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A Note on the Laminar Organization of Rat Visual Cortical Projections

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Introduction

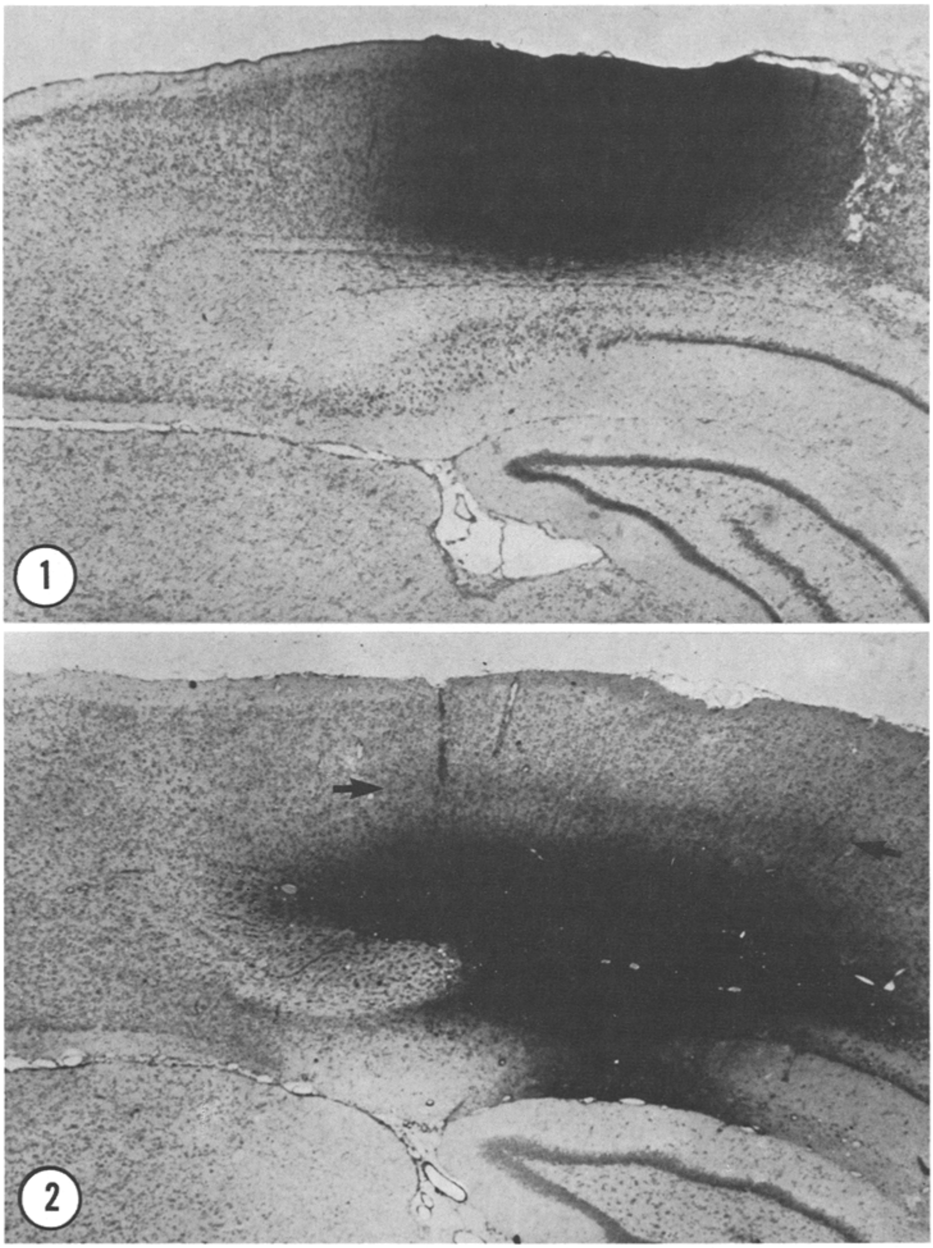
Following interruption of the rat corpus callosum, the lateral part of cerebral cortical area 17 and the adjacent area 18a contain terminal degeneration throughout all the layers of the visual cortex (Heimer et al., 1967; Lund and Lund, 1970; Jacobson, 1970). The terminal degeneration was described as dense in layers I and II, sparse in layers III and VI, and sporadic in layers IV and V. Experiments using superficial cortical lesions (Jacobson, 1971) and injections of horseradish peroxidase into superficial cortical layers (Jacobson and Trojanowski, 1974) both indicate that the supragranular layers of one hemisphere only connect with the supragranular layers of the opposite hemisphere. In the present study, the autoradiographic method for tracing neuroanatomical pathways (Cowan et al., 1972) has been employed to demonstrate the laminar projection of layers V and VI of area 18a to the infragranular layers of the contralateral hemisphere. The major advantage of this method is its ability to distinguish between fibers arising from a region as opposed to axons passing through the region.

Methods

The two cases presented in this paper were part of a larger study which included 23 albino rats with injections of L-[2,3-^{3}H]-proline into the lateral geniculate body, hippocampus and parts of the thalamus (Ribak and Peters, 1975). The procedure for the injections, the processing of the specimens into paraffin and the preparation of the autoradiographs were identical to that described in this earlier work (Ribak and Peters, 1975). Rat 43 had a 4 day survival time while rat 45 had a 7 day interval between the time of injection and the time of sacrifice.

Results

The injection site of rat 43 was located in the lateral part of area 17 (see Ribak and Peters, 1975) and the adjoining area 18a (Fig. 1). The entire depth of the cortex was labeled; the width of labeling in the deeper layers being less than in the upper layers. The injection site of the other case, rat 45, included layer VI and the lower part of layer V of areas 17 and 18a, as well as the subcortical white matter and the presubiculum (Fig. 2). Superficial to this injection



Figs. 1 and 2. Low magnification bright field photomicrographs of coronal sections through the rat visual cortex which have been processed for autoradiography to indicate the injection site of ^{3}H-proline. **Figure 1** shows the injection site of rat 43 which included all of the layers of the cortex in the lateral part of area 17 and the medial part of area 18a. A portion of area 18a to the right of the injection site was damaged during the experimental surgery. **Figure 2** shows the injection site of rat 45 which included layer VI and the lower part of layer V of the visual cortex, as well as the subcortical white matter and the presubiculum. The light band of label in layer IV (arrows) was interpreted as axon collaterals from the labeled neurons of layer VI. × 31.5

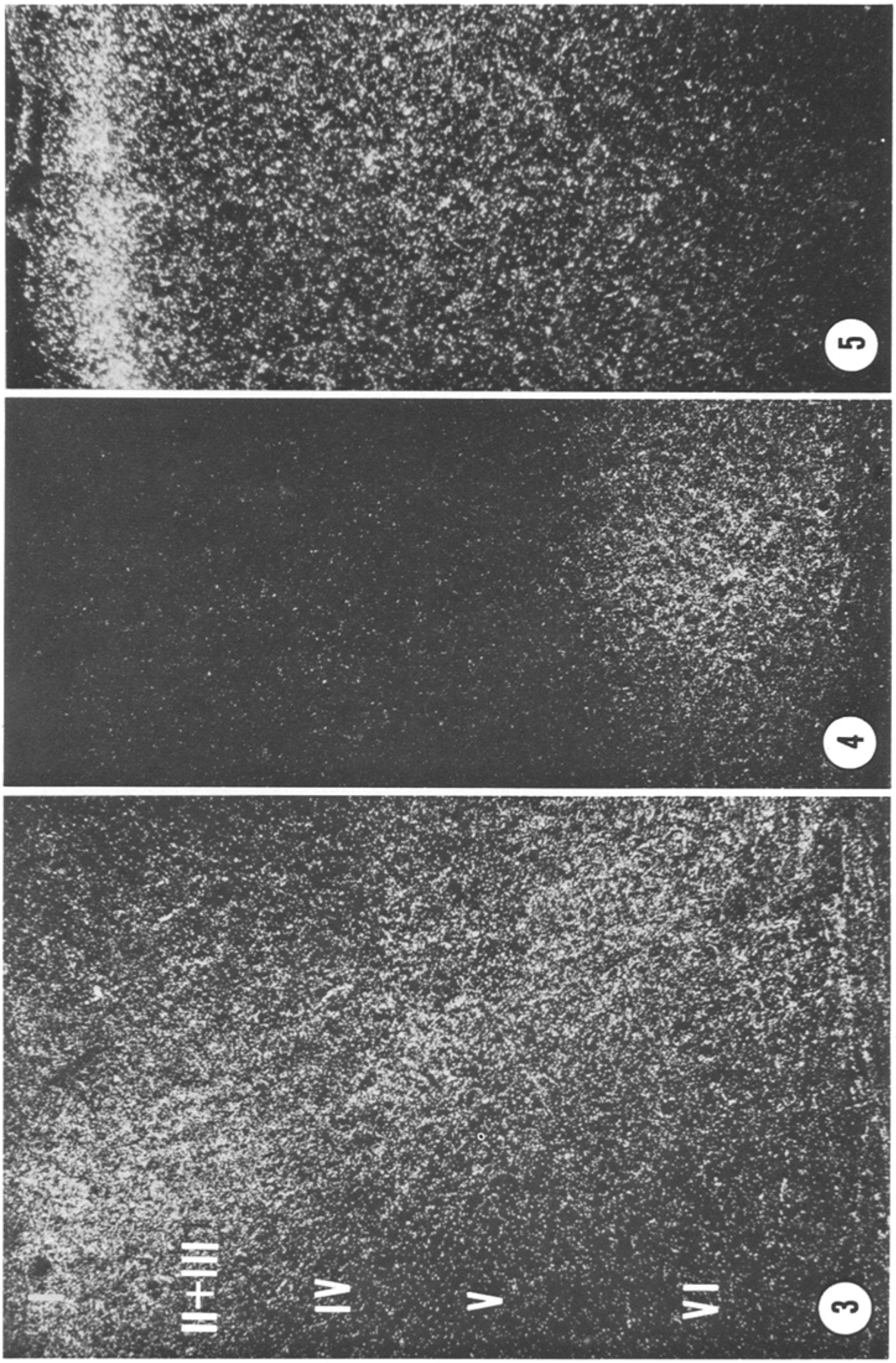
site, there was a distinct, light band of label in layer IV which was interpreted as having arisen from the axon collaterals of the labeled layer V and VI neurons.

In both animals, the following projections were observed from the visual cortex: a) commissural projections, b) ipsilateral descending projections to non-cortical structures and c) ipsilateral cortico-cortical projections. The differences in the location of the injection sites in these two cases gave rise to significant differences in the pattern of labeling at the terminal sites. This difference was illustrated best in the callosal projection. For example, in rat 43 (injection site included both the supra- and infragranular layers) the callosal projection was traced to the contralateral area 18a and lateral part of area 17. This projection displayed silver grains above background throughout all the layers with somewhat less label in layer IV (Fig. 3). Such a pattern of labeling was similar to that described for the commissural fibers in the rat somatosensory cortex (Wise and Jones, 1976).

In striking contrast, the contralateral area 18a in rat 45 (infragranular injection site) was labeled significantly only in layer VI (Fig. 4). This indicated that the deep layers of the cortex only send commissural fibers to the deep layers of the contralateral cortex. This finding was consistent with the physiological data on the stratified organization of the commissural projection (Grafstein, 1959) and the anatomically proven reciprocal commissural projection of the supragranular layers (Jacobson, 1971; Jacobson and Trojanowski, 1974), but it was unexpected because previous Golgi studies (Lorente de Nó, 1938) indicated that the neurons of layers V and VI send commissural fibers into layers II and III.

The ipsilateral descending projections to non-cortical structures formed a well-labeled and distinct fiber tract that could be traced from the white matter beneath areas 17 and 18a to their terminations. The first site of termination of this ipsilateral corticofugal fiber bundle was in the dorsal portion of the caudoputamen which confirms the findings of Killackey and Ryugo (1975). From the caudoputamen, the labeled fiber tract entered the brainstem to terminate in the following structures: the dorsal and ventral nuclei of the lateral geniculate body, the lateral posterior nucleus of the thalamus, the lateral terminal nucleus of the accessory optic tract, the zona incerta, the dorsolateral part of the pontine gray, the pretectal area and the superficial layers of the superior colliculus. These sites of termination are identical to those described in an earlier study (Nauta and Bucher, 1954). In addition, the present study did *not* show a corticogeniculate projection to the intergeniculate leaflet, that part of the lateral geniculate body situated between the ventral and dorsal subdivisions which has been shown to receive a bilateral projection from the retina (Hickey and Spear, 1976).

The third observed projection from the visual cortex was the ipsilateral cortico-cortical projection to area 18 on the medial aspect of area 17. Dense labeling occurred in the lower half of layer I and the upper half of layer II of area 18 (Fig. 5). In addition, the remaining layers were lightly labeled. The origin of this projection was probably area 18a (Krieg, 1946) since in a previous study area 17 was observed to project only to the lateral and anteromedial



Figs. 3, 4 and 5

peristriate cortices (Montero et al., 1973). This ipsilateral cortico-cortical projection was observed only in rat 43, the case where the injection site included both the supra- and infragranular layers. The cortico-cortical projection to the supragranular layers of area 18 was absent in rat 45, the case with the infragranular injection site. The difference in terminal labeling between these two cases suggests that the infragranular layers of the visual cortex do not send cortico-cortical fibers to the supragranular layers.

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References

Cowan, W.M., Gottlieb, D.I., Hendrickson, A.E., Price, J.L., Woolsey, T.A.: The autoradiographic demonstration of axonal connections in the central nervous system. Brain Res. **37**, 21–51 (1972)

Grafstein, B.: Organization of callosal connections in suprasylvian gyrus of cat. J. Neurophysiol. **22**, 504–515 (1959)

Heimer, L., Ebner, F.F., Nauta, W.J.H.: A note on the termination of commissural fibers in the neocortex. Brain Res. **5**, 171–177 (1967)

Hickey, T.L., Spear, P.D.: Retinogeniculate projections in hooded and albino rats: an autoradiographic study. Exp. Brain Res. **24**, 523–529 (1976)

Jacobson, S.: Distribution of commissural axon terminals in the rat neocortex. Exp. Neurol. **28**, 193–205 (1970)

Jacobson, S.: The laminar contributions to the callosal system in the albino rat. Anat. Rec. **169**, 346 (1971)

Jacobson, S., Trojanowski, J.: The cells of origin of the corpus callosum in rat, cat and rhesus monkey. Brain Res. **74**, 149–155 (1974)

Killackey, H.P., Ryugo, D.K.: The organization of unspecific thalamic projections to the telencephalon of the rat. Anat. Rec. **181**, 393 (1975)

Krieg, W.J.S.: Connections of the cerebral cortex. I. The albino rat. C. Extrinsic connections. J. comp. Neurol. **86**, 267–395 (1947)

Lorente de Nó, R.: Cerebral cortex: architecture, intracortical connections, motor projections. In: Physiology of the Nervous System (ed. J.F. Fulton), pp. 291–325. London: Oxford University Press 1938

Lund, J.S., Lund, R.D.: The termination of callosal fibers in the paravisual cortex of the rat. Brain Res. **17**, 25–45 (1970)

Figs. 3, 4 and 5. Darkfield photomicrographs of autoradiographs of the cerebral cortex. **Figure 3** shows the distribution of the commissural projection to the contralateral area 18a from rat 43 whose injection site included both the supra- and infragranular layers. All of the layers contain silver grains above background with somewhat less label in layer IV. **Figure 4** shows the commissural projection as it appeared in rat 45 where only the infragranular layers were included in the injection site. Most of the label is limited to layer VI and the lower part of layer V. **Figure 5** shows the ipsilateral cortico-cortical projection from area 18a to area 18. Most of the label is located in layer II and the lower half of layer I with significant label in the other layers. × 120

Montero, V.M., Bravo, H., Fernández, V.: Striate-peristriate cortico-cortical connections in the albino and gray rat. Brain Res. **53**, 202–207 (1973)

Nauta, W.J.H., Bucher, V.M.: Efferent connections of the striate cortex in the albino rat. J. comp. Neurol. **100**, 257–286 (1954)

Ribak, C.E., Peters, A.: An autoradiographic study of the projections from the lateral geniculate body of the rat. Brain Res. **92**, 341–368 (1975)

Wise, S.P., Jones, E.G.: The organization and postnatal development of the commissural projection of the rat somatic sensory cortex. J. comp. Neurol. **168**, 313–344 (1976)

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