

POSTNATAL DEVELOPMENT OF OCULAR DOMINANCE COLUMNS IN LAYER IV OF  
THE CAT'S VISUAL CORTEX, AND THE EFFECTS OF MONOCULAR DEPRIVATION\*

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The segregation of geniculocortical fibers representing the two eyes and the effects of monocular deprivation on this segregation were studied by transneuronal transport of radioactive proline injected into one eye, and by physiological recordings. In the normal adult animal, this autoradiographic technique (7) has demonstrated that geniculocortical terminals from the two eyes are partially segregated (6). We examined the physiological correlate of this anatomical segregation by recording from single cells in identified laminae of area 17 in cats in which one eye had previously been injected with radioactive label. In layer IV, most cells had simple receptive fields and about 20% of the cells were monocularly driven from each eye. Cells were clustered according to eye preference, and transitions between groups of cells dominated by one eye or the other were marked with electrolytic lesions. Figure 1A shows one such experiment in a normal cat. In this and similar experiments, a good correspondence was found between the distribution of cells in layer IV dominated by the injected eye and that of radioactively labelled terminals.

Previous work in the monkey has disclosed that the geniculocortical projection is initially overlapping (5). The afferents representing the two eyes begin to segregate apart from each other  
\* The experiments described here are presented fully in the two following papers: LeVay, S., Stryker, M.P., & Shatz, C.J., Ocular dominance columns and their development in layer IV of the cat's visual cortex: a quantitative study, in press, J. Comp. Neur., 1978; and Shatz, C.J. & Stryker, M.P., Ocular dominance in layer IV of the cat's visual cortex and the effects of monocular deprivation, in press, J. Physiol., 1978.

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at least 3 weeks prenatally, and the process of segregation is not complete until after 3 weeks postnatally (3,5). We investigated the possibility that such a process of segregation might begin postnatally in the cat and might therefore be more easily amenable to experimental intervention. As late as 15 days postnatally, radioactive label formed a continuous band in layer IV on both sides of the brain, suggesting that afferents serving the two eyes were intermingled. At 22 days of age, periodic variations in grain density first appeared in layer IV, but these variations were clear only in the hemisphere ipsilateral to the injected eye. Such variation was more distinct at 33 days of age and achieved approximately the adult appearance at 39 days. On the contralateral side such variation was not marked until 39 days, and even in the adult it was less striking than on the ipsilateral side.

Interpretation of these findings was complicated by the possibility that significant amounts of radioactivity might spill over into the inappropriate laminae of the lateral geniculate nucleus and label the wrong set of cortical afferents. This was studied in autoradiographs of 1  $\mu$ m Epon sections by measuring the ratio of labelling density over neuronal nuclei in laminae A and A1. We found that this spillover was always greater on the contralateral side, and greatest in the youngest animals. When spillover was taken into account quantitatively in the interpretation of the grain counts made from the cortical autoradiographs, as shown in Figure 2, three findings emerged: 1) At 8 and 15 days, the continuous appearance of radioactive label on the ipsilateral side was not due to spillover but reflected a real uniformity in the distribution of ipsilateral-eye afferents. 2) The continuous pattern of label seen prior to 39 days on the contralateral side is uninterpretable owing to spillover. Other considerations, however, make it seem likely that the process of segregation proceeds synchronously for the two sets of afferents. 3) In the adult, each eye's afferents occupy the centers of the appropriate ocular dominance columns almost exclusively, but they overlap at the borders. The overall dominance of the contralateral eye appears to reflect the greater size of the patches of terminals representing that eye rather than a continuity in the distribution of those terminals.

Physiological recordings allowed us to examine whether transient functional connections might originally be made uniformly along layer IV in an unsegregated pattern. Tangential penetrations through layer IV in kittens 10 to 17 days of age showed most of the cells to be nearly equally driven through the two eyes, in contrast to the adult. These findings suggest that functional connections may be broken and reformed during development, although other interpretations cannot yet be excluded. It is striking, however, that the onset of segregation coincides roughly with the beginning of the critical period of susceptibility to the effects of monocular deprivation (1).

In cats which had been monocularly deprived from birth until more than 9 months of age, afferents representing the deprived eye were still demonstrable autoradiographically, although very few cells are reported to be driven by that eye in similar animals studied by previous workers (1,4). We wondered whether the deprived-eye terminals, while still present, might somehow be functionally suppressed. Recordings from layer IV in monocularly deprived cats, however, also revealed a substantial input (22% of cortical cells driven) from the deprived eye; this is consistent with the anatomical findings. Responses from the deprived eye in layer IV were found to coincide with patches of label, when the deprived eye was injected (Figure 1B), or holes in the much more extensive distribution of label found when the non-deprived eye had been injected (Figure 1C). Most cells driven by the deprived eye had simple or circular receptive fields. Recordings from other cortical layers showed almost total dominance (93% of cortical cells driven) by the non-deprived eye, in harmony with the results of previous workers. Almost all cells with complex receptive fields were dominated by the non-deprived eye. These findings, then, do not provide evidence that thalamic afferents representing the deprived eye are functionally suppressed in layer IV of the cat's visual cortex. Rather, they show that an effect of monocular deprivation in the cat, as in the monkey (2,3), is to alter the development of the geniculocortical projection so as to provide a greater territory in layer IV for the non-deprived eye along with

a reduced territory for the deprived eye. It remains to be seen whether a similar process occurs at the further stages of visual processing carried out in other cortical layers.

The current findings on normal development suggest that the mechanism involved in the production of the altered geniculocortical projection by monocular deprivation does not necessarily involve axonal sprouting into "new" territory. As has been suggested for the monkey (3), it may instead involve a failure of the retraction of the non-deprived eye's afferents which would have occurred in the normal process of segregation.

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FIGURE LEGENDS

Figure 1

Reconstructions from parasagittal sections of electrode penetrations into the visual cortex (area 17) of one normal cat and two cats which had been monocularly deprived by lid suture from birth until more than 9 months of age. Approximately two weeks prior to the recording experiments, one eye of each animal was injected with a mixture of  $^3\text{H}$ -proline and  $^3\text{H}$ -fucose. The distribution of transneuronally-transported radioactivity in the cortex is indicated by stippling on the reconstructions; the stippled areas presumably represent the regions of termination of the geniculate fibers serving the injected eye.

Numbered arrows indicate the positions of electrolytic marking lesions made along the electrode track. Symbols refer to each unit recorded: units with simple-type receptive fields are denoted by circles; those with complex-type by squares; triangles indicate other receptive-field types (e.g., hypercomplex, etc.) and units that were not classified; and diamonds indicate unresolved background activity.

A. Two electrode penetrations in area 17 of a normal cat. Filled symbols refer to the units preferring the injected (ipsilateral) eye (ocular dominance groups 5-7). Half-filled symbols indicate units equally driven by the two eyes (group 4). In penetration 1, the electrode passed through the two patches of label in layer 4, one at the upper right open arrow, the other just following lesion 5. In both cases, cells were dominated by the injected eye.

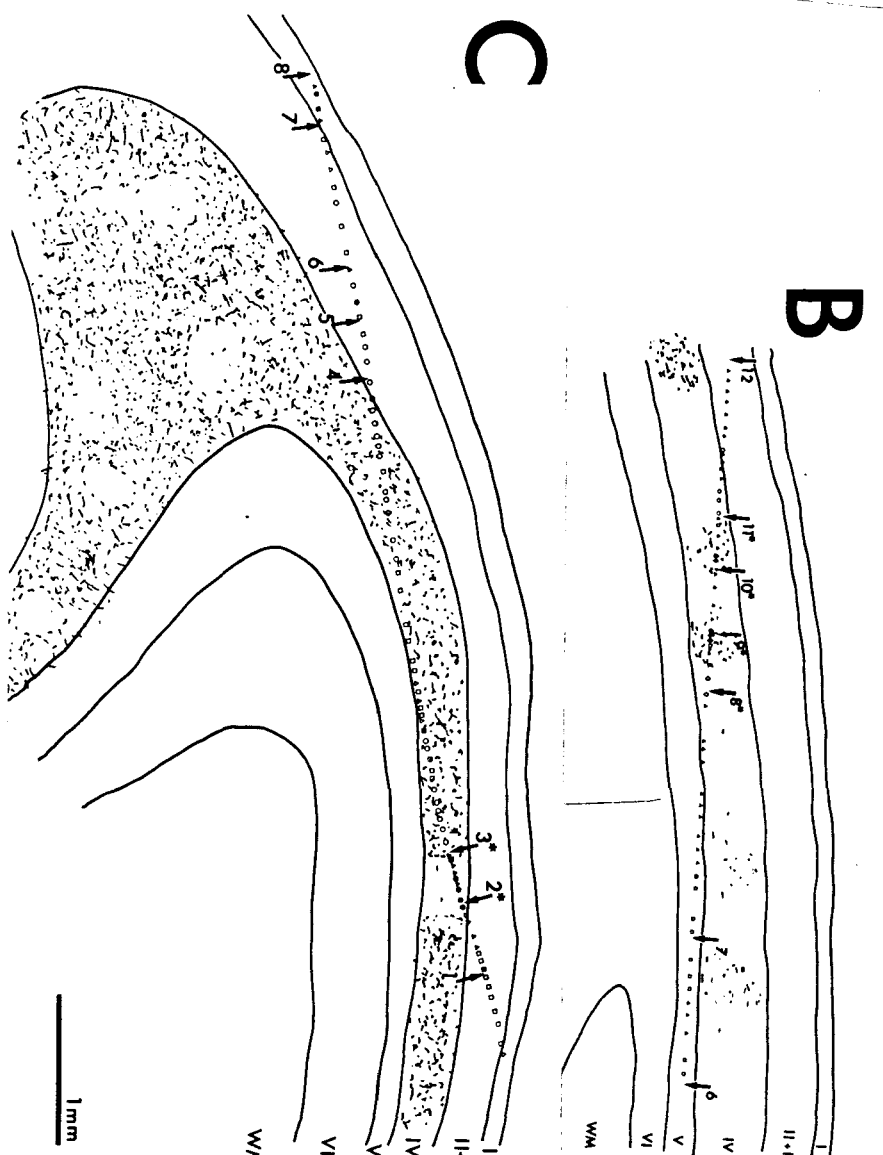
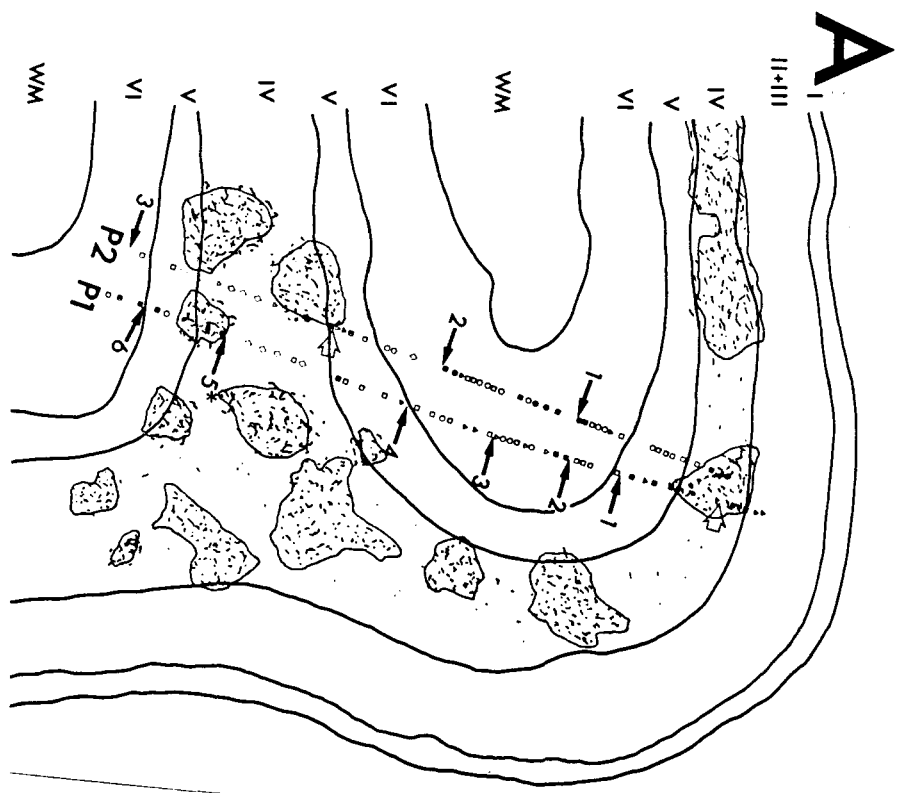
## Figure 1 (continued)

B. Electrode penetration in a monocularly deprived cat in which the deprived eye was injected. Filled symbols indicate units dominated by deprived (contralateral) eye. As the electrode passed through layer IV, two groups of units dominated by the deprived eye were encountered: the first was located near lesion 9; the second after lesion 10. Note that the regions occupied by patches of radioactive label occupy a smaller proportion of layer IV than in normal cats (A), and that units dominated by the deprived eye were found only in these patches.

C. Electrode penetration in a monocularly-deprived cat in which the non-deprived eye was injected. Filled symbols indicate cells driven by the deprived (ipsilateral) eye. As the electrode entered layer IV, a group of cells driven by the deprived eye was encountered between lesions 2 and 3. Positions of these lesions were found to coincide with a gap in the transneuronally-transported radioactive label. Note that the distribution of radioactive label within layer IV was more extensive than in normal cats(A).

Figure 2

Grain counts in successive  $12.5 \times 100 \mu\text{m}$  regions along the base of layer IV from autoradiographs of horizontal sections of the visual cortex on both sides of the brain. Shown are three from a series of eight animals. The counts in each bin were averaged with those of the four adjacent bins to obtain the smoothed values plotted here as dots. Ordinates show grain density in grains/ $1250 \mu\text{m}^2$ ; abscissas show distance along layer IV in mm. The stated age is the age at death; 2 mCi of  $^3\text{H}$ -proline was injected into one eye of each animal 8 days previously. The grains above background (dotted lines) reflect transneuronally transported label. Theoretical limits for the maximum and minimum cortical grain densities to be expected if the afferents serving the two eyes were completely segregated from each other in layer IV are indicated by solid lines. These theoretical limits were calculated from counts of the autoradiographic labelling of neuronal nuclei in laminae A and A1 of the lateral geniculate nucleus, on the assumption that geniculate neurons transport label to their cortical terminals in proportion to the labelling of their nuclei. Note that the labelling does not show periodic fluctuations on the ipsilateral side at 15 days, indicating a uniform distribution of afferents. By 39 days the fluctuations in grain density are nearly as pronounced as in the adult.

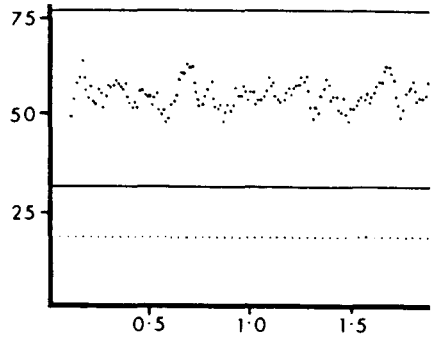


**C**

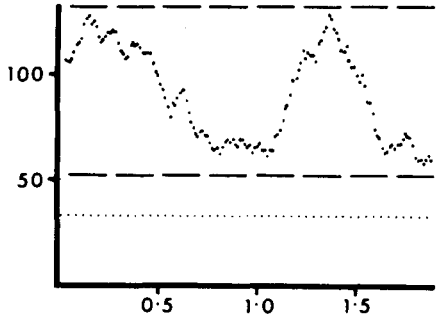
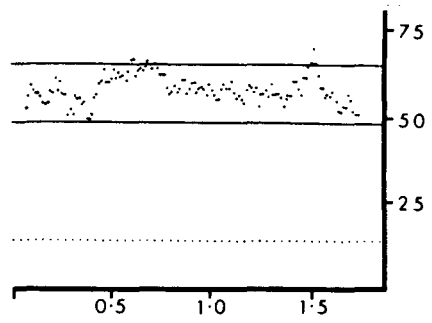
Figure 1

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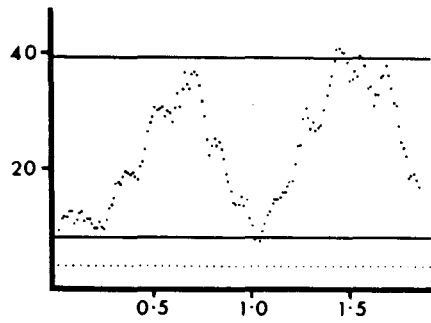
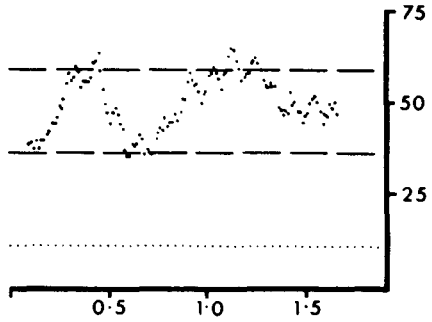
contra



15  
days



39  
days



adult

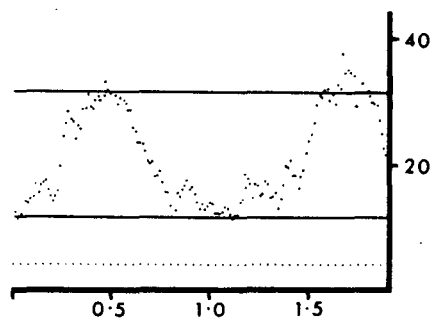


Figure 2