RECEPTIVE FIELDS OF CELLS IN STRIATE CORTEX OF VERY YOUNG, VISUALLY INEXPERIENCED KITTENS[1]

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INTRODUCTION

IN A SERIES OF STUDIES on the cat over the past 5 years we have recorded from single cells in the striate cortex and mapped receptive fields using patterned retinal stimulation. The results suggest that connections between geniculate and striate cortex, and between cortical cells, must be highly specific (5). Indeed, cells in the striate cortex respond in such a characteristic way that departures from the normal adult physiology should be easily recognizable.

In the present study we have made similar experiments in kittens ranging in age from 1–3 weeks. Our purpose was to learn the age at which cortical cells have normal, adult-type receptive fields, and to find out whether such fields exist even in animals that have had no patterned visual stimulation.

METHODS

Four kittens were included in this series. Three of these were from the same litter. The youngest was 8 days old at the time of the experiment, and had not yet opened its eyes. The second had both its eyes covered by translucent contact occluders at 9 days, at which time the eyes were just beginning to open; the experiment was done 1 week later, at 16 days of age. The third kitten had the right eye covered by a translucent occluder at 9 days, and the other eye was allowed to open normally; the experiment was done on the nineteenth day. The fourth kitten, from a different litter, was brought up normally and used in an experiment on the twentieth day, after 11 days of normal visual exposure. Thus two kittens had, at the time of the experiment, no patterned-light experience; the third had such experience in one eye only, and the fourth had normal visual stimulation in both eyes. Before the experiments the two kittens that had been exposed to patterned light were beginning to show following movements of the eyes and visually guided behavior.

Procedures for stimulating and recording have for the most part been described in previous papers (4, 5). A few modifications were necessary for newborn and very young kittens. Since doses of barbiturate large enough to give surgical anesthesia were usually lethal, the kittens were first given a small dose of thiopental (15–20 mg/kg.), and just before surgery the appropriate regions of skin were infiltrated with local anesthetic (Xylocaine, 2%). A few minutes after injection of the local anesthetic the animal usually fell asleep and showed no sign of discomfort during the surgery or the experiment. From observations on these and other newborn kittens we have the impression that the Xylocaine has central effects as well as local ones. Since eye movements were not troublesome, no paralyzing

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agent was used, and artificial respiration was not necessary. The skull, too soft to be held by ear plugs, was supported by cementing it to a modified Davies chamber (2) which was then clamped securely. The electrode was introduced through a hole in the skull and dura a few millimeters wide. Tungsten microelectrodes were used for recording, and several electrolytic lesions in each track served to identify recording sites in histological sections. All brains were examined histologically.

Patterned stimuli were shone on a diffusely lit screen which the kittens faced from a distance of 1.5 m. Background light was about 1 c.d/m^2, and stimuli were generally 0.5–1.5 log units brighter. Identification of area centralis and optic discs by our usual projection method (4) was difficult because the cornea and media have a cloudy appearance and because the tapetum in cats does not develop fully until 3–4 weeks after birth (3). Receptive-field position could therefore not be determined accurately, though it was our rough impression that fields were within about 10° of the center of gaze.

RESULTS

Cortical activity and responses in kittens without visual experience

Resting activity and responsiveness. Seventeen single cells were recorded from the two visually naïve kittens, nine from the 8-day-old and eight from the 16-day-old. Perhaps the most marked difference between these experiments and our usual recordings from cortex in adult cats was in the maintained activity and responsiveness of the cells. With steady diffuse background illumination cells tended to be silent or to fire at a very low rate. Perhaps partly because of this paucity of maintained activity the number of cells studied in a penetration was unusually small, a few in each passage from surface to white matter as against 20–30 in an ordinary adult penetration. Cells were not only sluggish in their spontaneous activity but also responded grudgingly to the most effective patterned stimuli. This relative difficulty in eliciting responses reminded one of similar difficulties in driving cells in very deeply anesthetized adult cats (5, p. 122). Just as in deeply anesthetized adults, some cells did not respond at all to patterned stimuli unless the stimuli were moving.

Finally, cortical cells, especially in the 8-day-old kitten, showed a marked tendency to fatigue. To be sure of obtaining brisk responses one sometimes had to wait for as long as a minute between stimuli. While a tendency to such fatigability is occasionally found in cells of mature cats, it is far from the rule, and when the depressed responsiveness occurs, it does not last nearly so long. The fatigue would seem to be cortical, since similar effects were not seen in geniculate cells, and since in a binocularly influenced unit the intervals between effective stimuli could not be shortened by stimulating first one eye and then the other.

Receptive-field characteristics. Except for this sluggishness, cortical cells of visually inexperienced kittens strongly resembled cells of mature cats in their responses to patterned stimuli. The cells responded poorly, and often not at all, to changes in diffuse retinal illumination. They responded best to straight-line stimuli (i.e., slits, dark bars, or edges), but only when these were appropriately oriented within the receptive fields, which averaged about 2–5° in diameter. The optimum orientation was found by moving the stimulus back and forth across the receptive field, adjusting the orientation

between stimuli. In Fig. 1, a single-unit recording obtained from the 8-day-old kitten, a long narrow rectangle of light was moved back and forth across the receptive field as shown. Brief responses were consistently obtained when the slit was oriented in a 1 o'clock–7 o'clock direction (*A*) whereas there was no response when it was oriented at 90° to this (*B*). A similar kind of preference in stimulus orientation was common to all of the units isolated. Several of the cells, especially those in the 8-day-old kitten, gave responses over a range of stimulus orientations that was unusually wide by adult standards, yet even in these cells stimulating at an orientation of 90° to the optimum evoked no response at all. Moreover, the responses to moving an optimally

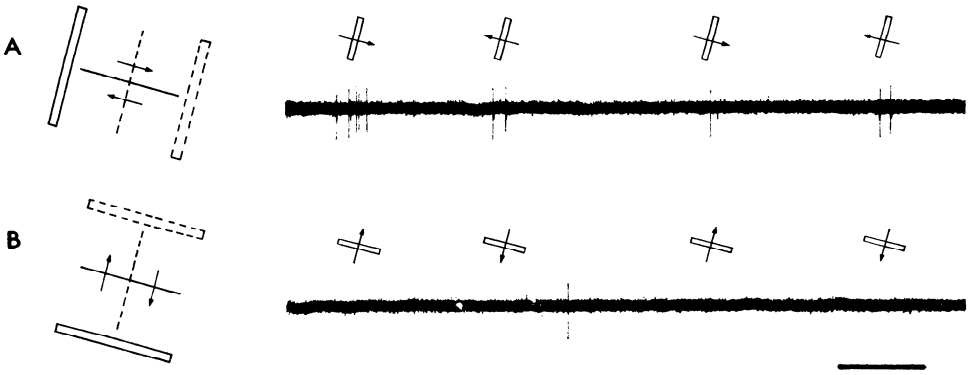

FIG. 1. Single-cell responses from cortex of an 8-day-old kitten with no previous visua experience. A rectangle of light 1°×5° is moved back and forth across the receptive field in the contralateral eye. Unit binocularly activated, ocular-dominance group 3. Receptive-field sizes about 5°×5°; fields situated in the central part of the contralateral visual field. *A:* stimulus oriented 12:30–6:30 (parallel to receptive-field axis). *B:* stimulus oriented 9:30–3:30 (at right angles to the optimal orientation). Rate of movement, 5°/sec. Time, 1 sec.

oriented stimulus across the receptive field were not necessarily the same for the two diametrically opposite directions of movement (see Fig. 4). As in the adult cat, this kind of directional preference varied from cell to cell; some cells responded equally well to the two opposing directions of movement, while some responded well to one direction and not at all to the other.

The combination of sluggish responses and poor optics made it difficult to map receptive fields in a detailed way. Of those that could be mapped, however, some were clearly "simple" in type and others were "complex" (5).

Binocular interaction. The great majority of cells recorded from the two immature kittens (16 out of 17) could be influenced from each eye separately. Just as in adult cats (5), the receptive fields of these cells were situated in corresponding regions in the two eyes, and the two fields were, as far as one could tell, identical in arrangement, in degree of complexity and in orientation. Furthermore, the two eyes often differed in their relative ability to influence a given cell. We have again subdivided cells into seven groups

Table 1. Distribution of cells among the ocular-dominance groups

Kitten	Number of Cells in Each Group						
	1	2	3	4	5	6	7
8-day-old	1	2	3	3			
16-day-old			5	2	1		
19-day-old*	1	1	2	2	3	2	
20-day-old	2	1	2		3	2	1
Totals	4	4	12	7	7	4	1

* Not included in histogram of Fig. 2.

according to the relative influence of the two eyes (see Fig. 2, legend). The distribution of cells among the groups is given in Table 1 and in the histogram of Fig. 2 (shaded portion). Comparison of this histogram with the corresponding one in the adult (9, Fig. 1) suggests that there is little or no difference in ocular-dominance distribution with age or visual experience.

Functional architecture. In penetrations perpendicular to the surface of the cortex and parallel to the radial fiber bundles there were long sequences of cells all having the same receptive-field orientation. In oblique penetrations more frequent shifts in orientation were seen. An oblique cortical penetration in the 16-day-old kitten is reconstructed in Fig. 3. Here there were three shifts in receptive-field orientation within a relatively short distance,

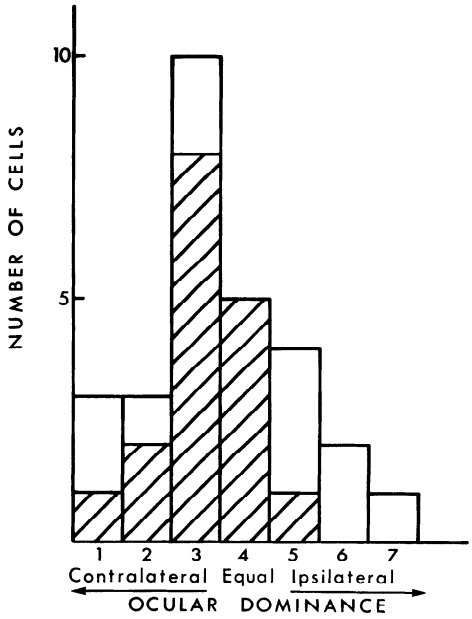

FIG. 2. Distribution of 28 cells among the seven ocular-dominance groups, defined as follows: cells of group 1 were driven only by the contralateral eye; for cells of group 2 there was marked dominance of the contralateral eye; for group 3, slight dominance. For cells in group 4 there was no obvious difference between the two eyes. In group 5 the ipsilateral eye dominated slightly, in group 6 markedly; and in group 7 the cells were driven only by the ipsilateral eye. The shaded portion refers to 17 cells recorded from two kittens with no prior visual experience (aged 8 and 16 days). The unshaded portion refers to cells recorded from the 20-day-old normal kitten.

and between each shift cells and unresolved background activity had the same field orientation. All of this is in good agreement with previous studies of the functional architecture of the visual cortex in adult cats (5), suggesting that the organization of cortex into columns of cells having common receptive-field orientations is already present in immature kittens that have never received patterned visual stimulation.

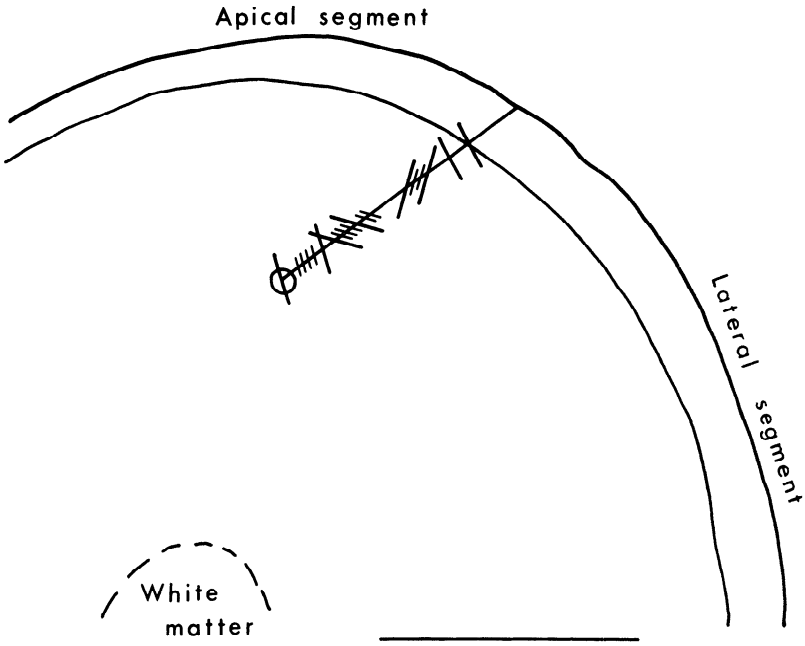

FIG. 3. Reconstruction of an oblique microelectrode penetration through the postlateral gyrus of a 16-day-old kitten without previous visual experience. Longer lines intersecting the electrode track represent single well-isolated cortical cells; directions of these lines represent receptive-field orientations, a line perpendicular to the track standing for a vertical orientation. Shorter lines show regions in which unresolved background activity was observed. At the end of a penetration an electrolytic lesion was made; this is indicated by the circle. Scale, 0.5 mm.

Kittens with visual experience

In their maintained activity, cortical cells of older, visually experienced kittens were much closer to normal. Most cells were active in the absence of patterned stimulation, so that isolation of single cells was much easier. Responses to restricted stimuli were brisker, and showed little of the fatigue that was so apparent in the 8-day-old kitten. As a rule the optimum stimulus was more precisely defined, especially the receptive-field orientation; in this respect these two kittens were closer to the adult than they were to the 8- and 16-day-old visually naïve kittens. Both simple and complex types of fields were mapped, and reconstructions of electrode penetrations again tended to confirm the columnar organization of the cortex. In the responses to stimula-

tion of the two eyes there were no obvious differences between the younger visually naïve kittens and the older experienced ones: the 11 cells recorded from the 20-day-old normal kitten varied greatly in ocular dominance, and are included in the histogram of Fig. 2, where they are represented by the unshaded portion.

The third, 19-day-old kitten was a useful control, since the right eye was covered from the time of normal eye-opening by a translucent occluder, and the left was allowed to remain uncovered. In the cortical recordings there was, on the whole, no obvious difference between the two eyes in their ability to influence cortical cells; the previously occluded eye was dominant about as often as the normal eye (see Table 1). In Fig. 4, a two-unit recording obtained from this kitten, a slit stimulus crossed the receptive field in three different orientations. The units responded well only to the second of these; to the first and third and to orientations still further from the optimum there was little or no response. The unit from which the smaller spikes were recorded gave hardly any responses to stimulation of the right eye (which had been covered), but responded well to the left. On the contrary, the cell giving the larger spikes strongly preferred the eye that had been occluded.

There was no tendency for cells dominated by the occluded eye to have less maintained activity or to respond less briskly and precisely than the other cells. We are therefore inclined to think that the sluggishness of maintained activity and responses in the first two kittens was related to age rather than to visual experience. This is simply a tentative impression, since the difference in the two groups of kittens may be more related to differences in the animals' susceptibility to anesthesia than to a difference in properties of cortical cells, especially since we know that suppression of maintained activity and of responses is a characteristic effect of anesthesia in adult cats.

What can be concluded from this kitten is that even as late as 19 days of age a cell need not have had previous patterned stimulation from an eye in order to respond normally to it. This will be of some interest when the effects of longer periods of monocular deprivation are considered, as discussed in the accompanying paper (9).

Discussion

The main result of this study has been to show that much of the richness of visual physiology in the cortex of the adult cat—the receptive-field organization, binocular interaction, and functional architecture—is present in very young kittens without visual experience. Our conclusion is that the neural connections subserving these functions must also be present, in large part, at or near the time of birth. This extends the work of the previous paper (8) in which we showed that visual experience was not necessary for the development of optic-nerve or geniculate receptive fields.

These findings were somewhat unexpected in view of behavioral observations in very young kittens. At birth a bright light evokes a lid reflex (10), as well as a sluggish pupillary response (1), suggesting that the visual system is

to some extent functional. Nevertheless, kittens appear quite unable to use their eyes at the time of normal eye-opening, which usually occurs between the sixth and the tenth day. Avoidance of objects is seen at the very earliest around 14 days, while pursuit, following movements, and visual placing

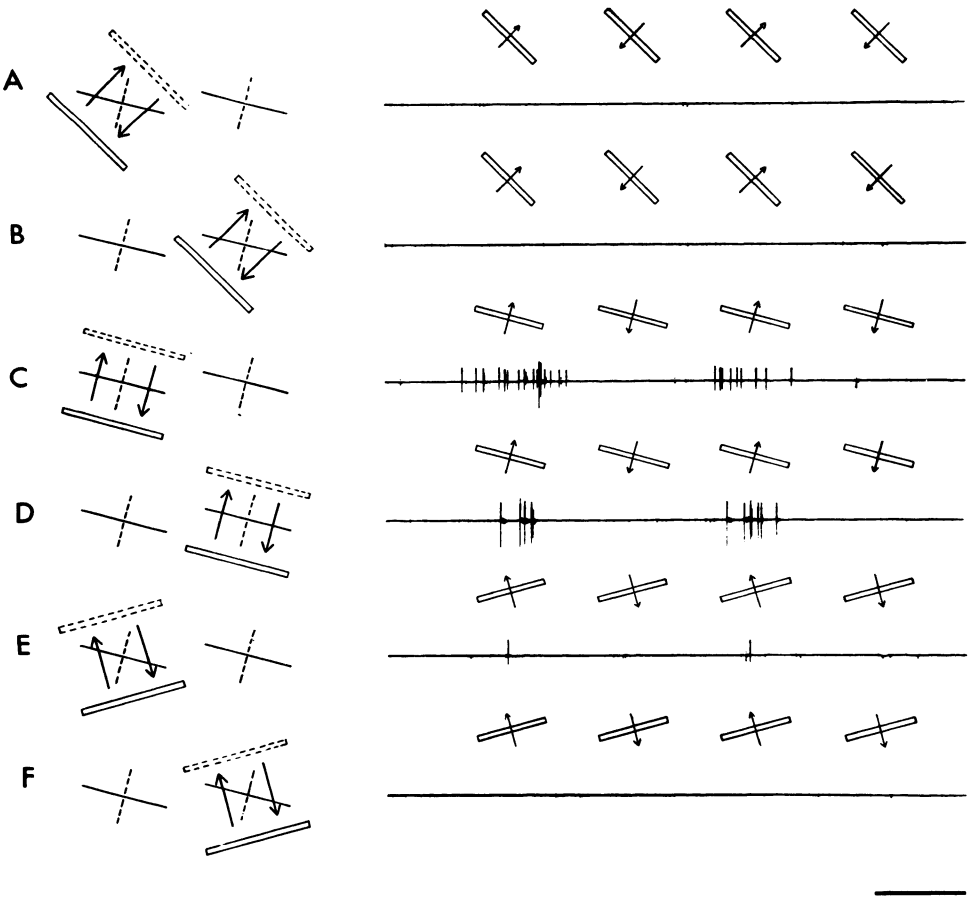

FIG. 4. Two-unit recording from a 19-day-old kitten whose right eye had been covered from the time of normal eye-opening by a translucent occluder. Each eye stimulated separately by a slit 0.5°×0.4°, moved across the receptive field at a rate of about 1°/sec. Size of fields 2°×4°. Time, 1 sec.

appear only at 20–25 days (10, 7). Visual acuity, measured by observing optokinetic nystagmus, increases rapidly from the second week and approaches adult levels by about the fourth week (7). To parallel this behavioral development in the first weeks we have in cortical cells only the increase in briskness of responses and extent of maintained activity—which may be related to differences in reaction or our experimental procedures rather than to real differences in the physiology—and the heightened precision of responses, especially to variations in stimulus orientation. This leads

one to wonder whether the inability of young kittens to use their vision is related not so much to incomplete development of the visual pathway as to a lack of visuomotor ability.

From the behavioral observations alone one might easily imagine that the improvement in visual skill during the first weeks after birth is closely paralleled by development in neural connections in the visual pathway. Such a concept has probably been reinforced by studies on the delay in development of visual ability produced by raising animals in darkness or in diffuse light (for reviews see ref. 6); it has been natural to assume that in the normal animal neural connections subserving vision are developed only if pattern stimuli fall on the retina. The present results make it clear that highly complex neural connections are possible without benefit of visual experience. In interpreting the results of visual deprivation, both the behavioral and the physiological, one must therefore consider the possibility that lack of stimulation may lead not simply to a failure in forming connections, but rather to the disruption of connections that were there from the start.

Summary

Responses of single cells to visual stimuli were studied in the striate cortex of very young kittens. Two animals, aged 8 and 16 days, had had no previous exposure to patterned stimuli. Responses of cortical cells in these animals were strikingly similar to those of adult cats. Fields were simple or complex, with a clear receptive-field orientation. Cells with similar orientations appeared to be grouped in columnar regions. The majority of cells were driven by the two eyes, with patterns of binocular interaction that were similar to those in the adult. Compared with cells in the mature cat, those in young kittens responded somewhat more sluggishly to visual stimuli, and receptive-field orientations tended to be not quite so well defined.

In two other kittens, one monocularly deprived by translucent occluder from birth for 19 days, the other a normal 20-day-old, responses to patterned stimulation of either eye were entirely normal by adult standards.

It is concluded that many of the connections responsible for the highly organized behavior of cells in the striate cortex must be present at birth or within a few days of it. The development of these connections occurs even in the absence of patterned visual experience.

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