

## The occipitotectal pathway of the rat

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### INTRODUCTION

A pathway arising within the visual cortex and terminating in the superior colliculus is described by many authors following demonstration of it experimentally by von Monakow (1889) in the cat and Ferrier & Turner (1897) in the monkey. However, considerable variation is found between descriptions regarding in which laminae these corticotectal fibres end. Whilst some such variation might be accounted for by species differences, discrepancies between accounts by various authors using the same animal can hardly be explained in this manner. Such confusion exists in work on this pathway in the rat, the animal of the present study.

Unfortunately none of the authors concerned made sufficient number of lesions within the visual area to determine whether the boundary of origin of the pathway is confluent with the boundary of the visual cortex. Their work indicates an occipitotectal pathway, but gives no indication of what relationship this pathway may have with the striatotectal pathway.

A further problem arises here as to the discrepancies between different accounts of the limits of the visual cortex in the rat. The frequently used maps of Le Messurier (1948) and of Krieg (1946) based on physiological and cytoarchitectonic criteria respectively show a more extensive visual area than that defined by Waller (1934) and Lashley (1941) using the criteria of a retrograde degeneration study. It is therefore of interest to find to which map of the visual area the area of origin of the occipitotectal pathway may correspond.

The possibility of localization of the occipitotectal projection, while indicated by Nauta & Bucher (1954) in two animals, has not been adequately surveyed. A preliminary report of the present work (Lund, 1964) indicates that part of the occipital area projects to the superficial laminae of the superior colliculus in the manner described by Nauta & Bucher (1954) and that the projection is topographically localized. The relationship of the origin of this pathway to the striate cortex, and the relationship of these to corticotectal fibres from neighbouring areas is discussed below. The experimental evidence for the conclusions and further details of the work are also described.

### MATERIALS AND METHODS

A total of thirty-eight albino rats has been used. In thirty-four, localized cortical lesions involving the occipital or parieto-occipital areas of one hemisphere were made under ether anaesthesia by suction or thermocoagulation. Following survival times of 7–10 days, the animals were sacrificed by perfusion with 10% neutral formol saline. In each animal, the cortex was removed from the rest of the forebrain by cutting through the rostral part of the thalamus, embedded in paraffin, and cut transversely

at  $15 \mu$ . Two series of every tenth section were taken for staining with the Nissl and Nauta-Glees (Guillery, Shirra & Webster, 1961) methods respectively. These were used for reconstructing the extent of the lesion. In doing this, the posterior border of the cortex and the mid-line were used as the co-ordinates from which measurements were taken. The lateral border of the cortex and the boundary of the lesion could then

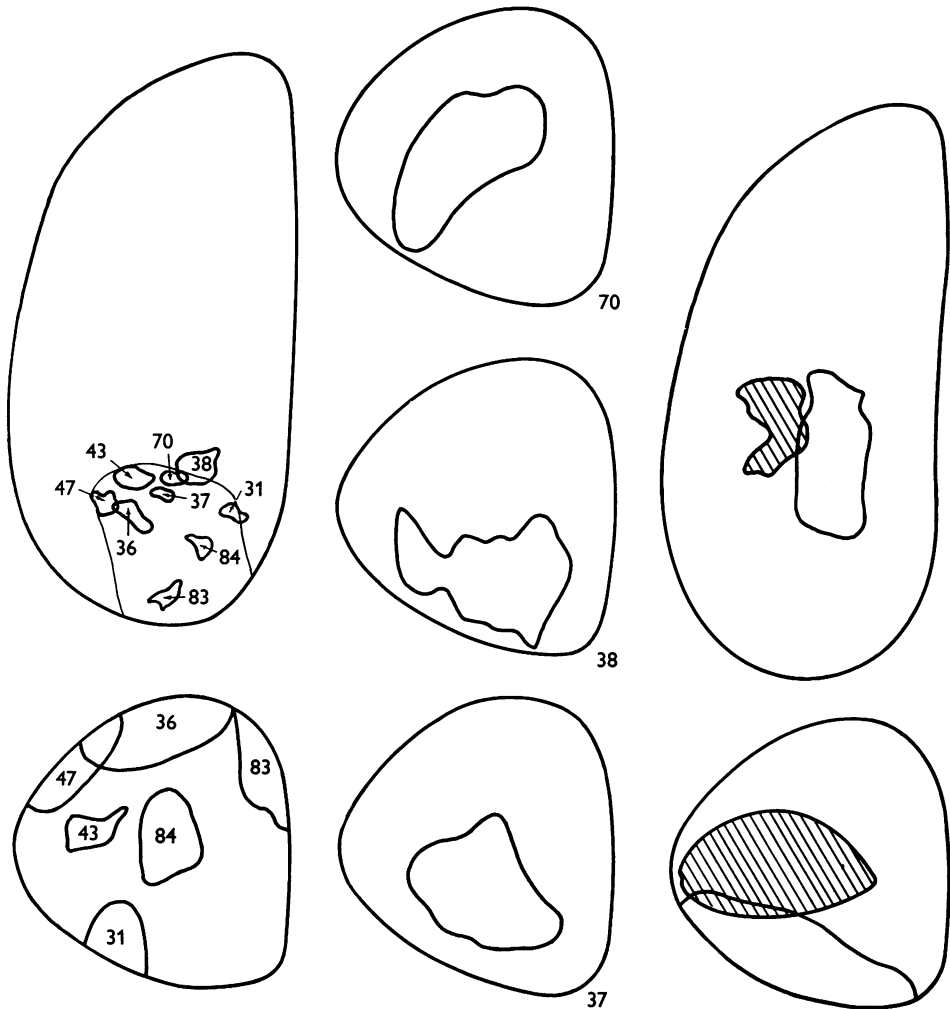


Fig. 1

Fig. 2

Fig. 1. Map of the left cortex and four maps of the left superior colliculus viewed from above, showing the cortical area within which lesions produce degeneration in the superficial laminae of the superior colliculus. A sample of lesions and their corresponding areas of degeneration is also shown, the numbering indicating the numbers of the individual brains. The scale of the colliculus is twice that of the cortex.

Fig. 2. Map of the left cortex and colliculus viewed from above, showing the two parts of the anterior cortical area and their differential projection to the deeper part of the superior colliculus.

be mapped out. From individual maps, the composite maps of Figs. 1 and 2 were constructed. In four brains with lesions extending into layer III or the superficial part of layer IV, no degeneration could be found in subcortical structures, although deeper lesions in similar areas produced typical degeneration patterns. As a result in the case of oblique or tapering lesions, measurements of their extent were taken at the depth of the lower border of layer IV. The extent of the lesion was taken to include the area of the cavity where it still existed and the area of cellular atrophy or gliosis bordering the cavity. The only lesions to invade the underlying white matter are in

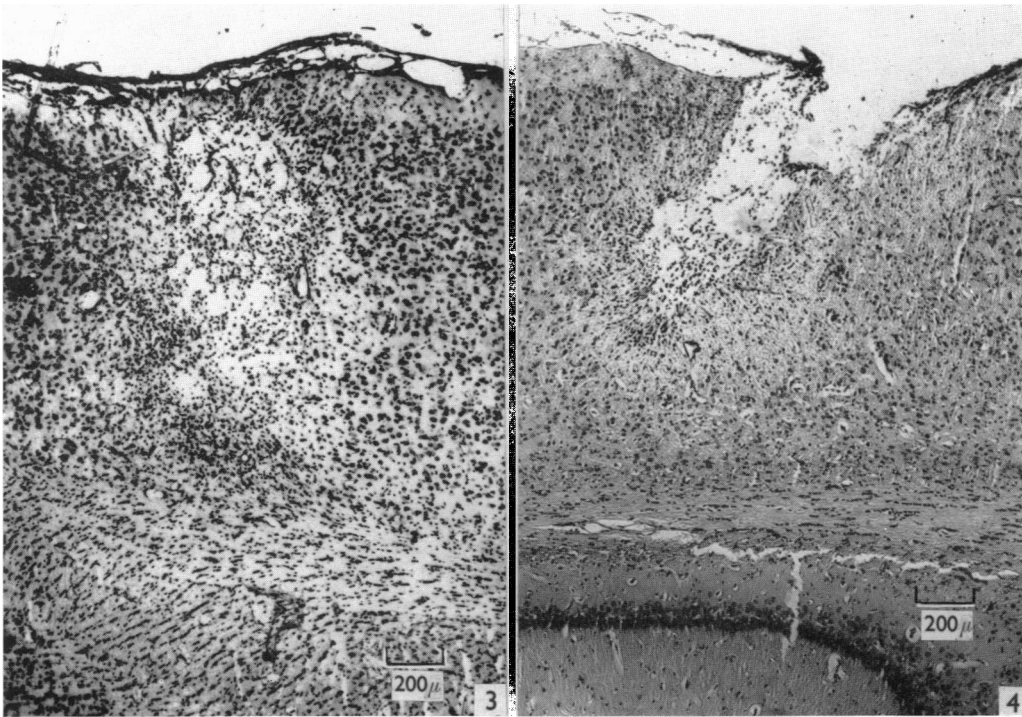


Fig. 3. Transverse section of the cortex of brain 70 at the point at which the lesion is most extensive. Nissl stain.

Fig. 4. Transverse section of the cortex of brain 43 at the point at which the lesion is most extensive. Nissl stain.

the two brains in which large lesions were made over a large part of the occipital area. In these only the surface fibres of the white matter are involved, there being no indication of damage to underlying structures in either Nissl-stained or Nauta-stained sections. Two micrographs of the deepest extent of the smaller lesions of brains 70 and 43 are shown in Figs. 3 and 4.

Parasagittal frozen sections were cut of the rest of the brain at  $30\ \mu$  for staining with the Nauta & Gyax method (1954) and some at  $15\ \mu$  for staining with the Glees method (1946). At least two series of every fifth section from each brain were stained by the former method. The sections were mounted randomly, and the extent of degeneration

assessed after which they were serialized. Serialization was done with reference to a Nissl-stained series of the same brain which had been mounted in serial order before staining. In addition, the sagittal length of the upper surface of the stratum opticum of the colliculus was measured for each section. Using these criteria, the series can be reconstructed. So that a base-line could be provided for making a map of the superior colliculus and the degeneration within it, a transverse cut was made through the inferior colliculus before sectioning. While allowance has been made, in making the map of the superior colliculus, for curvature in the sagittal plane, no account has been taken of the curvature in the transverse plane. In all cases assessment and measurements of the extent of degeneration were made on sections before serialization so that subjective bias in constructing a preconceived map could be avoided.

So that the degeneration in the superior colliculus could be directly compared with that resulting from optic nerve section, one optic nerve was cut in the orbit in a further four animals. Following a survival time of 8 days the animals were sacrificed and the brains stained with the Nauta and Gygax or the Glees method.

#### RESULTS

From a study of the cortical lesions producing and failing to produce degeneration in the superior colliculus, two cortical areas can be distinguished, one situated posteriorly (Fig. 1) and the other, which may be further subdivided, situated immediately anterior to the first (Fig. 2). The distinction between the two areas is made by the laminar distribution of their fibres within the superior colliculus. In view of the difficulties of correlating the boundaries of these areas with that of the visual cortex, they will be described at present as the anterior and posterior cortical areas.

Lesions within the posterior area (Fig. 1) produce a similar pattern of degeneration in the afferent pathway to the superior colliculus and in the terminal distribution in the colliculus. In all cases the collicular degeneration is restricted to the side of the lesion.

Degenerating fibres can be traced with the Nauta method running through the internal capsule to enter the lateral part of the cerebral peduncle. At the position where the latter is crossed by the optic tract, the fibres leave it to run with the tract, some in the brachium of the superior colliculus and other passing through the lateral geniculate and pretectal region. The two sets of fibres merge at the rostro-lateral border of the superior colliculus to form the stratum opticum, together with fibres of the optic tract. No degenerating fibres have been seen leaving the peduncle more caudally than the level at which it is related to the optic tract after lesions within this cortical area.

The fibres of cortical origin running in the stratum opticum terminate in this lamina and principally in the deeper part of the stratum griseum superficiale. Following lesions of the whole posterior cortical area, the whole area of each of these laminae shows preterminal degeneration. A few fibres separate from the deeper bundles of the stratum opticum. Whether these terminate in the stratum griseum intermedium is not clear, partly because the boundary between the stratum opticum and stratum griseum intermedium is poorly defined in the rat and also because neither the Glees nor the Nauta method is sufficiently reliable to differentiate terminal or preterminal degeneration from passage degeneration in this area

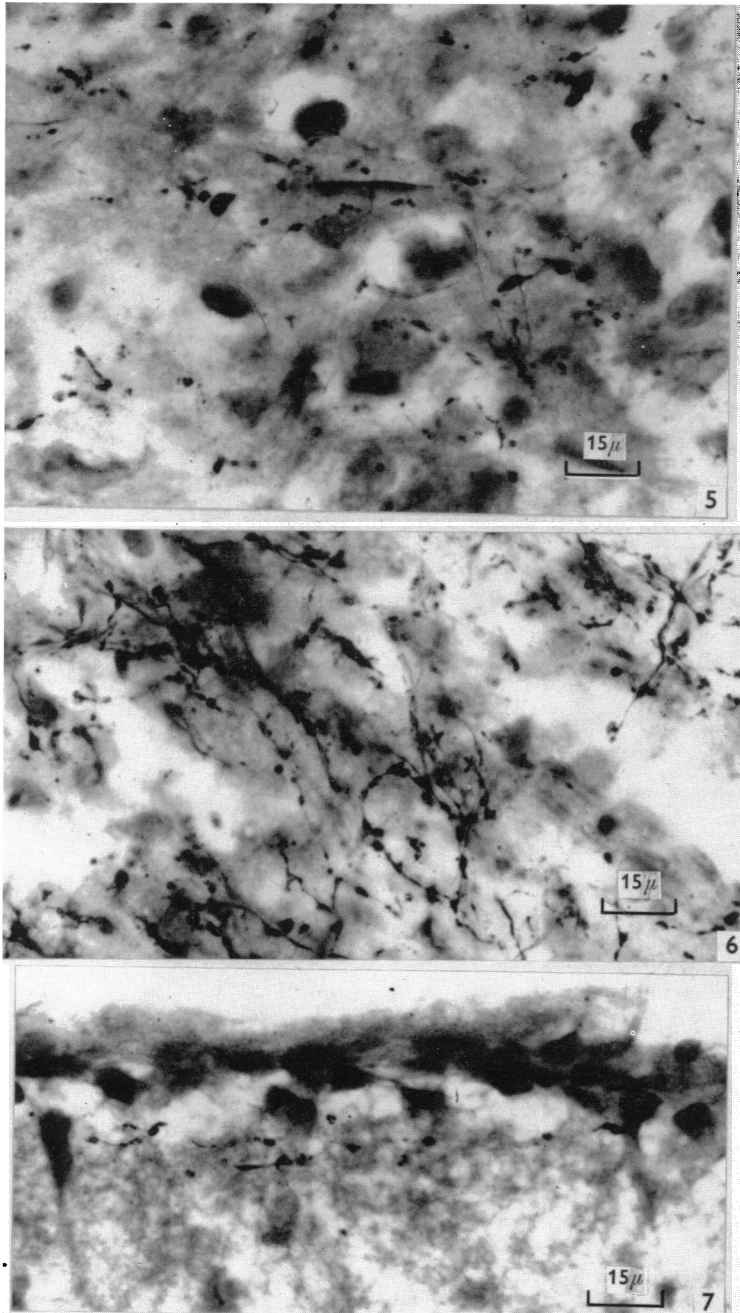
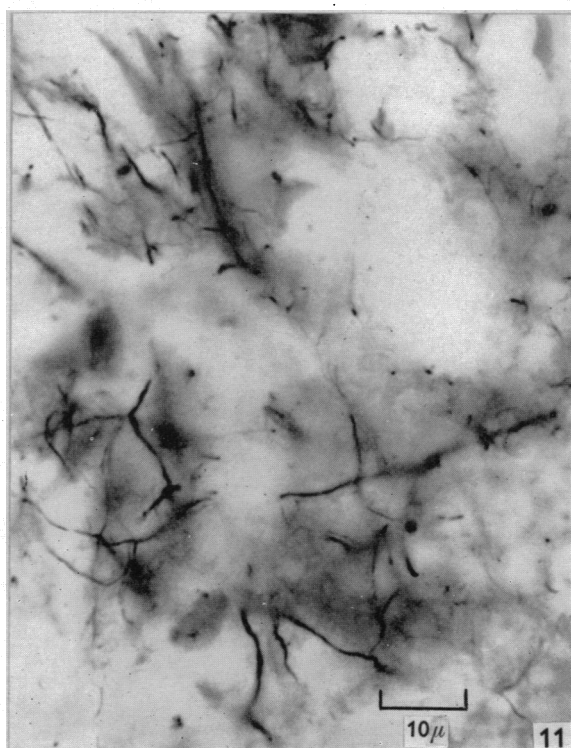
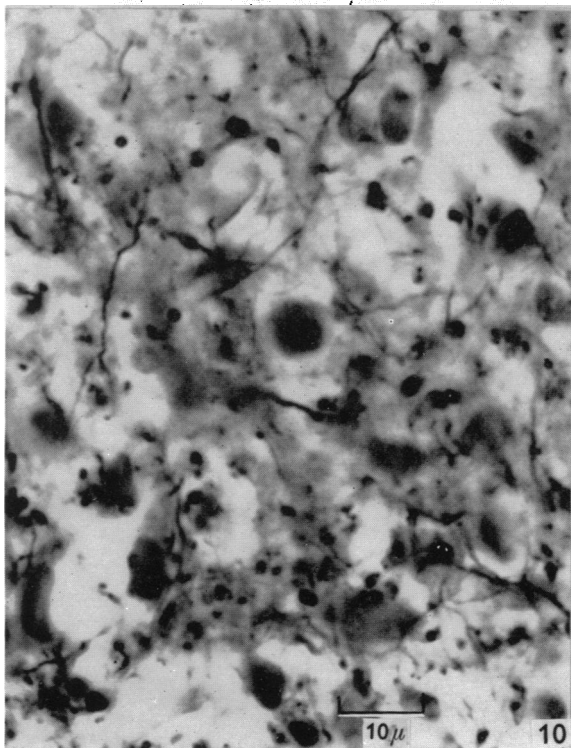
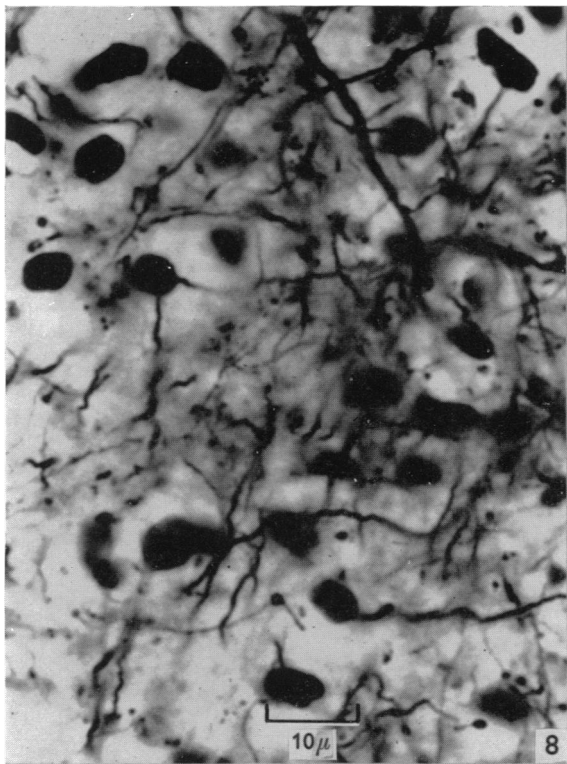


Fig. 5. Degeneration in the stratum griseum superficiale of the colliculus produced by a lesion involving the whole ipsi-lateral visual cortex. Nauta method.

Fig. 6. Degeneration in the same lamina produced by removal of contra-lateral eye. Nauta method.

Fig. 7. Degeneration in the stratum zonale of the colliculus after a large lesion in the ipsi-lateral visual cortex. Nauta method.



A few degenerating fibres run in the stratum zonale (Fig. 7). These appear continuous with those in the stratum opticum at the borders of the superior colliculus, especially anteriorly. None are seen to enter the stratum griseum superficiale, but degenerating fibres are found in close relation to cells in the stratum zonale, suggesting the possibility of termination of fibres there.

Following enucleation of the eye, degeneration is limited to the same laminae as after lesions in the posterior cortical areas. The most striking difference between the two is that the degenerating fibres produced by optic lesions are much thicker and more numerous, particularly in the stratum opticum and stratum griseum superficiale. This is shown in Figs. 5 and 6 of the stratum griseum superficiale. Degeneration is limited mainly to the deeper part of the lamina following cortical lesions, but that produced by eye enucleation is evenly distributed throughout the lamina. It becomes gradually more sparse nearer the surface as the number of passage fibres from the stratum opticum is reduced. The most peripheral degenerating fibres are closely related with those in the stratum zonale, and there appears to be some exchange of fibres between the two laminae. Normal material stained by the Glees method shows no clear boutons. Following lesions in the visual cortex or of the optic nerve, boutons terminaux are profuse. They are particularly evident in the stratum griseum superficiale, as shown in Figs. 8–11. After both types of lesion they appear frequently as rings of 1–3  $\mu$  diameter or as knobs and occasionally as reticulated structures. In neither case do they show a particular distribution, for example in relation to cell bodies, although some certainly are situated quite close to cell bodies, as can be seen from Fig. 8. As with the Nauta-stained sections degeneration is less profuse following cortical lesions. In addition, the rings appear to be mostly of smaller diameter. The degeneration in the stratum opticum appears similar to that described above, but its presence is frequently masked by degenerating passage fibres. Since degeneration in the stratum griseum superficiale is limited to one superior colliculus only following either type of lesion, the other side can be conveniently used as a control in material cut transversely.

In brains in which the lesions are placed within the anterior cortical areas (Fig. 2) degeneration is limited to the deeper of the afferent laminae of the superior colliculus, being found only in the stratum album intermedium and stratum griseum intermedium. None is found in the more superficial laminae. The fibres reach the colliculus either by running through the thalamus or by running in the lateral part of the cerebral peduncle to a point slightly rostral to the pons, where they arch dorsally to join the other group of fibres.

Lesions overlapping both the posterior and the anterior area give degeneration in

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Fig. 8. Transverse section of the stratum griseum superficiale of the superior colliculus on the side ipsi-lateral to a complete lesion of the visual cortex showing degeneration. Glees method.

Fig. 9. The same area of the contralateral colliculus of the same section showing absence of degeneration. Glees method.

Fig. 10. Transverse section of the stratum griseum superficiale of the colliculus showing degeneration after removal of the contralateral eye. Glees method.

Fig. 11. The same area of the contralateral colliculus of the same section as Fig. 10, showing absence of degeneration. Glees method.

all of the five most superficial laminae of the colliculus. An example of such a lesion is shown for brain 38 in Fig. 1. Two other lesions covering a similar area but not extending so far posterior show degeneration in the stratum album intermedium and stratum griseum intermedium, but show none in more superficial laminae of the colliculus. The distribution of degeneration in the superficial laminae of the colliculus in brain 38 resembles that in brain 70, both the cortical lesions and distribution of collicular overlapping slightly.

Lesions made lateral to either the anterior or the posterior area produce no degeneration in the superior colliculus. While the cortical area lying antero-laterally to the anterior area has not yet been fully investigated, no degeneration was found in the superior colliculus in three brains with lesions situated immediately anterior to the anterior area. Lesions situated medial to the posterior area give some degeneration in the most anterior part of the stratum album intermedium of the colliculus. This is continuous with degeneration found in the pretectum. However it is difficult to decide the exact boundary between pretectum and tectum, leaving some doubt as to exactly how much of the degeneration is situated within the colliculus. No similar degeneration could be found after lesions medial to the anterior area.

The present results indicate that there are two well-defined areas in the parieto-occipital and occipital regions of the cortex of the rat which project to the superior colliculus, and can be differentiated from one another by the pattern of their projection. The relationship of these to the visual cortex will be discussed later.

#### LOCALIZATION STUDY

Whilst lesions involving the whole of the posterior cortical area produce degeneration throughout the whole of the stratum opticum and deeper part of the stratum griseum superficiale, lesions damaging only part of the area produce localized degeneration in the laminae of the colliculus. Lesions in the antero-lateral and postero-medial parts produce degeneration in the antero-lateral and antero-medial quadrants of the colliculus respectively. The antero-medial part of the posterior cortical area projects to the postero-lateral quadrant of the colliculus, and the postero-medial to the antero-lateral quadrant. The pattern can be seen from Fig. 1. It fits well when applied to brains numbered 43, 47, 36, 83, 84, 31 (Fig. 1). However, there is a region in the anterior part of the posterior cortical area the pattern for which is less clear. The area of degeneration produced by small lesions, while approximately in the expected area, is much more extensive relative to size of lesion than of lesions placed elsewhere. Three such lesions are shown in Fig. 1 in brains 37, 38 and 70, the areas of degeneration in the colliculus in each of these brains being shown separately from the rest. While, as described earlier, the lesion in brain 38 is quite large, only a small part of it is in the posterior area. None of these lesions involves the underlying white matter, so that the possibility of damaging fibres projecting from a wider area of cortex must be discounted. The lesion in brain 70 is shown at its maximum depth in Fig. 3, compared with that for brain 43 (Fig. 4).

Little can be said as yet of localization of degeneration from lesions in the anterior cortical area. Lesions in the larger medial area (Fig. 2) produce degeneration in the posterior part of the superior colliculus, but there is no indication of systematic



localization within this area after small lesions. Lesions in the lateral area produce degeneration in the intermediate part of the colliculus. The four small lesions within the lateral area show indications of producing systematically localized degeneration, such that more lateral lesions produce areas of degeneration situated more laterally in the colliculus.

## DISCUSSION

The first account of a corticotectal pathway to the superior colliculus in the rat is by Clark (1933). He found, using the Marchi method, that the pathway originates only in the visual area (as mapped by Droogleever Fortuyn, 1914) and enters the colliculus by the stratum album intermedium to end there. Unfortunately he made only one lesion in the visual area, and this caused accessory damage to subcortical structures. Huber & Crosby (1943), in a general discussion of the corticotectal pathway in a number of animals including the rat, describe fibres entering the superior colliculus from the visual cortex by the stratum opticum. From here most fibres run deep to end in the stratum griseum intermedium. Collaterals are described running more superficially to end in the stratum griseum superficiale. Krieg (1947), using the Marchi method, was unable to trace degenerating fibres to the superior colliculus after small lesions in his area 17 (Krieg, 1946) in four animals. However, he found degeneration in the stratum opticum and stratum album intermedium after lesions in areas 18 and 18*a*. Only Nauta & Bucher (1954) describe the degeneration in the same laminae as in the present work. Both their lesions are in the posterior part of the visual cortex (defined by Krieg, 1946) and fall within the posterior area defined in Fig. 1.

The variation between descriptions might be accounted for in part by technical difficulties. A further problem is the variation in the limits of the visual cortex as defined by different authors. Maps have been prepared by Droogleever Fortuyn (1914), von Volkman (1926), Lashley (1941) and Krieg (1946) using cytoarchitectonic criteria. However, they vary considerably from the map by Droogleever Fortuyn where the visual cortex occupies the posterior 42% of the total sagittal length of the cortex to that by Lashley where it occupies only 28%. Krieg divides the visual area into areas 17, 18 and 18*a*. Differences may arise from the use of different strains of rat, but the principal cause is the poor criteria available for defining the area. The centre of the area is distinct, with a thick layer IV composed of many densely packed cells, but the gradation from this to the characteristic structure of neighbouring cortex is gradual, there being no sharp boundary between the two. This is particularly noticeable with the anterior and lateral borders, as Lashley (1941) indicated.

One must be cautious then in accepting the limits of the visual cortex defined by this method without first considering those found by using other techniques. By the evoked potential method after stimulating the optic nerve directly a visual area is given which exceeds the limits of any described above (Le Messurier, 1948). The two studies by Waller (1934) and Lashley (1934*b*) use the appearance of retrograde cell changes in the lateral geniculate body as an indication that cortical lesions were within the visual area. Their maps agree with one another and with the cytoarchitectonic map proposed by Lashley (1941).

The posterior area of the present study corresponds closely with the visual area defined by Waller (1934) and Lashley (1934*b*, 1941). It may therefore be presumed that

the origin of the corticotectal pathway ending in the more superficial laminae of the superior colliculus is the visual cortex.

The correlation of the more anterior projection area with cortical areas defined in other ways is difficult to decide. It would seem unjustified to separate off a posterior part of it from the rest on the grounds that it fell within the visual area of the more frequently used maps of Krieg or Le Messurier. This would imply that the organization of the afferent and efferent systems of this part of the cortex are unrelated to one another. The pathway compares closely in course and termination with the corticotectal pathway of the monkey arising in area 7, which is described by Swarcbart & Kuypers (1962). The area of origin of its fibres corresponds with the parietal area of Lashley's cytoarchitectonic maps, and to the cortical projection areas of the lateralis pars anterior and lateralis pars posterior thalamic nuclei from his retrograde degeneration studies (1941). It falls within the thalamic projection areas of the centromedian and lateral nuclei of Waller (1934). The two distinct areas within this region correspond well with the two thalamic projections areas described by each author. The presence of the more anterior area serves to limit the anterior boundary of the visual area very carefully. The medial projection area coincides with the cingulate area, but its details have not been investigated in this study.

The evidence of a localized corticotectal projection in the rat was shown by Nauta & Bucher (1954). The degeneration found after one lesion corresponds closely with that in brain 83 of this study. The second lesion, corresponding with that in brain 84, causes degeneration far in excess of what would be expected from the present work.

The localization study by Gerebtzoff & Wauters (1941) in rabbit and guinea-pig is based on only three limited lesions and shows a pattern such that the corticotectal pathway does not connect corresponding projection areas of the visual field in cortex and colliculus. Only the work of Crosby & Henderson (1948) on the monkey suggests this to be the case. Unfortunately the only experimental details given of the work on which these conclusions are based is that the histological preparations were stained by the Weil method. They describe the corticotectal pathway from the visual area as entering the superior colliculus in the stratum album intermedium and ending deep to the stratum opticum. This is contrary to the account by Swarcbart & Kuypers (1962) using the Nauta and Gyax method. It is difficult therefore to see how they arrived at their conclusions.

However, their assertions regarding the interrelation of retinotectal and corticotectal fibres are shown here to be correct for the rat at least. Both the retinotectal and retinogeniculo-cortical pathways have been mapped by Lashley (1934*a, b*). Relating these to the present map of the corticotectal pathway, it is shown that areas of cortex project to areas of colliculus receiving fibres from the same areas of the retina.

From the present work it is clear that the retinotectal and corticotectal fibres from the visual area are closely related in their terminal distribution. How they interact is unclear. They might end on different cells, or the same cells, or one might end pre-synaptically on the other. Only experimental studies using the Golgi method and the electron microscope will provide the answer.

The question of the interrelation of terminal distribution of corticotectal, spino-tectal and other tectal afferents to the stratum album intermedium and the stratum griseum intermedium presents further problems. It seems likely that the spino-tectal

pathway may end in relation to the corticotectal pathway from the parietal area in a similar manner to the retinotectal and corticotectal from the visual area.

The arrangement suggests that the afferent laminae consist of two blocks, one lying on the surface concerned with visual stimuli and the other lying below it concerned with somatosensory and other stimuli. Whether these two interact and how they might be related to the organization of the efferent system are problems which will be of considerable importance when assessing the role of the colliculus in relation to other parts of the nervous system.

The situation described here for the afferents from the visual system indicates that whatever the true function of the superior colliculus, its response to visual stimuli may be the result of the interaction of the two inputs, from visual cortex and retina respectively, rather than the autonomous functioning of one in the absence of the other, as is often assumed in behavioural experiments.

## SUMMARY

1. A study has been made in the albino rat of the organization of the pathway from the occipital cortex to the superior colliculus and its relationship with the retinotectal pathway.

2. One corticotectal pathway arises from an area coincident with the visual area defined by Lashley (1941), and terminates principally within the three most superficial laminae of the superior colliculus.

3. It is topographically localized and this localization can be related with that described for the retinotectal pathway.

4. Further corticotectal pathways arise from the areas anterior and medial to the visual area, but they project only to the stratum album and griseum intermedium.

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