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ANATOMICAL AND NEUROBEHAVIORAL INVESTIGATIONS
CONCERNING THE THALAMO-CORTICAL ORGANIZATION
OF THE RAT'S VISUAL SYSTEM

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the
Degree Doctor of Philosophy in the Graduate School
of The Ohio State University

By

Howard Clark Hughes, B.A., M.A.


* * * * *

The Ohio State University
1976

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Dedicated to my wife, Katherine B. Hughes, whose
patience, understanding and support made completion of this work
possible

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Presently, my principal interests are concerned with the anatomical and functional organization of the various thalamic projection systems and their associated cortical targets in the visual system.

COURSES TAUGHT:

Psychology 100 - Introductory Psychology I
Psychology 101 - Introductory Psychology II

PUBLISHED ABSTRACTS:

1. Berntson, G.G. and H.C. Hughes. Eating, grooming, threat and escape induced by medullary stimulation in the cat. Annual Meeting of the Society for Neuroscience, October, 1974, St. Louis, Missouri.
2. Martin, G.F., M.S. Beattie, H.C. Hughes and M. Linouts. Reticulo-olivary connections, their organization and possible significance. Annual Meeting of the Society for Neuroscience, November, 1976, Toronto, Canada.

PUBLICATIONS:

1. Berntson, G.G. and H.C. Hughes 1974 Medullary mechanisms for eating and grooming behaviors in the cat. Experimental Neurology, 44: 255-265.
2. Berntson, G.G. and H.C. Hughes 1976 Behavioral characteristics of grooming induced by hindbrain stimulation in the cat. Physiology and Behavior, 17: 165-168.

3. Berntson, G.G., H.C. Hughes and M.S. Beattie 1976 A comparison of hypothalamically induced biting attack with natural predatory behavior in the cat. Journal of Comparative and Physiological Psychology, 90: 167-178.
4. Hill, R.M., G.D. Ritchie, C.E. Bohman, S.A. Burns and H.C. Hughes 1976 Retinal blur and midbrain cell response. Experientia, 32: 481.
5. Hughes, H.C., P.M. Meyer, J.W. Meyer, D.R. Meyer and J.C. Bresnahan 1976 An inexpensive microphotometer for measuring grain densities in autoradiographs. Stain Technology, in press.
6. Martin, G.F., M.S. Beattie, J.C. Bresnahan, C.K. Henkel and H.C. Hughes 1975 Cortical and brainstem projections to the spinal cord of the American opossum, Didelphis marsupialis virginiana. Brain, Behavior and Evolution, 12 (4-6): 270-310.
7. Martin, G.F., M.S. Beattie, H.C. Hughes, M. Linauts and M. Panneton 1976 A study of reticulo-olivary connections in the North American opossum. Brain Research, submitted for publication.
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ABBREVIATIONS

CG	-	substantia grisea centralis
CM	-	nucleus centre median
CP	-	cerebral peduncle
DMH	-	nucleus dorsomedialis hypothalami
FR	-	fasciculus retroflexus
Hip	-	hippocampus
IC	-	inferior colliculus
IPN	-	nucleus interpeduncularis
LGNd	-	lateral geniculate nucleus, pars dorsalis
LGNv	-	lateral geniculate nucleus, pars ventralis
LM	-	lemniscus medialis
MG	-	medial geniculate nucleus
MRF	-	midbrain reticular formation
NAD	-	nucleus anterior dorsalis thalami
NAMT	-	nucleus anterior medialis thalami
NAVT	-	nucleus anterior ventralis thalami
NLP	-	nucleus lateralis posterior
NLT	-	nucleus lateralis thalami
NMT	-	nucleus medialis thalami
NP	-	nucleus pretectalis
N Pf	-	nucleus parafascicularis
NR	-	nucleus reticularis thalami
NS	-	nucleus suprageniculatus
NVTd	-	nucleus ventralis thalami, pars dorsalis
NVTv	-	nucleus ventralis thalami, pars ventralis
OT	-	optic tract
RBC	-	red blood cell
RN	-	nucleus ruber
SC	-	superior colliculus
SMT	-	stria medullaris thalami
SN	-	substantia nigra
III	-	oculomotor complex
TPO	-	nucleus posterior thalami
VMH	-	nucleus ventromedialis hypothalami
ZI	-	zona incerta

INTRODUCTION

A number of recent neuroanatomical investigations have described a retino-cortical pathway in addition to, and arranged in parallel with the geniculo-striate projection (Diamond and Hall, 1969; Diamond, Snyder, Killackey, Jane and Hall, 1970; Graybiel, 1970, 1972a,b; Niimi and Sprague, 1970; Harting, Diamond and Hall, 1973; see Jones, 1974 for a review; Benevento and Rezak, 1976). This recently identified network has features that are common to the various species in which it has been examined. Its ascending component is a pathway in which visual information is transmitted to the cortex via (1) the retinofugal projection to the superior colliculus and portions of the pre-tectum (Hayhow, Sefton and Webb, 1962; Laties and Sprague, 1966); through (2) the ascending connections of these midbrain visual centers to nuclei within posterior portions of the dorsal thalamus (Altman and Carpenter, 1961; Tarlov and Moore, 1966; Martin, 1969; Graybiel, 1972a; Harting, Hall, Diamond and Martin, 1973; Benevento and Fallon, 1975); and finally through (3) the projections of these various thalamic cell groups to multiple and sometimes overlapping fields within the peri-striate and temporal regions of the cortex (Le Gros Clark and Northfield, 1937; Chow, 1950; Clüver and Campos-Ortega, 1969; Diamond et. al., 1970; Graybiel, 1970, 1972a,b; Niimi and Sprague, 1970; Harting et. al., 1973; see Jones, 1974; Rosenquist, Edwards and Palmer, 1974; Maciewicz, 1975; Benevento and Rezak, 1976).

The present series of experiments is a reinvestigation of the thalamocortical organization of the rat's visual system in the light of these new developments. Two major questions were addressed. First, do the projections of Nucleus lateralis posterior (NLP) and the dorsal division of the lateral geniculate nucleus (LGNd) have features in common with analogous projections in other mammalian species? If so, does this second pathway to the cortex imply that in the rat, as in cats (Doty, 1971; Sprague, Levy DiBernardino and Conomy, 1973; Sprague, Levy, DiBernardino and Berlucchi, in press), rhesus monkeys (Pasik and Pasik, 1971), and tupaia (Killackey and Diamond, 1971; Ware, Diamond and Casagrande, 1974) that the classical projection to the striate cortex is not necessarily of pivotal importance for the cortical processing of visuospatial information? The anatomical problems were pursued through examinations of the projections of NLP and LGNd with the methods of autoradiography (Cowan, Gottlieb, Hendrickson, Price and Woolsey, 1972) and of retrograde transport of horseradish peroxidase (LeVail and LeVail, 1972). Concurrent neurobehavioral experiments assessed the discriminative behaviors of rats prepared with striate cortical ablations, bilateral electrolytic lesions of NLP, and combined ablations of areas 17 and NLP.

The anatomical results indicated that NLP provides afferents to an extensive peristriate cortical region and to a circumscribed zone in the temporal area just dorsal to the rhinal sulcus. Examination of the projections of the LGNd revealed, in addition to the well-known striate connections, extensive extra-striate projections which partially overlap the cortical field of NLP. These results provided

a framework for the interpretation of the neurobehavioral findings. The latter observations showed that the striate cortex of the rat is not essential for performances of visual-pattern tests, established a functional interaction between the two thalamo-cortical networks, and indicated that the NLP system is importantly involved in subserving the visual abilities of the hooded rat.

MATERIALS AND METHODS

Figure 1 presents the cytoarchitectural areas of the posterior neocortex of the rat as they were defined by Kriég (1946a,b). The cortical zones which are relevant to the present results are indicated by the hatched areas.

Sixty-six adult, male, Long-Evans hooded rats (300-450 gms) served as subjects. They were housed individually and provided with a diet of rat chow and water ad libitum. The surgical procedures were carried out while the animals were under anesthesia induced by intraperitoneal injection of sodium pentobarbital (60mg/kg).

Autoradiography Procedure

Hydraulic injections of 3H-leucine were made in NLP and LGNd following stereotaxic placement of a 36g Hamilton 5 μ l syringe. The 3H-leucine (New England Nuclear) was in aqueous (normal saline) solution concentrated to an activity of 10-20 μ Ci/.1 μ l. In most cases, .1-.3 μ l of this solution was injected at a rate of approximately .1 μ l/45 min. One week subsequent to the intracranial injections, the subjects were administered an overdose of sodium pentobarbital and were then perfused intracardially with normal saline followed by 10% formol saline. After post-fixing in the perfusate for at least 48 hrs., the brains were frozen and sectioned at 34 μ . Alternate sections through the dorsal thalamus and posterior cerebral cortex were

mounted in gelatin onto clean slides, and were then dried and dipped in Kodak NTB2 photographic emulsion (diluted 3:2). The prepared slides were placed in light-tight boxes and exposed for 4-5 weeks at 4°C. They were then developed and counterstained lightly with cresyl violet. The autoradiographs were examined by light and dark-field microscopy.

Horseradish Peroxidase Procedure

Retrograde labelling of thalamic projection neurons was accomplished through the use of the horseradish peroxidase (HRP) technique. Restricted cortical placements of 30-50% HRP in aqueous solution (normal saline) were administered hydraulically via a 36g Hamilton 5µl syringe into areas 18, 17 and 18A (see Fig. 1). The volumes of the placements varied from .1-.3µl and were injected at rates of .1-.2µl/40 min. The subjects were sacrificed with an overdose of sodium pentobarbital 24-36 hours after the completion of the injection. At that time intracardial perfusion of 0.5% procaine and saline was followed by fixation with a modified E.M. fixative (1.25% glutaraldehyde, 1% paraformaldehyde, 1% sucrose in phosphate buffer). The brains were left to postfix for 24 hours at 4°C and then were placed in a 30% sucrose in phosphate buffer solution for 24-36 hours. Frozen sections of 40µ were incubated in Tris buffer (pH 7.6) at 4°C and were then transferred to a solution of diaminobenzidine (DAB) and Tris buffer (60mg DAB/200ml Tris). After warming the solution to 37°C, the HRP-DAB reaction was catalyzed by addition of 8% H₂O₂

(15ml/400ml DAB/Tris solution). The reacted tissue was placed on chrome-alum-coated slides and lightly counterstained with cresyl violet. The HRP-labelled material was examined by dark- and light-field microscopy.

Retrograde Thalamic Degeneration

The thalamic afferents to the striate cortex (area 17) were also examined by determining the amount and locus of retrograde degeneration subsequent to circumscribed removal of area 17 (see Fig. 1). These de-striate preparations also participated in behavioral experiments designed to assess their residual capacities for brightness and pattern perception. The position and extent of the cortical lesions was determined through measurements taken relative to the intersection of the transverse and sagittal bone sutures (lambda). The coordinates (relative to lambda) were: AP; -0.6mm to $+2.4\text{mm}$; ML; 2.0mm to 5.0mm at the anterior edge, and 2.5mm to 5.5mm at the posterior edge. The bone overlying this cortical area was removed and the exposed tissue was aspirated with a fine glass pipette.

On the 28th to 32nd post-operative day, subjects were given an overdose of Sodium Pentobarbital and perfused intracardially with normal saline followed by formalin. The brains were removed and allowed to post-fix in the perfusate for at least 2 days. Prior to sectioning, the extents of the cortical lesions were measured and transferred to standardized diagrams of the dorsal aspect of the neocortical surface.

Frozen sections were cut at 30 μ . Every third section through the posterior thalamus and every 10th through the cortical lesions were stained with cresyl violet and examined microscopically for the presence of healthy neurons. Occasional cases were counter-stained with Luxol blue (Kluver-Barrera method) to facilitate identification of area 17 and the fiber systems within the thalamus.

Behavioral Methodology

Apparatus. The visual discrimination apparatus was a modification of that used by Thompson and Bryant (1955). Briefly, it consisted of a start box and an alley (45cm long) at the end of which were placed two stimulus panels, 8.5cm apart and separated by a partition that extended 7.5cm into the alley. The panels were placed in apertures that each led into the goal box. Subjects were trained to leave the start box, run down the alley and gain access to the goal box by pushing the correct stimulus door backward and entering the goal box. The rats were motivated with mild electrical shocks which were applied through a grid floor that extended from the start box to the goal box entrance.

The stimulus panels were 9 X 9cm, and subtended 53° of visual angle at the end of the partition (choice point for most subjects). The stimuli were illuminated by light reflected from a fluorescent lamp which was placed directly above the two stimulus panels. The luminances of the white and black stimuli used in the flux discrimination was 3.0 and 0.1 millilamberts respectively. The position of the correct (white) stimulus was varied quasi-randomly according to a

Gellermann series (1933), with the principal constraint being that the correct stimulus never appeared on the same side on more than 3 consecutive trials.

The pattern stimuli consisted of two identical panels of alternating white and black stripes (2.5cm/cycle) oriented 45° from horizontal. The luminance of the white stripes was the same as that for the white panel, and the same was true for the black stripes and black panel as all of the stimulus panels were made of the same plexiglass material. The correct stimulus in the pattern problems was that stripe orientation that was 45° to the left of vertical. The stimuli were designed so that rotation of 90° would reverse their orientation while 180° rotation would preserve the orientation but shift the phase of the grating 180° .

Training Procedure. The training procedure was similar to that which was previously employed in a long series of visual-discrimination studies in our laboratory (Meyer and Meyer, in press).

The principal difference from the standard method was that the pretraining stimuli were black, slotted panels such that the animals could readily see the interior of the goal compartment. This method was adopted because, in the usual pretraining procedures for experiments concerned with retentions of the black-white habit in the program of The Ohio State University, oblique-striped panels have been used for the pretraining stimuli. Since our principal interest was in learning of visual-pattern habits, the use of such cues was obviously precluded as a part of the pretraining procedure. The result was enhancement of the rate of preoperative learning of the black-white

habit, with the final criterion of performance being reached in approximately 9 fewer trials than is typically observed when the conventional methods are followed.

The experiment was carried out as follows: days 1-5, subjects were handled by experimenter 5 minutes daily; day 6, subjects were adapted to apparatus by being allowed free access to all of the compartments without being shocked; day 7, subjects were pre-trained to exit the start box, run down the alley and enter the goal box through identical neutral panels placed in the goal box entrances; days 8-9, subjects were trained on the black-white discrimination; day 10, subjects were assigned to groups based on matching their flux discrimination learning scores and given appropriate surgical treatments; days 11-21, post-operative recovery; day 22, subjects were retrained to criterion on the black-white discrimination; days 23-35, subjects were trained for initial acquisition of the pattern discrimination. The required performance criterion was 9/10 correct responses in all cases. Training on pattern discrimination was terminated if the subject failed to reach the 9/10 criterion after 12 training days (300 trials). The possible mediation of the habits by non-visual (i.e., olfactory) cues was minimized by periodic washing of the stimuli and alley with a dilute vinegar solution.

Surgical and Histological Procedures

Following attainment of criterion on original learning of the flux discrimination, the animals were assigned to one of the following groups on the basis of their learning scores: (1) a group in which

both the striate cortex (area 17) and N. Lateralis posterior was ablated; (2) a de-striate group; (3) a group in which NLP was destroyed and (4) an unoperated control group.

Thalamic lesions were accomplished through stereotaxic (AP +2.2, +3.0; Dv +1.0, +1.0; ML +2.5, 2.7) placement of a 0 insect pin whose tip had been filed flat to a circular diameter of approximately .25mm and which was insulated except for the cross-sectional area of the tip. Tissue destruction was affected by passage of an anodal DC current (.6mamp) for 4 seconds at each electrode placement. All of the cortical ablations were performed according to the procedure outlined in the section describing the anatomical methods.

Following completion of the surgeries, the animals were given intramuscular injections of a broad-band antibiotic and returned to their home cages for an 11-day post-operative convalescence. The histological examinations of the preparations which were studied with neurobehavioral techniques proceeded as outlined in the methodology for anatomical studies of de-striate subjects.

RESULTS

Anatomical Results

Projections of Nucleus Lateralis Posterior. The projections of NLP were examined autoradiographically in 2 cases, and by retrograde transport of HRP in four cases. Figure 2 shows the cortical projections of NLP demonstrated autoradiographically. The injection site in case LP2 (Fig. 2A, Sections A-C) included virtually the entire rostro-caudal extent of the nucleus. Rostrally, the labelled region extended into the caudal pole of N. Lateralis thalami. Medially, there was involvement of the lateral half of the anterior portion of N. Pretectalis, while light label extended laterally to the extreme medial portion of the LGNd. The hippocampus overlying the NLP was also very slightly involved.

The post-injection survival time of case LP2 was 1 week, and as Figure 2 A-D shows, the axons of projection cells were heavily labelled. These axons were observed to course rostrally through the nucleus and then to coalesce into a dense fascicle that exits from the thalamus via the superior thalamic radiation (Fig. 2A, Section A). At the level of its thalamic exit, the fiber bundle bifurcates within the medullary substance of the cortex. The majority of the labelled axons course dorsally and posteriorly, while the smaller inferior limb of the projection bends ventrally and terminates in a

circumscribed area immediately dorsal to the rhinal sulcus (Fig. 2A, Section A). This temporal field lies within the boundaries of area 20 as defined by Krieg (1946a,b). The superior limb, or dorsal division of the NLP projection continues within and immediately superficial to the medullary substance to terminate in areas 7, 18A, and 18 (Fig. 2 A-E).

A close examination of case LP 1 revealed a prominent laminar organization of the fiber terminations arising from NLP (Fig. 3). The pattern appears to be the same in all of the NLP-recipient zones. The heaviest thalamic input terminates in layer 4 and the deeper portion of layer 3. In addition, there is a smaller input to layer 1, and the grain density in layer 6 is above the background levels. However, much of the labelling in layer 6 can be attributed to axons of passage (Peters and Saldanha, 1976).

The organization of the NLP projection was also examined through retrograde labelling of thalamic neurons following injection of HRP into areas 17, 18, and 18A. Frequently, labelled axons were seen emanating from these cortical injection sites. Occasionally, heavily-labelled thalamic areas had a brownish hue when observed in bright-field. This probably was due to the anterograde transport of HRP by corticofugal axons.

Injections of HRP into area 18 resulted in labelling of cells in NLP, N. lateralis thalami (NLT), and the anterior dorsal (NAD), anterior medial (NAMT), and anterior ventral thalamic nuclei (NAVT). Retrograde incorporation of HRP in the latter cell groups is most likely attributable to ventral extension of the injection site into

the retrosplenial cingulate cortex (Domesick, 1972). The labelled neurons in NLP were confined to the anterior part of the nucleus (Fig. 4, Section E-F) and were generally less densely stained than the more rostrally situated cell groups.

Placement of HRP into area 17 revealed a very sparse projection from NLT and NLP to the striate cortex (Fig. 4A, B). Typically, the reaction product in these cells was very light, with several densely labelled neurons in each coronal section (Fig. 5B). Retrograde cell labelling was observed throughout the rostro-caudal extent of NLP and tended to be found in the more centrally located portions of the nucleus (Fig. 5A). While there was some indication that the medial portion of area 18A was involved in the injection site, the pattern of thalamic labelling in case HRP 5 was obviously different than in case HRP 2 (Fig. 6A). This suggests that the enzyme in area 18A was not sufficiently dense to result in retrograde uptake by thalamic cells projecting to area 18.

The projection of NLP to the lateral portion of area 18A is represented diagrammatically in Fig. 6A. As the figure indicates, a group of cells containing the reaction product extended laterally from the central portions of NLP through the ventromedial aspect of the LGNd and extended into a lamina subjacent to the optic tract along the dorsolateral aspect of the LGNd. In general, the cells within NLP were more densely labelled than cells in the LGNd (Figs. 6, B and C).

The arrangement of cells containing the reaction product following HRP placements in areas 18 and 18A suggests a regional

distribution of afferent neurons to these cortical areas. The more rostral parts of NLP project to 18 and a column of cells extending throughout the rostro-caudal axis of the nucleus and comprising its lateral aspect projects to area 18A (Figs. 4 and 6). Despite the relatively large injection site in case HRP 2, this case indicates that the thalamo-cortical organization of area 18A is characterized by a dramatic convergence of input from the LGNd and NLP.

Some Observations on the Projections of the Lateral Geniculate

Nucleus, pars dorsalis. The retrograde cell degeneration in the thalamus of de-striate rats is typified in Figure 7. Normal-appearing nerve cells were observed in the LGNd along the medial wall and in a dorsolateral lamina subjacent to the optic tract. Figure 7D shows that the transition between the degenerated portions of the nucleus and the lateral lamina is fairly abrupt. Examination of the surface diagrams indicated that there was little variability in the size of the lesions, an observation that probably accounts for the finding that the actual size of the ablation contributed little to the severity of retrograde thalamic cell changes (Fig. 9). Since the dorsolateral portion of the LGNd seemed so resistant to cell loss following striatotomy, a search for extra-striate geniculate projections was made using autoradiography and retrograde transport of HRP. The cortical distributions of silver grains were examined following injections of ³H-leucine into the LGNd. In three cases, these injections did not involve NLP. The results for case LGN 2 are presented in Figure 8. The injection site of case LGN 2 is clearly confined to the dorsal division of the lateral geniculate. It extends through the

middle 1/3 of the nucleus in the A-P plane and throughout this extent includes the dorso-lateral aspect that is unaffected by restricted striate removal (Fig. 7). The post-injection survival time was 1 week, and the axons of geniculate neurons are clearly labelled. These axons pass rostrally through the nucleus and leave the thalamus near the rostral pole of LGNd, via the superior thalamic radiation (Fig. 8). Following a trajectory similar to the NLP projection, these axons course through the superficial subcortical white matter to terminate within two spatially distinct cortical target areas. The major geniculate projection is confined to area 17 in all but its most posterior extent, where the label extends into the extreme medial portion of area 18A of Krieg (Fig. 8, C and D). Examination of Nissl stained material indicates this area has a fairly well-developed granular layer, which has lead Ribak and Peters (1975) and Montero, Bravo and Fernandez (1973) to consider it the caudal extension of area 17. In addition to these striate connections, the LGNd provides afferents to a portion of the lateral aspect of area 18A (Fig. 8, B and C).

The cortical afferents from LGNd have a laminar organization. The principal geniculo-cortical input is clearly confined to layers 4 and the deeper parts of 3, but light grain deposits in layers 1 and 6 also indicate a geniculate input, at least in those cortical regions in which layer 4 was most heavily labelled (Fig. 2D).

Injection of HRP into area 18A resulted in extensive retrograde cell labelling within LGNd (Fig. 6). The ventromedial and dorso-lateral aspect of the nucleus contained labelled neurons in all but

its most rostral portions (Fig. 6, B-F). There is also a suggestion of a laminar pattern of the lateral geniculate cells that project to area 18A. Comparison of Figure 6A, Figure 7, and Figure 9 indicates the close correspondence between the locations of neurons with extrastriate projections and the area that fails to show retrograde cell loss following a striate cortical ablation.

In case HRP 5 (Fig. 5A), the label was injected into area 17. As the figure shows in Sections A-E, a column of cells extending throughout the rostro-caudal axis of the geniculate projects to a single region within area 17. Rostrally, the labelled cells assume a ventromedial location, and the position of the labelled group migrates dorsally and laterally in the more posterior portions of the nucleus. The more-densely-labelled geniculate neurons were generally observed in the center of the column, with the more peripheral cells containing progressively smaller amounts of the reaction product (Fig. 5C).

Finally, no subcortical efferents of either NLP or LGNd were observed despite an extensive search, which focused especially on the di-mesencephalic juncture and the tectum.

Behavioral Results

Histological Reconstructions. Figure 9 presents the most and least accurate surgical outcomes for each of the three operated groups. The figure presents closely matched sections through three coronal planes (anterior, middle, and posterior) which were selected to illustrate the histological status of both the LGNd and the NLP. Analysis of the retrograde cell loss resulting from striate ablations has already been

described. Figure 9 reiterates the finding that, subsequent to circumscribed removal of area 17, neurons are consistently found along the medial and especially the dorsolateral aspects of the LGNd. Importantly, these areas correspond to those portions of the LGNd which were identified as having extra-striate projection fields, which suggests that the extra-striate connections are at least sustaining projections (Rose and Woolsey, 1959). According to electrophysiological studies by Montero, Brugge and Beitel (1968), these unaffected portions of the LGNd represent superior portions of the visual field, where the temporal field is represented laterally and the nasal field more medially. Virtually no detectable degeneration was noted in the NLP of any of the striate lesioned animals.

In subjects with lesions of NLP, damage to the overlying optic tract was also commonly observed (Figs. 9 and 10B). Encroachment of the gliotic scar in N. pretectalis (4 cases), the posterior thalamic nucleus (2 cases) or the ventral thalamic nucleus (1 case) was less frequently observed. In no case was significant damage to the LGNd observed, but minimal involvement of its medial aspect was noted in 2 cases. A photomicrograph of a typical thalamic lesion is provided in Figure 10B.

The histological reconstructions for subjects with combined ablations of area 17 and NLP were similar to those for subjects with striate or NLP ablations alone. Thus, the areas that failed to show retrograde changes in the de-striate preparations remained intact in the 17 + NLP preparations. The presence of normal cells along the medial wall of the LGNd in many cases suggested that the electrolytic

lesions did not contribute to the gliosis noted in the geniculate. As in Group NLP, occasional involvement of N. pretectalis (4 cases), the posterior thalamic nucleus (1 case) and the ventral thalamic nucleus (2 cases) was observed in addition to the frequent inclusion of the optic tract overlying NLP. Figure 10A shows the appearance of the thalamus in a typical case taken from Group 17 + NLP.

Eight subjects were excluded from consideration because their thalamic lesions proved to be inaccurately placed. Three of these rats were from Group NLP and five were from Group 17 + NLP. Also, three subjects were prepared with cortical ablations that were significantly larger than those for the acceptable de-striate preparations because we were interested in ascertaining whether the LGNd would completely degenerate if portions of areas 18 and 18A were included in the extirpation. Interestingly, the retrograde pictures for the latter animals were similar to those for the de-striate preparations, but they nonetheless failed to learn the pattern problem within the maximum of 300 trials. The inclusions and exclusions of subjects were made on the basis of the histological findings, and of course without reference to the outcomes from the neurobehavioral tests. There were ten animals in Group 17, nine in Group NLP, eleven in Group 17 + NLP, and ten in the unoperated Control Group.

Comparison of planimetric measurements of the cross-sectional areas of the thalamic lesions in Group NLP and Group 17 + NLP indicated that there were no systematic differences in the size of the NLP lesions in these two groups ($t = .60$, $df = 18$). Similar measurements of the cortical lesions confirmed the comparability of the

striate ablations in Group 17 and Group 17 + NLP ($t = 1.16$, $df = 19$).

Visual Performances. The behavioral results were assessed through the analysis of variance on trials to criterion. Individual between-group differences were assessed via the t -test, and with Dunnett's t when non-orthogonal comparisons required adjustments in the degrees of freedom (Winer, 1962; p. 89).

Preoperatively, the animals required an average of 16.20 trials to reach criterion on the black-white discrimination. Comparison between the subjects grouped according to their eventual treatment assignments indicated that there were no differences between the groups in terms of their original learning scores on the brightness habit ($F = .99$; $df = 3.36$).

All of the animals exhibited excellent post-operative retention of the black-white problem (Fig. 11). Despite these high performance levels, the analysis of variance revealed that there were reliable between-group differences in the numbers of trials required to regain criterion performance on the flux discrimination ($F = 7.17$, $df = 3,36$, $\alpha < .01$). Post-hoc comparisons revealed that the difference can be attributed to the poorer performance of Group 17 + NLP when compared to any of the other groups ($t = 2.25$, $df = 19$, $\alpha < .05$).

The numbers of trials to criterion on the pattern problem served to differentiate the treatment groups in a much more dramatic fashion. The mean numbers of trials required for attainment of 9/10 correct responses, along with their associated standard errors of the means (SEM), were as follows: Control, $\bar{X} = 28.3 \pm 3.61$; Group NLP; $\bar{X} = 33.56 \pm 4.72$; Group 17, $\bar{X} = 75.20, \pm 10.98$, Group 17 + NLP; $\bar{X} = 146.36$,

± 20.72 . The analysis of variance confirmed the reliability of these differences ($F = 18.35$, $df = 3,36$, $\alpha < .01$).

Figure 12 presents the mean numbers of trials required by each group to reach each of the successive criteria. The acquisition functions of the groups began to diverge at the 7/10 criterion, as reflected in the greater numbers of trials taken by Groups 17 and 17 + NLP to attain this modest degree of discriminative behavior. The difference between the groups increased as more stringent criteria of performance were reached. Post-hoc analyses of trials to the terminal 9/10 criterion indicated that while Group NLP was not impaired when compared to the normal animals ($t = .90$, $df = 17.00$), de-striate rats were significantly impaired relative to normal subjects (Dunnett's $t = 2.49$, $\alpha < .025$) and to NLP preparations (Dunnett's $t = 2.26$, $\alpha < .05$).

Importantly, however, Group 17 + NLP were much more severely impaired than the de-striate subjects ($t = 2.94$, $df = 19$, $\alpha < .01$). This result shows that although NLP lesions have virtually inconsequential effects upon visual-pattern learning when the striate cortex is intact, they markedly potentiate the deficit produced by a striate cortical ablation. Thus, lesions of NLP have different consequences when they occur in isolation as opposed to when they are combined with striate cortical damage.

DISCUSSION

Anatomical Results

The results of these experiments show that the organization of the rat's visual system is characterized by parallel thalamic projections which each provide afferents to several different cortical fields. NLP projects to a neocortical expanse that includes area 18A and at least some portions of areas 18, 7, and 20. It also may have an extremely sparse connection with the striate cortex (area 17). The LGNd, in addition to its well-established linkage to area 17, also projects to area 18A and to the cortex caudal and medial to Krieg's area 17. Examination of cases in which 3H-leucine was placed in LGNd, or HRP was injected into area 18 did not reveal comparable geniculate projections to area 18, but perhaps further studies will show that such projections exist.

Although extra-striate geniculate projections have been described in the cat (Minkowski, 1914; Wilson and Cragg, 1967; Niimi and Sprague, 1970; Burrows and Hayhow, 1971; Rosenquist et al., 1974; Maciewicz, 1975) and in the squirrel monkey (Wong-Riley, 1976), the present results are the first demonstration of analogous connections in the rat. Ribak and Peters (1975) described the projections of the LGNd in the albino rat as being largely confined to area 17. The

absence of a geniculate projection to the lateral field in area 18A of albinos is in contrast to the present results, and must tentatively be attributed to differences between the strains. Such a suggestion is not unreasonable in light of the fact that differences between the organization of the retino-fugal projections in these strains have already been described (Lund, 1965; Giolli and Creel, 1974; Lund, Lund and Wise, 1974; Hickey and Spear, 1976).

The fact that there is presently a lack of consensus with respect to the posteromedial extent of area 17 makes interpretations of the nature of the geniculate projection to this area necessarily equivocal. Krieg (1946a,b) described the peristriate cortex as completely surrounding area 17 in all but its anterior aspect. The electrophysiological results of Adams and Forrester (1968) seemed to be consistent with Krieg's definition of the field. Also, the evoked-potential map of Montero (1973) permitted a similar conclusion. However, the unit map of V-I of Montero, Rojas and Torrealba (1973) extends to the posterior margin of the cerebral hemisphere, and Ribak and Peters (1975) have argued on cytoarchitectural grounds that the posteromedial cortex should be included in area 17. Ribak and Peters have also described a geniculo-cortical projection to the subzone in question, and the present results are completely consistent with their observations on this point. Therefore, regardless of whether the posteromedial cortex is a part of 17 or, instead, is a part of 18A, it is clear that this region is heavily supplied with a projection from the LGNd.

Placement of HRP into area 17 illustrates the nature of the highly topographic geniculostriate projection. Our results with this procedure, in confirmation of the classical retrograde degeneration findings of Lashley (1934), show that a column of cells which projects to the same area within the striate cortex runs throughout the rostrocaudal axis of the nucleus. The oblique orientation of this column is consistent with the lines of projection first discovered in the cat by Bishop, Kozak, Levick and Vakkur (1962) and subsequently described in the rat by Montero, Brugge and Beitel (1963). These lines of projection represent the projection of retinal points onto the LGNd, and may be mediated by the longitudinal retinofugal fiber system (Montero and Guillery, 1968).

Some Comments on the Organization of the Lateral Geniculate Nucleus in the Rat.

The projections of the feline geniculate have been investigated by a number of workers (e.g., Wilson and Cragg, 1967; Niimi and Sprague, 1970; Rosenquist, Palmer and Edwards, 1974; Maclewicz, 1975). The results of these and other investigations have indicated that, in the cat, the LGNd is so intricately organized in terms of its afferent and efferent connections that it is more properly regarded as a nuclear complex than as a unitary structure. The present findings with regard to the geniculocortical system of the rat suggest that this complex organization is not specific to the cat. Thus the rat's LGNd has been shown to project beyond the boundaries of area 17, and the extra-striate cortical projections seem to be regionally specific.

There is no indication of heterogeneity in Nissl-stained sections of the rats' LGNd, but it has been observed and described by Cunningham and Lund (1971) on the basis of the regional distribution of neurofibrillary and Fink-Heimer degeneration following enucleation. The degeneration patterns form at least three definable laminae. The most dorsal of these laminae corresponds closely to the dorsolateral lamina that projects to area 18A. Interestingly, this area is also the only sector of the LGNd that contains synaptic glomeruli (Cunningham and Lund, 1971) similar to those found in lamina A in the cat (Guillery, 1969). Golgi studies on the rat LGNd (Kriebel, 1975) have shown that a distinct morphological cell type is found only in this area (Kriebel's type 2). These neurons, according to Kriebel, resemble cells found in Golgi preparations of laminae A and A1 in the cat. Both laminae A and A1 in the cat and the lateral crescent of the rat project to the peristriate cortex (Rosenquist et al., 1974; the present paper). Thus the results of this and other studies using rats, when compared with the available data for the cat, suggest that there are parallels between the organization of the rat and cat lateral geniculate nucleus in terms of lamination, cell morphology, synaptic organization, and cortical connections.

Neurobehavioral Results

Postoperative Retention of Flux Discrimination. It has long been recognized that animals with radical ablations of the posterior isocortex suffer from deficits in the retention of pre-operatively learned flux discriminations (Lashley, 1935; Horel, Bettinger, Royce

and Meyer, 1966; see Meyer and Meyer, in press, for review). The expected mean numbers of trials required by these preparations to regain pre-operative performance levels is 23 ± 3 when trained in accordance with the procedures used in this investigation (Glendenning, 1972). The excellent retention of pre-operatively learned black-white discrimination habits by the de-striate rats in the present study shows that these impairments of retention are not specifically related to the removal of area 17 in the radical preparations. Indeed, the group-mean postoperative performance of de-striate preparations is only two trials more than that of normal control animals.

Although the experiments described above were carried out with subjects whose lesions typically included areas 17, 18A, 18, 7 and 20 as defined by Krieg, results from other recent studies suggest that lesions of the striate and peristriate cortex are probably sufficient for production of complete impairments of retention of the black-white habit. An example is provided by the work of Scheff and his associates (Scheff and Wright, in press; Scheff, Wright, Morgan and Bowers, in press). The experiments concerned the effects of interoperative practice with this task upon ultimate retention of the black-white habit following the second of two unilateral posterior cortical ablations. That is, Scheff et al. were examining the bases of Thompson's (1960) observation that protection of retention is produced by and is also explicitly a function of interoperative training.

After having replicated Thompson's findings with animals prepared with posterior lesions which were largely confined to the striate-peristriate cortex, Scheff and his colleagues studied the

effects of third-stage ablations of the cortex immediately anterior to the striate-peristriate region. When they retrained the subjects for a third time, they found that retention of the habit was impaired, although the habit had been partially retained following the second unilateral ablation provided that the animals had previously been given interoperative training on the habit. They also showed that comparable, but far-anterior third-stage ablations do not produce impairments of retention. In addition, they showed that interoperative training alters the visually-evoked responses which can be recorded from the cortical subregions whose third-stage removals are followed by ultimate impairments of retention of the habit.

These important findings have suggested the induction of visual functions by a combination of cortical ablations and postoperative training in systems which do not ordinarily perform visual functions. Notably, however, the regions which Scheff et al. describe as the contiguous-to-visual cortex includes area 7 as defined by Krieg. Our own findings show that NLP, in addition to projecting to the extra-striate cortex and to Krieg's area 20, also projects to area 7. Further, our results for retention of the black-white habit by subjects prepared with ablations of area 17 and NLP suggest that damage to the NLP projections result in a modest potentiation of the trivial impairments which are seen in de-striate subjects. Hence it is possible to entertain the view that the Scheff et al. findings were results of enhancements, via training, of the functions of one of the forebrain's intrinsically-visual mechanisms, and not of vicarious reorganization of the functions of extra-visual systems.

Postoperative Learning of Visual Pattern Discriminations. Radical bilateral posterior ablations permanently suppress performance of visual-pattern problems of the kind employed in this investigation (Horel et al., 1966). Importantly, the problem was insoluble in terms of over-all differences in flux, over-all differences in contour, local differences in flux, local differences in contour, or differences in quantities of retinal signals which might arise from horizontal scannings of the stripes on the panels. These specifications are significant because rats prepared with lesions of the striate and the extra-striate cortex (areas 17, 18 and 18A of Krieg) can eventually master problems if the stimuli are different with respect to contour (Mize, Wetzel and Thompson, 1971; Weiskrantz, 1974) or problems which present arrays of vertical and horizontal stripes (Cowey and Weiskrantz, 1971; Spear and Barbas, 1975).

The results of the present pattern-learning study have shown that bilateral ablations of area 17 have only a relatively modest effect upon the rate of postoperative acquisition of the oblique-stripes discrimination habit. These findings are consistent with a number of recent observations concerning the visuospatial capacities of other mammalian species following removal of the striate cortex. Thus, cats (Levy, DiBerardino and Conomy, 1973; Sprague, Levy, DiBerardino and Berlucchi, in press; Berkley, Sprague and Bloom, 1976), tupaia (Killackey and Diamond, 1971; Ware, Diamond and Casagrande, 1974), rabbits (Murphy and Stewart, 1974), and rhesus monkeys (Pasik and Pasik, 1971) have all been reported to be capable of mastering visual-pattern problems after having been prepared with

ablations of the striate cortex.

One of the best-remembered statements of Lashley (1939) was his claim that approximately 700 cells of the LGNd are sufficient to permit visual-pattern learning by rats with near-total ablations of the striate region. This statement has come to be regarded as a truth, as it must be if the striate cortex is in fact of pivotal importance in perceptions of visuospatial patterns. However, although it has become the custom to describe preparations with lesions which extend far beyond the boundaries of the striate cortex as animals with striate lesions, the bulk of the available evidence suggests that striate-extra-striate lesions do not produce impairments of visual-pattern learning simply because they guarantee complete destruction of the striate cortex. Hence, the traditional concept that total degeneration of the LGNd is an appropriate criterion of completeness of striate ablations needs to be abandoned, as is clear from our results and from the anatomical findings of Doty (1971) and Niimi and Sprague (1970) with respect to de-striate cats.

Comparisons between the learning scores for the four experimental groups this experiment shows that striate and extra-striate mechanisms interact in mediating learned visual functions in rats. This conclusion rests on our demonstration that although NLP ablations by themselves produce no discernable effects upon retention of brightness habits or upon acquisition of visual-pattern habits, identical lesions in combination with striate cortical damage results in behavioral impairments that exceed the expected consequences of the cortical lesions alone.

A likely explanation of the dynamics underlying this observation derives from the nature of the two major afferent channels to peristriate visual cortex in the rat. The geniculostriate extra-striate channel involves the projection of the LGNd to the striate cortex (Lashley, 1941; Ribak and Peters, 1975) and the efferent connections of area 17 to 18 and 18A (Nauta and Bucher, 1954; Montero et al., 1973). An alternate source of afferent information to areas 18 and 18A lies in the cortical projections of N. lateralis posterior. Thus, the connectivity of this system, when examined in conjunction with the present behavioral findings, leads to the suggestion that under circumstances in which one of these parallel-conducting thalamocortical systems is damaged, visual information can still be transmitted through the remaining, intact portion of the ascending pathways to extra-striate cortex. An implication of this suggestion is that the presence of the geniculostriate system masks the effect of damage to the NLP projection more completely than does the NLP projection compensate for striate cortical damage. The emphasis, however, should be placed on the establishment of extra-geniculostriate mechanisms having an important role of any kind, and in attempts to establish what that role might be.

ILLUSTRATIONS

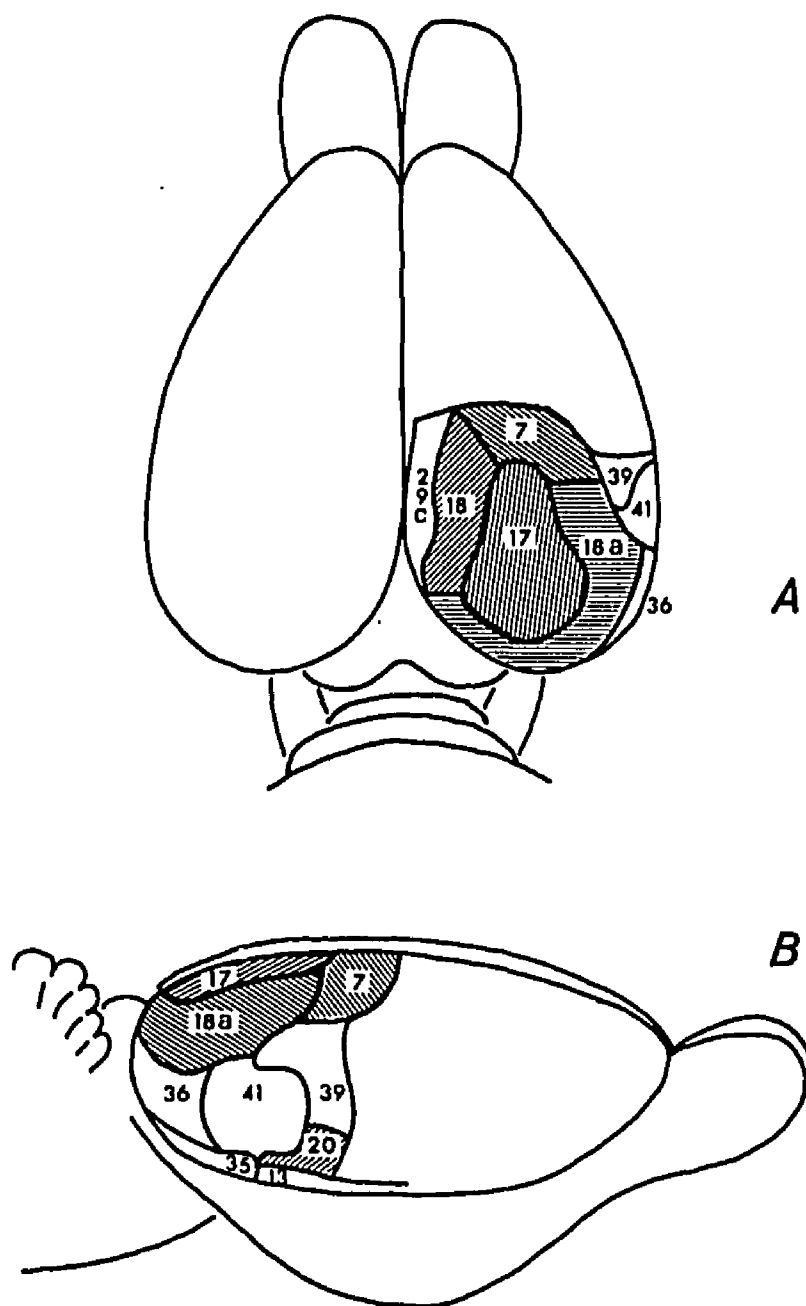


Figure 1. Cytoarchitectural fields of the posterior cortex in the rat. (Adapted from Krieg, 1946).

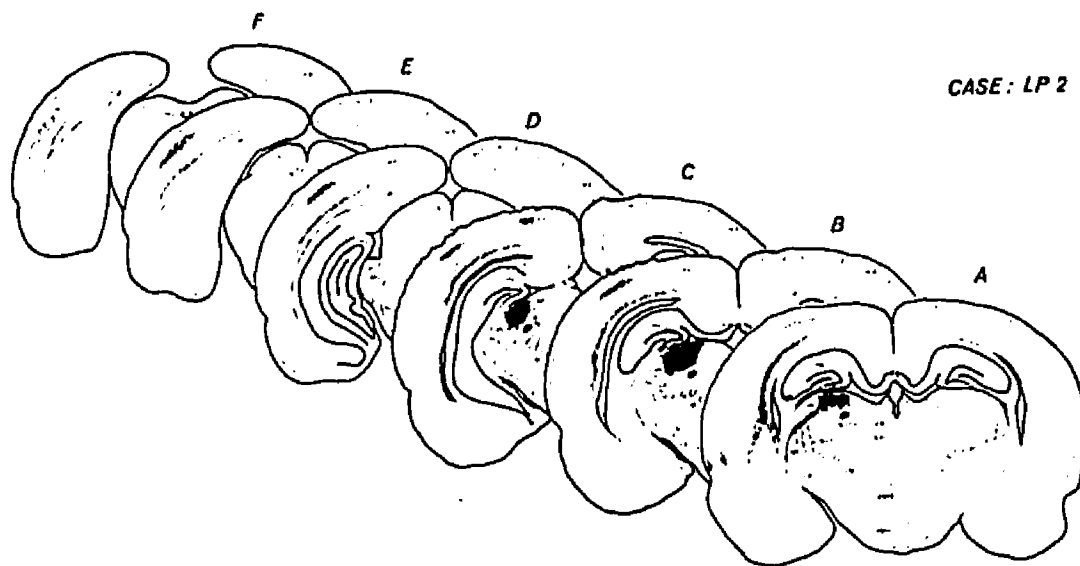


Figure 2. Autoradiographic demonstration of the projections of Nucleus lateralis posterior. The location of the injection site is indicated by the dark arrows in sections A, B and C.

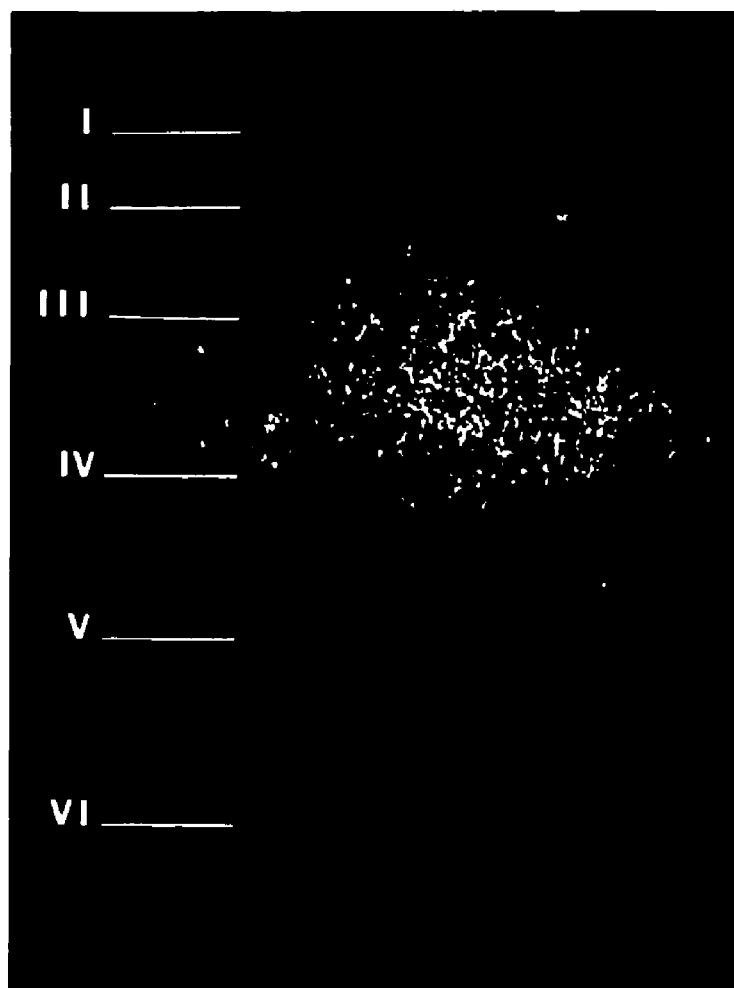
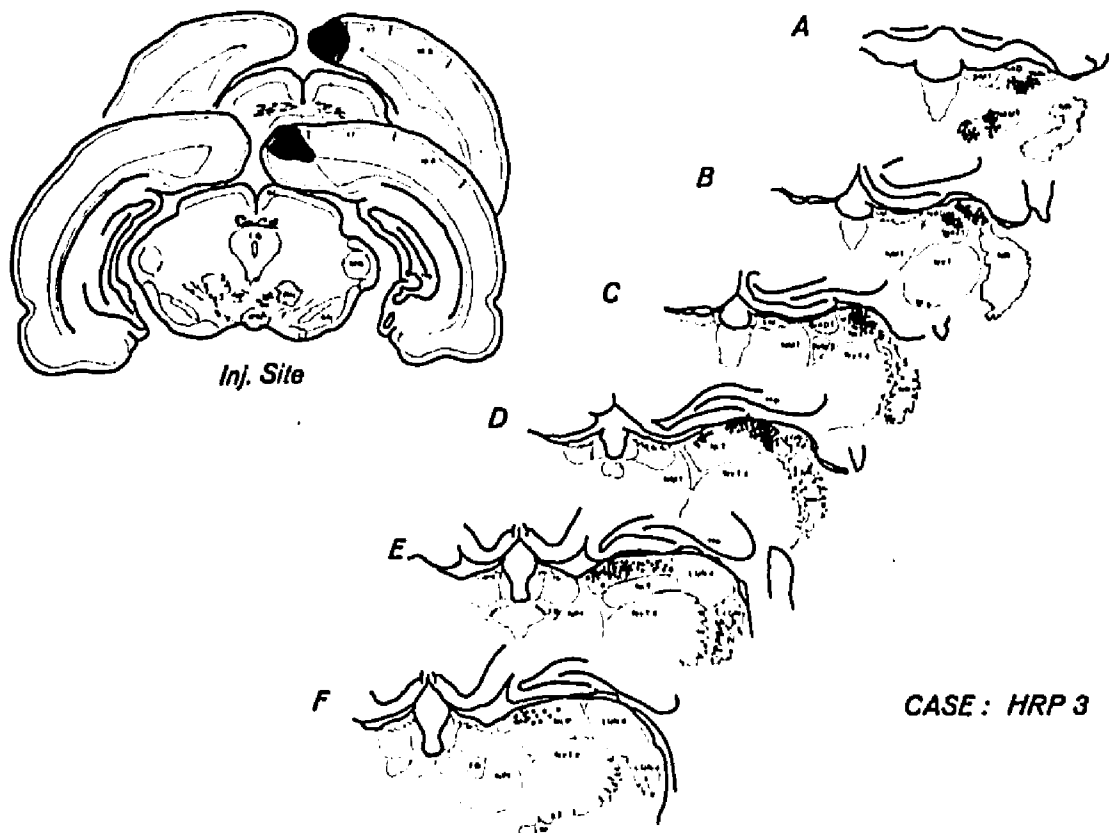
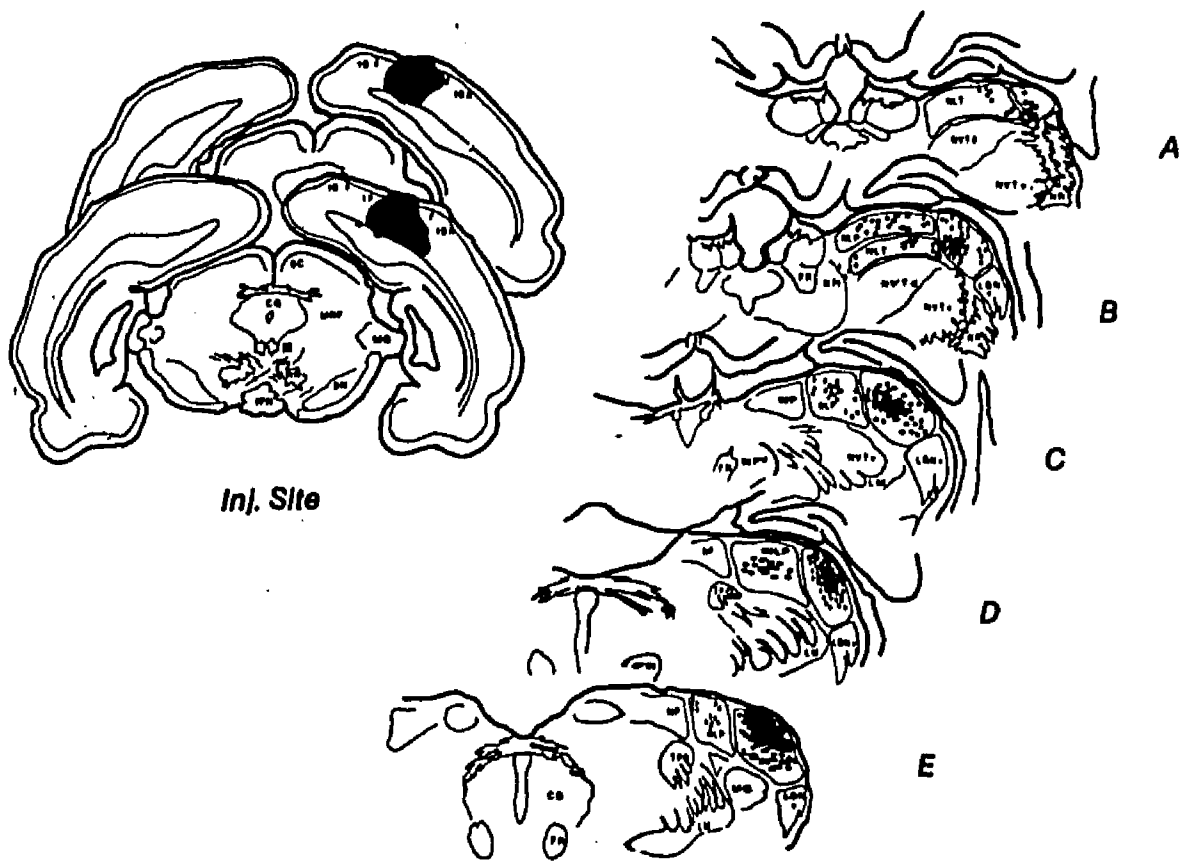


Figure 3. Laminar distribution of silver grains in area 18A following injections of ^3H -leucine into NLP. Cortical laminae are indicated at left. Dark field illumination taken from case NLP 1.



CASE: HRP 3

Figure 4. Drawings of thalamic sections selected to illustrate retrograde cell labelling resulting from injection of horseradish peroxidase into area 18. Light labelling is indicated by open circles, heavily labelled neurons are indicated by filled circles.

**A**

CASE: HRP 5

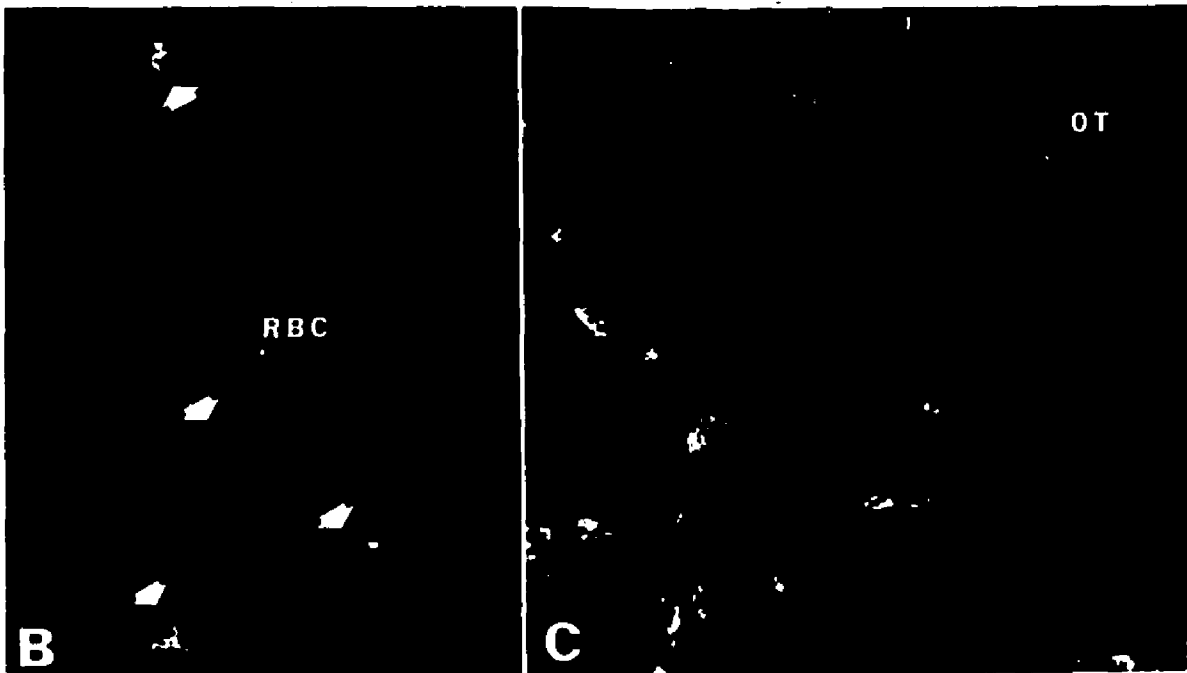


Figure 5. A. Drawings of selected thalamic sections illustrating retrograde uptake of HRP following injection into area 17.
 B. Appearance of labelled cells in NLP, dark field illumination.
 C. Appearance of labelled cells in LGNd, dark field illumination.

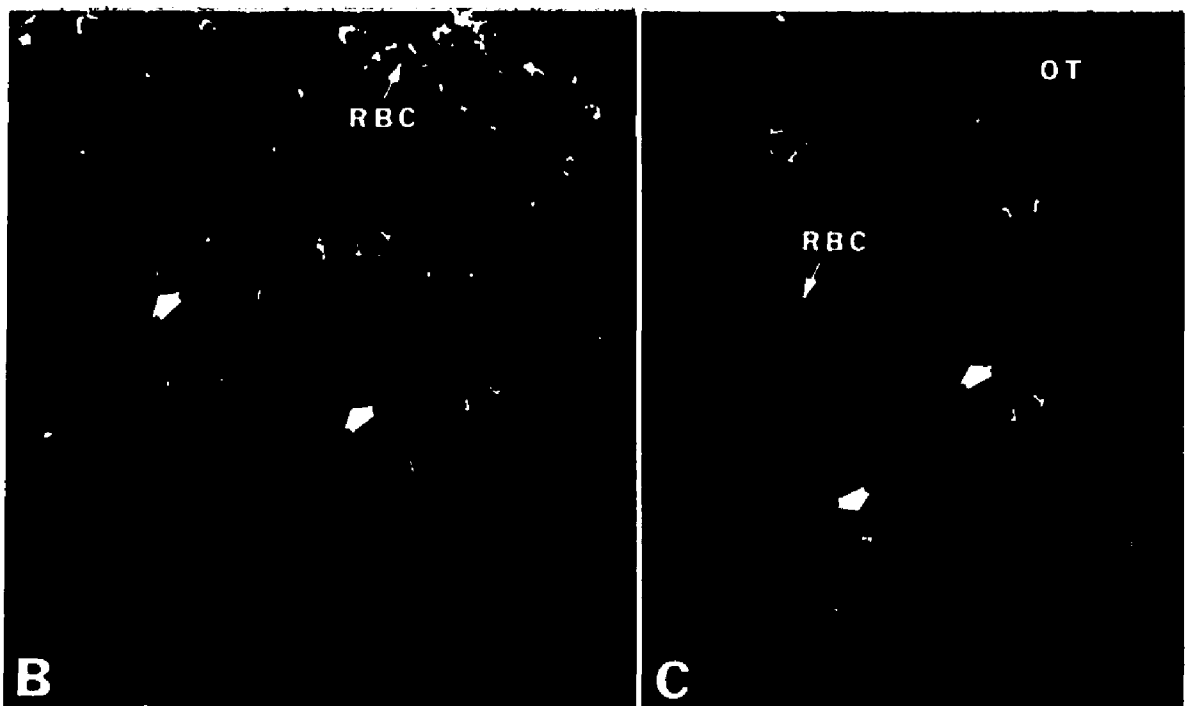
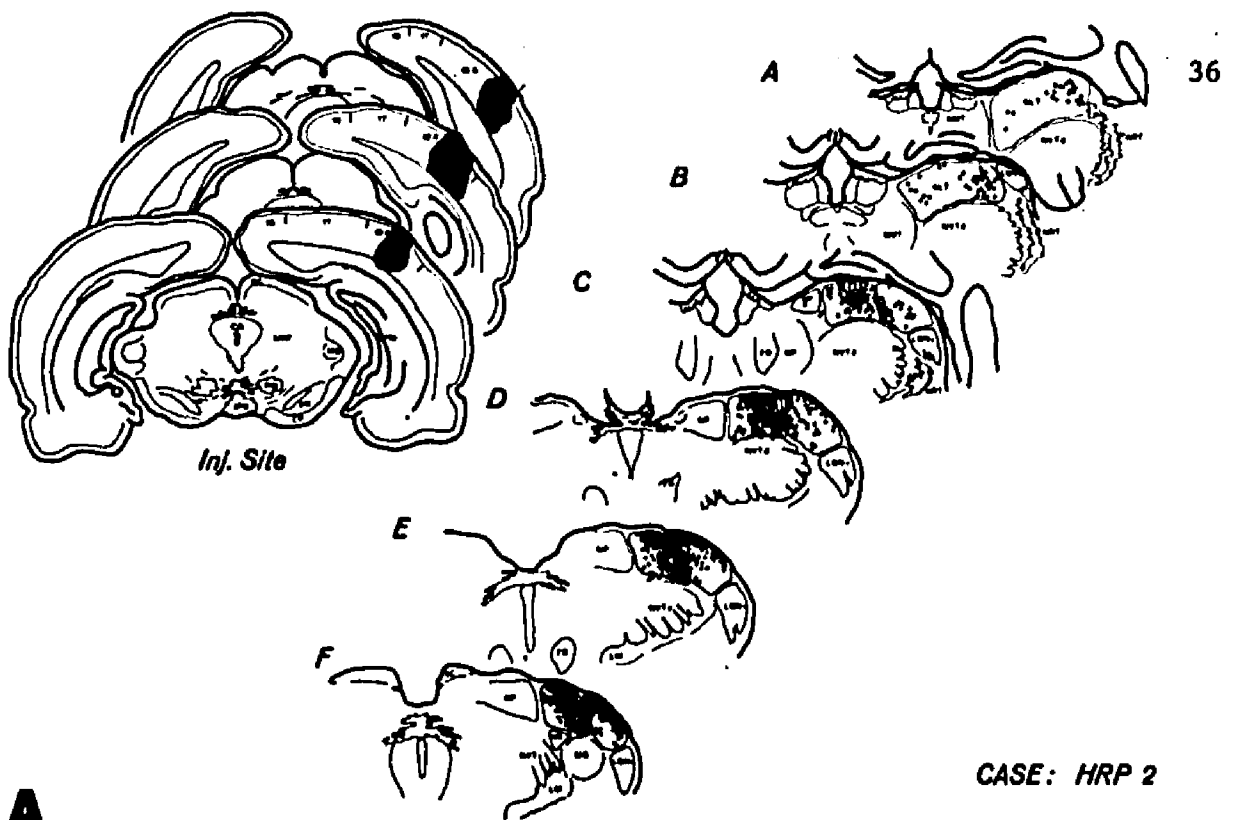


Figure 6. A. Drawing of thalamic sections selected to illustrate retrograde incorporation of HRP following injection into area 18A. Light labelling is indicated by open circles, heavily labelled neurons by filled circles. Note the accumulation of labelled cells in the lateral half of NLP and in the dorsolateral portion of the LGN.

B. Dark field photomicrograph of HRP-labelled neurons in NLP.

C. Dark field photomicrograph of HRP-labelled neurons in LGNd.

Lightly labelled neurons are indicated by open arrows.

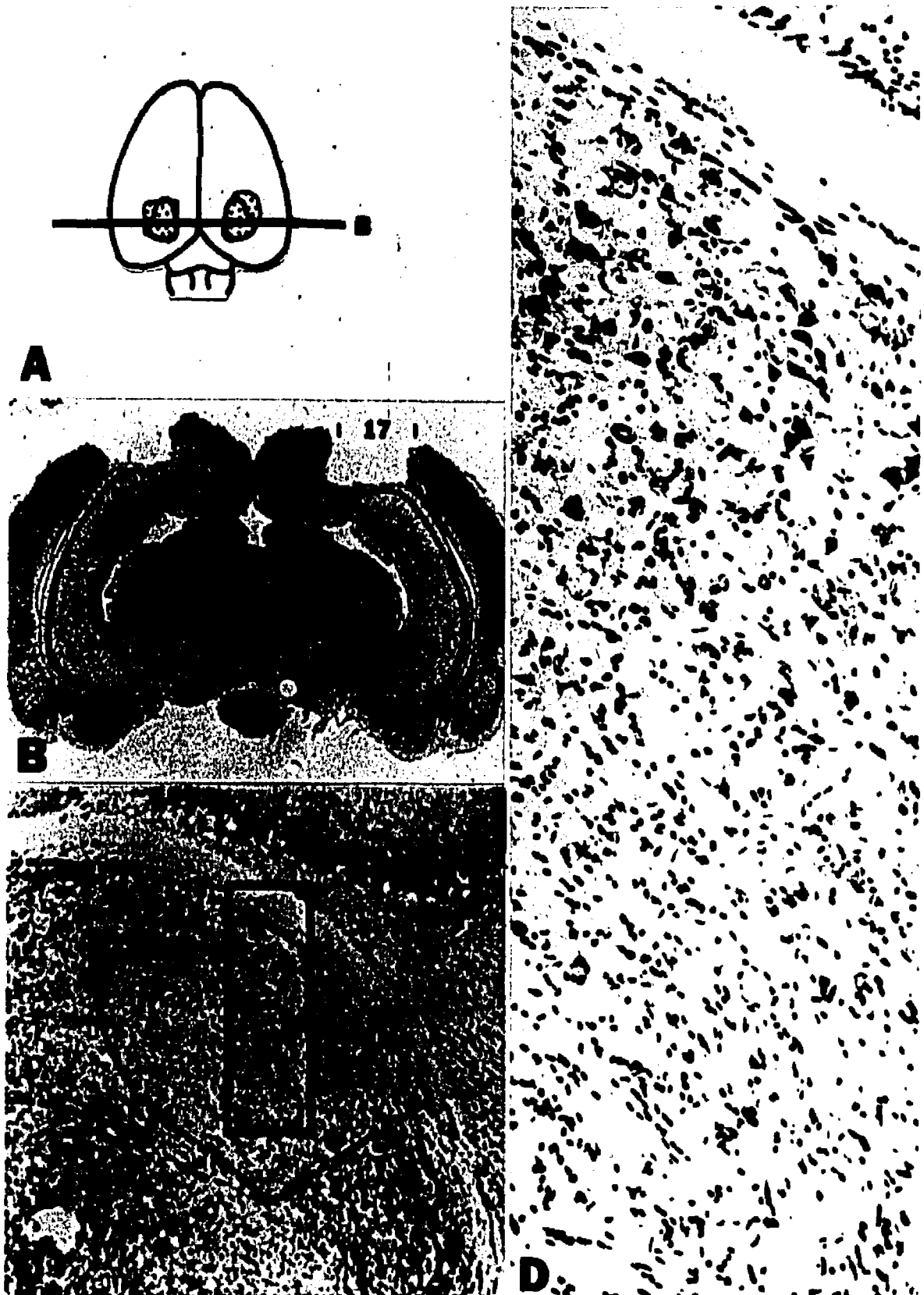


Figure 7. A. Dorsal view of bilateral ablation of area 17 (outlined with heavy black line). Lesion extent is indicated by stippling.
 B. Photomicrograph of section through the lesion site. Nissl stain.
 C. Photomicrograph taken from right LGNd showing area which is degenerated following removal of striate cortex.
 D. Higher power view of LGNd showing transition between degenerated and intact portions of LGNd.



Figure 8. Drawings made from sections selected to illustrate the cortical distribution of silver grains following injection of 3H-leucine into the LGNd.



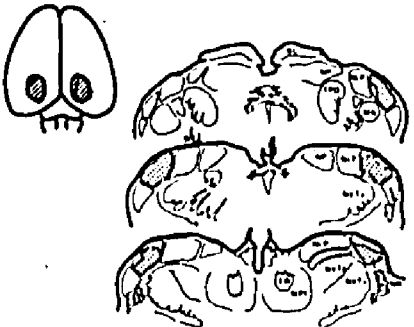
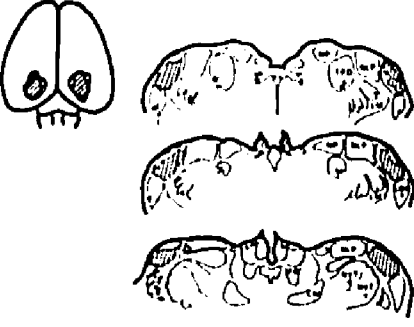
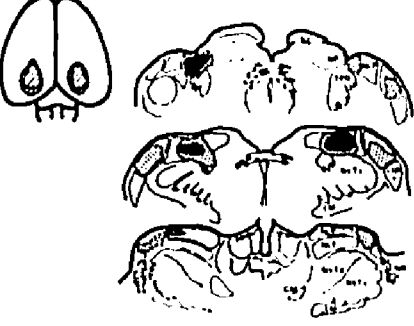
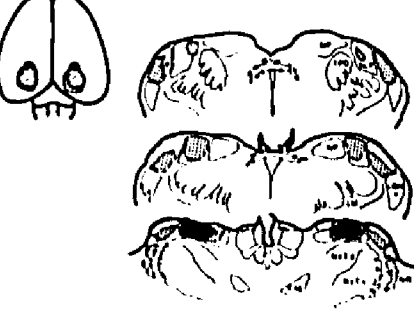
GROUP	MOST ACCURATE LESIONS	LEAST ACCURATE LESIONS
N. LATERALIS POSTERIOR		
AREA 17		
AREA 17 PLUS N. LATERALIS POSTERIOR		

Figure 9. Least and most accurate lesions in each of the three operated groups.



Figure 10. A. Photomicrograph of the thalamus of a typical case taken from Group 17 + LP.
B. Photomicrograph of the thalamus of a typical case taken from Group LP.

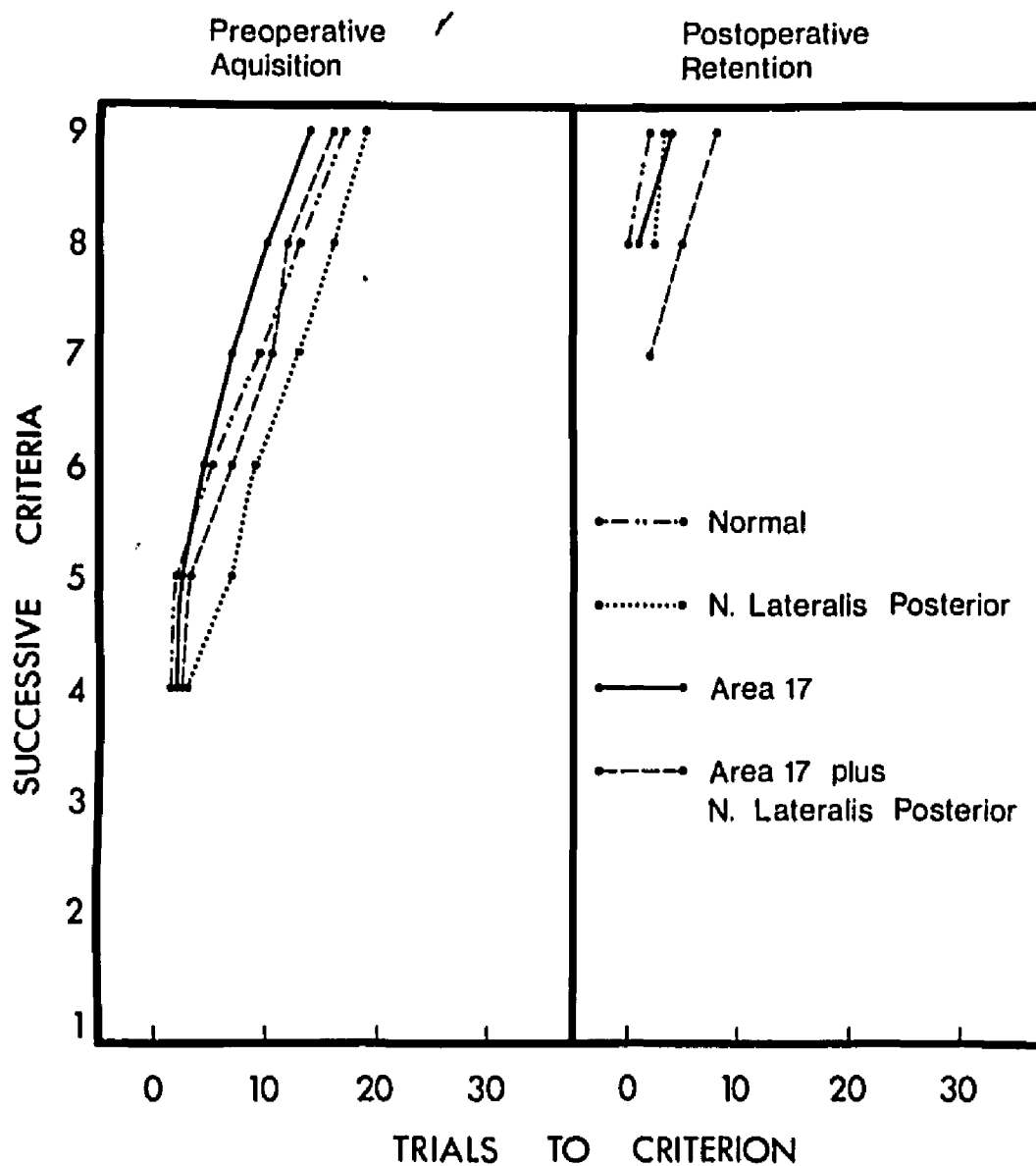


Figure 11. Preoperative acquisition and postoperative retention of flux discrimination for each of the three experimental groups and the normal control group. Data points represent group-mean numbers of trials (abscissae) needed to perform at each successive criterion (ordinates).

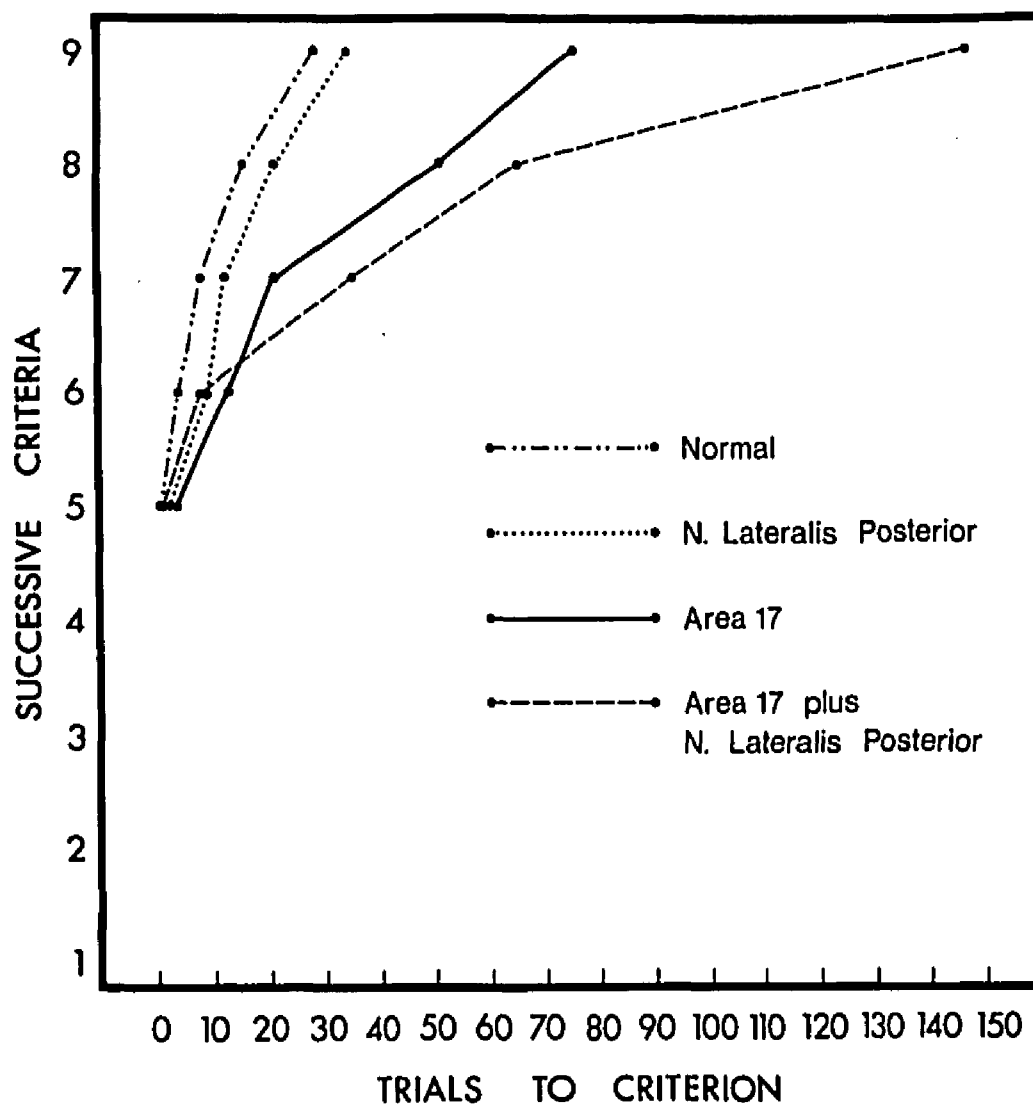


Figure 12. Postoperative acquisition of pattern discrimination for each of the three experimental groups and for the normal control group. Data points represent group-mean numbers of trials (abscissae) needed to perform at each successive criterion (ordinates).

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