EARLY DEVELOPMENT OF VISUAL CORTICAL CELLS IN NORMAL AND DARK-REARED KITTENS: RELATIONSHIP BETWEEN ORIENTATION SELECTIVITY AND OCULAR DOMINANCE

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(Received 22 July 1977)

SUMMARY

1. 535 units were recorded in the primary visual cortex in twelve normally reared and fifteen dark-reared kittens aged between 8 and 50 days. These results were pooled with a previous study of 582 units recorded from thirty-five kittens reared in similar conditions.

2. These 1117 cells were classified into four functional classes of neurones: (a) visually unresponsive cells, (b) non-specific cells which were sensitive to spots or slits of light moving in any direction, (c) immature cells which were preferentially activated by a rectilinear stimulus but unselective regarding its precise orientation and (d) specific cells that appeared to be as selective for orientation as the simple or complex cells in the adult cat.

3. The results confirm that cells having the same orientation-specific response properties as adult cortical visual neurones are present in the earliest stages of post-natal development, independently of visual experience. However, to maintain and develop these specific cells after the third week of post-natal life, visual experience is necessary.

4. The ocular dominance of visual cells is not constant from the earliest stages of development. A significant increase in binocularly driven neurones occurs with age.

5. Before 3 weeks of age, whatever the rearing conditions, there are more specific cells coding horizontal and vertical orientations than those coding oblique orientations. These ‘horizontal and vertical detectors’ are preferentially driven by the contralateral eye.

6. After 4 weeks of age, specific neurones are found at all orientations in normally reared kittens. At this stage of development the ocular dominance is independent of orientation preference, of the functional class of neurones considered and of the rearing conditions. The proportion of binocularly driven cells is slightly below adult standards.

7. A hypothesis of differential plasticity is proposed: contralateral, monocular ‘horizontal and vertical detectors’ are supposed to be stable; they would remain so until they become binocular. Binocular cells, for which competition between two inputs occurs, are the labile units which can be despecified or specified under the control of visual experience.
INTRODUCTION

After extensive study of feature detectors at the cortical level in the adult cat (Hubel & Wiesel, 1959, 1962, 1963a), numerous workers have directed their attention to the existence of specific functional properties before visual experience (Hubel & Wiesel, 1963b; Barlow & Pettigrew, 1971; Pettigrew, 1974; Buisseret & Imbert, 1976; Blakemore & Van Sluyters, 1975; Leventhal & Hirsch, 1975; Sherk & Stryker, 1976; Singer & Tretter, 1976). Whilst it is commonly thought that binocular interaction is present at eye opening (Hubel & Wiesel, 1963b), there is controversy concerning the presence of orientation specific units in young, visually inexperienced kittens. Is orientation selectivity an inborn feature of visual cortical cells?

On the basis of a small sample of cells \( n = 17 \) in very young kittens, Hubel & Wiesel (1963b) concluded that orientation-specific cells are present in naïve cortices by 8 days of age and that binocularity is of adult standard. In contrast, Pettigrew (1974) claimed that before the fourth post-natal week, neurones in both normal and binocularly deprived kittens show similar directional properties but in both cases lack proper orientation selectivity and disparity selectivity. Blakemore & Van Sluyters (1975) agreed with some of Pettigrew's results, but noted a considerably greater degree of inherent organization in deprived cortices. Moreover they found orientation-selective cells in normally reared and in binocularly deprived kittens at eye opening and showed that in visually deprived animals less than 3 weeks old, specific cells were usually simple and monocular. Similarly, Buisseret & Imbert (1976) reported that 23% of recorded visual cells presented adult characteristics of orientation specificity, in both normally and dark-reared kittens as soon as the first visual responses appeared. These authors also confirmed, with more numerous data, that up to the end of the third week the specific cells are generally monocularly driven whatever the rearing condition.

The factors that could contribute to these conflicting results have been discussed in detail by Pettigrew (1974) and Barlow (1975). One problem is that many authors pooled results obtained from kittens of different ages (Hubel & Wiesel, 1963b; Pettigrew, 1974; Blakemore & Van Sluyters, 1975; Buisseret & Imbert, 1976), and reared in different conditions (Hubel & Wiesel, 1963b); Blakemore & Van Sluyters, 1975; Pettigrew, 1974), making physiological assumptions which need to be proved.

In order to see if sampling could be responsible for such discrepant views, we have extended a previously published study of the developmental properties of visual cortical cells (Buisseret & Imbert, 1976). The sample of cells has been doubled \( n = 1,117 \) taken from a total of sixty-two kittens reared in the same restricted conditions. Two groups were compared: the first group was normally reared, that is to say with natural alternation of day and night and the second was reared in complete darkness from the first or second day of age up to the day of the acute experiment.

This quantitative analysis has led us to a detailed study of ocular dominance, orientation preference and the possible relationships between these two functional properties. A hypothesis of differential plasticity is proposed.

Two brief accounts of these results have already been published (Frégnac & Imbert, 1977a, b).
METHODS

For the new results, twenty-seven kittens aged from 1 to 7 weeks were used. Twelve of these, from four different litters, were reared in a normal visual environment; fifteen, from five other litters, were reared in complete darkness from the second day after birth. The kittens were anaesthetized with Pentothal given i.p. (40 mg/kg) and were placed with the minimum of trauma in the stereotaxic visual apparatus modified according to Rose (1970). A small opening was made in the skull above the primary visual cortex (area 17 according to stereotaxic co-ordinates). The kitten was paralysed with flaxedil (10 mg/kg.hr) and maintained under artificial respiration. The experiments normally continued for up to 8 hr. Further Pentothal (one tenth of the initial dose) was given half-way through the experiment to ensure continued anaesthesia. The pupil was dilated with atropine and a contact lens applied to correct the refraction error and to protect the cornea from drying. Strict precautions were taken with the dark-reared kittens in order to avoid any unwanted visual experience.

At the start of the experiment, the kitten was placed 40 cm in front of a faintly lighted screen. For very young kittens, cloudy optics caused by a persistent hyaloid artery make the estimation of the visual axis difficult. Judging from the recording sites, and from the projections of optic disks when possible, the receptive fields studied were within 10° of the area centralis. Tungsten micro-electrodes of impedance ranging from 1 to 15 MΩ were used to record extracellularly from cortical neurones. The size, shape and position of the receptive fields were mapped by manually projecting small spots or slits of light. On completion of these hand-controlled examinations, selected neurones were studied quantitatively using computer-programmed visual stimuli. The computer construction of orientation tuning curves from averaged responses to moving or stationary stimuli of random orientation gave estimates (with an accuracy of ± 5°) of optimal orientations identical to those obtained from the preliminary examinations (see also Hubel & Wiesel, 1974; Blasdell, Mitchell, Muir & Pettigrew, 1977). After the complete characterization of the receptive field properties of one recorded visual cell, the micro-electrode was stepped 50 μm deeper before proceeding to the identification of a new cell (Stryker & Sherk, 1975). Tracks were terminated at a depth of 4000 μm from the pial surface and a limited number of neurones were recorded per track (see Table 1) in order to avoid any sampling bias due to the columnar organization of orientation preference in the visual cortex.

The receptive field characteristics of the cells were systematically studied in the following ways:

(a) With small, stationary spots, in order to determine the ON and OFF regions within the receptive field and its limits.

(b) With stationary bars or slits to determine the ON and OFF regions within the receptive field, its limits and its orientation stricto sensu.

(c) With orientated bars or slits moving across the receptive field to determine directional asymmetry.

(d) With spots moving across the receptive field to compare the responses observed with those observed in (c). When static criteria (b) were ineffective in the assessment of orientation specificity, the cell was classified orientation-specific if the range of orientation for moving stimuli to which it responded was narrower using bars or slits than with spots (Pettigrew, 1974).

Action potentials from afferent lateral geniculate nucleus (LGN) fibres were occasionally encountered in a cortical track. A studied unit was considered as a geniculate afferent when a rapid positive monophasic wave form was recorded, when the responses were strictly monocular, if the receptive field was circular with typical organized ON-OFF responses, and when the responses followed highly repetitive stimulation. These were discarded from our results.

RESULTS

535 units were recorded, 342 in the normally reared and 193 in the dark-reared kittens. Among these units 210 normally reared and 105 dark-reared were activated by visual activation. These results were pooled with previous results obtained using the same techniques and the same conditions of rearing. Buissaret & Imbert (1976) used a combination of Pentothal and N₂O anaesthesia. No qualitative difference has
<table>
<thead>
<tr>
<th>Rearing conditions</th>
<th>8-11</th>
<th>12-17</th>
<th>18-28</th>
<th>29-50</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Normal</td>
<td>Normal</td>
<td>Dark</td>
<td>Normal</td>
<td>Dark</td>
</tr>
<tr>
<td>No. of kittens</td>
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<td>8</td>
<td>7</td>
<td>8</td>
<td>14</td>
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<tr>
<td>No. of tracks</td>
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<td>18</td>
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<td>68</td>
</tr>
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<td>94</td>
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<td>246</td>
</tr>
<tr>
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<td>5.6</td>
<td>5.2</td>
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<td>3.6</td>
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<tr>
<td>No. of visually unresponsive cells</td>
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<td>60</td>
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</tr>
<tr>
<td>No. of visually excitable cells</td>
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<td>44</td>
<td>88</td>
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<tr>
<td>No. of visual cells per kitten (average)</td>
<td>1</td>
<td>15</td>
<td>6</td>
<td>11</td>
<td>11</td>
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</tbody>
</table>

* Visually unresponsive cells were not systematically studied for six normally reared kittens.
been found by anaesthetizing kittens only with Penthotal. Table 1 gives the total distribution of 1117 cells according to four age groups: 8–11, 12–17, 18–28 and 29–50 days.

Four types of cells were defined according to their responses to the four tests (see Methods).

*Type 1; visually unresponsive units*

These had very low spontaneous activity (0·1–0·5 impulses/per sec) and could not be driven by visual stimuli. In most cases they were only discovered when mechanically stimulated by the advancing electrode.

*Type 2; non-specific units*

The receptive fields of these cells were usually circular and often very large (5–15°). They were activated equally well by bars or spots of light moving in any direction over their visual field.

*Type 3; immature units*

The receptive fields of these cells tended to be rectangular (10° × 8°) and the response to rectilinear stimuli was greater than to spots. When moving stimuli were used, their selectivity as a function of the direction of movement was greater when bars or slits were used than with spots. They exhibited a degree of orientation selectivity although responding to a range of orientation up to 45° either side of the optimal orientation. In all cases there was a clear null orientation, orthogonal to the optimal, which had no effect.

*Type 4; specific units*

These cells were orientation-specific and exhibited all the characteristics of simple or complex cells in the adult cat (Hubel & Wiesel, 1962; Pettigrew, 1974; Henry, *et al.* 1974). The receptive fields were smaller in size (2° × 4°) than those of immature cells.

In order to allocate a cell to one of the four types described above, we were sometimes obliged to put greatest weight on one decision criterion (see Methods (*d*)). This was done in the most conservative way so as to avoid making cells appear specific in terms of orientation selectivity unless they fulfilled all the criteria given above.

Polar diagrams of orientation preference were drawn for specific cells by taking as the optimal orientation the optimal orientation corresponding to the dominant eye, or the average orientation when both eyes were equally effective in driving the cell.

The distribution of orientation preference of specific cells (type 4) was estimated by grouping them in eight categories 22·5° wide – that is, roughly half the width of their tuning curves. Statistical calculations (χ² test with Yates’s correction and Snedecor test applied to the distribution of deviations from the mean) were carried out where the pooled results obtained from comparable kittens gave a mean of at least ten cells per orientation class; eighty cells were required to establish a polar diagram. For immature cells the optimal orientation was arbitrarily chosen as the mean of the range of orientations to which the cell responded. Statistical tests were performed if the pooled results obtained from comparable kittens gave a mean at least of twenty cells per orientation class of 45° width.
(1) Receptive field properties and visual experience

The distribution of the different cell types in three age groups (total, 1050 cells) is shown in Fig. 1. The age groups were chosen arbitrarily and are the same as those used in the previous study (Buisseret & Imbert, 1976). To construct Fig. 1 the pooled results obtained in both studies have been taken, since the present results do not differ significantly from those already published by Buisseret & Imbert. The only point of discrepancy is that we found a smaller percentage of visual cells in dark-reared kittens than in normally reared kittens.

Contingency tables were prepared for different functional types at different ages and under the different rearing conditions. Chi-square tests* showed that the following trends are all significant ($P < 0.005$, d.f. = 2). The proportions of non-specific, immature and specific cells for each rearing condition are no longer comparable between 17 and 28 days. After 28 days a clear-cut effect appears: in normally reared kittens the proportion of specific cells increases while in dark-reared kittens the proportion of non-specific cells becomes predominant. At this age the distributions of the different types of visual cells for each rearing condition are significantly different.

The same tests applied to the proportions of the different types of cells for each rearing condition before 17 days did not give significant results. Neither is the change

* d.f. = number of degrees of freedom for establishing the contingency table. $P =$ level of significance of the $\chi^2$ test or probability that the value of $\chi^2$ calculated from the contingency table was larger than some critical value. $\chi^2$ is calculated with and without correction of continuity since we use discrete data and small samples (Yates's correction) and the smaller $\chi^2$ is considered for the decision criterion. When $P < 0.005$, we conclude that observed frequencies differ significantly from expected frequencies computed on the basis of a hypothesis. The commonly assumed hypothesis is that the two classifications are independent of each other.
DEVELOPMENTAL PROPERTIES OF VISUAL CELLS

In the percentage for each type of neurone before 17 days and between 17 and 28 days significant, whatever the rearing condition considered.

In summary, these results obtained from the study of 1050 cells confirm that cells having some of the highly specific response properties of adult visual cortical neurones, especially concerning orientation selectivity, are present in the earliest stages of post-natal development, independently of visual experience. However, a crucial evolution occurs between 17 and 28 days, implying that visual experience is necessary to maintain and develop these specific cells after the third week of post-natal life.

<table>
<thead>
<tr>
<th>TABLE 2. Properties of different types of visually responsive units at different ages</th>
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<td>Age group (days) ...</td>
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<tr>
<td>Rearing conditions</td>
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<tr>
<td>Non-specific cells</td>
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<td>Immature cells</td>
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<tr>
<td>Specific cells</td>
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</table>

Since these results were consistent with data obtained by Hubel & Wiesel (1963b) and Blakemore & Van Sluyters (1975), who estimated the beginning of the labile period to be 19 or 23 days, we decided to carry out a detailed analysis of orientation preference and ocular dominance for the two post-natal stages of development:

(a) before the beginning of the so-called 'critical period', which is around 21 days;
(b) after the time it takes for specific cells to become the majority of visual cells if a normal environment is present or to disappear if the visual environment is absent, i.e. 28 days.

Our analysis does not use results pooled from kittens reared in different environmental conditions. It is assumed that results obtained from kittens under 3 weeks of age (or over 4 weeks) are comparable if the rearing conditions were identical.

(2) Ocular dominance and rearing conditions

Ocular dominance can be studied by classifying visual cells into two groups: cells which are activated only by one eye (monocular) and cells which are activated by both eyes (binocular), or into five groups ranging from contralateral monocular activation to ipsilateral monocular activation via three groups of binocular activation.

For the limited number of cells (457) with which we were able to study binocular interaction, it appeared (Fig. 2) that ocular dominance was unaffected by the rearing conditions.

It is interesting to note that the ocular dominance of the visual cells was not constant from the earliest stages of development; a significant increase in binocularly driven neurones occurred with increasing post-natal age. It can be seen that between 28 and 50 days the proportion of binocularly driven cells was still slightly below adult standards.

The lower part of Fig. 2 presents ocular dominance histograms that indicate a slight majority of visual neurones influenced preferentially by the contralateral eye for
kittens over 4 weeks of age. It shows clearly that for kittens younger than 3 weeks, whatever their rearing conditions, most of the monocular neurones recorded were controlled by the contralateral eye.

(3) **Ocular dominance and receptive field properties**

It has already been noted (Imbert & Buisseret, 1975) that ocular-dominance histograms are not significantly different for 6-week-old kittens reared normally or in total darkness. (It must be emphasized that these histograms are obtained mainly from specific cells in normally reared kittens and from non-specific cells in dark-reared kittens.) This is also true for kittens over 28 days of age when the analysis

![Diagram](image)

**Fig. 2.** Ocular dominance histogram, post-natal and rearing conditions. The upper part represents histograms for two classes of visual cells. I, monocularly driven; II, binocularly driven in two rearing conditions. \( n \) = no. of cells; \( m \) = no. of kittens. The lower part shows histograms for two rearing conditions with five classes of visual cells: 1, responding only to the contralateral eye; 2, preferentially activated by the contralateral eye; 3, equally activated by both eyes; 4, preferentially activated by the ipsilateral eye; 5, responding only to the ipsilateral eye. The figure is divided into two halves: left, kittens under 3 weeks of age; right, kittens over 4 weeks of age. \( \chi^2 \) tests showed a significant increase in binocular neurones by comparing kittens before 3 weeks of age and after 4 weeks of age \((P < 0.005; \text{D.F.} = 1 \text{ or D.F.} = 4)\) whatever the rearing condition. No significant effects were found when testing if ocular dominance and rearing conditions were independent classifications, for each age class considered.

is restricted to specific cells in normally reared kittens and non-specific cells in dark-reared kittens, for two or five classes of ocular dominance. The results obtained by the analysis of all visual cells still hold for the analysis made for each type of neurone shown in Fig. 3, though the sample size is reduced for each histogram. Thus
the distribution of ocular dominance appears to be unaffected by the rearing conditions, whatever the type of visual neurone considered.

The ocular dominance histogram for non-specific cells shows a small peak for the class of cells equally influenced by both eyes, whatever the rearing condition. In contrast, the histograms for immature cells and specific cells are somewhat different and give in both cases a rather large percentage of monocular contralateral cells without the presence of a peak representing 'binocular' cells.

![Diagram of Ocular Dominance Histograms](image)

*Fig. 3. Ocular dominance histograms for the different classes of visual cells. From top to bottom: histograms for both rearing conditions for three classes of visual cells; 1–5, classes of ocular dominance (see Fig. 2). The ocular dominance histograms are not significantly affected by the rearing conditions.*

In summary, it appears that the contralateral dominance observed in Fig. 2 is mainly due to immature and specific cells, though the percentage of 'monocular' cells is much higher the younger the kitten, whatever the functional class of the neurones considered. Thus it is possible that ocular dominance in very young kittens is related to receptive field properties.

(4) **Distribution of orientation preference**

By pooling results obtained from comparable kittens and maintaining the statistical restrictions given above, the distribution of orientation preference in the naive cortex may be determined.

Results shown in Fig. 4 concern only specific cells from normally reared kittens because the optimal orientation to which the cells respond may be established with...
most confidence in these animals. For dark-reared kittens, in order to increase the sample, pooled results are given for immature and specific cells, there being no significant difference between the orientation preference distributions of the two groups.

Before 3 weeks of age, whatever the rearing conditions, we found more specific cells coding horizontal and vertical orientations than responding to oblique orientations. After 4 weeks of age there seemed to be no asymmetry in the distribution of orientation preference exhibited by specific neurones in normally reared kittens. No polar diagrams are shown for dark-reared kittens because specific cells or immature cells were recorded less and less in increasingly older kittens.

Fig. 4. Polar diagrams of orientation preference. The number of specific cells recorded from comparable kittens is plotted versus the mean polar orientation of each orientation class of 22.5° width (0–22.5°, 22.5–45°, 45–67.5°, 67.5–90°, 90–112.5°, 112.5–135°, 135–157.5°, 157.5–180°). The length of each bar indicates the number of specific cells for one class of orientation. The number of specific cells (n) and kittens (m) are given for each polar diagram.

In order to determine whether these results were due to sampling bias, the normalized deviation from a uniform distribution for each of the eight orientation classes is plotted in Fig. 5. From these graphs the density histograms of deviation values may be estimated.

χ² tests and Snedecor tests applied to the distribution of deviation from equal subdivision lead to the same conclusions. Sampling bias may be responsible for the irregularities of the orientation preference distribution observed for kittens over 4 weeks of age. The slight dominance of oblique orientation in Fig. 4C is not significant (P > 0.05; D.F. = 1) and the density histogram (Fig. 5, II) is centred on a null mean value. For kittens under 3 weeks of age, vertical and horizontal orien-
DEVELOPMENTAL PROPERTIES OF VISUAL CELLS

Sections are more common than oblique ones and the density histogram shows the existence of two heterogenous distributions with non-null mean values. The peak corresponding to positive deviation from equidistribution is obtained for horizontal and vertical orientations (± 22.5°) and the peak corresponding to negative deviation from equidistribution is obtained for oblique orientations (± 22.5°). The fact that the same trend was observed for normally reared and dark-reared kittens under 3 weeks of age strongly supports the coherence of our data.

Fig. 5. Orientation preference: deviation from equirepartition. (I) Polar representation; the ordinate represents the percentage (Δ) of deviation from equal subdivision for the proportion of specific cells found for one of the eight classes of orientation. The abscissa gives the classes of orientation. (II) Density histogram: the ordinate gives the percentage (%) of classes of orientation for which the deviation from equirepartition belongs to an interval with the form, [(2K - 1).12.5%, (2K + 1).12.5%] K ∈ Z.

In summary, the distribution of orientation preference does not seem to be constant during the first stages of post-natal development. Before 21 days many more cells responded preferentially to vertical and horizontal orientation than to oblique stimuli.
(5) Orientation preference and ocular dominance

The non-homogeneity of orientation representation by specific cells in kittens under 3 weeks of age may suggest that the difference in ocular dominance histograms shown in Fig. 3 between non-specific cells and immature or specific cells is linked to the orientation preference property. The problem is to know if the peak of monocular contralateral cells is due to a certain subclass of specific cells.

![Graph showing orientation preference and ocular dominance](image)

Specific cells (●●● normally reared; ●● dark reared kittens):
(1) vertical and horizontal
(2) oblique
(4) any orientation
(5) any orientation

Non-specific cells: (3) (○○○ normally reared; ○○ dark reared kittens).

Fig. 6. Relationship between orientation preference and ocular dominance. The percentage of binocular cells is plotted for specific cells: (1) responding preferentially to horizontal and vertical orientation, (2) responding preferentially to oblique orientations, (4) and (5) whatever their orientation preference; class (3) represents the percentage of binocular non-specific cells. The classes (1)–(3) show results obtained in normally reared and dark-reared kittens under 3 weeks old. Class 4 shows results obtained in normally reared kittens between 28 and 50 days old. The percentage of binocular cells would be the same for non-specific cells in dark-reared kittens over 4 weeks old and is not shown in the Figure. These data show that the ocular dominance histograms are not significantly affected by the rearing condition.

The specific cells may be divided into two functional classes, one composed of specific cells responding preferentially to horizontal and vertical orientations (HV ± 22.5°) and the other composed of specific cells responding preferentially to oblique orientations (DD ± 22.5°). It is important to ensure that the ocular dominance histograms are still unaffected by the rearing conditions. In order to avoid sampling fluctuations due to too many classes, since we divided our sample population into
two populations, we considered the simplest ocular dominance histograms in two classes: ‘monocular’ cells and ‘binocular’ cells. In this case, ocular dominance is independent of rearing conditions for HV cells and DD cells.

The results in Fig. 6 show that HV cells are not comparable to other visual cells before 21 days. These cells were mostly monocular and mainly driven by the contralateral eye. On the other hand, a greater proportion of the DD cells were binocularly activated and their ocular dominance histogram was not significantly different from the distribution obtained for non-specific cells.

In summary, for kittens under 3 weeks old, with or without visual experience, ocular dominance and orientation preference appear as two linked parameters characterizing the intrinsic organization of visual cortex. Most of the specific cells in kittens under 3 weeks old are contralaterally dominated and have horizontal or vertical orientation preference. Beyond 4 weeks, ocular dominance is independent of orientation preference, of the functional class of neurones considered and of rearing conditions.

(6) Orientation preference and orientation selectivity

The conclusions drawn from the study of immature cells according to the statistical restrictions given above are the same as those obtained from the study of specific cells. There is no significant difference in the distribution of orientation preference for specific and immature cells. Thus, as noted in paragraph (3), there being no significant difference in their ocular dominance histograms, the only way to distinguish immature cells from specific cells is to compare their tuning curves. Immature cells may be defined as a transitory type of cell having a competence for a large range of orientations. They are present at eye opening and disappear after 40 days in both dark- and normally reared kittens.

DISCUSSION

It is already known that the specific responses of cortical visual neurones to the orientation, direction, size, position and luminance of a visual stimulus appear in very young kittens, independently of visual experience. Orientation-selective neurones have been recorded in normally reared kittens as early as 8 days by Hubel & Wiesel (1963b), at 9 days by Blakemore & Van Sluyters (1975), and at 12 days by ourselves (Frégnac & Imbert, 1977b), and in dark-reared kittens as early as 14 days by ourselves (1977a), and 19 days by Blakemore & Van Sluyters (1975).

These data may seem surprising if one considers the poorness of the kitten’s optics (Thorn, Gollender & Erickson, 1976) and the very low percentage (2%) of synapses present at eye opening (Cragg, 1974) but they indicate without doubt the existence of innately specified orientation-selective cells. One of our aims was to determine at what post-natal age such specific cells could be recorded. Here, although visual responses were recorded in 9-day-old kittens, orientation-selective cells were only observed in kittens that were 12 or more days old. This confirms the data reported by Buisseret & Imbert (1976).

Our results bear mainly on the description of the functional state of the visual cortex before the beginning of the critical period and enable us to describe the initial state, before visual experience rules development.
The first important conclusion is that the ocular dominance of visual cells is not constant from the earliest stages of development. This is in contradiction with the commonly accepted idea that the property of binocularity for cortical cells is essentially fully established before visual experience occurs (Hubel & Wiesel, 1963b; Barlow, 1975; Grobstein & Chow, 1975).

The ocular dominance histograms in the normal adult cat show that the majority of cells are preferentially activated by the contralateral eye (Hubel & Wiesel, 1963a; Albus, 1975a; Kratz & Spear, 1976). It is worth while to note that Noda, Creutzfeldt & Freeman, (1971), working with awake cats, found five times as many visual cells dominated by the contralateral eye as those dominated by the ipsilateral eye. In anaesthetized cats there exists a discrepancy between the results of Wilson & Sherman (1976) and Albus (1975b, c) as to whether or not the distribution of ocular dominance is related to receptive field properties and retinal eccentricity. According to Albus, the contralateral predominance is observed within the 4° of the area centralis and decreases with retinal eccentricity. Moreover a higher proportion of simple cells are monocularly activated than complex cells. According to Wilson, the percentage of binocular cells remains constant with retinal eccentricity, but contralateral dominance is perhaps more predominant for cells receiving an input from the area centralis.

Our study of kittens over 4 weeks of age confirms a slight dominance in the proportion of contralateral cells. We cannot reinterpret our results according to Albus's remarks, since classification into simple or complex types is less clear in young kittens, but the fact that we found the same contralateral dominance for specific cells in normally reared kittens as for non-specific cells in dark-reared kittens indicates that there is no clear relationship between receptive field properties and ocular dominance in older kittens.

In younger kittens, recent results suggest that a larger percentage of specific cells might be monocularly driven than in the adult cat. This is true for binocularly deprived kittens (Blakemore & Van Sluyters, 1975; Sherk & Stryker, 1976; Kratz & Spear, 1976) and dark-reared kittens (Buisseret & Imbert, 1976) but there exists a discrepancy between conclusions concerning normally reared kittens (Blakemore & Van Sluyters, 1975; Buisseret & Imbert, 1976). Our quantitative data allows us to state that in kittens under 3 weeks of age, whatever the rearing conditions (normally or dark reared) and whatever the receptive field properties, a higher percentage of cortical cells are driven by the contralateral eye than in kittens over 4 weeks of age and adult cats. It is also clear that at this early stage of development the subclass of orientation-specific cells and immature cells which respond preferentially to horizontal and vertical orientations is composed mainly of contralateral monocular cells.

It is known from prenatal study of the visual pathways in the cat (Anker, 1977) that the projection of the optic tract to the contralateral LGN is the more marked. The major afferent and efferent pathways are fully developed before birth. Thus it could be that the slight overall contralateral dominance observed in ocular dominance histograms of the adult cat is the residue of an imbalance between ipsilateral and contralateral projections of the optic tract via the LGN. The increase in the proportion of binocular neurones observed with post-natal age may be related either to the late development of intracortical connexions or to the maturation of afferent
Developmental Properties of Visual Cells

Geniculo-cortical synapses, which has been shown to occur in the second post-natal week (Cragg, 1974).

The second point of our study concerns the distribution of orientation preference. In the adult cat there is no evidence for a meridional bias in the distribution of orientation preference across the population of neurones in the visual cortex. Physiological studies (Campbell, Maffei & Piccolino, 1973; Blasdell et al. 1977) show no convincing meridional bias in visual acuity. Electrophysiological data have not clarified the situation and disagreement persists concerning the existence of asymmetries in the distribution of orientation preference exhibited by visual cortical cells in normal adult cats (Pettigrew, Nikara & Bishop, 1968; Noda, Freeman, Gies & Creutzfeldt, 1971; Rose & Blakemore, 1974; Barlow, 1975; Wilson & Sherman, 1976; Leventhal & Hirsch, 1975, 1977). A recapitulation of the different conclusions inferred from previous studies by applying $\chi^2$ tests to reject (or retain) the hypothesis of a uniform distribution of orientation preference (with a level of significance $\alpha = 0.005$) is shown in Table 3 and raises some doubts concerning the cohesion of experimental data obtained by different workers.

Table 3. Distribution of orientation preference in the adult cat. $\chi^2$ tests are applied to the distribution of orientation-selective cells function of certain classes of orientation.

<table>
<thead>
<tr>
<th>Authors</th>
<th>Functional type of visual cells</th>
<th>$W$</th>
<th>Classes of orientation</th>
<th>D.F.</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pettigrew et al. (1968)</td>
<td>Simple unimodal directional units</td>
<td>10°</td>
<td>HV versus DD</td>
<td>17</td>
<td>*</td>
</tr>
<tr>
<td>Noda et al (1971)</td>
<td>Orientation-selective cells (awake cat)</td>
<td>22.5°</td>
<td>—</td>
<td>7</td>
<td>N.S.</td>
</tr>
<tr>
<td>Rose &amp; Blakemore (1973)</td>
<td>Simple cells</td>
<td>45°</td>
<td>—</td>
<td>3</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td>Complex cells</td>
<td>45°</td>
<td>—</td>
<td>3</td>
<td>N.S.</td>
</tr>
<tr>
<td>Henry et al. (1974)</td>
<td>Complex cells</td>
<td>10°</td>
<td>—</td>
<td>17</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Orientation-selective cells</td>
<td>20°</td>
<td>H.V. versus DD</td>
<td>1</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>40°</td>
<td>HV DD</td>
<td>1</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>30°</td>
<td>D versus D</td>
<td>1</td>
<td>*</td>
</tr>
<tr>
<td>Leventhal &amp; Hirsch (1975)</td>
<td>Orientation-selective cells</td>
<td>45°</td>
<td>—</td>
<td>3</td>
<td>N.S.</td>
</tr>
<tr>
<td>Albus (1975)</td>
<td>Simple cells</td>
<td>20°</td>
<td>—</td>
<td>8</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td>Complex cells</td>
<td>20°</td>
<td>—</td>
<td>8</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td>Orientation-selective cells</td>
<td>20°</td>
<td>—</td>
<td>8</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>40°</td>
<td>HV versus DD</td>
<td>1</td>
<td>*</td>
</tr>
</tbody>
</table>

$W$, angular width of the classes of orientation; D.F., number of degrees of freedom equal to the number of classes of orientation minus one. The null hypothesis is that the expected distribution is a uniform distribution. The level of significance is 0.005. N.S., $\chi^2$ tests do not give significant orientations. * $\chi^2$ test gives significant result.

Our own results for kittens over 4 weeks of age show that the distribution of orientation preference in immature and orientation-specific cells is very like that of the adult cat although complete specificity of the visual response is not fully achieved.

In very young kittens, before the beginning of the critical period, there is clear
evidence that a larger proportion of neurones respond preferentially to horizontal and vertical orientations than to oblique stimuli. Our results fit well with those obtained previously by Leventhal and Hirsch (1975). These authors showed the presence of units exhibiting preference for horizontal and vertical lines in cats exposed with goggles to diagonal patterns. Their conclusion was that such units maintain and develop their intrinsic specificity even when horizontal and vertical lines are excluded from the animal's environment. They proposed that cells displaying a preference for diagonal lines may be recruited from a population of neurones uncommitted initially, whose orientation-specificity is affected by the animal's early experience, and suggested that these cells receive the neuronal inputs necessary for proper development and function from cells having an intrinsic preference for horizontal and for vertical orientation. More recently the same authors (Leventhal & Hirsch, 1977) have studied the effect of early experience on orientation selectivity in the visual cortex of adult cats. In normal cats, neurones displaying orientation preference to horizontal and vertical lines have the smallest receptive fields, located within 10° of the area centralis and respond only to low rates of stimulus motion. In pattern-deprived animals nearly all orientation-selective cells are 'horizontal and vertical detectors' with small receptive fields and are mainly driven by one eye, whatever the retinal eccentricity. Although our results are in agreement with these data, two differences may be noted. Firstly, these authors used pooled results from pattern-deprived animals and dark-reared cats. In our own experiments we could not record a significant number of orientation-selective cells in dark-reared kittens over 4 weeks of age (< 5%). Moreover it has been shown by Kratz & Spear (1976) that pattern deprivation results in an asynchrony between visual inputs and may lead to an abnormal ocular dominance histogram. It is probable that pattern-deprived cats and dark-reared kittens are not at all comparable. Secondly, we did not observe that horizontal and vertical orientation preferences could be linked to receptive field size. The non-uniformity in the distribution of orientation preference was observed for both immature cells and specific cells. Immature cells had receptive fields mostly larger than 2°. Thus it seems that the dichotomy used by Hirsch & Leventhal is not appropriate for characterizing receptive field properties in young kittens. We would agree, however, that the visual system's preferential response to horizontal and vertical lines is determined intrinsically and this probably reflects the response properties and distribution of certain cortical neurones already present in kittens under 3 weeks of age, reared with or without visual experience.

Rather than totally accepting Leventhal & Hirsch's conclusions we propose a simpler hypothesis of 'differential modifiability' linked to the property of binocularity.

We suppose that binocularly driven cells are the modifiable cells which may be specified or despecified in terms of orientation selectivity under the control of visual experience. We suggest that the monocular 'horizontal and vertical detectors' recorded in very young kittens form a special subpopulation of the visual cortex which receives projections mainly from the contralateral eye at the time of eye opening. These 'monocular' cells are stable and resistant to the absence of visual input or to the selective exposure to an orientation to which they do not respond as long as they are influenced only by one eye. If no binocular competition is aroused by
the rearing conditions and visual environment, the level of binocularity increases with post-natal age for visual cortical cells. ‘Horizontal and vertical detectors’ which were still monocularly driven at 3 weeks of age become mainly binocularly driven after 4 weeks of age and can be affected by visual experience. Thus the absence of visual environment may lead to a complete loss of orientation selectivity because the development of binocularity remains unaffected.

We wish to thank Miss P. Saillour for her valuable technical assistance and Dr E. Gary-Bobo for help in some of the experiments. We gratefully acknowledge the assistance of Mrs F. Bordeaux with the care of the animals, of Miss J. Soupault and Mrs J. Pinot who typed the manuscript and of Dr K. Grant for help with the English. This work has been supported by grants from the CNRS (RCP 080348) and the INSERM (ATP 6-74-27 and CL 76-4-045-6).

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