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EARLY POST-NATAL DEVELOPMENT OF NEURONAL FUNCTION IN THE KITTEN'S VISUAL CORTEX: A LAMINAR ANALYSIS

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SUMMARY

1. The normal post-natal development of visual cortical functions was studied by recording extracellularly from 612 single neurones in the striate and parastriate cortex of anaesthetized and paralysed kittens, ranging in age from 6 to 24 days. Analyses have been made of laminar differences in the developmental trends of receptive field properties such as orientation specificity and spatial organization of 'on' and 'off' zones.

2. At the beginning of the second post-natal week the majority of neurones (76%) only respond to light 'off' (unimodal 'off' neurones). Only later does the frequency of occurrence of unimodal 'on' neurones and of bimodal or multimodal neurones (with spatially segregated 'on' and 'off' zones arranged side by side) increase so that, by the middle of the fourth week, about equal numbers of these three receptive field types are found. The proportion of 'on–off' neurones (with spatially coincident 'on' and 'off' zones) remains low (between 9% and 12%) during the early post-natal period.

3. In layers 4 and 6 of areas 17 and 18 the frequency of occurrence of visual neurones is quite normal even in the youngest kittens, whereas the probability of recording neurones in layers 2/3 and 5 in kittens less than 14 days old is remarkably low and only gradually improves up to the middle of the fourth week. A very rudimentary order in the spatial arrangement of orientation-specific neurones and ocular dominance distribution is observed even in very young kittens. This order improves rapidly and reaches adult levels during the fourth post-natal week.

4. In visually inexperienced kittens, on average 11% of all responsive neurones are selective for the orientation of elongated visual stimuli, and 58% are biased. The proportion of orientation-selective cells begins to increase rapidly about two days after lid opening, and proportions of orientation-selective cells similar to that in the adult are reached by the end of the fourth post-natal week. Orientation-selective neurones in kittens less than 10 days old are only found in layers 4 and 6 and the lower part of layer 3. In layers 2/3 and 5 they are first seen in larger proportions by the beginning of the third post-natal week.

5. Our results show that, during the first post-natal month, the time course of the functional development of visual cortical neurones depends on receptive field type

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and on intracortical location. Implications of our findings for the development of intracortical connectivity and the generation of 'simple' receptive fields are discussed. In addition, possible mechanisms for, and functional implications of the late generation of 'complex' fields are suggested.

INTRODUCTION

Previous studies concerned with the development of the functional organization of the kitten's visual cortex have produced conflicting results. Hubel & Wiesel (1963) found receptive field types and functional properties such as orientational and directional specificity to be well developed, although neurones responded only sluggishly to visual stimuli and did not follow repetitive stimulation. On the other hand Pettigrew (1974) found no cell in the early post-natal period having orientational selectivity and only some possessing selectivity for the direction of stimulus motion. Other investigators have claimed that, shortly after birth, a small proportion of neurones in the kitten's visual cortex respond specifically to stimulus orientation and that, as a function of a developmental process, the immature cortex reaches a functional state similar to that in the adult cat by the beginning of the second post-natal month – provided that the kitten has experienced a normal visual environment (Blakemore & Van Sluyters, 1975; Buisseret & Imbert, 1976; Frégnac & Imbert, 1978; Bonds, 1979).

The conclusions drawn from these studies about the functional development of the immature cortex of kittens less than 12 days old have, however, relied on small sample sizes. In addition, little attention has been paid to receptive field structure and laminar distribution of visually responsive neurones. Hubel & Wiesel (1963) identified receptive fields in an 8-day-old kitten resembling the simple and complex fields described in adult cats (Hubel & Wiesel, 1962). In a 9-day-old kitten, Blakemore & Van Sluyters (1975) found orientation-specific neurones from layers 4 to 6 with simple receptive fields.

Our aims in conducting this study were therefore: (1) to reinvestigate the development of orientation specificity and other functional properties of neurones in the visual cortex of very young kittens by applying quantitative analysis to a representative sample of cells, (2) to give particular consideration to classification of receptive field types by evaluating response to stationary stimuli and assessing summatory behaviour, and (3) by establishing the laminar distribution of classified cells to gain some understanding of the development of afferent and intracortical connectivity.

A preliminary report of our experiments has been published previously (Wolf & Albus, 1981).

METHODS

Animals and surgical preparation

The experiments were performed on thirty-one normal kittens ranging in age from 6 to 24 days (Table 1). Four of the nine kittens studied in the youngest age group (6–9 days) had their eyes still closed at the beginning of the experiment, one kitten (6 days) had one eye partially and the other fully opened, whereas the remaining four had had their eyes open for at least one day. As eye opening takes place in the normal animal between days 6 and 9 post-natally, all the older kittens had at least two days visual experience by the start of the experiment.

Surgical anaesthesia was induced with an intraperitoneal injection of pentobarbitone (40 mg kg^{-1} body weight). In some cases this was supplemented by 0·4–0·8 % (v/v) fluothane in oxygen delivered through a mask. After one of the jugular veins was catheterized and a cannula inserted into the trachea, gallamine triethiodide (4–6 mg) was administered I.V. and the kitten was artificially ventilated with a mixture of 67 % N_2O, 30 % O_2, and 3 % CO_2. Throughout the experiment, pentobarbitone (2 mg kg^{-1} h^{-1}), gallamine triethiodide (15 mg kg^{-1} h^{-1}), prednisolone (0·6 mg h^{-1}), and laevulose (100 mg h^{-1}) in Ringer solution was given intravenously at a rate of 1·2–3·0 ml h^{-1}. The electrocardiogram was continuously monitored and cardiac accelerations to noxious stimuli were not observed during the experiments. End-expiratory CO_2 was monitored and held at about 5·5 % (v/v) by adjusting the stroke volume of the ventilation pump (40 strokes min^{-1}). The animals' temperatures were maintained at 38 °C by a thermostatically controlled heating blanket and monitored via a rectal thermistor. After the nictitating membranes were retracted with neosynephrine, the pupils dilated with atropine, and neutral contact lenses applied to protect the corneae from drying, the kitten was mounted in a stereotaxic frame (Horsley & Clarke, 1908). The head was retained in stereotaxic coordinates by a metal bar fixed to the skull with dental acrylic which additionally formed a reinforcing layer on the skull. A small opening was then made above the visual cortex, from stereotaxic coordinates A4 to P1 and L0 to L5. Around the craniotomy a well of acrylic was made. After cutting a small hole in the dura, the electrode tip was lowered to the pial surface and the brain covered with 4 % agar in Ringer solution to reduce cerebral pulsation.

Recording methods and visual stimulation

Extracellular recordings from single cells were made with tungsten micro-electrodes insulated with glass and having impedances of 7–11 MΩ at 1 kHz a.c. (exposed tungsten 4–6 μm, diameter at the exit from the glass 2–4 μm). The spikes were conventionally amplified, displayed on an oscilloscope and monitored aurally. As the electrode was advanced through the cortical layers at an oblique angle in a rostro-caudal direction, a hand-held projection lamp was used to produce moving and stationary light stimuli of different sizes and shapes (spots, bars, edges) on a dimly illuminated tangent screen (luminance 1–2 cd m^{-2}) positioned at a distance of 57 cm from the kitten's eyes. The luminance of the light stimulus was normally 1–2 log units above background. Neurones which were evident only by their spontaneous activity and could not reliably be activated by visual stimulation, or which were silent and produced only injury discharges when impaled by the electrode, were classified as visually unresponsive.

On isolation of units, monocular receptive fields were mapped as 'minimum response fields' (Barlow, Blakemore & Pettigrew, 1967). Orientational and directional asymmetries in the response to moving and/or stationary bars and edges, as well as velocity response range, were then qualitatively determined for the dominant eye. In order to assess the summation properties of the neurones, bars of different lengths and widths were used and the spatial extent of excitatory subregions was evaluated with small flashing spots. When possible, the receptive field in the non-dominant eye was also investigated and binocular interactions were examined.

For quantitative analysis of response characteristics, we employed a computer-controlled stimulation and spike-acquisition programme. With this programme, moving or stationary stimuli could be presented with direction and velocity of movement, presentation time and interstimulus interval being adjustable. The orientation of an elongated moving stimulus was always orthogonal to the direction of movement. To compensate for response variability, stimuli were interleaved (the method of Henry, Bishop, Tupper & Dreher, 1973). For assessment of orientation specificity, at least four different stimulus orientations (i.e. eight different directions of movement) including the optimum orientation determined manually and the orientation orthogonal to it, were presented quasi-randomly at least five times. Using these data, the computer was able to construct orientation tuning curves. To assess receptive field structure, stationary stimuli were flashed at each position in the receptive field and the responses so obtained were averaged over ten presentations.

There was some uncertainty in determining the eccentricity of the receptive fields in relation to the area centralis, since the cloudy optic media during the early post-natal phase (Thorn, Gollender & Erickson, 1976) prevented us from plotting optic disks and other retinal landmarks for younger animals in our sample. To measure the eccentricity of the receptive fields for kittens younger than 18 days, the perpendicular projection of the kitten's nose on to the tangent screen was considered as the centre of gaze. We estimate the error with this method to be less than 10 deg, based on comparisons with measurements of eccentricity from receptive field positions and stereotaxic coordinates of the recording electrodes.

Cell classification

On the basis of the division of the receptive field into 'on' and 'off' zones, cells were divided into three groups: (i) neurones responding exclusively to light on or to light off are classified as *unimodal 'on'* or *unimodal 'off'* cells respectively, (ii) neurones having receptive fields with both (or several) 'on' and 'off' zones, generally arranged side by side, are described as *bimodal* (or *multimodal*) cells, (iii) if there was no spatial segregation between 'on' and 'off' discharge areas, i.e. if the neurone responded to both phases of a flashing stimulus anywhere in its field, it was classified as an *'on–off'* neurone.

For those cells investigated quantitatively, an orientation specificity index (*OSI*) was calculated from the mean response to stimulation with an optimally oriented slit or bar (*optimum response*) moved in the preferred direction of movement (for moving stimuli), or flashed on and off at the optimum orientation (for stationary stimuli), and the mean response (for moving stimuli, the average of the responses to both directions of movement) to the same stimulus orthogonally oriented (+/− 15 deg) to the optimum (*non-optimum response*), through an application of the formula,

$$OSI \text{ (in \%)} = (1 - \text{non-optimum response/optimum response}) \times 100,$$

where response rates have been corrected for spontaneous activity. Cells with an orientation specificity index of greater than or equal to 90 % were classified as orientation *selective*, those with an index in the intermediate range (50–90 %) as orientation *biased*, and cells with an index of less than 50 % as orientation *non-specific*. The same scheme for classification of orientation specificity was applied by Bonds (1979). Since both orientation-selective and orientation-biased cells display orientation specificity, though to different degrees, they are grouped together as orientation *specific* in the following discussion, in contrast to the non-specific or *non-oriented* cells.

For cells which could only be qualitatively tested for orientation specificity a slightly different scheme was found necessary. Neurones unresponsive to the orientation orthogonal to the optimum were considered to be orientation selective and those displaying a clear-cut preference for one orientation but without an orientation at which they did not respond were considered to be orientation biased; those neurones which showed either no preference or only a slight preference for one orientation were classified as orientation non-specific. None of the neurones classified qualitatively as orientation selective required reclassification upon subsequent testing with the quantitative method. Discrepancies arose only in some cases between cells falling into the biased and non-specific classes. In these cases, the neurones in question were placed into the non-specific category. Whereas all orientation-specific neurones were also tested with small spots of light, only a small number (less than 3 %) were found to have similar tuning properties for both spots and bars of light moving across their receptive fields. Some of these neurones displayed directional selectivity and, because of their small number, they are combined with the group of orientation-specific cells.

Direction specificity was defined in relation to responses in the preferred and non-preferred directions for an optimally oriented slit. A direction specificity index (*DSI*) was calculated by applying the same formula as for computation of the orientation specificity index and allowed three groups to be defined; direction selective ($DSI \geqslant 90\,\%$), direction biased ($DSI = 50$–$90\,\%$), and direction non-specific ($DSI < 50\,\%$).

Examples of quantitative tuning functions of neurones from 6- and 7-day-old kittens are shown in Fig. 1. These curves have been selected in order to demonstrate that all variations of orientation specificity are present in the kitten's cortex as early as at the end of the first post-natal week. The limited number of orientations in these cases are not a reflexion of the testing of the total population; for most neurones in kittens older than 10 days, the response was determined at eight or more different orientations. Neurones in *A* and *E* are non-specific to stimulus orientation, cells in *B*, *C*, *F* and *G* are orientation biased, and cells in *D* and *H* are orientation selective. The cells in *A–C* were classified as directionally non-specific, the others as direction biased.

We used a 5-point scale to classify cells for ocular dominance (o.d.). The o.d. group 1 neurones could be stimulated through the contralateral eye and the o.d. group 5 cells through the ipsilateral eye only. The other units responded to stimulation of both eyes: those in o.d. group 2 responded more to contralateral, in o.d. group 4 more to ipsilateral, and in o.d. group 3 equally well to ipsi- and contralateral stimulation. Neurones responding only to binocular stimulation were also classified as o.d. group 3.

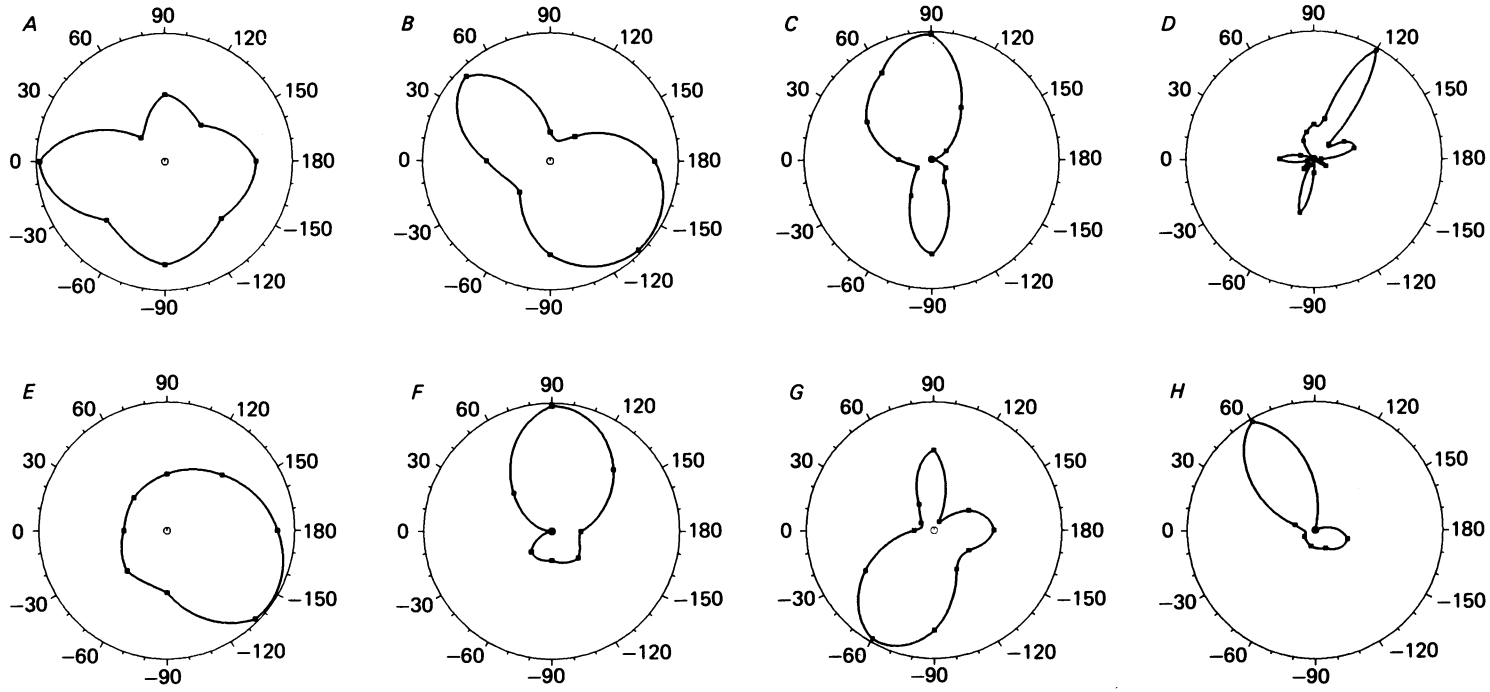

Fig. 1. Orientation tuning of neurones in the visual cortex of 6- and 7-day-old kittens. Four of the cells (*A*, *D*, *F* and *G*) are from kittens which had their eyelids still closed on the day of the experiment. Stimuli were light bars (length 20–40 deg, width 2–5 deg) moving at velocities between 5 deg s^{-1} and 10 deg s^{-1} (except for *C*, where the velocity was 20 deg s^{-1}) perpendicular to the long axis of the stimulus. Responses were calculated from the average number of action potentials in the response profile of the peri-stimulus time histograms. Responses were normalized and are plotted in a polar diagram as a function of *direction* of movement. The curves are interpolated between data points (two on each side, parabolic interpolation of fourth power), such that the 'optimum response' could come to lie between points (e.g. in *E*). *A*, 7 days old, area 17, layer 6; maximum response 2·7 spikes s^{-1}. *B*, 6 days old, area 17, layer 6; orientation specificity index (*OSI*) = 69%; maximum response 3·2 spikes s^{-1}. *C*, 7 days old, area 18, layer 3; *OSI* = 88%, orientation tuning width (at half-height) 118 deg; maximum response 3·8 spikes s^{-1}. *D*, 7 days old, area 17, layer 4; *OSI* = 94%; orientation tuning width 21 deg; maximum response 2·2 spikes s^{-1}. *E*, 7 days old, area 17, layer 6; maximum response 2·1 spikes s^{-1}. *F*, 7 days old, area 17, layer 4; *OSI* = 88%; orientation tuning width 102 deg; maximum response 2·8 spikes s^{-1}. *G*, 7 days old, area 17, layer 6; *OSI* = 78%; maximum response 1·1 spikes s^{-1}. *H*, 6 days old, area 17, layer 4; *OSI* = 95%; orientation tuning width 54 deg; maximum response 2·2 spikes s^{-1}. Spontaneous discharge of the cells was in every case lower than 0·03 spikes s^{-1}. Intervals between single stimuli were 10 s. Each stimulus was presented ten times in *A*, *E*, *F* and *G*, and five times in the other cells. See text for further information.

TABLE 1. Total number of visual cells recorded in each individual kitten in cortical areas 17 and 18

Kitten's age (days)		No. of visual cells	Cells in area		Eccentricity of receptive fields (deg)		
			17	18	< 15	15–30	> 30
A							
6	+/0	9	9	—	3	2	4
7 (1)	0/0	13	13	—	6	7	—
7 (2)	+/+	24	—	24	—	24	—
7 (3)	0/0	30	30	—	1	11	18
7 (4)	0/0	12	12	—	12	—	—
7 (5)	+/+	11	11	—	4	—	7
8 (1)	+/+	25	25	—	25	—	—
8 (2)	+/+	6	6	—	6	—	—
9	0/0	14	14	—	14	—	—
B							
10 (1)		24	24	—	24	—	—
10 (2)		22	22	—	22	—	—
10 (3)		16	16	—	—	5	11
10 (4)		35	35	—	35	—	—
11		26	26	—	25	—	—
12 (1)		10	10	—	—	10	—
12 (2)		20	—	20	—	—	20
13 (1)		9	No histology			No eccentricity	
13 (2)		13	8	5	13	—	—
C							
14		33	9	24	—	33	—
15		27	27	—	27	—	—
16		17	17	—	—	17	—
18 (1)		30	30	—	3	27	—
18 (2)		23	23	—	23	—	—
18 (3)		28	28	—	28	—	—
D							
20 (1)		6	6	—		No eccentricity	
20 (2)		15	15	—	1	14	—
20 (3)		14	14	—	14	—	—
23		5	No histology		5	—	—
24 (1)		11	No histology		—	—	11
24 (2)		32	25	—	4	28	—
24 (3)		19	19	—	19	—	—
6–9		144	120	24	71	44	29
10–13		175	141	25	119	15	31
14–18		158	134	24	81	77	—
20–24		102	79	—	43	42	11
Total		579	474	73	314	178	71

The last three columns give the quantity of visual cells collated for three different eccentricity ranges. A–D indicate the division of the kittens into four age groups (6–9, 10–13, 14–18, 20–24 days, respectively) the data for which are summed up in the last five rows. The numbers in parentheses after some ages distinguish between kittens of the same age and are also referred to in the text or in Figures if necessary. For the kittens of the youngest age group, the state of the eyelids on the day of the experiment is indicated (+, open; 0, closed).

Histological reconstructions

On completion of the experiment, the kitten was killed with an overdose of pentobarbitone (200 mg I.V.), perfused transcardially with a buffered solution of 4% formaldehyde and 2% glutaraldehyde, and the brain was removed. After fixation, blocks of the brain in the region of each penetration were cut on a freezing microtome in 60 μm sections in a coronal and in some cases in an oblique plane, parallel to the electrode track. After the sections were stained with thionine, the electrode track was reconstructed from electrolytic lesions which had been made at intervals of 1–2 mm during retraction of the electrode (4–6 μA for 10 s, electrode negative), and from other landmarks, such as entry into and exit from the white matter. Cell positions were placed between those marker points by interpolation. The 17–18 border and the laminar position of the cells were then determined by the criteria of Otsuka & Hassler (1962). Cells for which the laminar position could not unambiguously be assigned (in most cases the cells lying in the border region of two layers) were not included in the quantitative analysis of laminar distribution.

RESULTS

Of the 612 neurones recorded in the striate and parastriate cortex of 6–24-day-old kittens, on average only 5% could not be activated by visual stimuli, their proportion decreasing from 8% in the youngest to 3% in the older kittens. Most of the non-visual neurones were located in the supragranular layers, but some of them, particularly in the younger animals, were also found in layers 4–6. In the following discussion descriptions refer only to those neurones which were visually responsive.

The majority of the visual neurones recorded were found in area 17 (Table 1). For analysis of receptive field properties, cells from areas 17 and 18 were grouped together but only cells from area 17 were considered in the analysis of laminar distribution of cells.

Receptive fields were located between 0 and 50 deg from the area centralis with the majority distributed in the lower hemifield (Table 1). The sizes of receptive fields located at the same eccentricity varied considerably, though average field size increased with eccentricity from the visual axis. For eccentricities between 0 and 15 deg, for example, the receptive fields measured between 2 and 10 deg across in the youngest age group (6–9 days). Receptive field size was also found to decrease with age. Cells with small fields could always be recorded in the same penetrations as those with large fields.

The kittens were divided into four groups according to their age (Table 1). Since we did not observe any difference in the proportion of selective neurones between initial and final phases of an experiment (frequently lasting for more than 20 h), visual experience in the experimental setting does not seem to improve the specificity of the visual cortex in anaesthetized and paralysed animals. Cells recorded on the second day of an experiment were therefore associated with the age of the kitten at the start of the experiment.

The marked sluggishness and extreme response fatigue of cells in the cortex of very young kittens to both moving and stationary stimuli reported by Hubel & Wiesel (1963), Pettigrew (1974), Blakemore & van Sluyters (1975), Buisseret & Imbert (1976), and Bonds (1979) and confirmed in this study made it necessary to adopt interstimulus intervals of up to 20 s between stimulus presentations to elicit reliable responses. Neurones, particularly in the two youngest age groups, fired only a few spikes per stimulus presentation. Average discharge rates, measured over the whole

response profile to optimum stimuli, were generally less than 5 spikes per second in kittens younger than 14 days (see also Figs. 1, 3, 4 and 5).

Receptive field structure

Stationary stimulation. In all age groups the majority of neurones responded to moving as well as to stationary stimuli. However, in the youngest animals, one-third of all cells could not be driven by flashed stimuli. The proportion of cells responding exclusively to moving stimuli was 30–34% between post-natal days 6 and 13, declining to 20% during the third week and reaching 10% at the beginning of the

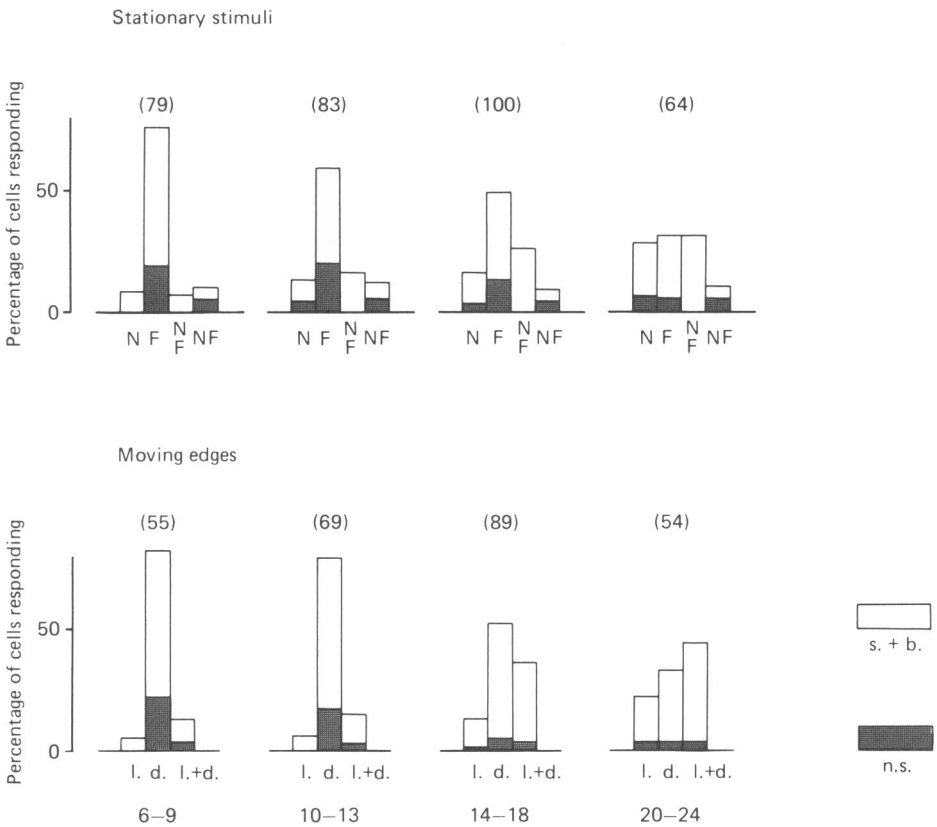

Fig. 2. Development of receptive field types for neurones in the kitten's visual cortex as revealed by stationary stimulation (upper row of histograms) and by stimulation with moving edges (lower row of histograms). The proportions of the different receptive field types of cells selective or biased to stimulus orientation (s.+b.) and non-specific to the orientation of a stimulus (n.s.) are indicated as percentages of the total number of cells per age group responding to stationary stimuli (upper) or to moving edges (lower). Total numbers of cells examined per age group and stimulus situation are given above each histogram, age groups (in days post-natal) are indicated at the bottom of the Figure. Neurones with unimodal 'on' or 'off' receptive fields are indicated by N or F respectively, with bi- or multimodal fields by N over F and those with 'on–off' fields by NF. Neurones responding exclusively to a moving light edge are denoted by l., those responding exclusively to a dark edge by d., and those responding to both light and dark edges by l.+d.

fourth week (cf. Pettigrew, 1974; Blakemore & Van Sluyters, 1975; Buisseret & Imbert, 1976; Frégnac & Imbert, 1978; Bonds, 1979).

Up to day 18, the proportion of unimodal 'off' neurones is larger than that of any other receptive field configuration. This is true for orientation-specific neurones (selective and biased) as well as for those with non-oriented receptive fields (i.e. orientation-non-specific cells). The proportion of 'off' cells decreased from 75·9 % of the neurones responding to stationary stimuli in the youngest kittens to 31·3 % in the oldest (Fig. 2). Unimodal 'on' neurones were rarely encountered in the youngest age group (7·6 % of the neurones activated by stationary stimuli), but gradually increased in number almost to the level of 'off' cells by the beginning of the fourth post-natal week (28·1 % in the 20–24-day group).

Bimodal or multimodal receptive fields (with spatially segregated 'on' and 'off' zones) were also rarely seen in the youngest age group, but their number consistently increased from being initially 6·3 % to reach 31·3 % (Fig. 2). Neurones with 'on–off' fields were rare at all ages, representing between 9 and 12 % of the total population of cells driven by stationary stimuli. Within the orientation-specific group, between 6 and 10 % had spatially coincident 'on' and 'off' regions.

Moving light and dark edges. Neuronal responses to moving light and/or dark edges could be elicited from 40–60 % of the visual cells in each age group (Fig. 2). Since, primarily in the younger animals, a proportion of visually driven cells could not be activated by stationary stimuli, and since not all cells responding to stationary stimuli were examined with moving edges, the population of neurones discharging to moving edges is not identical with the one responding to flashed stimuli (cf. Palmer & Davis, 1981*b*). Nevertheless, the developmental changes in receptive field types are also clearly revealed by the following testing procedure. Up to the end of the second post-natal week, 79–82 % of all neurones examined with moving edges responded to dark edges only, greatly outnumbering the units responding to light edges only (about 6 %) or to dark and light edges (13–15 %). During the third week a gradual change occurred, so that by the beginning of the fourth week 22 % of the neurones responded exclusively to light edges and 33 % to dark edges, while 44 % responded to both light and dark edges. This means that the relative strength of the 'off' mechanism in the cortex of very young kittens, and the increase in the strength of the 'on' component during the first post-natal month, is observed with moving edges as well as with stationary stimuli.

Receptive field types. Marked differences in distribution of receptive field types are apparent in comparisons between immature and adult cat cortices. Unimodal 'on' and 'off' neurones constitute nearly 85 % of the population of neurones which are activated by stationary stimuli in kittens at the time of eye opening. Even at the beginning of the fourth post-natal week this category still accounts for 60 % of visually responsive neurones, in contrast to the situation in the adult cat where such neurones constitute only 20–30 % of cells (Singer, Tretter & Cynader, 1975; Kato, Bishop & Orban, 1978; Palmer & Davis, 1981*a*). Some of the properties of unimodal cells are illustrated in the response histograms to different configurations and positions of stationary light stimuli (Figs. 3 and 4 *A* and *B*).

Summation of response within the receptive field, as illustrated in Fig. 3 *A* (position 6 *vs.* positions 1–4), was found in most units. In the youngest animals, a light spot

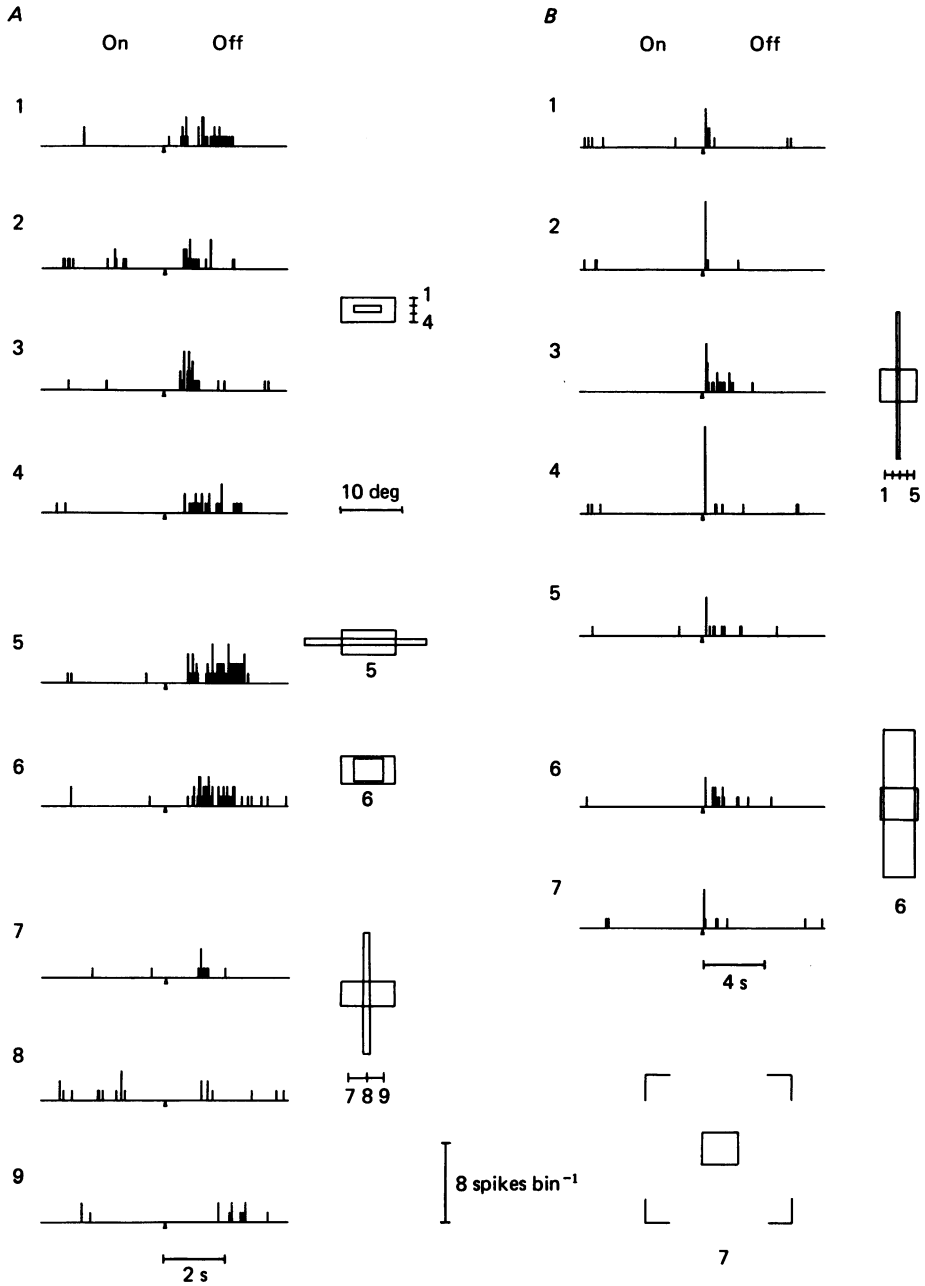

Fig. 3. Receptive field types in the kitten's visual cortex as revealed by stationary stimulation at different positions within the field. Receptive field sizes, stimulus sizes and stimulus positions are schematically drawn. Numbers at each drawing correspond to numbers in the upper left-hand corner of the peri-stimulus time histograms (p.s.t.h.s) and indicate different stimulus positions and stimulus configurations. P.s.t.h.s for both cells were obtained by stimulating the contralateral eye. Each stimulus was presented ten times per position. Stimuli were optimally oriented in *A* (1–6) and in *B* (1–6), and orthogonally to the optimum in *A* (7–9); the stimulus in *B* (7) was a large square (25 × 25 deg) of light. In each p.s.t.h. the response to light on is to the left and to light off, to the right. Each half of the p.s.t.h.s comprises 100 bins (bin-width = 40 ms in *A* and 80 ms in *B*). Scales indicate data acquisition time, number of spikes per bin and, for the drawings, degrees

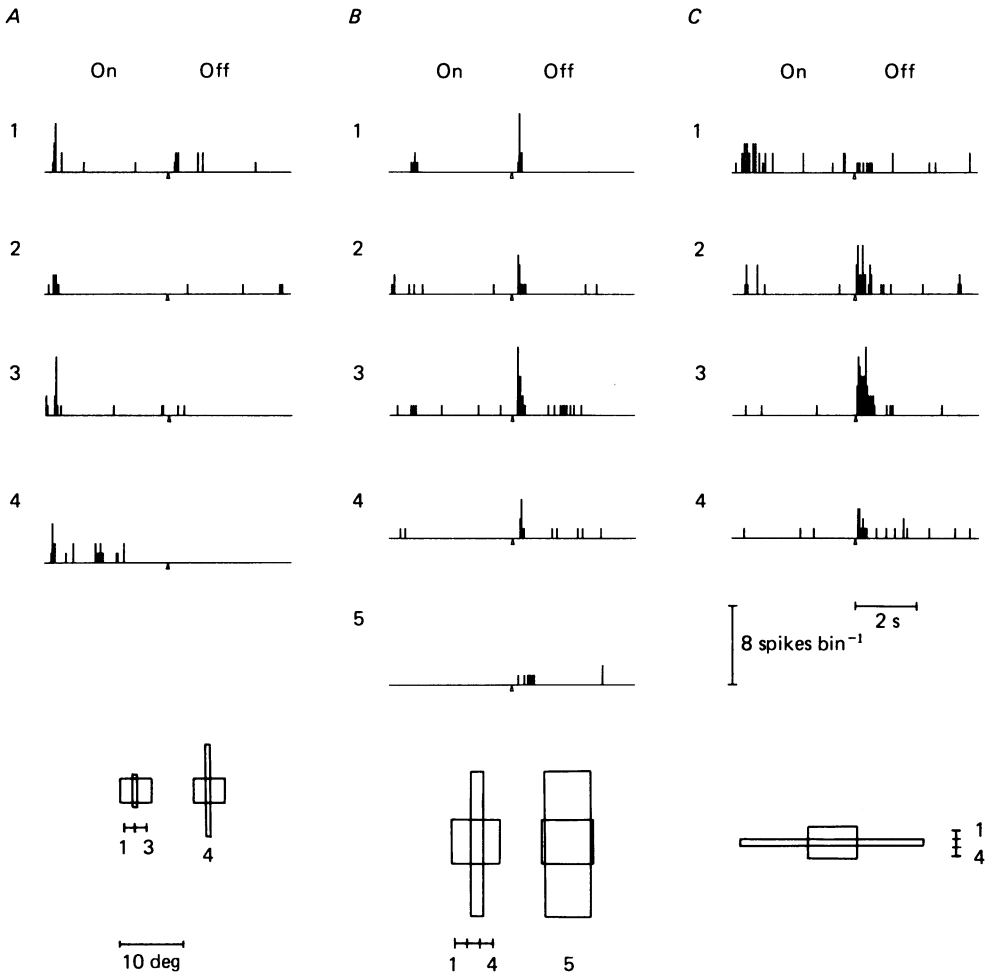

Fig. 4. Receptive field types in the kitten's visual cortex as revealed by stationary stimulation, P.s.t.h.s for the neurones in *A* and *C* were obtained by stimulating the ipsilateral eye and for *B*, the contralateral eye. Each stimulus was presented ten times per stimulus position. Bin-width was 40 ms for all p.s.t.h.s. *A*, unimodal 'on' cell, recorded from area 18, lamina 4, in a 7-day-old kitten. The neurone was orientation and direction biased, and belonged to ocular dominance group 4. Size of the receptive field was 4 × 5 deg, its eccentricity was 23 deg in the lower visual field. *B*, unimodal 'off' cell, recorded from area 17, at the border of laminae 3–4 in a 7-day-old kitten. The neurone was orientation and direction biased, and was dominated by the contralateral eye (o.d. group 2). Size of the receptive field was 7 × 8 deg, its eccentricity was 27 deg in the lower visual field. *C*, bimodal cell recorded from area 18, lamina 4, in a 14-day-old kitten. The neurone was orientation and direction selective, and belonged to o.d. group 4. Receptive field size was 5 × 8 deg, its eccentricity was 18 deg in the lower visual field. For further details see legend to Fig. 3.

in the visual field. *A*, unimodal 'off' neurone with sustained properties recorded from area 17, layer 4, in an 8-day-old kitten. The unit was orientation biased (compare position 5 to positions 7–9), directionally non-specific, and binocularly driven (o.d. group 3). The receptive field had a size of 4 × 9 deg and its centre was positioned at an eccentricity of 9 deg in the lower visual field. *B*, unimodal 'off' neurone with transient properties from area 18, layer 3, in a 7-day-old animal. The cell was orientation selective, directionally non-specific, and was activated only through the contralateral eye. Size of the receptive field was 5 × 5·5 deg, eccentricity was 26 deg in the lower visual field.

had to have a diameter of at least 1–2 deg to be able to elicit a reliable response. However, many neurones, particularly those with a very low response amplitude, required larger spots or broad and/or long bars to be activated at all. This was also the case for the neurones illustrated in Figs. 3*B* and 4*B*. Both did not discharge to a small spot or to a short bar, only to a stimulus covering the whole receptive field area or to a long bar. In addition, these examples show that a reduction in response was produced as the stimulus was enlarged to cover a significant part of the receptive field surround (Fig. 3*B*, position 6 *vs.* position 3; Fig. 4*B*, position 5 *vs.* positions 1–4), showing that the excitatory regions seem to be flanked by weak inhibitory regions as early as at the beginning of the second post-natal week.

An interesting observation, especially in kittens younger than two weeks, was that some of the unimodal neurones responded very weakly to opposite contrast of the stimulus. This is well illustrated for an 'off' cell in Fig. 3*A*, position 2 and for an 'on' cell in Fig. 4*A*, position 1. Normally this was only detected using quantitative methods. A criterion was adopted that, for a neurone to be classified as unimodal, the response to the non-preferred contrast should be less than 10% of that to the preferred contrast, and that the response was elicited only infrequently and with a marked variation in response latency. For the examples in Figs. 3*A* and 4*A* the non-dominant response was elicited in only two or three out of ten stimulus cycles.

Although orientation-specific unimodal neurones cannot unequivocally be correlated with the 'simple' category of Hubel & Wiesel (1962), they may indeed represent the simplest type of neurone in the visual cortex, for several reasons: they have a simple (in the semantic sense) receptive field structure; they are the first to be encountered in large numbers during post-natal functional development; they are very often excited only monosynaptically by thalamo-cortical afferents (Singer *et al.* 1975) and they appear to be positioned at an early stage in information processing (Toyama, Kimura & Tanaka, 1981).

On the other hand, neurones with bimodal receptive fields (Fig. 4*C*) without doubt meet the requirements for the simple neurone type of Hubel & Wiesel (1962). Although those encountered during the second post-natal week generally had a marked region of overlap between 'on' and 'off' discharge areas, they behaved in every other respect like simple cells. They showed summation within single excitatory regions and their responses were always reduced when the stimulus was so broad that it covered both the excitatory 'on' and 'off' zones, even without stimulating regions outside the receptive field. These zones are therefore organized in a mutually antagonistic manner as in the adult cat (Hubel & Wiesel, 1962). In addition, the responses of bimodal (and multimodal) neurones were in every case orientation selective (see Fig. 2). Multimodal receptive fields were not observed in the very young animals. From the onset of the third week, however, the arrangement of the receptive fields became more variable and the first field which clearly had three 'on' and 'off' discharge areas, spatially displaced, was recorded from an 18-day-old kitten.

Orientation-biased and orientation-selective 'on–off' neurones were rarely encountered (see also Fig. 2). Moreover, this population had heterogeneous properties since a marked difference was observed between the 'on–off' cells found in younger kittens and those in older ones. The vast majority of 'on–off' neurones recorded from kittens younger than two weeks were unresponsive to small spots of light (1–2 deg diameter). However, these neurones showed a clear summation of response both within the

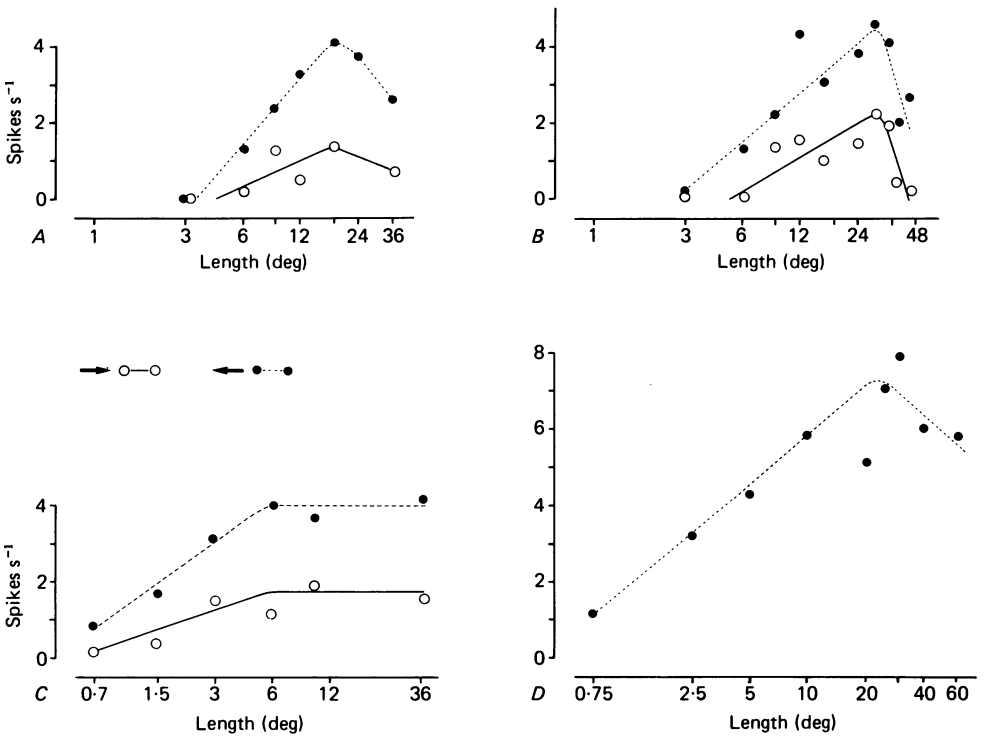

Fig. 5. Length summation and end inhibition of neurones in the kitten's visual cortex. A light slit (width 1·0 deg in *A* and *B*, 1·5 deg in *C* and *D*) of the optimum orientation was moved back and forth across the receptive fields at the preferred velocity, ten times for each stimulus length. Response amplitude was calculated from the average number of action potentials measured across the whole response profile and plotted as a function of stimulus length, abscissa scaled logarithmically. The preferred direction of movement is indicated by filled circles and a dashed line, the non-preferred direction by open circles and a continuous line. Curves are fitted by hand. *A*, cell from the border of layers 3–4 in area 17 of a 7-day-old kitten. Receptive field size 7 × 7 deg. *B*, cell from layer 3 in area 18 of a 7-day-old kitten. Receptive field size (length × width) 8 × 6 deg. *C*, cell from layer 6 in area 17 of a 12-day-old kitten. Receptive field size 4 × 3 deg. *D*, cell from layer 4 in area 18 of a 14-day-old kitten. Receptive field size 8 × 6 deg. All cells were orientation biased. Note that the neurone in *D* was direction selective.

receptive field and even when the stimulus extended to regions outside it. When stimulated with larger stimuli, discharges to 'on' and 'off' were unequal, the 'off' component dominating the 'on' component (for the majority of cases) or vice versa. It would appear, therefore, that there are distinct excitatory 'on' and 'off' regions within the receptive field but, because of an overlap in those regions, they could not be reliably identified with stationary stimuli of dimensions required to elicit a response. In older kittens, on the other hand, an increasing number of 'on–off' neurones responded to stimuli much smaller than the receptive field area and gave reliable discharges of about equal strength to both contrasts of a small spot or bar flashed on and off at any position within the receptive field. In addition, response summation in these neurones appeared to be non-linear. The discharge amplitudes were maximal to small spots and did not increase to larger stationary stimuli. In some cases, they were even less when the stimulus covered the whole field.

Because of its spatial summation properties, only this latter type of receptive field can be considered to be identical to the 'complex' field found in adult cats (Hubel & Wiesel, 1962; Singer, Tretter & Cynader, 1975; Gilbert, 1977; Kato, Bishop & Orban, 1978). Thus, typical complex cells were not observed in the kitten's visual cortex during the second post-natal week, the first one to be encountered being located in lamina 5 of area 17 in a 15-day-old kitten. Complex cells remained small in number throughout the third week, their proportion representing 5·6 % of orientation-specific neurones present between days 20 and 24.

Response summation along the axis of the receptive field was observed in more than 95 % of all orientation-specific neurones (Fig. 3*A*, position 5 *vs.* positions 1–4; Fig. 4*A*, position 4 *vs.* positions 1–3). It was found, especially in the younger kittens, to be effective over a much larger area outside the minimum response field than in adult animals (Fig. 5). The two neurones from 7-day-old kittens (Fig. 5*A* and *B*) only start to fire when the slit is more than 3 deg long. Their discharge rate is related linearly to the logarithm of slit length, up to 18 deg in *A*, and up to 30 deg in *B*, although the receptive field sizes are much smaller. Beyond an age of 12 days, minimal stimulus length could well be less than 1 deg, as can be seen from the length–response curves for neurones recorded in a 12- and a 14-day-old kitten (Fig. 5*C* and *D*).

Many of the orientation-specific neurones in the visual cortex of very young kittens also showed suppression of their discharges from regions outside their receptive fields, and this was found to be increasingly more pronounced in older kittens. Typically, in the youngest animals, diffuse stimuli still elicited a response in many orientation-specific cells. This is illustrated for an orientation-selective, unimodal 'off' neurone from a 7-day-old animal in Fig. 3*B*, position 7. On the other hand, in kittens older than two weeks, orientation-specific units, especially those which were orientation selective, rarely responded to diffuse visual stimuli. The results of Derrington & Fuchs (1981) are in agreement with this. These authors demonstrated the increasing efficacy of surround inhibition in the visual cortex of young kittens in the context of a study of the post-natal development of spatial frequency selectivity.

The length–response curves in Fig. 5 demonstrate that even in the youngest animals some cells may be strongly suppressed when the stimulus is lengthened, thus resembling the 'hypercomplex' type neurones (Hubel & Wiesel, 1965; Kato *et al.* 1978). For the neurones in Fig. 5*B* and *D*, slit length has to be 3–4 times as long as the corresponding dimension of the excitatory receptive field area before inhibition is observed, and typically this end-inhibition only occurred with stimulus lengths much longer than that required in adult cats. End-inhibition was found in cells of all layers, though rarely in layer 6, in both areas 17 and 18 (Fig. 5*C*, cf. Gilbert, 1977).

Response summation within the receptive field was also seen in neurones unspecific to stimulus orientation or direction of movement. However, suppression from the surround was found in only about 50 % of the non-specific cells. In the remaining neurones, the response either continued to increase in strength when additional surround areas were stimulated or remained unchanged. As for orientation-specific neurones, an excitatory response could not be elicited by stimulating the surround areas of non-specific cells alone. The shape of the action potentials from these units, as well as their binocularity, precludes the possibility that these recordings were from geniculo-cortical axons.

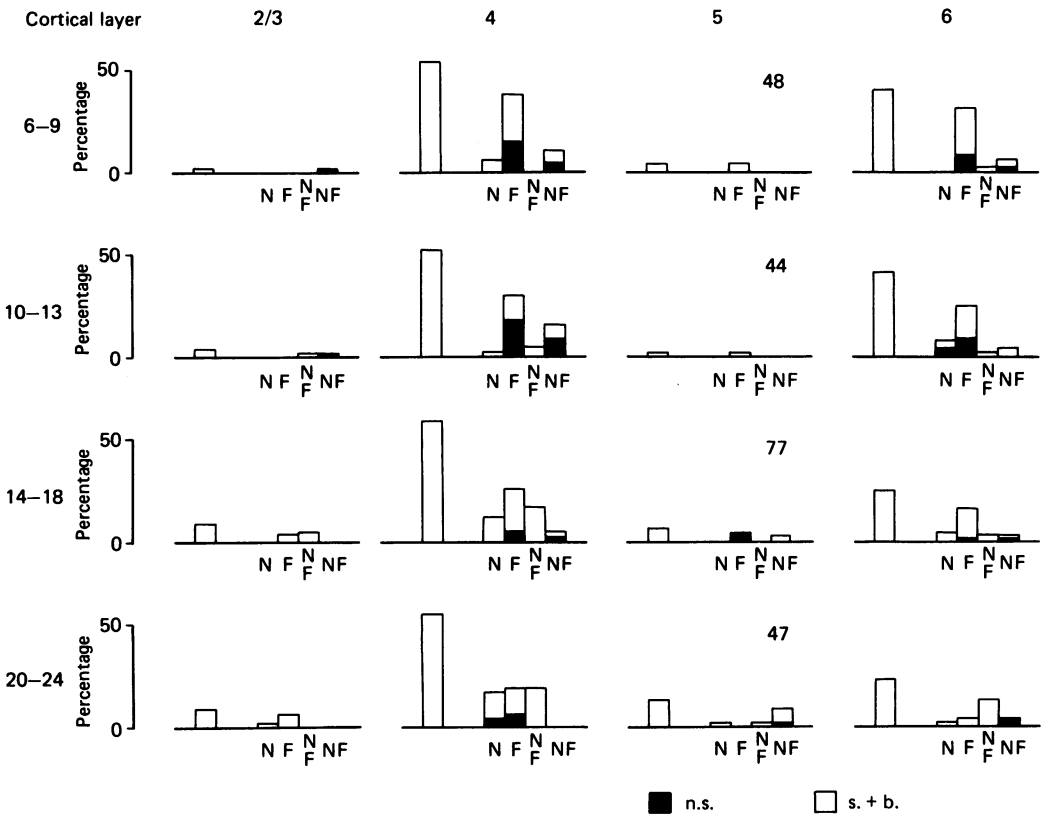

Fig. 6. Laminar distribution of receptive field types in the visual cortex (area 17) of young kittens. Layers are indicated by the numbers at the top of each column, age groups by numbers at the left-hand side of each row of histograms. The percentages of neurones in each layer are indicated by a bar (without subscript) at the left-hand side of each histogram representing one lamina. Neurones are further differentiated according to the spatial arrangement of 'on' and 'off' zones within their receptive fields and with respect to orientation specificity. The numbers above each row of histograms give the total number of units which responded to stationary stimuli, whose orientation specificity could be tested, and which could reliably be located from the histological reconstructions. For further information see legend to Fig. 2.

Laminar distribution of receptive field types. The laminar distributions of cells in area 17 activated by stationary stimuli are shown in Fig. 6. The change from an 'off'-cell-dominated distribution to a larger representation of unimodal 'on' and bimodal or multimodal neurones can be seen in all layers of the visual cortex. As one would expect from a consideration of the dimensions of the different cortical laminae, most neurones, orientation-specific as well as non-specific, were recorded from layers 4 and 6. The proportion of neurones encountered in both laminae 2/3 and 5, however, is comparatively small during the second post-natal week (between 6 and 7 %) and only increases gradually during the third and fourth week (16 % in 14–18-day-old kittens and 21 % in the 20–24-day-old animals), but still does not reach proportions found in the adult cat. To gain an impression of the actual proportions of cells in

relation to cortical lamination, the numbers of visually responsive neurones encountered in individual laminae of area 17 per unit cortical distance are given in Table 2. A significant increase in the frequency of recording neurones is found for layers 2/3 and 5 not before the end of the second post-natal week, whereas in layers 4 and 6 no consistent change is seen.

Interestingly, the few orientation-specific 'on–off' cells recorded up to the end of

TABLE 2. Frequency of visually responsive neurones within individual laminae of the kitten striate cortex at different ages during post-natal development

Age group (days)	Layer 2/3	Layer 4	Layer 5	Layer 6	All layers	Distance (μm)
6–9	1·3	6·9	2·2	4·3	4·0	29338
10–13	1·6	8·5	2·6	5·9	5·2	21976
14–18	3·7	8·3	6·1	5·5	6·3	25015
20–24	3·5	7·0	7·0	6·5	6·1	11570

The average numbers of neurones recorded in each layer per thousand micrometre penetration distance (columns 2–5) are given for each age group together with the average number of cells in all laminae (column 6). The total sampling distances through layers 2 to 6 are indicated in the last column. For further information see text.

the second post-natal week were almost exclusively found in layer 4 (Fig. 6). This additionally distinguishes them from 'on–off' cells found later on during development. Also, in 6–18-day-old kittens a number of 'on–off' neurones which did not display orientation specificity were seen in this layer. As orientation-specific as well as orientation-non-specific 'on–off' neurones were not found, in our sample, in layer 4 of older animals and since it is generally accepted that the middle layers primarily contain unimodal and simple cells in the adult cat (Hubel & Wiesel, 1962; Singer *et al.* 1975; Kato *et al.* 1978; Bullier & Henry, 1979*b*), their existence in this layer could reflect a transient stage in the development of layer 4 simple cells, i.e. neurones with bimodal receptive fields. It might also partly be due to light scatter caused by the poor quality of the kittens' optic media (cf. Discussion).

Orientational specificity

The proportion of orientation-selective cells increases from an average of 15% at the end of the first post-natal week (age group 6–9 days) to 72% at the beginning of the fourth week (age group 20–24 days) in both areas 17 and 18, accompanied by a decrease in the proportion of orientation-biased and non-specific neurones (Fig. 7 and Table 3). In spite of the inter-individual scatter in the distributions of orientation-specific and non-specific cells the developmental trend is quite marked.

In the 6–9-day-old group of kittens there was no significant difference in the distribution of orientation-specific or non-specific neurones between animals which had their eyelids still not opened at the beginning of the experiment and those with 1–2 days of visual experience. In one of the 7-day-old visually inexperienced kittens, no orientation-selective cells could be detected but 63% of the neurones were biased. In the two remaining 7-day-old, and in the 9-day-old kitten with its eyelids unopened on the day of the recording session, the percentages of orientation-selective neurones were 7, 18 and 21% respectively, and for this group of kittens 50–64% biased neurones were found. Less than one-third (18–33%) of all neurones recorded in these kittens did not show any orientation specificity. For visually inexperienced kittens in the

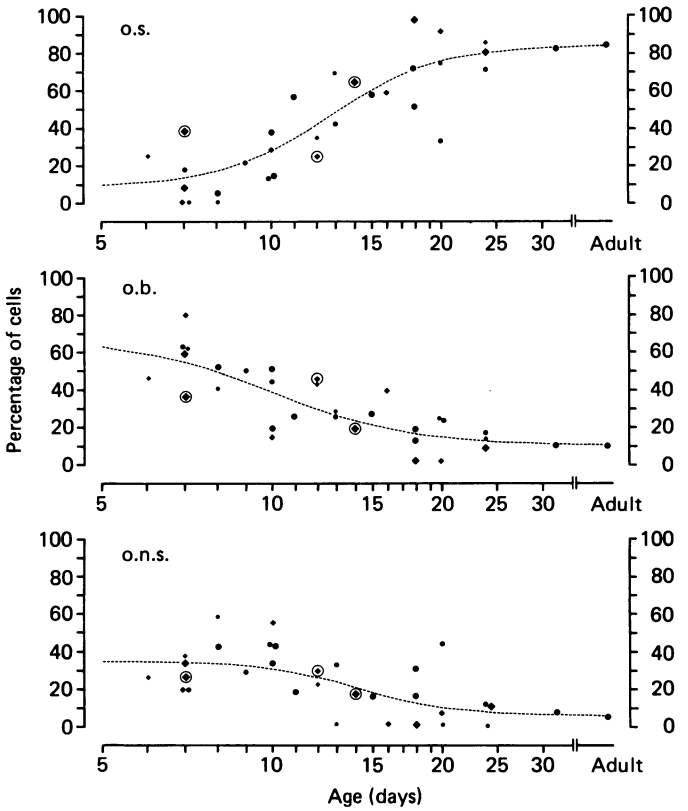

Fig. 7. Post-natal development of orientation specificity in the kitten's visual cortex. The relative numbers of orientation-selective (o.s.), orientation-biased (o.b.), and orientation-non-specific neurones (o.n.s.) are given for each kitten as percentages of all cells tested for orientation specificity in that kitten and are plotted as a function of kitten age. The data points at 32 days were calculated from seventy neurones recorded in 4- to 5-week-old kittens of the study of Beckmann & Albus (1982), the values for adult cats were calculated from 700 neurones of the work of Albus (1975*a*). Filled circles indicate data from kittens in which the majority of neurones had their receptive fields within 15 deg of the area centralis, diamonds those with eccentricities greater than 15 deg. Neuronal populations recorded from area 18 are indicated by circles around the symbols (see also Table 1). The size of the symbols tries to reflect the numbers of cells in each kitten: small, less than ten; medium, between ten and twenty; large, more than twenty neurones tested per kitten. Smooth symmetrical sigmoidal curves have been fitted, by applying the least-squares criterion, to the data (see also Rodbard & Hutt, 1974), weighting each point with the number of cells tested in the corresponding kitten. The curves are described by the equation

$$y = \frac{a-d}{1-(x/c)^b} + d,$$

where a is the upper asymptote, b is the slope coefficient, c is the value of the independent variable at the point of symmetry, and d is the lower asymptote. Note that the abscissa is scaled logarithmically.

youngest age group, the proportions were, on average, as follows: orientation selective, 11·7 %; orientation biased, 58·3 %; orientation non-specific, 30 % ($N = 60$) and for visually experienced kittens: orientation selective, 17·6 %; biased, 50 %; non-specific, 32·4 % ($N = 68$). The pooled results for both inexperienced and experienced animals are given in Table 3.

Our results clearly indicate that, when orientation specificity is considered for very young kittens either with or without visual experience, the visual cortex is still at an immature stage at the end of the first post-natal week. A state comparable to that of the adult is not reached before the fourth post-natal week. In Fig. 7, the developmental trends are highlighted by curves fitted to the data. As can be seen, the steepest increase in the percentage of orientation-selective cells occurs between post-natal days 10 and 16, i.e. the rapid development of orientation selectivity starts well after natural lid opening (2–3 days on average) on the basis of a relatively high proportion of orientation-biased cells.

Our data do not reveal differences in the development of orientation selectivity between areas 17 and 18, nor between paracentral and peripheral parts of the visual field representation in area 17 (Fig. 7). In area 18, for a 7-day-old kitten, the proportion of orientation-selective neurones recorded from intermediate parts of the representation was higher than that for peripheral parts of the visual field found in a 12-day-old kitten. The percentage of non-specific cells, however, was about the same in both animals. Whether these proportions reflect true differences in the rate of development of orientation selectivity at different eccentricities rather than inter-individual variability cannot be determined from the limited sample of units recorded in area 18.

The increase in the proportion of orientation-selective neurones during the first post-natal month is accompanied by a decrease in the width of orientation tuning in these cells, i.e. there is a 'sharpening' of orientation selectivity which is most noticeable during the third post-natal week. The mean values (± 1 S.D.) of the widths of the orientation turning curves measured at half the maximum response (width at half-height) decreased from 48·4 deg ($\pm 14{\cdot}2$, $N = 18$) in the youngest age group, over 45·6 deg ($\pm 14{\cdot}7$, $N = 48$) between days 10 and 13, to 36·5 deg ($\pm 12{\cdot}9$, $N = 94$) between days 14 and 18, and finally to 31·1 deg ($\pm 11{\cdot}9$, $N = 60$) in our oldest kittens, closely matching the value found in adult cats (Albus, 1975*a*; Heggelund & Albus, 1978; cf. Bonds, 1979). A significant difference in tuning widths between monocularly and binocularly driven orientation-selective neurones was not observed.

Correlating orientation specificity with ocular dominance, we observed a slight predominance of monocularly activated orientation-*selective* neurones during the third and fourth post-natal weeks (77·5% monocular *vs.* 65·0% binocular). The accompanying over-representation of binocularly driven *biased* cells might be due to the appearance of an increasing number of neurones in layers 2/3 and 5, possibly even complex cells, during this period. Our results only partly support earlier findings (Buisseret & Imbert, 1976) that in young kittens monocular neurones, and especially those which are exclusively driven by the contralateral eye, are more often orientation selective than cells driven by both eyes. In kittens less than 14 days old there is no discernible difference. During this stage of development, most of the monocular neurones (90%) are driven by the contralateral eye (see also Table 3).

Also, our results do not support the observation by Frégnac & Imbert (1978) of an over-representation of vertical and horizontal orientations in normal kittens younger than 3 weeks old (see Fig. 8*A–C*). When considering orientation-*specific* (selective and biased) cells receiving only monocular input, irrespective of whether all or only contralaterally innervated cells are included, there is no evidence of a bias

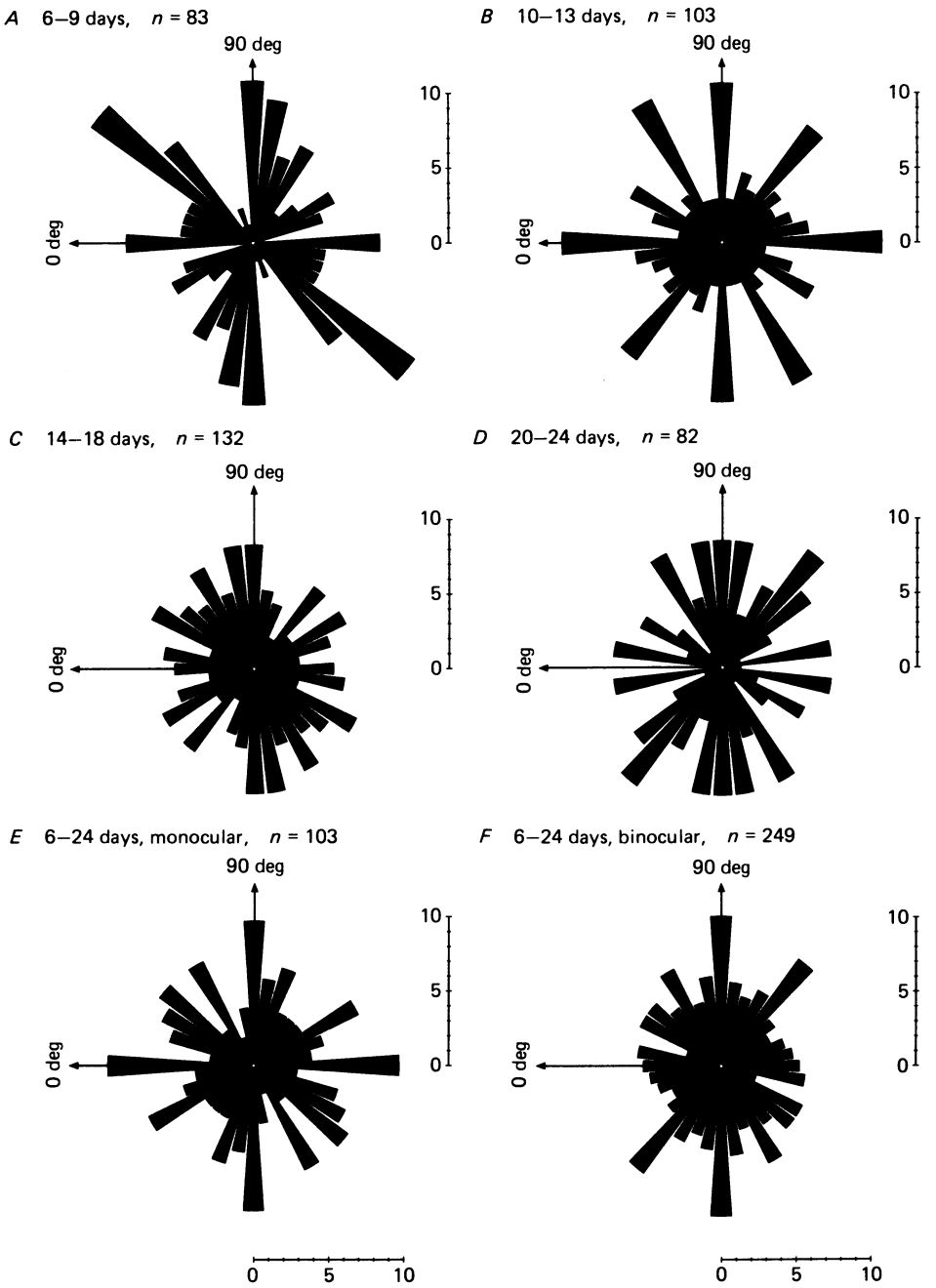

Fig. 8. Distribution of optimum orientations in the kitten's visual cortex for orientation-specific neurones. Each segment (width 10 deg) of the polar histograms indicates by its radius the percentage of neurones with optimum orientations falling within that particular range of angle. 0 deg corresponds to vertical, 90 deg to horizontal. Scale bars indicate percentages. Since direction specificity was not taken into account, the polar diagrams are radially symmetrical around their centres. The kittens' ages and the total number of cells tested are given above each histogram. *A–D*, distributions of optimum orientations for the four distinct age groups. *E*, distribution of optimum orientations for all monocular neurones (o.d. groups 1 and 5). *F*, distribution of optimum orientations for all binocular neurones (o.d. groups 2, 3 and 4). In kittens between 6 and 13 days old, orientation tuning was quantitatively measured for sixty-two neurones.

in the distribution of preferred orientations for vertical and horizontal (Fig. 8*E* for ocular dominance groups 1 and 5). Dividing the orientation-specific neurones of all age groups which were exclusively driven by the contralateral eye into four orientation groups (class width 40 deg), the percentages were, for preferred orientations at 0 deg (the vertical), 24·1; at 90 deg (the horizontal), 26·2; at +45 deg, 29·0; and at −45 deg, 20·7 ($N = 79$), thus yielding nearly the same proportion of neurones

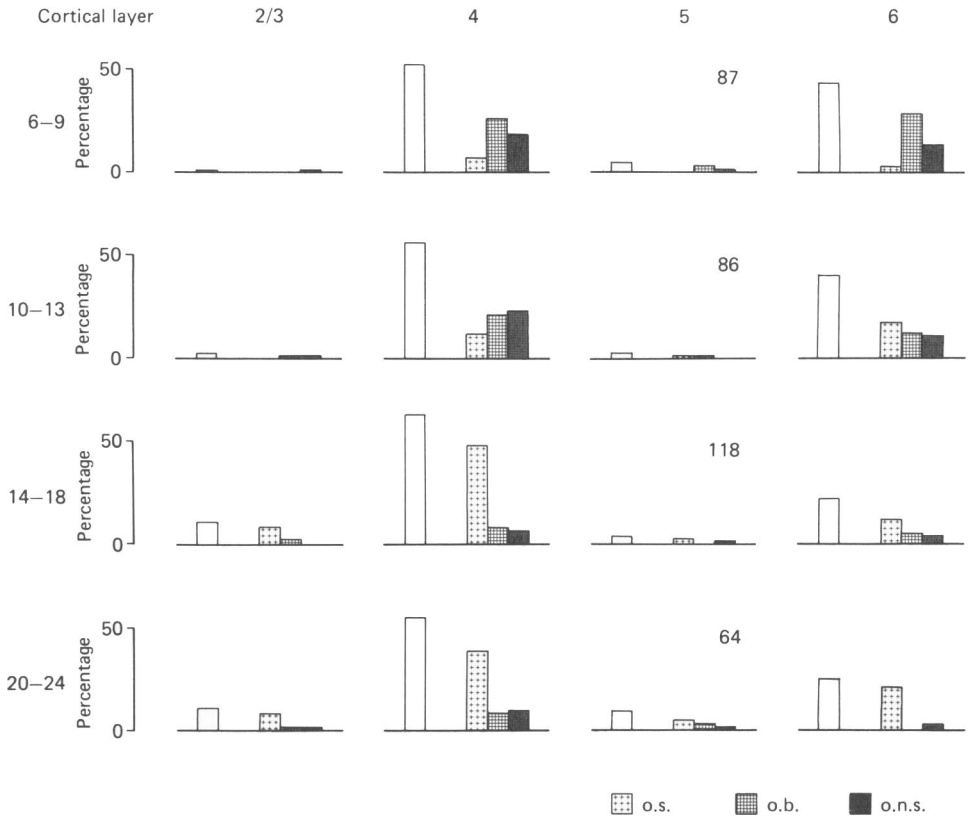

Fig. 9. Laminar analysis of the development of orientation specificity in the kitten's visual cortex (area 17). Orientation selective (o.s.), biased (o.b.), and non-specific (o.n.s.) neurones are indicated by different hatchings, the open bars give the percentages of neurones per layer in each age group. For further information see legend to Fig. 6.

responding preferentially to the horizontal and vertical as to the oblique orientations. Adopting a similar analysis to orientation-*selective* cells (i.e. those cells closely corresponding to the orientation-*specific* neurones in Frégnac & Imbert's (1978) study) a slight over-representation of horizontal, but not vertical orientations, was seen. The percentages were: vertical, 19·8; horizontal, 32·6; +45 deg, 27·6; and −45 deg, 20·0 ($N = 210$). All ocular dominance groups were considered. We also found no significant difference in the distribution of optimum orientations between neurones whose receptive fields were located within 15 deg and those with receptive fields located outside 15 deg of the visual axis.

The high proportion of cells responding to oblique orientations (around 40–50 deg)

in 6–9-day-old kittens (Fig. 8*A*) is unexpected. Also, for kittens older than 2 weeks, neurones responding preferentially to horizontal orientations (90 deg) seem to be slightly over-represented (Fig. 8*C* and *D*), especially when compared to neurones responding best to vertical edges. This is also reflected in Fig. 8*F*, where the optimum orientations for all binocular cells are plotted. At the moment it is not possible to decide whether these asymmetries reflect sampling biases rather than a genuine over-representation of particular orientations.

Laminar distribution of orientation specificity. The laminar distribution of all neurones in area 17 whose orientation specificity could be tested with moving or stationary stimuli is illustrated in Fig. 9. Orientation-selective cells in 6–9-day-old kittens were all located in layers 4 and 6. In both of these layers, the steep increase in the proportion of orientation-selective cells between days 10 and 18 (see also Fig. 7) is evident. On the other hand in lamina 2/3 only non-specific, and in lamina 5 non-specific and a few biased neurones, were recorded in the youngest age group. From day 14 onwards, however, orientation-selective neurones are also seen more frequently than biased and non-specific cells in those layers.

To draw any firm conclusion from this is hindered by the fact that the neuronal activity in laminae 2/3 and 5 during the second and the first half of the third post-natal week is relatively sparse (see also Fig. 6 and Figs. 10 and 11). This is reflected in a low percentage of neurones recorded (less than 5 %) from both layers 2/3 and 5. The proportion of these cells increases to about 15 % during the third week and to 20 % by the beginning of the fourth week (see also Table 2).

Direction specificity, ocular dominance, and velocity tuning

In addition to orientation specificity, other functional parameters such as directional specificity, ocular dominance, binocular interactions and velocity tuning were tested (Table 3). A significant increase of cells selective for the direction of movement of a light spot or bar can be observed during the first post-natal month. Their proportion increases from about 5 % in the second post-natal week to 28 % at the beginning of the fourth week, which is approximately equal to the number of directionally selective cells found in the adult cat (Albus, 1980). These results are in agreement with previous findings of Pettigrew (1974) and Bonds (1979).

The change in the ocular dominance distribution during the early post-natal period is analysed in detail in Table 3. During the whole of the first post-natal month the ratio of monocularly driven to binocularly driven neurones remains about constant, monocular neurones comprising between 25 and 34 % of all neurones recorded. There is a considerable change, however, from a contralaterally (o.d. groups 1 and 2) dominated population to a population in which contralaterally and ipsilaterally (o.d. groups 4 and 5) dominated neurones are about evenly distributed. This change becomes even more obvious if only neurones driven by one eye (group 1 and group 5) are considered. Initially, at the end of the first week, the proportion of group 1 neurones is relatively high (31 %) and decreases to about 20 % by the fourth week. During the same time, the number of group 5 neurones increases from 3 % to about 15 %, while the percentage of cells receiving equal input from both eyes does not change significantly. The initial dominance by the contralateral eye is seen for all neurones, regardless of eccentricity. During the first post-natal month there is

TABLE 3. Development of orientation specificity, direction specificity, ocular dominance, and velocity range in the kitten's visual cortex

Age group (days)		6–9	10–13	14–18	20–24
Orientation	*N*	128	149	148	84
	s.	14·8	32·9	68·2	71·4
	b.	53·9	34·2	18·3	14·3
	n.s.	31·3	32·9	13·5	14·3
Direction	*N*	128	145	145	86
	s.	7·8	3·5	22·7	27·9
	b.	37·5	32·4	35·2	32·6
	n.s.	54·7	64·1	42·1	39·5
Ocular	*N*	129	149	135	86
dominance	1	31·0	22·8	13·3	19·7
	2	26·4	24·8	30·4	19·8
	3	24·0	30·2	28·1	22·1
	4	15·5	18·1	16·3	23·2
	5	3·1	4·1	11·9	15·2
Velocity	*N*	128	141	133	75
	1–5	43·0	34·7	31·6	20·0
	−20	51·6	59·6	48·1	57·3
	−50	5·5	5·7	18·8	16·0
	> 50	0	0	1·5	6·7

The number of neurones analysed for each parameter is expressed as the percentage of the total number of cells tested in each age group (listed in the row *N*) with respect to this parameter. Orientation and direction: s., selective; b., biased; n.s., non-specific. Ocular dominance: 1, contralateral eye; 5, ipsilateral eye. Velocity: cut-off velocities in deg s^{-1}. For further information see text.

therefore a shift in ocular dominance from contralateral dominance to an equal representation of both eyes (cf. Le Vay, Stryker & Shatz, 1978), resembling closely the distribution usually found in recordings from paracentral regions of the adult cat's area 17 (Albus, 1975*b*).

In addition to stimulating each eye separately, we have quantitatively examined binocular interactions for sixty-one neurones of 6–13-day-old kittens for neurones with monocular receptive fields located within 10 deg of each other. For forty neurones, the response to binocular stimulation was stronger than the sum of the monocular responses (binocular facilitation). In five cases, the binocular response approximated the sum of the monocular responses (binocular summation) and in the remaining sixteen cases the binocular response was less than the sum of the monocular responses or even less than the response of the non-dominant eye (binocular suppression). These findings show that not only binocular facilitation (Pettigrew, 1974) but also a pronounced binocular inhibition may already occur in kittens less than 2 weeks old.

Stimulus velocity-response curves were prepared for a total of forty neurones in addition to the qualitative tests of velocity-response range carried out for the majority of neurones (Table 3). Even in the youngest animals, orientation-specific neurones were well tuned for the velocity of a moving light stimulus. Optimum velocities, as measured on the basis of the average discharge rate per response profile (equal time intervals for any velocity), were between 3 and 20 deg s^{-1}. During the second post-natal week only a few neurones (5–6%) could be activated by stimuli

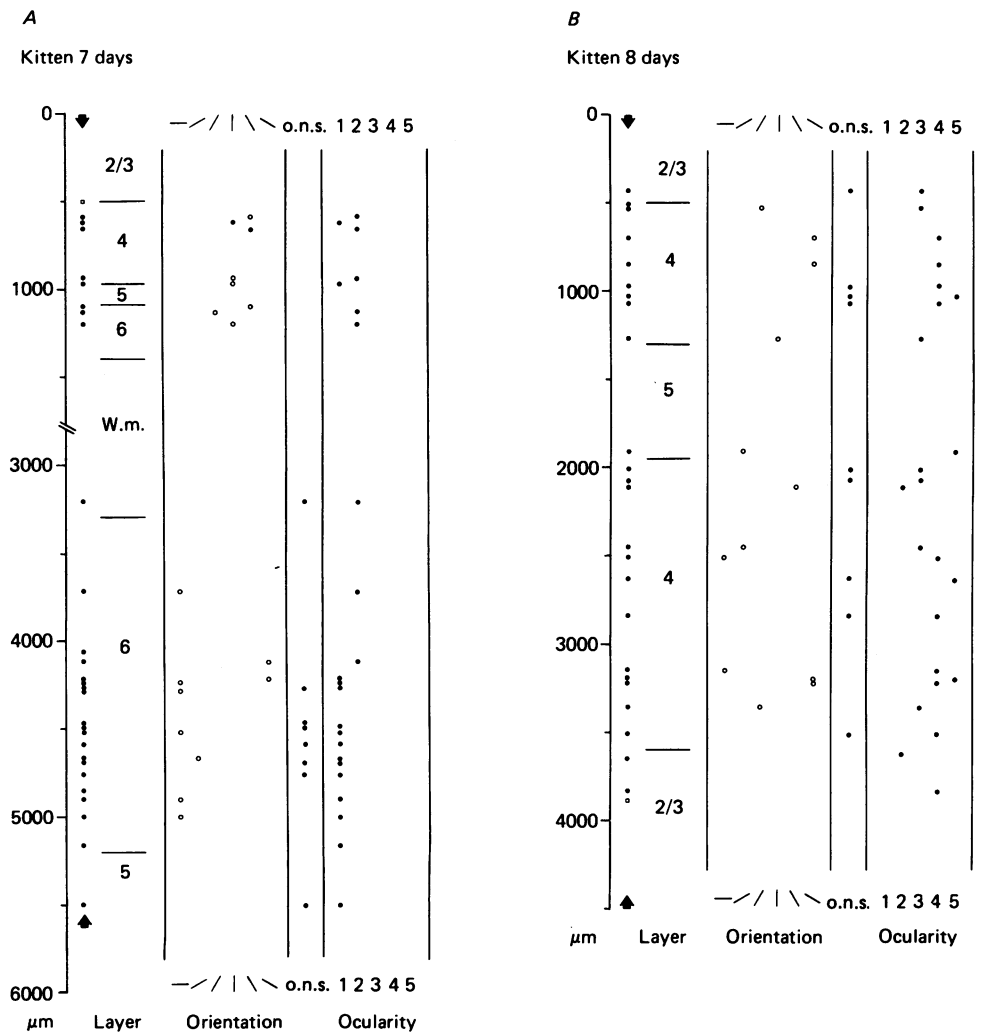

Fig. 10. Functional architecture of the kitten's visual cortex. Schematic reconstructions of the tangential electrode penetrations through area 17 for kitten 7 (3) in *A* and for kitten 8 (2) in *B*. Scale and columns indicate, from left to right: penetration distance in μm; cortical layers (denoted by numbers at the left of the diagrams, w.m.: white matter); optimum orientations of orientation-selective (filled circles) and orientation-biased (open circles) neurones, orientation-non-specific cells (o.n.s.), and ocular dominance (1, contralateral eye; 5, ipsilateral eye only). On the right-hand side of the distance scale the positions of all neurones encountered are marked (filled circles, visual cells; open squares, non-visual cells). The arrows indicate the entrance of the electrode into layer 2 and the lesions at the end of the penetrations. In *B* the electrode left the cortex at the end of the penetration.

moving at 20–50 deg s^{-1}, and none by stimuli moving even faster. The proportion of the units responding to these velocities (> 20 deg s^{-1}) increased to 22% by the beginning of the fourth week.

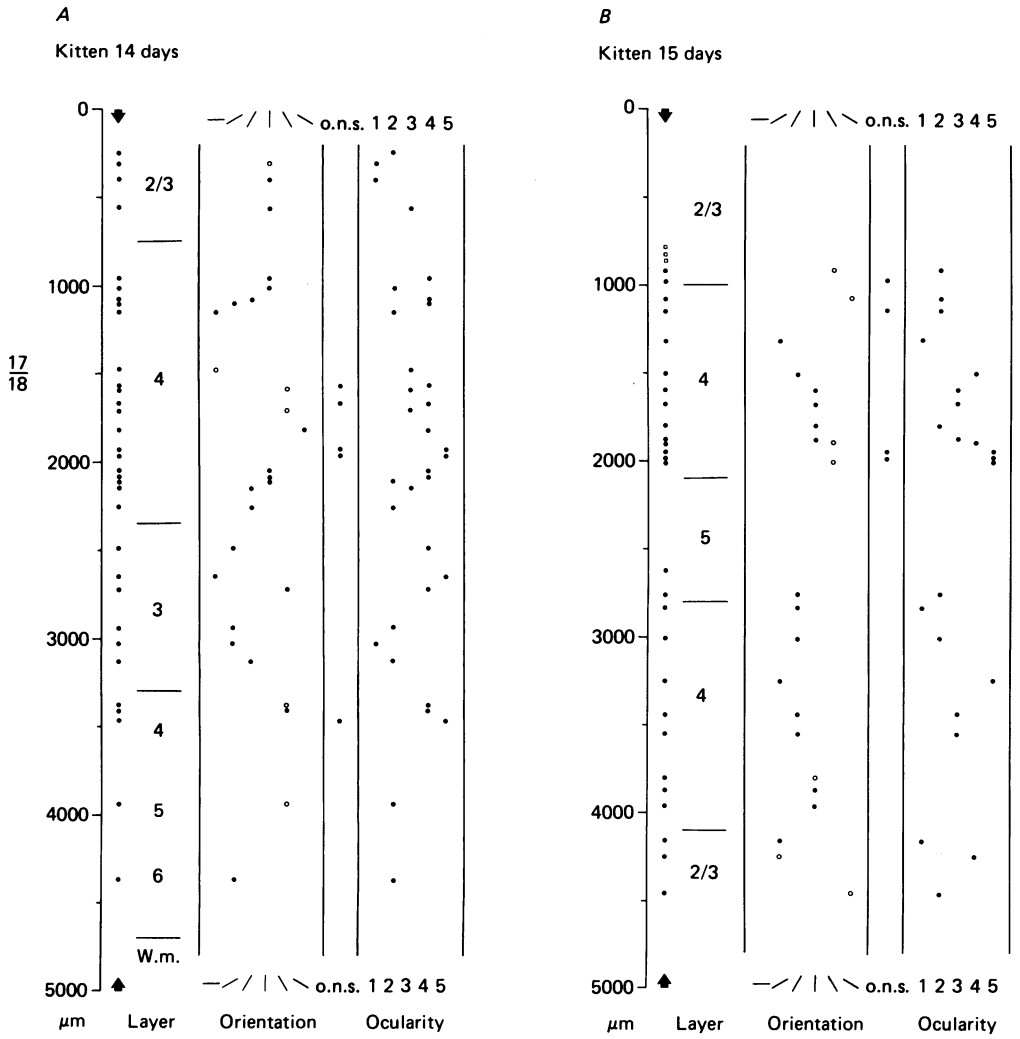

Fig. 11. Functional architecture of the kitten's visual cortex. Schematic reconstructions of the electrode penetrations for the 14-day-old kitten in *A* and for the 15-day-old kitten in *B*. The penetration in *A* started in area 17 and ended in area 18; the approximate border between the two areas is indicated. The penetration in *B* was through area 17. Since layer 3 in area 18 is broader as compared to area 17, the electrode re-entered the lower part of layer 3 in the penetration reconstructed in *A* before rapidly leaving the grey matter. In *B* the electrode left the cortex at the end of the penetration. For further information see legend to Fig. 10.

Functional architecture of the immature visual cortex

In long tangential penetrations through areas 17 or 18 of young kittens, the density of visually driven cells is on average lower than in adult cats. Nevertheless, for very young animals some parts of the electrode penetrations were densely packed with visually responsive neurones, as can be seen from Table 2 and as is also evident in Figs. 10 and 11. These segments were always confined to layers 4 and 6 and, in area 18, to the lower part of layer 3. The few neurones recorded in layer 2/3 during the

second post-natal week were located close to the 3–4 boundary; this was also the case in the penetration shown in Fig. 11*A*, where, due to the plane of the histological section, the neurones in lamina 2/3 appear to be located further towards the pial surface.

The finding that neither visually responsive neurones nor background activity were evenly distributed across all cortical layers was unexpected (Table 2). We first thought that superficially located cells might have been damaged by surgical manipulations, but even in electrode penetrations which re-entered the cortex in the medial bank of the postlateral gyrus after having traversed the white matter, visual activity ceased above layer 4 and only sporadically could cells be recorded from the lower part of layer 3. This is illustrated in the track reconstructions of the penetrations in the kittens 8 and 15 days old (Figs. 10*B* and 11*B*), where the electrode left the cortex at the end of the penetrations. We also noticed a 'gap' in recordable neurones and of background activity between layers 4 and 6 which was evident in all kittens younger than 14 days and can be seen in all track reconstructions. In the 8- and 15-day-old kittens (Figs. 10*B* and 11*B*), the electrode traversed a long distance tangentially through layer 5 and then re-entered lamina 4, clearly demonstrating the rarity of visually driven neurones in layer 5. With increasing age, however, the situation changed. As can be seen from Table 2, the recording density of visually responsive neurones in layers 2/3 and 5 increased significantly during development. The number of neurones encountered per unit cortical distance in layer 5 matched that of layers 4 and 6 by the beginning of the fourth post-natal week. In layer 2/3, the frequency of recording neurones did not increase equally quickly but, nevertheless, it amounted to 50% compared to that in the deeper layers.

Our results indicate that, by the beginning of the third post-natal week, the characteristic spatial organization of the orientation domain is well developed in areas 17 and 18 (Fig. 11; cf. Blakemore & Van Sluyters, 1975). Regular shifts in optimum orientations were usually observed in the rostro-caudally coursing tangential penetrations, suggesting that the system of orientation subunits was crossed by the electrode in an approximately perpendicular direction. In animals younger than 14 days, definite statements on the spatial organization of the orientation domain cannot be made on the basis of single penetrations, because the number of orientation-specific neurones was so small. We have therefore calculated the differences in optimum orientations for neurones less than 100 μm apart. These differences (mean $\pm$ 1 S.D.) were found to be $36{\cdot}1 \pm 23{\cdot}9$ deg ($N = 31$) in the youngest age group (6–9 days) and decreased to $25{\cdot}3 \pm 22{\cdot}8$ deg ($N = 103$) between post-natal days 10 and 18, to finally reach $19{\cdot}7 \pm 19{\cdot}1$ deg ($N = 34$) in the oldest age group (20–24 days). The corresponding mean value derived from rostro-caudal tangential penetrations is 18 deg in adult cats (Albus, 1975*a*). Our results demonstrate that already in very young kittens there is some order in the spatial arrangement of orientation-specific neurones, but that it still has to develop during the first post-natal month to attain the regular spatial arrangement found in adult animals.

As with the orientation domain, the ocular dominance system seems to be well developed by the beginning of the third post-natal week. This is indicated by the regular shifts in ocular dominance seen over most parts of electrode penetrations in these kittens (Fig. 11). Regular shifts in ocular dominance appeared even in the

youngest animals, though not as clearly as in older ones (Fig. 10*B*). The predominance of neurones driven exclusively by the contralateral eye, as can be seen in Fig. 10*A*, is probably due to the fact that the electrode entered the monocular segment in area 17 (kitten 7 (3), see also Table 1). The dominance of the contralateral eye was observable, however, even in kittens in which the receptive fields were located less than 15 deg from the area centralis.

DISCUSSION

The marked fatiguability and extreme sluggishness of neurones in the visual cortex of very young (1–2-week-old) kittens has already been reported by Hubel & Wiesel (1963). In spite of the poor response quality, the majority of visual cortical cells were reliably activated even with repetitive visual stimulation when an interstimulus interval of between several seconds and half a minute was adopted to compensate for response habituation. No correlation of discharge rates with response specificity was observed. Neurones showing very weak responses could well be highly orientation selective (Fig. 1, cf. Bonds, 1979).

Although, in kittens less than 1 month old, the response rates of visual cortical neurones vary considerably over time, the tuning properties do not change significantly. In the youngest kittens, especially, the variability of response to an optimum simulus exceeds 1·0 in many cases, where variability is expressed by the ratio (1 S.D./mean response). Response variability in the adult animal, however, also increases considerably when the mean discharge rates are less than 5 Hz (Heggelund & Albus, 1978).

The cloudy optics of the kitten's eyes do not seem to interfere seriously with studying the specificity of neuronal responses in the visual cortex. Cells adjacent to each other and representing the same area in the visual field could have large and small receptive fields as well as highly orientation-selective and orientation-non-specific response properties. In addition, bimodal or multimodal cells were encountered in the same penetrations as 'on–off' cells, even in the younger kittens. Our conclusions are therefore similar to those of Bonds (1979), who showed that gross optical degradation of the visual input in an adult animal did not significantly change orientational or directional selectivity of single cortical cells.

The development of orientation selectivity

Our findings confirm the conclusion from earlier studies on the post-natal development of orientation specificity (Hubel & Wiesel, 1963; Blakemore & Van Sluyters, 1975; Buisseret & Imbert, 1976; Frégnac & Imbert, 1978; Bonds, 1979) that, even when the strictest criteria are adopted, there are a significant number of orientation-selective cells in the visual cortex of visually inexperienced kittens. Also, the proportion of orientation-based cells was found to be very high in these animals. In particular, the proportions of orientation-specific and non-specific neurones in these kittens are not significantly different from the proportions found in kittens of the same age which have had visual experience of about 1 day. The proportion and rate of increase in numbers of orientation-selective neurones found during normal development closely matches that reported by both Blakemore & Van Sluyters (1975) and by Bonds (1979) who adopted a similar scheme for classifying orientation specificity.

The proportion of orientation-selective cells, in our sample, was found to increase rapidly about 2–3 days after lid opening around the tenth day post-natally. Interestingly, the proportion of orientation-selective neurones found at that time is about the same as that observed by Blakemore & Van Sluyters (1975), Frégnac & Imbert (1978), and Bonds (1979) in binocularly deprived (dark-reared) kittens during the third and fourth post-natal weeks. This suggests quite strongly that visual experience assumes an active role in the development of response specificity in the visual cortex of kittens as early as 2 days after natural lid opening.

The initial generation of orientation specificity, however, takes place well before lid opening, and the connexions of the early orientation-selective cells are obviously genetically predetermined. The rapid elaboration of orientation selectivity after lid opening therefore does not start on the basis of a neuronal population totally unspecific for stimulus orientation as proposed by Frégnac (1979). Since we did not observe differences in the frequency of orientation-selective neurones in very young animals between areas 17 and 18, nor between paracentral and peripheral parts of the visual field representation, they seem to be evenly distributed, on a global scale, across the striate and parastriate cortices. There was also a tendency for neighbouring orientation-selective cells to have similar orientation preference (cf. Blakemore & Van Sluyters, 1975; Sherk & Stryker, 1976). However, the organization of the orientation domain is significantly less precise in the visual cortex of young kittens than that found in the cortex of adults. These findings suggest that the early orientation-selective neurones may provide a framework and serve as a guiding structure for the further development of orientation selectivity and the regular arrangement of the orientation domain, a suggestion very similar to that of Blakemore (1977).

The predominance of horizontal and vertical orientations reported by Frégnac & Imbert (1978) in the visual cortex of normal kittens less than 3 weeks old was not seen in our sample. One possible reason to explain the discrepancy between the two results may be that we sampled the majority of neurones from paracentral to intermediate parts of the visual field representation, whereas Frégnac & Imbert (1978) only recorded neurones with eccentricities of less than 10 deg. The relative number of neurones responding preferentially to horizontal or vertical contours is also high near the cortical projection of the area centralis and low in more eccentric regions in the adult cat (Leventhal & Hirsch, 1980).

Intracortical inhibition seems to play at least some role in determining orientation specificity of the early orientation-selective cells with unimodal receptive fields. First, for many of them we have detected inhibitory regions outside the excitatory receptive field area, sometimes resembling the 'inhibitory side-bands' described by Bishop, Coombs & Henry (1973). As reported by Daniels, Pettigrew & Norman (1978), surround inhibition in neurones of the lateral geniculate nucleus (l.g.n.), which could theoretically also account for the observed inhibition, does not arise before the third post-natal week. Secondly, Purpura, Shofer & Scarff (1965) have demonstrated, in the early post-natal cortex, powerful and long-lasting post-synaptic inhibition in single neurones. This does not, however, preclude the possibility that an orientationally tuned excitatory input to the orientation-selective or -biased cells also plays a role, but makes its involvement unnecessary (cf. Vidyasagar & Urbàs, 1982; Wolf, Albus & Beckmann, 1982). On the other hand, the primary role of intracortical inhibition

for the generation of orientation specificity in bimodal and multimodal neurones cannot be denied, since we could demonstrate for all of them a mutual response antagonism between 'on' and 'off' zones.

Our experiments confirm earlier findings that the tuning widths of orientation-selective cells further decrease with increasing post-natal age (Blakemore & Van Sluyters, 1975; Bonds, 1979). The sharpening of orientation tuning is most probably associated with the appearance of bimodal receptive fields, because all of the cells having such fields were orientation selective, the majority of them to a high degree.

Recently, differences in the development of orientation specificity between the various layers of the striate cortex have been reported by Tsumoto & Suda (1982). Our results do not support the conclusion of these authors that the maturation of functional properties of cortical cells begins in layer 5, and occurs only much later in layer 2/3 and the lower half of layer 6. In our sample, when considering only the percentages of orientation-specific neurones for the different cortical laminae (see also Fig. 9), orientation specificity seems to develop quite uniformly throughout the vertical extent of the striate cortex, though the sample size for layers 2/3 and 5 is very small. However, considering the probability of recording visually responsive neurones (see also Table 2) it becomes evident that, up to the end of the second post-natal week, the number of orientation-specific neurones per unit cortical volume is low in layers 2/3 and 5 compared to that of layers 4 and 6 and remains quite low in layer 2/3 during the first post-natal month. In contrast to this, Tsumoto & Suda (1982) based their conclusion on only the percentages of orientation-specific neurones in individual cortical layers. In addition, their sample sizes, for all layers, in kittens less than 1 month old, are quite small. It would appear therefore, from our results, that the initial functional development of neurones in the visual cortex takes place in layers 4 and 6, i.e. those layers which receive the main body of afferents from the lateral geniculate nucleus (Le Vay & Gilbert, 1976), and precedes the maturation of neurones in layer 5 and, especially, in layer 2/3.

The development of receptive field types

We have shown that the adult types of simple and complex receptive fields only emerged at the beginning of the third post-natal week. Up to the end of the second week, no complex receptive field was identified and the proportion of simple fields was still less than 15% of neurones responding to stationary stimuli. The majority of neurones found, at that time, had receptive fields with a single excitatory region responding to light off.

Surprisingly, neurones similar to the ones we have recorded in areas 17 and 18 at the end of the first post-natal week were found by Hoffmann & Cynader (1977) in monocularly deprived cats. These animals had been raised with the lids of one eye sutured. After the non-deprived eye had been enucleated, at the age of 6 months, they were allowed to see through the formerly deprived eye for another year. Interestingly, most neurones then recorded had receptive fields consisting of a single excitatory region responding to light off. They did not respond specifically to the orientation or to the direction of movement of a light bar, and were all located in or below layer 4 of the visual cortex. The findings of Hoffmann & Cynader (1977) in combination with our results suggest that, under monocular deprivation, the

neurones receiving their main afferents from the deprived eye may retain their immature connectivity, which is unmasked only when the afferents from the experienced eye are functionally and/or anatomically removed.

The under-representation of the 'on' response in the visual cortex is certainly not caused by an under-representation of 'on'-centre cells in the lateral geniculate nucleus (Daniels *et al.* 1978; Beckmann & Albus, 1982). Since kittens have their eyelids still closed during the first post-natal days, the spontaneous activity in the retinal and geniculate 'off' systems would be higher than in the 'on' systems during this time and could lead to an earlier strengthening of synapses subserving 'off' responses in the visual cortex. So far a predominance of the cortical 'off' system has not been reported in older, dark-reared kittens (for a review see Movshon & Van Sluyters, 1981). However, the synaptic densities are much higher in the visual cortex of these deprived animals (Cragg, 1975*b*; Winfield, 1981) than in the visual cortex of 1–2-week-old normal kittens (Cragg, 1975*a*) which makes a direct comparison of both types of cortex difficult.

Several arguments can be brought forward in order to explain the gradual increase in the complexity of receptive field organization during the early post-natal period. The under-representation of the 'on' response certainly is a major factor for the delay in the development of the various simple receptive field types and probably also of the complex fields. Another reason for the under-representation, or even the lack of complex receptive fields, could be that polysynaptic inputs are not yet effective. Two results from our experiments point in this direction. First, neurones having complex receptive fields are not found during the second post-natal week and their proportion still remains very low during the third week. It is known from the studies of Singer *et al.* (1975) and of Bullier & Henry (1979*a*) that complex cells receive polysynaptic inputs much more often than simple cells. Secondly, we have found that the recording probability of single neurones was relatively low in cortical layers 2/3 and 5 as compared to layers 4 and 6, during the second post-natal week. Also, unresolved background activity was usually absent in layers 2/3 and 5. Singer *et al.* (1975) and Bullier & Henry (1979*b*) have convincingly demonstrated that, in the adult animal, polysynaptic inputs preferentially contact neurones in these latter layers. In addition, Beckmann & Albus (1982) have shown, with electrophysiological methods, that relatively few neurones in young kittens receive di- or polysynaptic inputs.

Ineffectiveness of polysynaptic inputs in the kitten's visual cortex could arise from either an insufficient excitatory drive and/or by a dominance of inhibitory post-synaptic processes. It has been shown that the intracortical axonal projections are still sprouting in the early post-natal period (Morest, 1969; Molliver & Van der Loos, 1970). In addition, the synaptic density of neurones in layer 2/3 is lower than that in other layers at, or shortly after, birth (Molliver & Van der Loos, 1970; Cragg, 1975*a*). If this correlates with neuronal activity, it would indirectly account for reduced neuronal activity in layer 5, the neurones of which were shown by Gilbert & Wiesel (1979) and by Lund, Henry, MacQueen & Harvey (1979) to receive a strong excitatory projection from the supragranular layers. A further reduction in excitatory drive for the pyramidal cells in layers 2/3 and 5 could result from the fact that the basal and apical dendrites reach their full size only later during the post-natal period (Noback & Purpura, 1961; Morest, 1969; Molliver & Van der Loos, 1970). The

under-representation of excitatory synaptic connexions of intracortical and/or associational origin could lead to a situation in which many neurones become dominated by intracortical inhibitory inputs (Purpura *et al.* 1965). This hypothetical inhibition should arise from other cortical neurones, i.e. from those with unimodal receptive fields which are the only cell type shown to be active in large numbers in the early post-natal period. It should affect neurones which have, or which develop, more complex receptive field types, i.e. either bimodal and multimodal neurones (which correspond to the classical simple category) or 'on–off' neurones (which correspond to the complex category). In fact, inhibitory connexions from neurones responding exclusively to light on or to light off which contact neurones with simple fields and those with complex fields, but not vice versa, have recently been demonstrated in adult cats (Toyama, Kimura & Tanaka, 1981).

Since earlier reports (Singer *et al.* 1975), that neurones with bimodal or multimodal simple fields receive polysynaptic inputs more often than neurones with unimodal fields, have not been confirmed by others (Bullier & Henry, 1979*a*), the importance of polysynaptic connexions for the generation of bi- or multimodal fields remains unclear. Especially in the younger kittens, a number of 'on–off' cells were observed in layer 4 of area 17. It is conceivable that the GABA-ergic inhibitory input to these neurones is not, at that stage, fully developed. This type of inhibition has been shown in the adult animal to be necessary to maintain the separation of the simple cell receptive field into 'on' and 'off' excitatory zones (Sillito, 1975).

The gap in visual activity in layer 5 of the visual cortex during the second post-natal week, and the under-representation of complex receptive fields, implies that the corticofugal pathways originating in that layer are either non-functional, or only function at a very low level, during the early post-natal period. The projection from layer 5 to the superior colliculus, amongst others, is present around the time of birth (Anker, 1977). This could explain the finding of Stein & Gallagher (1981) that the development of direction selectivity and of binocularity in neurones of the superior colliculus, which depends on the effectiveness of the cortical control over this structure, does not develop before the end of the second post-natal week. Our results could also explain why the naso-temporal component of the horizontal optokinetic nystagmus, which has been shown by Wood, Spear & Braun (1973), Hoffmann (1979), and Schoppmann (1981) to depend on cortico-pretectal efferents originating in layer 5 of the visual cortex, develops later than the temporo-nasal component during normal development (Van Hof-Van Duin, 1978).

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