# VISUAL CORTICAL CELLS: THEIR DEVELOPMENTAL PROPERTIES IN NORMAL AND DARK REARED KITTENS

BY P. BUISSERET AND M. IMBERT

*From the Laboratoire de Neurophysiologie,*
*Collège de France 75231, Paris Cedex 05, France*

## SUMMARY

1. 582 units were recorded in area 17 in twenty-one normally reared kittens, and fourteen dark reared ones, aged between 8 and 42 days.

2. Four classes of neurones were defined: (*a*) non-activable cells that cannot be excited by any peripheral stimulation; (*b*) non-specific cells that are sensitive to a visual stimulus moving in any direction; (*c*) immature cells that are preferentially excited by a rectilinear stimulus but are unselective for its precise orientation; (*d*) specific cells that appear to be as selective for orientation as the simple or complex cells of the adult cat.

3. 23 % of the cells presenting adult characteristics of specificity in terms of directionality and orientation are present in both the normally reared and in the dark reared kittens as soon as the first visual response (12 days) appears.

4. In normally reared kittens the proportion of specific cells increases with age, while that of the non-specific cells decreases.

5. Up to 3 weeks of age there is no significant difference in the proportion of the different types of cells in the dark reared from the normal kittens. But thereafter in the dark reared kittens the specific cells tend to disappear while the non-specific cells increase in number.

6. This confirms the view that cells with some highly specific response properties of the adult visual cortical neurones, especially in relation to orientation specificity, are present in the earliest stages in the absence of all visual experience.

However, visual experience is necessary to maintain and develop these specific cells after the third week of post-natal life.

## INTRODUCTION

Since the discovery by Hubel & Wiesel of specific visual detectors at the cortical level in the adult cat, numerous workers have shown that selective

visual experience can lead to modification in the proportions of the various functional types of unit recorded electrophysiologically from the cortex. Selective visual experience is effective in this respect only when it occurs during a limited critical period of post-natal development and when the cat has had no previous visual experience.

As far as binocular properties of cortical cells are concerned, agreement seems to have been reached: the ocular dominance distribution is constant from the earliest stages. According to Barlow & Pettigrew (1971) and Petti-grew (1974), 'direction sensitivity' seems also to be an inborn feature. On the other hand, according to the same workers, 'orientation selectivity' would appear to require an appropriate visual experience. Here their evidence is in conflict with the results of Hubel & Wiesel (1963), recently reaffirmed by T. N. Wiesel (1972, personal communication), showing that orientation selectivity, along with all other specific properties of adult cortical neurones, is already present by 8 days of age; this is the time of eyelid opening, and thus before any environmental interaction.

In order to see whether differences in techniques, rearing conditions, and in the criteria used for orientation specificity could account for these dis-crepant views, we have studied the responses of visual cortical neurones in kittens at a whole series of different ages.

Two groups were compared. The first group was normally reared, that is to say reared with natural alternation of day and night. The second group was reared in complete darkness from the first or second day of age up to the day of the acute experiment.

A brief account of some of these experiments has been given elsewhere (Buisseret & Imbert, 1975).

## METHODS

Thirty-five kittens, aged from 1 to 6 weeks were used; twenty-one of them, from seven different litters, were reared in a normal visual environment; fourteen from seven other litters were reared in complete darkness from the second day after birth. The kittens were anaesthetized with Pentothal given I.P. and placed with the minimum of trauma in the stereotaxic visual apparatus modified according to Rose (1970). A small skull opening above the primary visual cortex (area 17) was per-formed. The kitten was paralysed with Flaxedil and kept under artificial respiration with $O_2$ and $N_2O$. The experiment normally continued for up to 8 hr. Further Pento-thal was invariably given half way through the experiment to ensure continued anaesthesia. The pupil was dilated with atropine, and a contact lens placed to correct the refraction error and to protect the cornea from drying up. Severe precautions were necessary concerning the dark reared kittens in order to avoid any unwanted visual experience.

At the start of the experiment, the kitten was placed in front of a faintly lighted screen. Metallic micro-electrodes were used to record from the cortical neurones extracellularly. The size, shape, position, and other characteristics of the receptive field were mapped by manually projecting small spots or slits of light. On completion

of the preliminary, rather qualitative examination, the neurones were studied using computer programmed visual stimuli. The cells' responses as well as the stimulus parameters were stored on a magnetic tape and polygraph. The computer was then used to analyse the data.

## RESULTS

582 units were recorded: 275 in the normally reared (NR), and 307 in the dark reared (DR). Among these units 190 NR and 213 DR were activated by visual stimulation. Table 1 gives the distribution of these units according to four age groups: 8–11, 12–17, 18–28, 29–42 days. The visual cortical cells are distributed in five classes according to their ocular dominance: (1) cells activated only by the contralateral eye; (2) cells preferentially activated by the contralateral eye; (3) cells equally activated by both eyes; (4) cells preferentially activated by the ipsilateral eye; (5) cells activated only by the ipsilateral eye.

TABLE 1. Age distribution of all units studied

|  | 8–11 | 12–17 | | 18–28 | | 29–42 | | Total | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | NR | NR | DR | NR | DR | NR | DR | NR | DR |
| No. of kittens | 4 | 6 | 4 | 5 | 4 | 6 | 6 | 21 | 14 |
| No. of tracks (cortical penetration) | 12 | 21 | 17 | 16 | 24 | 21 | 36 | 70 | 77 |
| No. of cells | 26 | 93 | 80 | 84 | 92 | 72 | 135 | 275 | 307 |
| No. of cells per track (average) | 2·2 | 4·4 | 4·7 | 5·2 | 3·8 | 3·4 | 3·7 | 3·9 | 4·0 |
| No. of non-activatable cells | 23 | 32 | 37 | 27 | 33 | — | 24 | — | — |
| No. of visually excitable cells | (3) | 61 | 43 | 57 | 59 | 72 | 111 | 190 | 213 |
| No. of visual cells per kitten | 1 | 10 | 11 | 11 | 15 | 12 | 19 | 11* | 15 |

\* Age group 8–11 not included.
NR, normally reared; DR, dark reared.

The receptive field characteristics of the cell were systematically studied in the following ways.

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

(b) With spots moving across the receptive field, in order to find out about directionality.

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

(d) With oriented bars or slits moving across a receptive field to determine directionality.

Four types of cells were defined in function of these terms (Imbert & Buisseret, 1975).

### Type 1: Non-activable units

Characteristically they have almost no spontaneous activity. However, they are identifiable because they can be mechanically activated either by advance of the electrode or by stray vibration. These mechanically generated discharges stop rapidly after the exciting stimulus, and the cells them remain silent. They cannot be stimulated by any peripheral stimulation. The only way to check whether the silent cell is still present is to reactive it mechanically.

### Type 2: Non-specific units

The receptive fields are characteristically circular. The cells are sensitive to a stimulus moving in any direction. Normally a circular stimulus is more efficient than a rectilinear one.

### Type 3: Immature units

The receptive fields of these units tend to be rectangular ($10° \times 8°$) and the cells generally prefer a moving rectilinear stimulus (slit or bar) to a spot moving. They are best activated when the stimulus moves in a direction orthogonal to the optimal orientation of their receptive field. However, this orientation is rather imprecise since the cell can be activated by orientations up to $45°$ on both sides of the optimal one. But in all cases there exists a direction in which the stimulus is ineffective (it is in fact a two-way direction).

### Type 4: specific units

The specific cells have all the characteristics of the simple or complex cells in an adult cat. The receptive field is rectangular and smaller in size than the one of an immature cell (roughly $4° \times 2°$). These cells are activated by bars or slits moving in a precise direction (two-way or one-way). All other directions are ineffective. The orthogonal orientation of the stimulus in respect to the movement is critical.

For the purpose of allocating a cell to one of the four types described above, we were sometimes obliged to put greatest weight on particular aspect of their behaviour. This was always done in the most conservative way so as to avoid making cells appear specific unless they fulfilled all criteria. For instance, a cell presenting a strong directional selectivity but no ineffective direction would be classified as non-specific. Again, a cell presenting some specific characteristics, such as separate ON and OFF

regions within its receptive field, would be classified as immature rather than specific, if it were activated by movement above 30 ° on both sides of the preferred direction.

*Receptive field properties of cortical cells in normally reared kittens*

*Age group: 8–11 days*

During this period, twenty-three out of twenty-six recorded units were non-activable. Sometimes, mechanically stimulated potentials were of a very high amplitude and long duration (5–10 msec). These potentials could often be recorded for 100–200 $\mu$m of cortical penetration. Among the recorded cells, three were found to have a very poor spontaneous activity
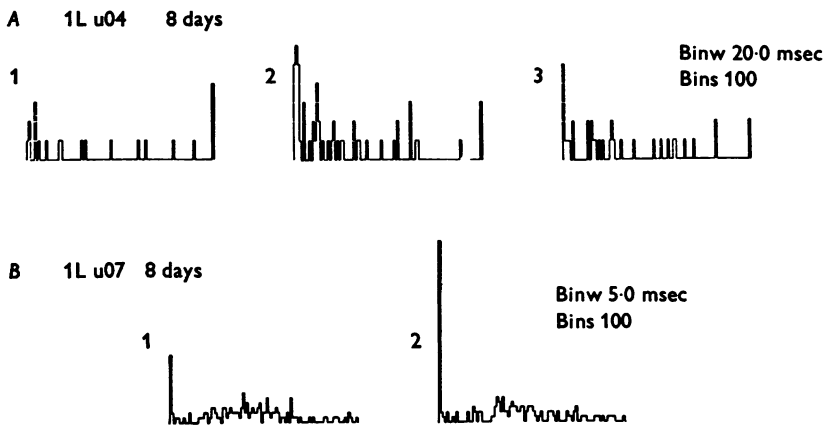


Fig. 1. Spontaneous activity of a poorly activable cell recorded in a 8 day old normally reared kitten. Time interval histogram showing the distribution of interval between impulses. Time of analysis: 50 sec. *A*, first example (1) spontaneous activity recorded in a kitten adapted at a mesopic level (control); (2) modification of this spontaneous activity by a flashing full field stimulus (1 flash/sec for 400 msec); (3) by presentation of a random contrasted moving pattern. *B*, second example (1) a control similar to that of *A*1; (2) visual stimulation similar to that described in *A*3.

modifiable by visual stimulation. There is no region in the visual field associated with this cell. The only way to modify spontaneous activity is to sweep the screen with complex, contrasting patterns. Such spontaneous activity modifications in an 8 day old kitten are illustrated in Fig. 1. In *A* the time interval histograms were carried out in three data collecting periods of 50 sec each, corresponding to three different visual conditions. In *A*1 the time interval histogram is carried out with the kitten adapted at a constant low mesopic visual luminance level (control). In *A*2 and *A*3 the

activity is analysed during the repetitive presentation of flashes lasting 400 msec each (2), and during the presentation of a contrasted moving random pattern (3). In both cases the spontaneous activity increases. Another cell is illustrated in Fig. 1*B*. During the control period of the data recording (1), the spontaneous activity is slightly more prominent. The random movement of the contrasted stimulus (2) only causes an increase in the shortest intervals.

### Age group: 12–17 days

From the beginning of this period, the visual units come into evidence already with spatially localized fields and definite characteristics of the trigger feature. They can then be classified according to the types defined above. Table 2 gives the distribution of the visual units during this period. As soon as the visual responses appear, about 25 % of the units are clearly and positively specific. An example of such a specific unit recorded in a 15 day old kitten is given in Fig. 2*B*. This cell, in contrast with the non-specific one illustrated in Fig. 2*A*, is only activated in a one way, horizontal direction by a vertically oriented moving bar (left histogram). There is no response for the movement of the stimulus in a vertical direction (central histogram). A longer vertically orientated bar moving horizontally (right histogram) gives a bimodal response. This kind of response probably reveals an inhibitory influence from the side regions of the receptive field (complex or hypercomplex cells, according to Hubel & Wiesel). It is noteworthy that the size of the receptive field is usually greater than that recorded in adult animals.

TABLE 2. Properties of different types of visually responsive units at different ages

| | Age group 12–17 | | Age group 18–28 | | Age group 29–42 | |
|---|---|---|---|---|---|---|
| | NR (%) | DR (%) | NR (%) | DR (%) | NR (%) | DR (%) |
| Non-specific | 23 | 40 | 9 | 56 | — | 94 |
| Immature | 54 | 37 | 49 | 30 | 24 | 4 |
| Specific | 23 | 23 | 42 | 14 | 76 | 2 |

Age group in days. NR, normally reared; DR, dark reared.

### Age group: 18–28 days

During this period, all three types of visual units (non-specific, immature and specific) continue to be found. However, there is a change in their distribution (Table 2, second column). The non-specific types decrease, whereas the specific ones increase. A specific cell (simple cell) in a
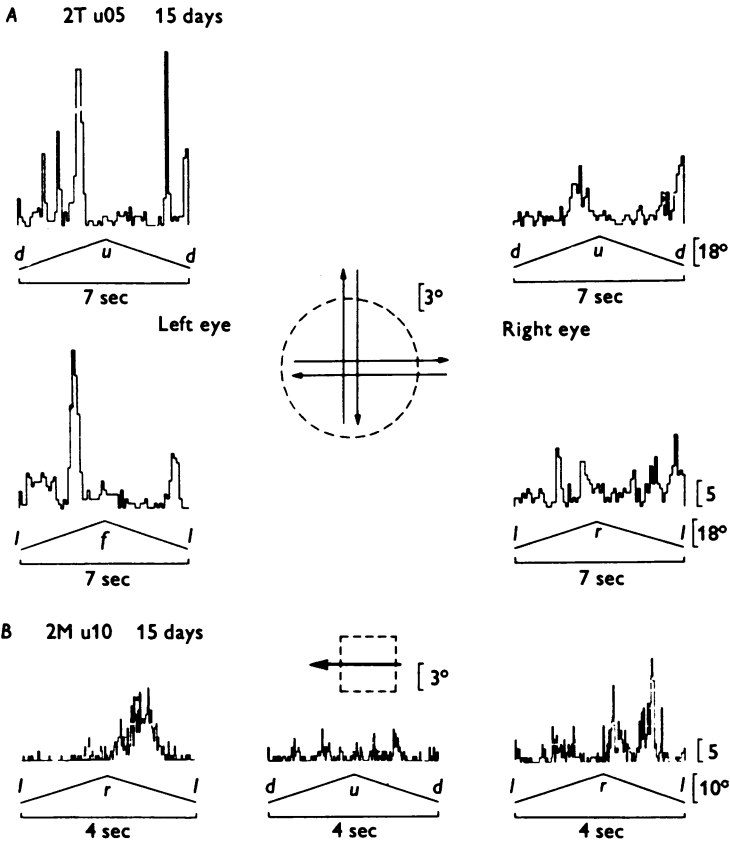
Fig. 2. Post-stimulus time histogram recorded in two 15 day old normally reared kittens. The histogram is the distribution of impulses occurring at various times after the onset of the stimulation. Bin-width (Binw) 100 msec for *A* and 20 msec for *B*; number of repeats (*n*) 14; the vertical calibration (number of impulses) is given near the right histograms. In the centre; diagram of the receptive field and direction of movement of the activating stimulus. *A*, non-specific cell binocularly activated with a left dominance. On the left, histograms formed by a moving spot presented to the left eye, on the upper left, from down (*d*) to up (*u*) and up to down. Lower left, from left (*l*) to right (*r*) and right to left. On the right, histograms formed by a moving spot presented to the right eye. Upper right-vertical movements. Lower right-horizontal movements. *B*, specific cell monocularly activated by the contralateral eye. Histogram formed by a vertically oriented slit moving across the receptive field. On the left, movement from left (*l*) to right (*r*) and from right to left. In the centre, movement from down (*d*) to up (*u*) and up to down. On the right, movement from right to left and left to right (on the right the slit is longer than on the left).

19 day old kitten is illustrated in Fig. 3. The stationary flashing of a horizontally orientated bar reveals two spatially separated ON and OFF regions within the receptive field. Moreover this cell is selectively activated by a horizontally orientated bar, moving in a one-way vertical direction.
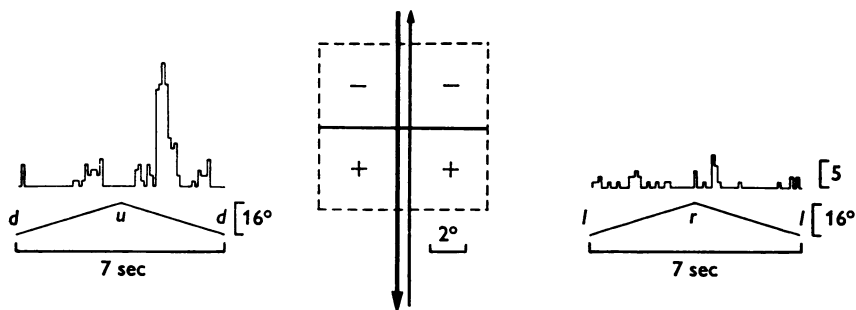


3G u19    23 days

Fig. 3. Specific cells monocularly driven. Post-stimulus time histogram recorded in a 23 day old NR kitten. Binw 100 msec.; $n = 14$. In the centre, diagram of the receptive field, $+$ ON region, $-$ OFF region, and direction of movement of the slit. The thickness of the arrow indicates the strength of the response. On the left, histogram formed by a horizontal slit moving from down ($d$) to up ($u$) and up to down. On the right, histogram formed by the movement from the left ($l$) to the right ($r$) and the right to the left by the same slit, vertically oriented.

*Age group: 29–42 days*

During this period the non-specific cells tend to disappear (Table 2, third column). The percentage of specific units increases so that at 42 days most of the cells are specific.

*Receptive field properties of cortical cells in dark reared kittens*

*Age group: 12–17 days*

In dark reared kittens the first visual responses appear at the same time as in normally reared kittens. During this period, the forty-three visually activated cells studied were again readily classified as non-specific, immature, or specific. Table 2 (first column) shows that the distribution of the cells according to the four types defined above is almost the same as the one observed for the normally reared kittens (Fig. 7). In particular the percentage of the specific units (23 %) is the same in both cases. For this age group, it is impossible to define by electrophysiological recordings whether the kitten has been normally or dark reared.

*Age group: 18–28 days*

Two examples of specific units in a 19 day old kitten are illustrated in Fig. 4. These two cells have horizontally orientated perceptive fields, and are sensitive to the movement of stimuli in a vertical direction. One of the
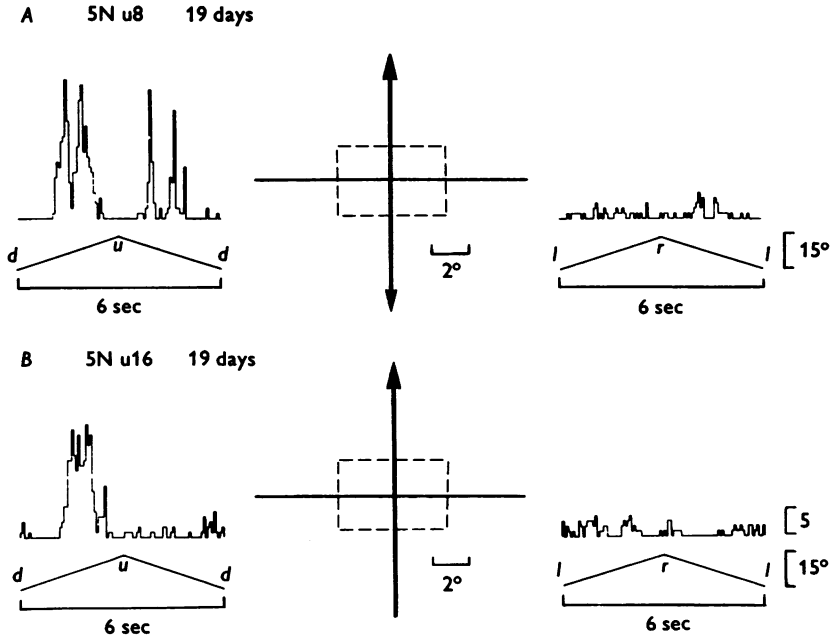


Fig. 4. Post-stimulus time histogram of two specific cells in a 19 day old DR kitten. Binw 60 msec; $n = 14$ $A$; in the centre, diagram of the receptive field and direction of movement of the activating stimulus. The thickness of the arrow indicated the strength of the response. On the left, histogram formed by a horizontally orientated slit moving from down ($d$) to up ($u$) and from up to down. On the right, histogram formed by the same but vertically oriented slit moving from right ($r$) to left ($l$) and left to right. $B$, the same for another cell. In $A$, a specific cell monocularly activated by the contralateral eye. The cell responds to a two-way vertical direction. In $B$, a binocular specific cell, mostly activated by the contralateral eye in a one-way direction.

cells is activated in a two-way direction ($A$), and the other only in a one-way direction ($B$). During this period, the number of specific cells decreases, and the number of non-specific cells increases (Table 2, second column).

*Age group: 29–42 days*

The non-specific units become by far the most numerous, but the other types can still be found especially during the fifth week (Table 2, third column). An example of these non-specific cells is shown in Fig. 5. This unit is binocularly activated by a stimulus of any shape (preferentially a
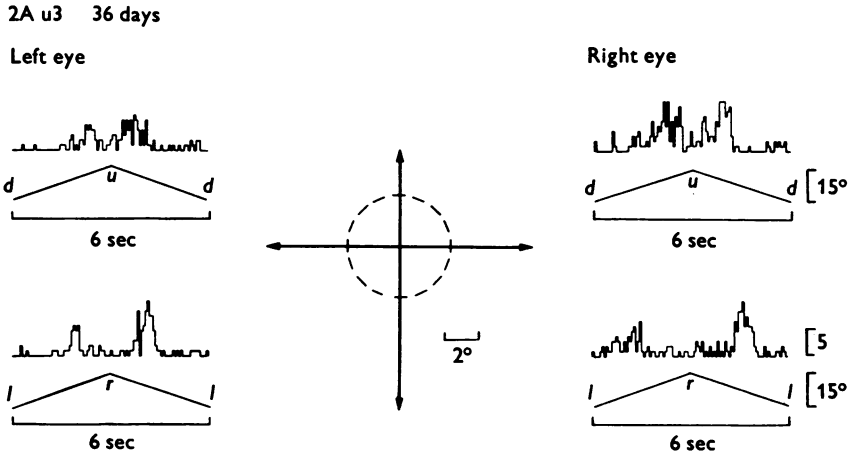
2A u3    36 days

Left eye                                          Right eye



Fig. 5. Post-stimulus time histogram recorded in a 36 day old DR kitten showing a non-specific cell binocularly activated. Binw 60 msec; $n = 14$. Diagram of the receptive field and direction of movement of the activating stimulus. On the left, histogram formed by left eye stimulation. Upper left, a spot moving vertically from down ($d$) to up ($u$) and up to down. Lower left, a spot moving horizontally from left ($l$) to right ($r$) and right to left. On the right, the same thing for right eye stimulation.

spot), moving across the receptive field in any direction. Note that activation is less prominent than for the specific unit. It is therefore difficult to determine the limits of the receptive field. The properties of an immature unit are illustrated in Fig. 6. The cell is preferentially activated by a horizontally directed movement and does not respond to vertical movement. However, responses can still be obtained for intermediary directions. Fig. 7 is a quantitative summary of the results described above. First of all, whatever the rearing conditions, as soon as the first clear visual responses appear about 25 % of the recorded cells are specific. Secondly, with normally reared kittens the specific cells tend to increase and the non-specific and immature decrease. Thirdly, in the dark reared kittens, the characteristics of the early specific units progressively disappear until all the units are non-specific.

In a previous work (Imbert & Buisseret, 1975) it was shown that the distribution of cells according to their ocular dominance was not different in either group, normally or dark reared, and was similar to that previously
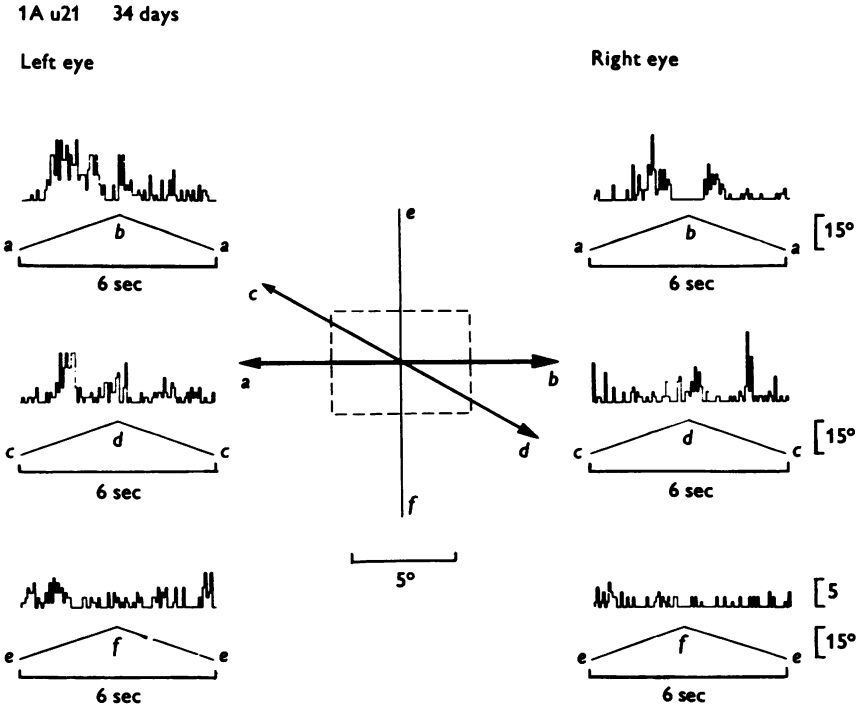


Fig. 6. Post-stimulus time histogram recorded in a 34 day old DR kitten showing a binocularly activated immature cell. The preferred direction is horizontal, and the ineffective direction is vertical. Binw 60 msec; $n = 14$. In the centre, diagram of the receptive field, the thickness of the arrows indicate the strength of the responses. In each case the slit is perpendicularly orientated to the movement in the direction indicated by the arrows. The letters under the histogram correspond to the same letters in the central diagram, indicating direction of the moving slit. The left histograms were obtained by left eye stimulation, and the right histograms for right eye stimulation.

described for 'adult' cells. In this paper we confirm on the whole this statement. However up to the end of the third week the specific cells, in the normally or dark reared kittens, are generally monocularly driven, in contrast with the specific ones of the adult cortex.
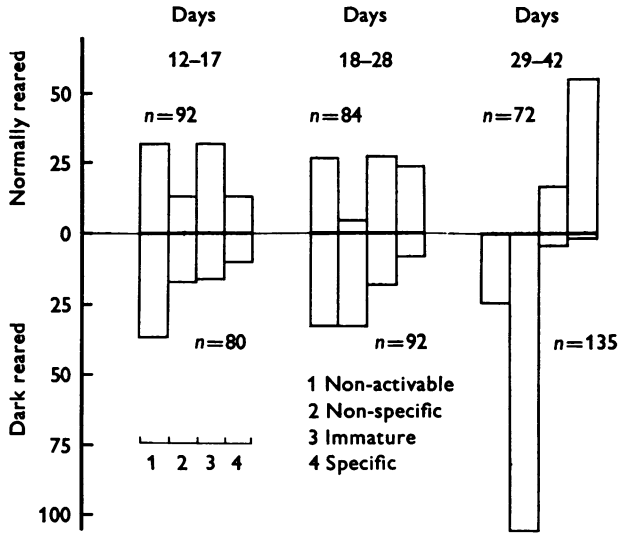
Fig. 7. Distribution of the different types of cells in three age groups in the NR kittens (upper part), and the DR kittens (lower part). See text for details.

## DISCUSSION

Our experiments are in agreement with those of Hubel & Wiesel (1963), in showing the presence of specific units in young, visually inexperienced kittens. In a 15 day old kitten, 23 % of the cells have some similar characteristics of specificity as in the adult cat. However most of these units are monocularly driven. We have been able to pay particular attention to orientation selectivity of these cells, by using stationary flashing bar instead of a moving one. Our results concerning the first appearance of oriented cells differs entirely from those of Barlow & Pettigrew (1971), and Pettigrew (1974), who claim that the first orientation selective cells appear only at the end of the fourth week. We must say that most of the Barlow & Pettigrew (1971) and Pettigrew (1974) studies were concerned with disparity selectivity, which we did not study. However, we can agree with Pettigrew (1974) that it is excessive to classify many of the units isolated at an early stage as specific in term of orientation selectivity. Although they are driven by a moving bar in a loosely delimited direction (failing to respond to the orthogonal direction), they respond in the same way to any type of stimulus irrespective of its configuration. Since they do not satisfy all the criteria of orientation, we have delimited such cells from the 'specific' cells and classified them as 'immature'. These cells could correspond to the 'complementary cells' of Pettigrew & Garey (1974). It seems

likely that Hubel & Wiesel (1963) considered some units as specific that we would consider immature. They used only a moving bar as stimulus, and observed that the cells gave responses over a range of stimulus orientation that was unusually wide by adult standards. We agree with Hubel & Wiesel (1963) as to the quality of the cellular response in a very young kitten is concerned. The cells' spontaneous activity is very poor or non-existent. They are sluggish in their responses, and show a marked tendency to fatigue. Also, with 8–11 day old kittens, we recorded (apart from non-activable units), three cells whose spontaneous activity was modified by random moving patterns (Fig. 1). When Hubel & Wiesel mention that 'some cells did not respond at all to patterned stimuli unless the stimuli were moving' either they were referring to units of the same type as the three just mentioned, or to units which we could classify as non-specific.

Throughout our experiment, we give to each kitten an age in days, measured from birth onwards; so do also the other authors mentioned in this paper. This may be a source of difficulty when comparing results. For some kittens, there appeared to be a discrepancy between their age in days and their 'developmental' age, as inferred from their electrophysiological behaviour. Other factors may also interfere, such as premature birth, number of kittens per litter, season of birth, mother's breed, age . . . These factors clearly play a role in the animal's somatic weight and are responsible for variations in development. Such variations might account for the slight differences in the chronological time of appearance of orientation specificity in our results and in those of Hubel & Wiesel (1963); but such variations cannot account for the larger discrepancy between our results and those of Barlow & Pettigrew (1971).

In this study, we have opted for extreme rearing conditions: namely complete deprivation of light. It is only in this case that one can rigorously consider that a kitten has had no previous visual experience (cf. Imbert & Buisseret, 1975).

But Pettigrew (1974) puts a 4 week old kitten reared with sutured eyelids (thus lacking in form experience) in the same category as a very young and normally reared one. Our results show that this is totally inappropriate. We have studied the development of dark reared kittens' receptive field properties age group by age group. This has demonstrated that at 15 days receptive field properties are the same irrespective of rearing conditions. However, the cortical cell responses of the dark reared kittens (and of the normally reared) are both progressively transformed so that a 6 week old dark reared kitten cannot be equated with a 15 day old one, whether reared normally or in the dark. Pettigrew (1974) did study the development of normally reared kittens, week by week, but he included all the findings from the dark reared kittens of 2–6 weeks age in the same

histogram (Pettigrew, 1974, Fig. 8). This may indicate that he did not discriminate between any changes in the receptive field properties in his 'form' inexperienced kittens between 2 and 6 weeks.

Pettigrew has stated (1974) that 'visual experience must in some way be responsible for the setting up of specific sets of connexions *de novo*' but this appears to derive from two observations which we cannot support. The first is that 'a large proportion of cells in older binocularly deprived cortex fail to respond to any visual input . . .' Table 1 shows that for the oldest dark reared kittens (29–42 days), there are only twenty-four non-activable units out of 135 recorded or 17 %, which is hardly a 'large proportion'. Moreover, the proportion of non-activable cells for the older kittens is smaller than for the younger ones. This indicates a decrease with age in the number of cells of this type. His second statement is that 'very few cells are recorded in tracks through immature cortex'. In Table 1, the number of units per penetration is given in function of age group and rearing condition. There is no notable difference in the number of units by track terms of the age and rearing conditions of the kittens, apart from the first age group in which these units are very scarce. On the main issue, our findings are simply that some specific visual connexions develop in kittens reared in complete darkness from birth and so cannot be attributed to 'visual experience . . . setting up . . . connections *de novo*'.

However, for specificity to be maintained and to continue to develop, the kitten must be allowed visual experience by its third week of life so connectivity is dependent upon functioning as well as upon innate developmental factors.

Note added in proof. Since this paper was submitted, Blakemore & Van Sluyters (*J. Physiol.*, 1975, **248**, 663–716) have published similar results concerning the existence of cells presenting some orientation selectivity in 3 week old deprived animals which are mostly monocularly driven, and the progressive degradation of this specificity following prolonged deprivation.

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