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SPATIOTEMPORAL RECEPTIVE FIELD STRUCTURE OF NEURONS IN THE LATERAL GENICULATE NUCLEUS OF BINOCULARLY DEPRIVED CATS

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Abstract. Twelve cats were binocularly deprived of pattern vision from the time of eye opening by rearing in masks. Six cats were raised in masks for 5 to 7 months until an acute experiment (group D) and 6 others were additionally trained in visual pattern discrimination for 2 to 5 months following the initial deprivation period (group DV). In all cats the receptive fields (RFs) of neurons in lateral geniculate nucleus were analyzed with three-dimensional computer plots (response planes). The percentage of neurons encountered with homogeneous RFs (Y cells) was 7% in D cats and 16% in DV cats. Both values are much lower than in normal cats. Y-type neurons had weakly developed surrounds of their RFs and more phasic responses than normal. Surrounds of heterogeneous (X cell) RFs were also weak or absent. X-type receptive field centers were enlarged in both D and DV animals when compared to a sample from normal cats. They were also larger in D than in DV cats, particularly within 8 degrees of eccentricity. The late components of the response patterns of X cells were weak or absent. Seven percent of neurons found in the middle of the A laminae in DV cats had an atypical (ON-OFF like) structure of their receptive field which might indicate that they were like immature X or Y neurons.

INTRODUCTION

Visual deprivation may affect both structure and function of the cat's dorsal lateral geniculate nucleus (see 32 for review). Most studies agree that mean soma size (9, 10, 30, 33, 37 but 20) and proportion of encountered Y cells (11, 20, 31 but 6, 29) are smaller in deprived laminae. These effects are more severe in monocularly deprived animals but were also observed in binocularly deprived cats (9, 10, 31, 37).

Whether visual deprivation also causes a change in the organization of the receptive fields of relay cells is still controversial. Originally, Wiesel and Hubel (36) concluded that monocular eyelid suture does not affect the receptive field properties of LGN neurons (although they found some cells with abnormally large centers) and this suggestion was supported by Sherman et al. (31). Later on Maffei and Fiorentini (24) found a deficit in spatial resolution of cells in the deprived lamina of monocularly sutured cats. This finding was confirmed in several subsequent studies (11, 22, 23, 26, 28, see however 5, 29). The effect was most marked for X cells representing different parts of the visual field, including the monocular segment (22). This would implay that the resolution deficit in X cells is not due to "binocular competition" as has been suggested for the Y pathway (31, 32). No comparable data are available for binocularly sutured cats but surprisingly, dark rearing was reported to affect only temporal (5) but not spatial (5, 26) resolution of X cells. On the other hand both monocular and binocular atropine application (14) was claimed to lower spatial acuity of LGN X cells. These ambigous results obtained in binocularly deprived cats prompted us to reinvestigate the deprivation effect on organisation of LGN cell receptive fields using a uniquely sensitive method which encompasses both spatial and temporal properties of the receptive field — the response plane technique (34).

Since the receptive fields of cells in deprived animals were found to be affected we further examined the effect of postdeprivational visual experience on geniculate receptive field properties. Any recovery of receptive field structure could form the substrate for earlier observed behavioral improvement in such animals (27, 40).

METHODS

Twelve cats were binocularly deprived of pattern vision by rearing in masks from the time of eye opening (21). The masks prevented pattern vision, but allowed access of scattered light to the retinae. The reduction of eye illumination varied from 1 log unit to 6.5 log units (Sixtar light

meter) depending on the intensity of stains produced by eye secretions. The average reduction was comparable to that produced by eyelid suture (according to our measurements, a gray eyelid reduces the illumination by about 5 log units). The illumination of cats cages varied with weather and time of day from 1.4 do 58 lx. The masks, made of white double linen, were changed daily. During changing the cat's eyes were kept closed by the experimenter and washed with a weak antiseptic solution (for details see 21). The effectiveness of visual deprivation with masks has been confirmed before by the presence of several typical post-deprivational deficits, both at the behavioral and single unit level (4, 25, 41).

Six cats (group D) wore masks for 5 to 7 months up to the time of an acute experiment. The remaining six cats (group DV) were reared in masks to an age of 5 to 8 months and thereafter raised with open eyes and trained in visual pattern discrimination tasks for another 2 to 5 months before the experiment.

For the acute experiments brainstem transections were performed at the pretrigeminal level under ether anaesthesia, which was subsequently discontinued (43). The femoral vein and trachea were cannulated. The animals were paralysed with gallamine triethiodide (Flaxedil: initial dose -100 mg, maintenance dose -20 mg/h) and artificially ventilated with room air. End — expiratory CO_2 was maintained at 3.5-4% by adjusting the tidal volume delivered by the respirator. Temperature was kept as 38°C with an automatic heating pad. Fluid balance was main stained by subcutaneous injection of 5% glucose in saline solution. The eyelids and nictitating membranes were retracted with neosynephrine and pupils dilated with atropine. Contact lenses were used to protect the corneas and correct the refractive state of the eyes. The recording started not earlier than 2 h after the surgery.

Hubel-type tungsten microelectrodes were used for single cell recording from the LGN. In four experiments an array of five tungsten in lacquer stimulating electrodes was additionally inserted into the visual cortex and used for antidromic activation of LGN relay cells. The stimulating electrodes and recording microelectrode were positioned within the cortex and the openings were sealed with agar. The stimulated part of the cortex was usually smaller than the investigated region of the LGN. Cells recorded outside the zone of stimulation were classified on the bases of position and physiological properties, as were cells in experiments without cortical electrodes. For future track reconstruction, small electrolytic lesions were made with the microelectrode at selected depths in a penetration. After the experiment the brains were perfused with formaline and fixed for further histological procedure.

Visual stimuli were displayed on a white tangent screen located 57 cm in front of the cat's eye. A handheld projector was used for the initial plotting of the cells receptive fields. A bar of light subtending 0.4 x 0.75 degrees was used for more qualitative analysis (see below). We have used a slightly wider bar than in the original experiments on normal cats (34, 39) to allow faster analysis. It was shown previously that the stimulus size does not influence the overall structure of the receptive fields as revealed by the response plane method (34, 38). The stimulus intensity was 10 cd/m^2 and the background level was routinely 1 cd/m^2.

Data analysis was done on-line with a Cromemco Z-80 computer. Spatiotemporal firing patterns were analyzed in terms of "response planes" and "contour planes" (34). Under computer control the bar of light was switched on and off at 30 different positions along the vertical diameter of the receptive field. The step size was usually 0.5°. Each particular position of the slit corresponded to one peristimulus time (PST) histogram. One complete traverse of the stimulus added one repetition to each of 30 PST histograms. Fifteen repetitions were routinely used. All PST histograms were displayed together to form a plot of the averaged time course of cell firing rate (Z axis) as a function of time counted from stimulus onset (X axis) and location of the stimulus in space (Y axis). One PST histogram (the lowest in each response plane) was taken without a stimulus and, therefore, represented spontaneous activity.

For further analysis horizontal slices through the response plane at variable levels were used. When the PST histogram in the response plane exceeded the selected level of firing frequency a line was drawn in the plane. This form of display was called contour plane (34). The contour planes taken at the spontaneous firing level (see Figs. 1-3) consist of holes and solid regions representing domains of lowered and increased probability of cell firing or respectively, "inhibitory" and "excitatory" domains.

The terminology used in present study was adapted from Stevens and Gerstein (34):

Area: a region of space. Does not take temporal variation into account.

Domain: a portion of the response or contour plane. This encompasses both a region of space and a period of time.

Inhibitory domain: a domain within which the firing probability is below the spontaneous level.

Excitatory domain: a domain within which the firing probability is above spontaneous level.

Primary excilatory (PE) domain: strongest excitatory domain. Always corresponds to the classic center response.

Secondary excitatory (SE) domain: second strongest excitatory domain. Corresponds to the classic excitatory surround.

Primary inhibitory (PI) domain: strongest inhibitory domain.

Secondary inhibitory (SI) domain: second strongest inhibitory domain. Corresponds to the classic inhibitory surround.

Tertiary domain: occasionaly seen, weak inhibitory or excitatory domain which generally follows one of the four domain types described above.

Homogeneous receptive field: response plane of such field has very little domain variation as a function of space. It has been shown (34) that cells with such a domain arrangement are Y cells according to the linear summation test (5).

Heterogeneous receptive field: response plane of such field shows a considerable domain variation as a function of space. Such a domain arrangement characterizes X cells (34).

RESULTS

The receptive fields of 100 LGN cells were analyzed in animals reared in masks until the acute experiment (group D) und 105 units in cats with period of normal vision following initial deprivation (group DV). Since many abnormal receptive fields were encountered in the visually deprived animals it was essential to select only the laminae A and A1 units. The selection was based on the histological reconstructions of electrode tracks and sequence of the RFs in the track. In the four final experiments we also used antidromic stimulation to identify LGN relay cells. Since the latter criterion was not available in most experiments, it is possible that some of the studied cells were intrageniculate interneurons (38). Fifty six neurons in group D animals and 66 cells in group DV cats were selected as located within the main laminae. Response planes of these neurones were compared with data obtained previously from normal cats by means of the same type of electrodes and method of analysis (34, 39).

Cells with homogeneous receptive fields (Y type). The most striking effect of visual deprivation was the small number of Y cells encountered; only 8% of cells in group D animals and 18% in DV cats had homogeneous RFs, which are specific for Y-type LGN neurons (see Methods). This should be compared to the 48% of neurones with homogeneous RFs found in normal cats (34). The response planes of Y cells in normal cats were characterized by following features:

1. Small variation in response latencies for primary and secondary domains as a functions of space.

2. More transient responses than in X type planes.

3. Spatial overlap of PE and SI domains in Y-ON cells and the PI and SE domains in Y-OFF cells.

The response planes of Y units from visually deprived cats satisfied the above characteristics. The primary excitatory domains were as strong as in normal animals and the general arrangement of the domains were the same. The only difference was that the SE and both inhibitory domains seemed to be weaker. There was no difference between D and DV cats in this respect. Figure 1 shows a montage of all of the Y-type receptive fields found in group D cats.

Cells with heterogeneous receptive fields (X type). Heterogeneous receptive fields typical for X-cells were found for 92% of the units in D cats and for 75% of cells in DV animals. In both groups of visually deprived animals, the X-type neurons had grossly normal response properties when tested with the handheld projector. Response plane analysis frequently showed deficits, however, mainly in the secondary and tertiary domains. To reinforce this observation the response planes were arbitrally classified into four subgroups according to the strenght of the consecutive domains and the proportion of each subgroup estimated. The group I response planes had all the primary and secondary domains well developed. They were undistinguishable from the planes obtained in normal cats. On the other end of the scale, group IV planes showed only strongest domain, usually the primary response from the neuron receptive field center. In between, group II contained the response planes with visible, clear domain structure, but with incomplete set of domains or with some domains poorly developed. Group III contained the response planes that showed the one strongest domain (like in group IV) plus "something" — the remineders of other domains. To make the assignment more reliable the flexibility of computer graphics was used extensively. The response planes were magnified, rotated, the contour planes were built at various levels to detect the specific domains.

Neurons ascribed to different subgroups were found intermingled with each other in the same electrode tracks in all experiments. Thus, observed differences cannot be due to the difference in optical properties of the eyes or to changes in the state of the animals.

Figure 2 shows the variability of X-ON response planes encountered in group D animals. These planes, when recorded in normal cats, had the following characteristics (34):

1. Spatially nonoverlapping PE and SI domains.

2. A center response (PE) more sustained than in Y-type fields.

3. The latency of the SE domain varied as a function of space, beeing longer towards the RF center.

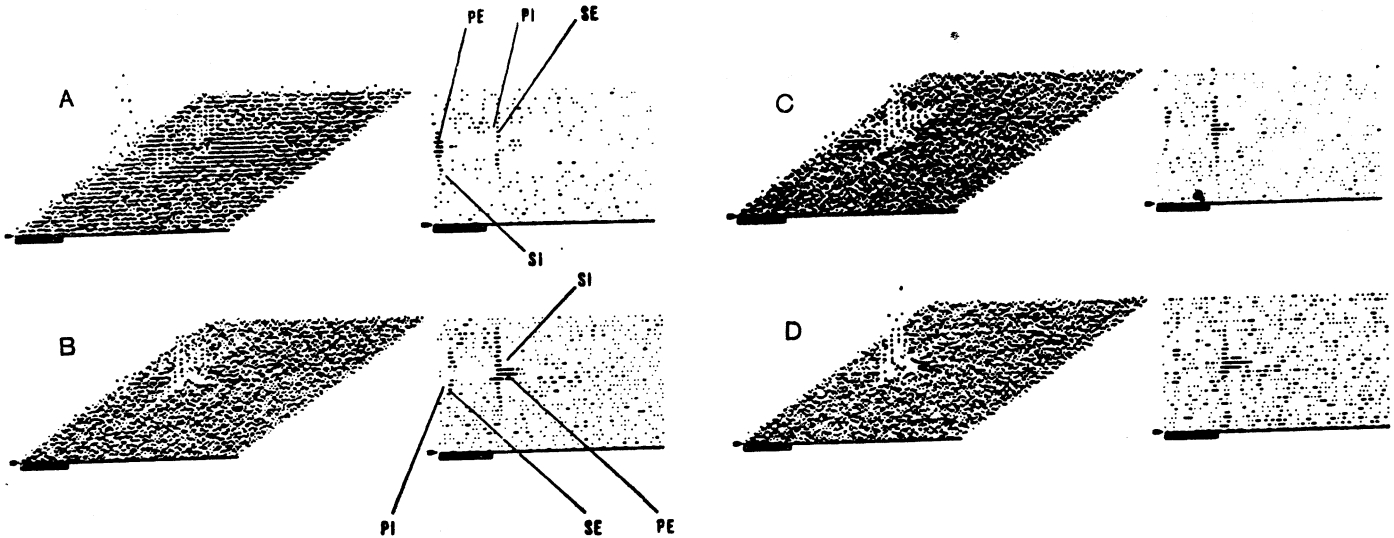

Fig. 1. Montage of homogeneous response planes obtained from four cells in group *D* cats. To the right of each response plane is the corresponding contour plane taken at the level of spontaneous firing. Dark bars under the planes represent the stimulus on time (300 ms). All response planes were obtained with 0.5° step size. Background and stimulus intensities were 1 and 10 cd/m^2 correspondingly. Fifteen repetitions of the stimulus in each position. Four main domains in ON-center (A) and OFF-center (B) fields are indicated (see Methods). Arrows indicate the lowermost histogram obtained without stimulation and therefore representing the spontaneous firing level.

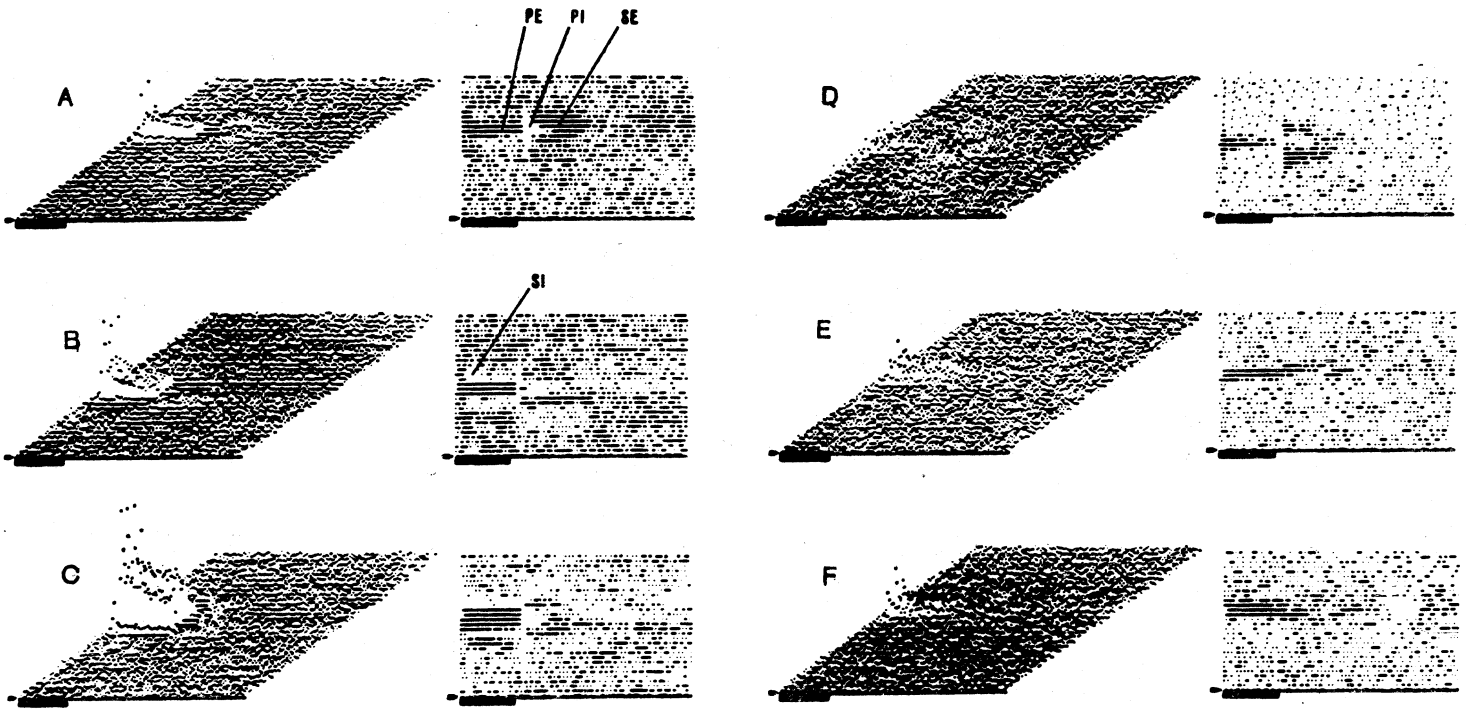

Fig. 2. Montage of heterogeneous-ON, response and contour planes to show variability. All planes show responses of cells from group *D* cats. Recording parameters as in Fig. 1.

The response plane ilustrated in Fig. 2*A*, is typical for the first subgroup (group I) of cells which had the most complete response planes. The excitatory domains PE and SE can easily be seen. The inhibitory domain PI is also well developed, while the inhibitory domains SI are weak compared to those in response planes of cells from normal cats. Figures 2*B* and 2*C* show response planes exemplifying the cells in group II. In both cases the PE domains are strong but the SE domains are poorly developed. The inhibitory domains PI are also weak although present in both response planes. The overall RF structure is therefore less clear. Figure 2*D* show an example of group III cell. In this response plane the PE and both inhibitory domains are weak, with the strongest cell response in the SE domain. Finally, the response planes in Figs. 2*E* and 2*F* represent the group IV cells. Here only the PE domains can be clearly distinguished with only a hint of the SE domains. The PE domains are decaying slowly after end of the stimulus forming the "tab of excitation" as described previousely for retinal ganglion cells (34).

A similar montage of X-OFF response planes is shown in Fig. 3. The archetypal X-OFF field had been characterized in normal cats (34) by:

1. Spatially nonoverlapping PI and SE domains.
2. A center response (PE) which was more sustained, compared to Y-OFF type fields.
3. The longest latency of PE domain in the spatial center of the RF.

In visually deprived animals the heterogeneous RFs did not always fully satisfy the last statement (Fig. 3*C*, *D* and *F*). Other features, however, justify the inclusion of these cells into the X-type class. The example in Fig. 3*A* represents the cells in group I with the most complete response planes (note however, the rather phasic component of PE domain). This neuron was recorded in a DV cat. In group D animals type I response planes were not found. All other examples shown in Fig. 3 were recorded in D cats. Figure 3*B* shows a response plane exemplifying group II cells. This cell has almost complete heterogeneous type characteristics except that the PI domain is weaker than found for normal OFF cells (34, 39). The response planes in Fig. 3*C* and *D* represent group III cells. All the secondary domains are poorly developed, the PE domains exhibit some degree of spatial homogeneouity, but the SE domains are still typical for X cells. Figure 3*E* and *F* represent the group IV cells with only the strongest tonic-like PE domains clearly discernible in the response planes. Several of the heterogeneous-OFF type cells from group III and IV (see Fig. 3*D*, *F*) showed some homogeneous features. We have used the grating test for spatial summation (34) on 5 cells of this type. All of them revealed a specific position of the grating which gave no response, proving that they were indeed the X cells.

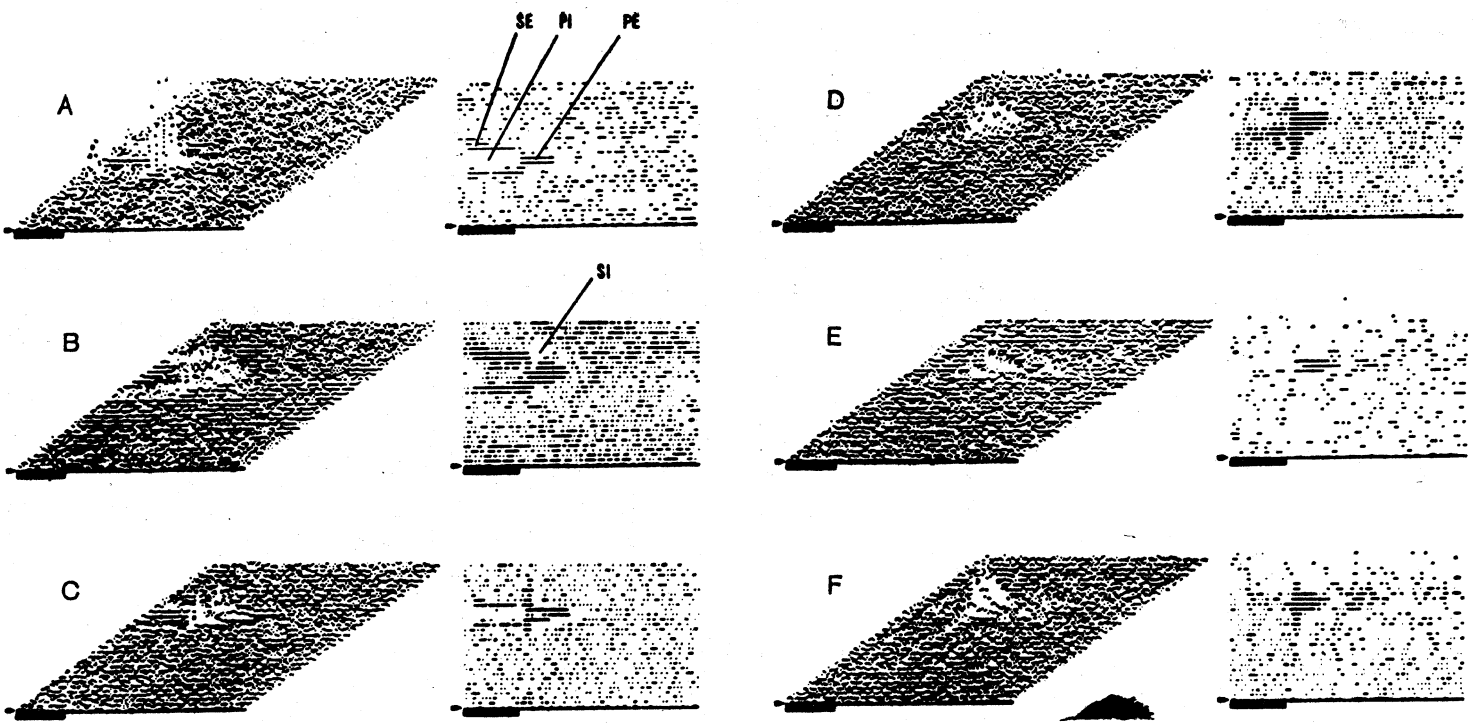

Fig. 3. Montage of heterogeneous-OFF (X-OFF) response and contour planes to show variability. Planes in A characterise the cells, found in DV cat. The remaining examples were encountered in *D* cats. Other explanations as in Fig. 1.

In normal cats the response planes show some degree of variability, including deficits in individual domains (Stevens and Gerstein (34); Figs. 8 and 9). A comparison of the percentages of different response planes subgroups in D, DV and normal cats is given in Table I. The data for normal animals were obtained by reprocessing the X-type response planes of 37 cells from an earlier study by Wróbel and Gerstein (39).

It is clearly apparent from Table I that compared to normal, the cells in deprived animals tend to show more deficits in the domain organization of their receptive fields. The Kolmogorov-Smirnov test was used for statistical analysis of the data from Table I. Sample sizes were

TABLE I

Distribution of different response planes subgroups in normal deprived cats

Cell type	Group of cats	Percent of response planes in arbitrary subgroups[a]				Total number of cells
		I	II	III	IV	
X-ON	D	6	14	47	33	36
	DV	7	45	48	0	32
	Normal	21	54	25	0	24
X-OFF	D	0	38	24	38	16
	DV	19	25	40	16	16
	Normal	33	56	11	0	13

[a] arbitrary subgroups were defined in page 266.

enlarged by summing ON and OFF type cells of the same subgroup. Significant differences ($P < 0.05$) were found between the distributions of cells within both deprived groups (D and DV) and normal animals and between D and DV groups of cats.

The presented data show that 5-7 months of binocular deprivation of pattern vision results in a changed RF structure of LGN neurons. These changes affect mainly the surround of X-type cells, where both SI and SE domains are weaker than in normal receptive fields. The Y-type cells, rarely encountered, show similar deficits. Postdeprivational visual experience (2-5 months) restores significantly but not fully the normal RF structure.

Receptive field center diameters. The diameter of the receptive field center of LGN cells is determined by connectivity and the internal balance of excitation and inhibition. Within the class of X or Y cells (the X cells were the only sample large enough to be analyzed) it depends on eccentricity and background illumination. Since spontaneous contour planes (i.e. the slice through the response plane at the level of sponta-

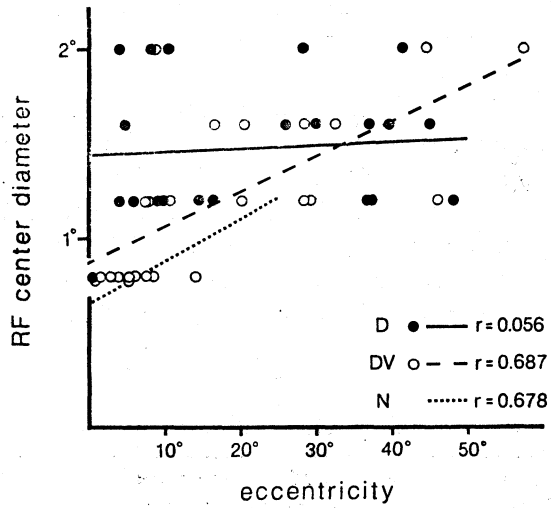

Fig. 4. Receptive field (RF) center diameters as measured in D (filled) and DV (unfilled circles) cats. The corresponding regression lines were calculated. Regression line (dotted) for the normal sample (N) represents the distribution reprocessed from (40).

neous firing, see Methods) allow rather accurate and objective measurement of RF diameter, an attempt was made to measure the field center diameters using constant background illumination, stimulus size and intensity. Figure 4 shows the RF center diameters of ON-center X cells measured in D and DV cats. Within the D group there is no correlation between eccentricity and RF center diameter, but for DV cats the positive correlation is significant (t-test, $P < 0.001$). This difference is related to many small center diameter fields found in DV cats within 8 degrees of eccentricity. Only one such small field was found in the corresponding area in the D group. The regression coefficient in the DV group is similar to that found in normal cats (dotted line in Fig. 4; data obtained by using the same method have been reprocessed from Ref. 39) although the diameters of normal RF centers seem to be samewhat smaller on the average. The last observation, however, can not be confirmed statistically since a smaller size stimulus was used in the experiments on normal cats (39).

The samples of receptive fields centers measured in D and DV animals were similarly distributed through the visual field (Kolmogorov-Smirnov test) and both groups could be therefore compared directly. Statistical analysis revealed a significant difference between distributions of RF center diameters in group D and DV animals (Kolmogorov-Smirnov test, $P < 0.05$).

We conclude that receptive field center diameters are generally bigger in D than in DV cats especially within 8 degrees of eccentricity. Thus, following the postdeprivational visual experience, the RF diameter — eccentricity relationship shifts toward that observed in normal cats.

Cells with atypical, ON-OFF type response planes. Eight neurons, all found in the DV sample, could not be simply attributed to any of the classes described above. Their response planes showed qualitative deficits of both the spatial and temporal arrangement of domains. One such cell is presented in Fig. 5*A*. The cell responded vigorously in a sus-

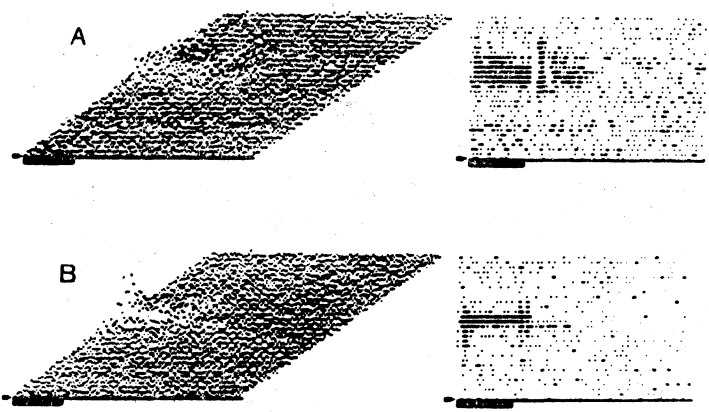

Fig. 5. Two examples of cells lacking typical primary inhibitory domain in their response planes. Other explanations as in Fig. 1.

tained manner during stimulus on time but only a short lasting PI domain could be observed after stimulus end. A phasic excitatory domain developed shortly afterwards in the receptive field center. An example of another cell of a similar type is shown in Fig. 5*B*. Here, the response plane is completely lacking the PI domain and instead, an excitatory response follows immediately the stimulus offset. Note, that this OFF response clearly differs from the "tab of excitation" seen in Figs. 2*E*, *F*. Because of weak or absent primary inhibitory domains these cells resemble the ON-OFF type neurons as described before in young kittens (3).

It should be noted that all of these cells were located within the main A and A1 geniculate laminae. All ON-OFF type cells found above the first relay cell in the track were excluded from this sample as they could correspond to perigeniculate neurons. Neither of two other cells showing this type of RFs and encountered in vicinity of the interlaminar layer were considered for analysis. Cells with ON-OFF type receptive

fields are extremely rare within the main laminae of normal animals (34) and could not be found in specially designed experiments (1). It is clear that their presence in deprived cats results from abnormal development.

DISCUSSION

Our experiments show, that lack of pattern vision during the early period of life affects both X and Y-type cells in the lateral geniculate nucleus. In agreement with previous studies (11, 20, 31) we found a major abnormality in the proportion of X and Y-type geniculate cells in deprived cats. In addition, the receptive fields of both neuronal classes differed from comparable samples in normal animals (38, 39). Deficits could be revealed in the spatial structures of the receptive fields as well as in the temporal properties of the responses. The most obvious change was a weakening of the receptive fields surrounds of both X and Y cells. Also later components, including the postphasic inhibition and tertiary domains were weak or absent. The primary excitatory domains within Y cells tend to be more phasic. A period of normal vision, following the 6 months of deprivation caused a small restitution in the percentage of encountered Y cells. The receptive field center diameters of the X cells became smaller presumably due to an overall improvement in the center — surround organisation. Finally, several cells with atypical ON-OFF responses were also found in deprived animals.

The lateral geniculate nucleus seems to be the first processing center in the visual pathway that is affected by visual deprivation (2, 19, 32, 36, see however different results obtained on squinted animals-15). Whether the effect results from lack of normal development and/or reorganisation of the geniculate circuitry or is secondary to an abnormal development of other visual centers is still unclear (32). The decreased number of Y cells encountered in the LGN of visually deprived cats was first described by Sherman et al. (31) and generally confirmed in several subsequent studies in monocularly and binocularly lid sutured cats (8, 11, 20, 31 but 6, 29). The present confirmation of this post-deprivational deficit indicate that our method of deprivation produces comparable changes to that of lid suturing not only in the colliculus superior (4) and visual cortex (25) but also in the lateral geniculate nucleus. It has been shown that cell shrinkage and associated electrode sampling bias cannot entirely explain the loss of recorded Y cells in deprived geniculate (7, 32, 33). The physiological mechanism underlying this effect is unknown; a delayed maturation in Y pathway (3) may be considered as one of possible explanations (7, 35, see also below).

The described abnormalities of the X cells receptive fields, such as larger field centers, weak or absent surrounds, altered time patterns of the responses might be expected to give a reduced spatial resolution. Such changes have been described in monocularly deprived animals (11, 13, 22, 23, 24, 26, 28 but 5, 29) for cells in both monocular and binocular segments. This finding would suggest that binocular competition does not play an important role in the development of this deficit. Surprisingly, a number of studies on binocularly sutured (31) and dark reared (18, 26) animals failed to demonstrate a decrease in X cells resolving power. Such effects have been observed, however, after squint operation (17) and in bilaterally atropinized cats (14). Although evoked by different deprivation methods, these results fit well with our data.

In their original paper Wiesel and Hubel (36) have reported that 4 out of 20 geniculate cells in a deprived LGN layer had larger then normal receptive field centers, sluggish responses and showed weaker peripheral suppression. In contrast, Lehmkuhle et al. (23) have found that monocular lid suture, despite its effect on spatial resolution of X cells does not change the center diameters and lateral inhibition within their receptive fields (as estimated for 9 cells from area response function). The latter findings hardly agree with our observations. The discrepancy might be partly due to the method of analysis. It has been reported for example, that sensitivity within the retinal ganglion cell receptive field, when measured by means of small light bar (as in our experiment), accompany the decrease in spatial acuity in squinted cats (15). Further experiments in our laboratory are in progress to clarify the above discussed discrepancies.

The partial return of Y cells number and the improvement of the X cells receptive field structure after prolonged period of normal vision may explain behavioural improvement of such animals (27, 40). Previous experiments gave inconsistent results whether postdeprivational visual experience increases the ratio of encountered Y cells (8, 12, 42 but 20, 26). A cortical origin of such increase was postulated (32, 42) but evidences against this hypothesis have also been reported (26). Since all these experiments were performed on monocularly sutured cats any comparison with our results is difficult. The effect of eye opening on X cell responses have not been studied quantitatively in lid sutured cats (20, 32). In dark reared animals Mower et al. (26) have found slight improvement in visual acuity of X cells with receptive fields within 2° of eccentricity, after 4-6 months long monocular visual experience. It is worth stressing, that the partial return of the center/surround organisation as observed for X cells in the retrained (DV) cats cannot be attributed only to a longer survival time of these animals. Two cats in

this group were studied at the same age as the oldest deprived (D) animals and the differences were the same as for the rest of the animals. Thus, visual experience appears to be the important differentiating factor between the studied groups.

Cells with ON-OFF receptive fields are extremely rare in normal LGN and were usually reported to be located within interlaminar layer (24, 34). The ON-OFF cells found in the present study were all positively shown to be located within the main laminae. Similarly abnormal geniculate receptive fields were reported after TTX induced silencing of the retinal activity during critical period (1). It is very unlikely that deprivation of pattern vision can arrest the spontaneous activity of some ganglion and geniculate cells in similarly severe manner (7). The common factor in both experiments may be a delayed maturation of the LGN. The central histograms of response planes in Fig. 5*A*, *B* are very similar to the responses of ON-OFF type cells found by Daniels et al. (3) in normal young kittens. These authors found that the ratio of such cells diminishes from 40% in newborn animals to about 8% in oldest age group studied (6 weeks). Could it be that such atypical connectivity persisted longer in deprived cats?

The qualitative agreement of our data with the description of immature receptive field properties in young normal kittens is indeed remarkable. Two main differences between normal and deprived animals were observed in our experiment: the relatively small number of Y cells and abnormal surrounds of X and Y receptive fields. Similarly, Daniels et al. (3) have shown that X cells mature before Y neurons (see also 35) and for both cell types the surround responses develop later then the center responses. Thus, as suggested by Ikeda et al. (16), the arrest or delayed development of the retino-geniculate pathway after pattern deprivation, might be the main source of most of the deficits observed in present experiment.

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