The structure and connections of the inferior colliculus

AN INVESTIGATION OF THE LOWER AUDITORY SYSTEM

J. van Noort

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Proefschrift

Ter verkrijging van de graad van doctor in de Geneeskunde
aan de Rijksuniversiteit te Leiden,
op gezag van de Rector Magnificus Dr. L. Kukenheim Ezn.,
Hoogleraar in de Faculteit der Letteren,
ten overstaan van een Commissie uit de Senaat te verdedigen
op dinsdag 24 juni 1969 te klokke 15.15 uur, door

Jan van Noort

geboren te Hilversum in 1934

TE ASSEN BIJ
VAN GORCUM & COMP. N.V. – DR. H. J. PRAKKE & H. M. G. PRAKKE

PROMOTOR: PROF. DR. W. J. C. VERHAART

This investigation was made under the supervision of Dr. J. Voogd in the Laboratory of Neuro-anatomy of the State University Leiden. The three-dimensional drawings are made by Mr. J. Tinkelenberg.

The publication of this dissertation was made possible through a grant from the Netherlands Organization for the Advancement of Pure Research (Z.W.O.).

Aan mijn ouders
Aan mijn vrouw

Contents

Introduction

I

The aim of this study was initially to find the anatomical substrate of the acoustic recurrent system, physiologically shown by Desmedt and Mechelse (1957, 1958). Although one such system was found, it seemed not the one wanted because it showed a different location. On further investigation its origin could be localized in the inferior colliculus (IC) and its termination in the dorsal cochlear nuclei of both sides. It proved to be necessary, however, to study the structure and the connections of the collicle anew, because the short and in certain details deficient description of Cajal was the latest one up to 1964.

The use of both the Nauta-Gygax and the Häggqvist methods proved to reveal many more details in both its structure and connections than have been described by previous authors. The study of the connections gradually enlarged to one of the whole auditory system, caudal to the IC, but from the rostral part, only its direct connections have been paid attention to. It soon became apparent that the IC is the main relay centre of both the ascending and the descending auditory pathways, as no single fibre passes it uninterruptedly in either direction. For a proper understanding of its role in frequency analysis, binaural hearing and its influence on more caudal auditory centres, detailed information of the structure and the fibre connections of the cochlear nuclei and the superior olivary complex is indispensable, however.

Methods 2

Experiments were carried out in fullgrown cats.

Except for the standard series from which the schemes are drawn and series B 132 which was paraffin embedded and stained according to Häggqvist's method, all the brains have been cut in frozen sections, which were stained according to the Nauta-Gygax 1954 method with a slight modification (a.o. the original ammoniacal silver solution of 1951 was used instead of the Laidlaw solution).

OPERATION TECHNIQUE

After the intra-abdominal administration of hexobarbitone sodium, the animal was placed in the Horsley-Clarke frame and usually a stereotactic operation was carried out. Special arrangements had to be made to evade the bony tentorium. Usually the auditory structures have been reached with an electrode, entering the skull from dorsocaudal to ventrorostral under an angle of ± 40 degrees with the vertical plane. The lesions were made with a Wyss high frequency coagulation apparatus. The cochlear lesions have been made through the bulla tympanica with a small dental drill, but in a small number of experiments the auditory structures were reached through the base of the skull. The last 50 experiments have all been carried out in duplo, one for a transversal the other for a parasagittal series.

The average survival time was 10 days, when in a deep hexobarbitone sodium anaesthesia the animals were perfused with a 10% formalin solution in tapwater. The brains were stereotactically cut into blocks, the plane of section for the transverse series tilting at an angle of 70° with the horizontal plane. In this way the IC remains connected with the brain stem, whereas when sectioned in the stereotactic plane its caudalmost part falls apart from it.

Its disadvantage is evidently that the preparations differ from the pictures of the stereotactic atlas. The blocks remained in neutral formalin for 1-3 months, after which they were cut in sections of 24 mu.

STAINING PROCEDURES

For the IC special series from alcohol-fixed material embedded in celloidine, were stained according to the methods of Nissl and of Klüver and Barrera. The sections of the standard series made from paraffin-embedded brains are somewhat deformed, as is visible in the schemes, and in both series they are compressed dorsoventrally.

For the different staining techniques I refer to literature. (Nauta and Gygax 1951, 1954, Busch 1961, Klüver and Barrera 1953 and Glees 1946).

DRAWINGS AND RECONSTRUCTIONS

For the transversal schemes one half of the sections was depicted and duplicated. The parasagittal series used for the schemes deviates a few degrees from the sagittal plane, but it was used because it was very well stained, and had coordinate marks.

In most of the schemes all the visible degeneration is indicated by dots, but only part of it is described in the text. Large dots combined with smaller ones indicate a higher concentration of degeneration than small ones alone, but this has nothing to do with the calibre of the degenerated fibres.

The three-dimensional quasi-transparant reconstructions of the cochlear nuclear complex are made from reconstructions on glassplates. The sections were depicted on glass and put together in the right sequence and at regular distances.

Almost all lesions of the cochlea have been identified macroscopically only, but B 206 and B 207 have been sectioned and stained for microscopical control.

The structure of the inferior colliculus

3

The inferior colliculus (IC) may be divided into
a. a central nucleus *b.* a lateral zone.
The central nucleus (CN) falls into
1. a dorsal part 2. a ventral part.

Although distinguishable from the IC the parabrachial area (PB) (Moore and Goldberg, 1963) is closely related especially to its lateral zone.

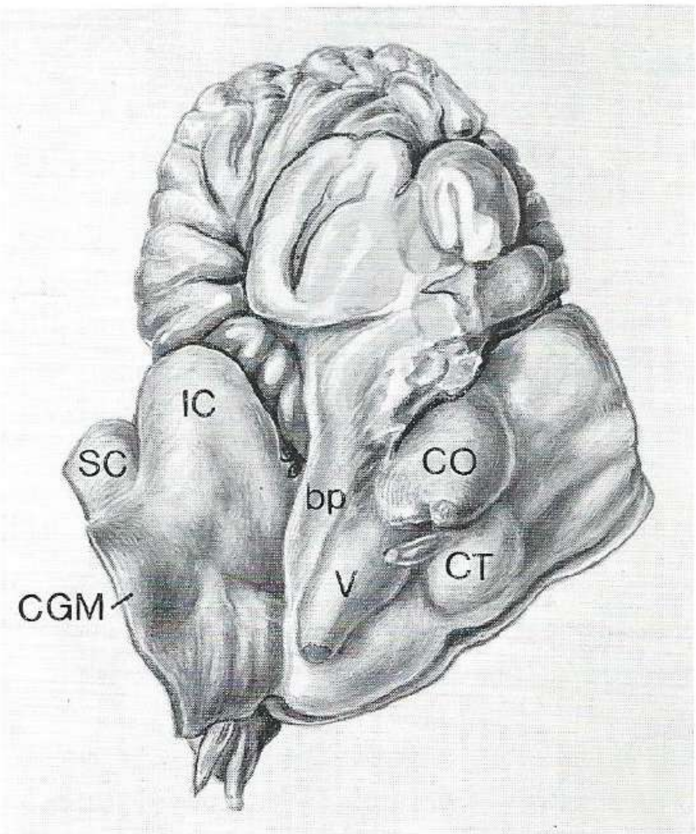


Fig. 1. Brain stem of the cat (cerebellum hemisphere partly removed) seen from ventrolaterally.

GROSS ANATOMY OF THE IC

Lateroventral view (fig. 1): After removal of the cerebral hemisphere the oval IC becomes visible. Two peduncles connecting the collicle with the surrounding structures may be distinguished; the brachium of the IC (bci) extending rostroventrally, and the lateral lemniscus extending caudoventrally. The commissure of the IC is hidden from view.

Within the collicle (fig. 2) the central nucleus (CN) appears to have a processus at its rostroventral side to be called the proc. rostroventralis. It belongs to the pars ventralis of the CN, whereas the pars dorsalis occupies the dorsal part of the CN. The boundary dividing ventral from dorsal part of the CN is schematically depicted by the oblique plane in fig. 2.

The zona lateralis is a fibro-cellular layer lateral and even laterocaudal to the CN.

Because of its intimate relationship to the IC the nucleus parabrachialis (PB) is mentioned here, but it will be described in the next chapter. Its localization medial to the brachium of the IC (bci), but lateral to the ventral part of the CN is shown in fig. 3.

MICROSCOPICAL ANATOMY OF THE IC

For the study of the microscopical anatomy of the IC several staining techniques (Häggqvist, Nissl, Klüver, Nauta) and normal as well as experimental materials have been used.

The experiments giving information about the origin and course of the fibres mentioned in this chapter will be described in detail in the next chapter.

THE BORDERS OF THE CN

Caudomedially and dorsally the CN forms the border of the IC.

Laterally and laterocaudally the zona lateralis covers the CN and its rostral border is formed by the fibres of the collicular commissure and by laterally directed fibres which join the bci. Ventrally this border gives way to the protruding proc. rostroventralis.

The CN in its medioventral part is sharply delineated by fibres nearly all from the IC itself. In its lateral part the entering lateral lemniscus makes a sharp bordering difficult. Because of its larger cells the processus rostroventralis can be distinguished from the smaller cells of the reticular substance, and is partly surrounded by tectofugal fibres.

The medial border with the small lamina of reticular substance which separates it from the central grey is sharp. Only over a small area the central grey matter and the CN meet, just caudal to the commissure of the IC. In Nauta-stained sections the border between them is occasionally difficult to recognise.

THE CYTOARCHITECTURE

The dorsal part of the CN is composed of densely packed small cells of a uniform character, more or less directed from caudoventral to rostrodorsal.

Its ventral part contrarily consists of widely spread fairly large cells without a special orientation, with a minority of smaller cells lying between them. At the entrance of the lateral lemniscus (ll) the cells lie still wider apart.

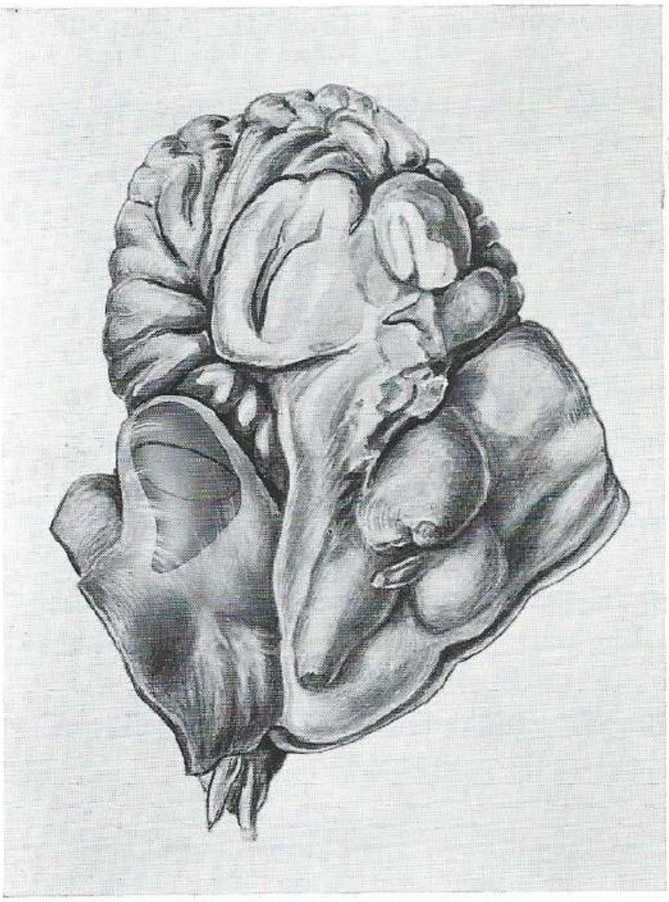


Fig. 2. Semintransparant view of the central nucleus of the IC divided in a dorsal and a ventral part by an oblique plane.

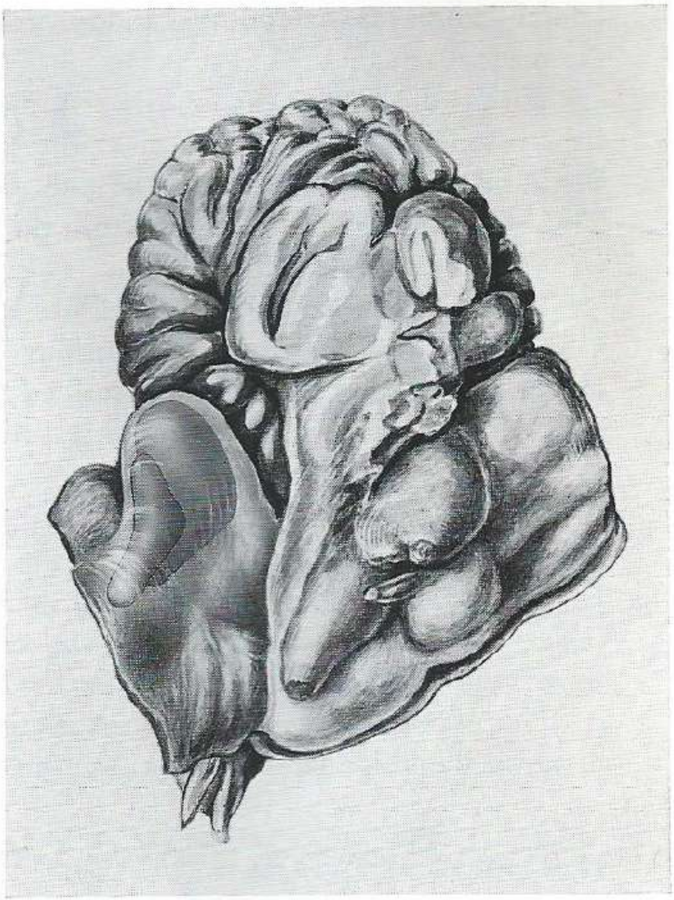


Fig. 3. The parabrachial nucleus is here depicted laterally to the central nucleus.

The lateral zone: This complex area is composed of

1. The bci.
2. A fibrocellular layer medial to it and lateral to the CN which rostrally merges with the PB.
3. A fibrocellular area with thin fibres and small cells caudaolaterally in the IC also found lateral to the ll.
4. A few very large cells (the largest found in the IC) caudolaterally in the ventral half of the lateral zone. They are surrounded by fibres on their way to the bci.

Ad 1. Between the fibres of the bci small flat cells are found.

Ad 2. Different types of cells can be distinguished in this layer.

It is characteristic that no lateral lemniscus fibres terminate there, which gives this zone a deeper blue aspect in Häggqvist-stained material than the ventral part of the CN which is the only endstation of the ll, as will appear below.

The fibres of the IC: the lateral half of the IC is covered by a layer of thin fibres, which becomes thicker from medial to lateral. Nearly all these surface fibres enter the bci

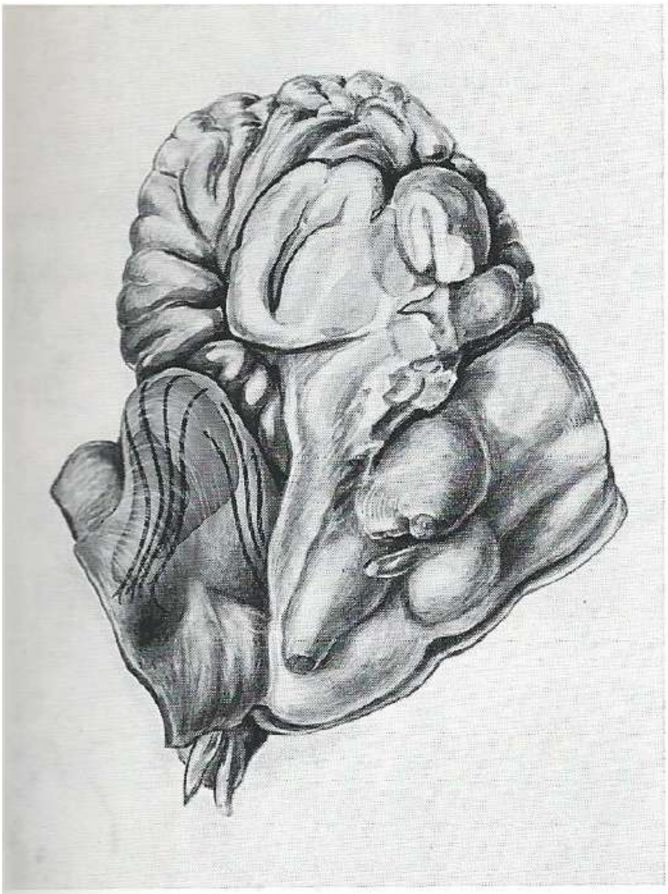


Fig. 4. Superficial efferent fibres running from the IC ventrorostrally to the CGM and ventrocaudally (recurrent fibres).

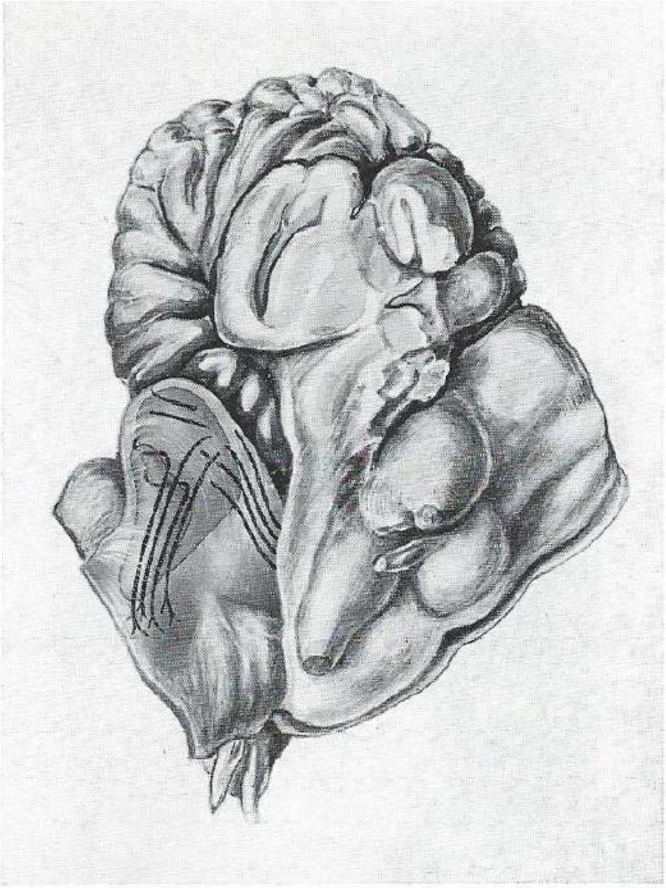


Fig. 5. Deeper layer of efferent fibres demonstrating the peculiar route of a number of them in between the CN and PB.

in its surface zone. The remaining fibres descending from the caudolateral side of the IC pass on the surface to the ll where they form an oblique bundle running to the lateral basal pontine nuclei (fig. 4). Under these surface fibres a deep-set fibre system is found taking a different course and apparently avoiding the area where the ll enters the IC. The majority of the cells in the medial half of the IC send their axons rostrally around the entering ll. Within the lateral zone two ways can be followed, either rostrally straight into the bci or first curving caudoventrally and subsequently rostroventrally again. In this way they run in the same direction as the bci and join it in its medial part. These caudally curving fibres caudally border the PB (see fig. 5).

The minority of the cells in the medial part of the IC send their axons caudally around the entering lemniscus and subsequently join the bci.

The cells homolaterally projecting in the lateral half of the IC send their axons straight laterally. A series of horizontal sections through the IC may elucidate this description (fig. 6).

With the aid of diagrams (fig. 6) the IC will be described in horizontal sections from dorsal to ventral.

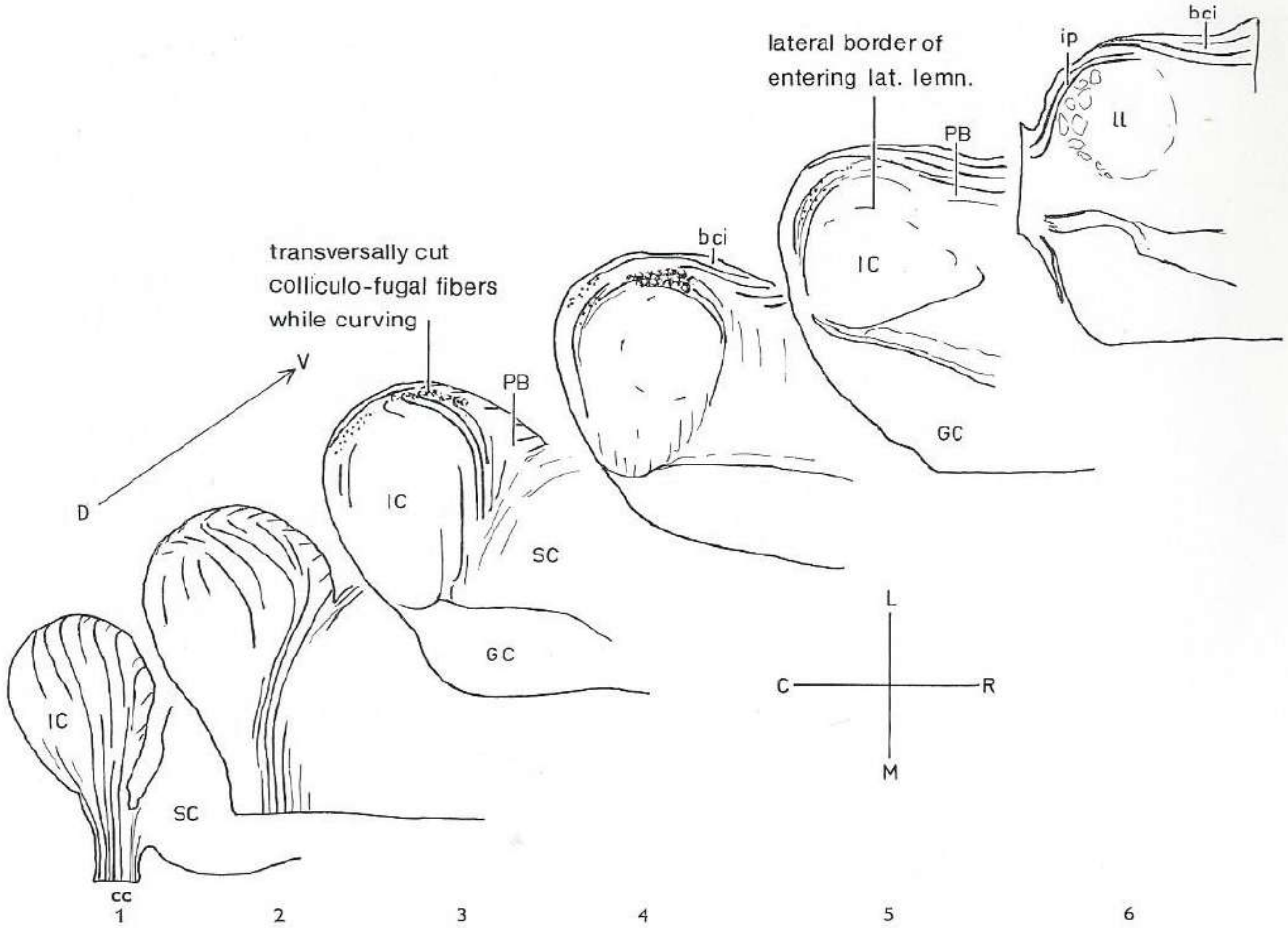


Fig. 6. Horizontal section through the IC. Demonstrated is the course of the efferent fibers.

The first diagram (fig. 6) shows the fibres of the commissure of the IC (cc) partly running laterally to contribute to the surface fibre layer of the IC partly entering the grey substance of the IC, and either originating or terminating there. The same holds good for the fibres of the surface fibre layer seen in the caudal half of the IC.

The second diagram demonstrates that fibres originating rostrally in the IC necessarily curve caudoventrally to enter the bci.

In the third diagram these fibres are also visible, with the PB located rostral to these curving fibres. At the caudolateral side of the IC small transversally cut fibres descend along the lateral side of the ll.

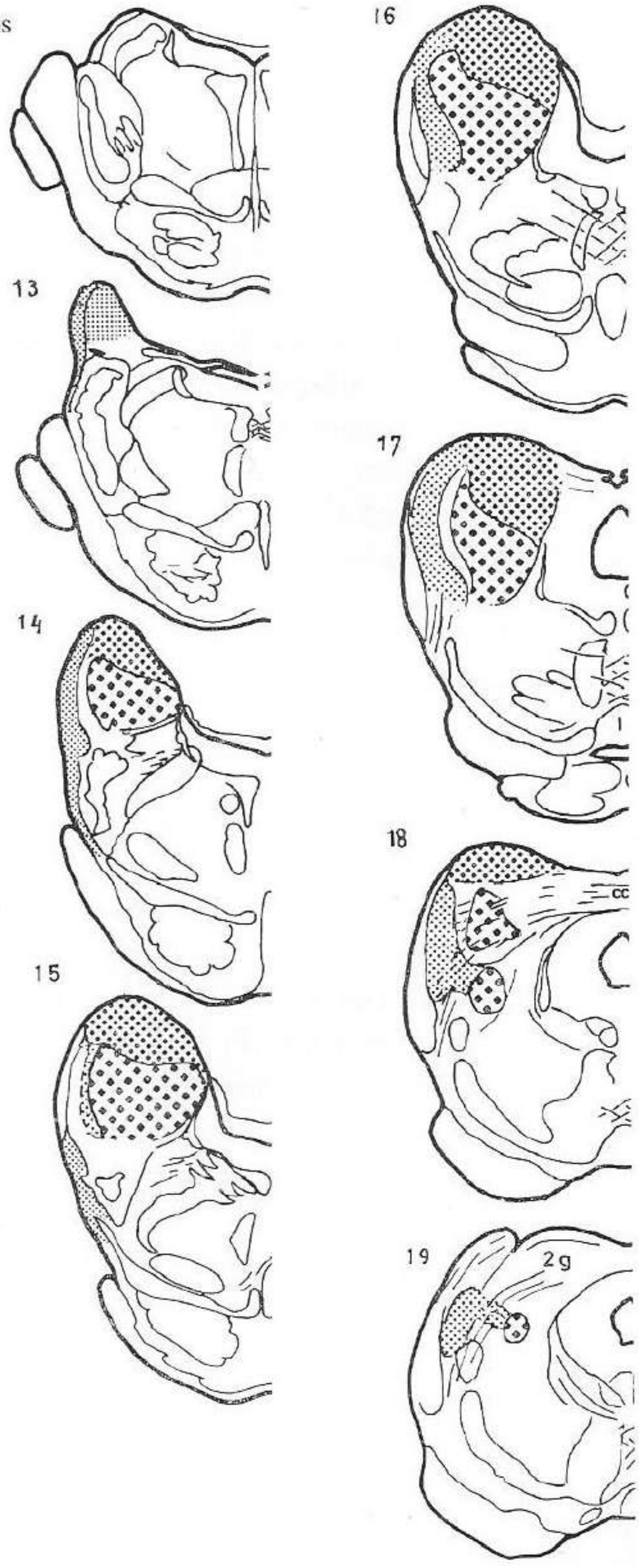
In diagrams 4 and 5 longitudinally sectioned rostrally directed fibres running along the caudal and lateral sides of the entering lemniscus may be observed. In diagram 5 the processus rostroventralis is visible.

In diagram 6 the ll is seen and at its laterocaudal border the isthmoperipeduncular bundle (ip). This bundle will be described below.

TRANSVERSAL SECTIONS (CAUDAL TO ROSTRAL, FIG. 7):

Diagram 13: The lateral zone of the IC contains the same type of cells as those found lateral to the ll, but medially in the IC the cells stain paler and are slightly smaller and

Fig. 7. Transversal sections demonstrating the subdivisions of the IC.



this part should probably be differentiated from the area lateral to it. The fibres in this section run in two different directions mainly.

1. From the top of the IC fibres stream lateroventralward, partly passing caudolaterally along the ll, partly travelling rostralward to form the bci.

2. The other group of fibres derives from the medioventral part of the IC, and

forms the fibre layer that gives the ventromedial border its sharp outline. At more rostral levels the fibres pass laterodorsally to concentrate between the lateral zone and the CN.

Diagram 14: The lateral zone still resembles the area lateral to the ll. It contains fine fibres descending from the dorsal part of the IC, mixed with scattered cells. Medial to this zone a fibre layer is found, of which the origin has been described under 2 in diagram 13. A remarkable feature of this fibre layer is the presence of a small number of large cells (in fact the largest of all the cells in the IC) isolated among the surrounding fibres. These cells are also present in diagram 15 and in diagram 16. Medial to this fibre layer the area of termination of the ll, in casu the ventral part of the CN is seen. Its cells are wider apart and the presence of larger cells allows a differentiation from the dorsal part of CN which is crowded with small cells. In the dorsal as well as the ventral part efferent fibres run laterally, whereas dorsally only small and ventrally also coarse ones are present. The same differentiation of dorsal and ventral part is found at the more rostral levels.

Diagram 15: The lateral zone is now occupied by fibres of the bci. Medially we can distinguish the fibres originating in the ventromedial part of IC (see description diagram 13. 2, pag. 9), that have taken the caudal course to the lateral side. At the level of this diagram these fibres are incorporated into the bci.

Diagram 16: Between the bci and the ventral part of the CN we find a zone of grey matter with various kinds of cells, which do not differ from those of the ventral part of the CN. The zone looks different, however, because the lemniscal fibres do not enter it. At more rostral levels the zone has the same appearance, and more caudally in diagram 15 it is just visible as a small zone still lateral to the CN.

At all levels the ll fibres radiate from the entrance dorsalward into the ventral part of the CN.

At the present level and at that of diagram 17 only a few efferent fibres in the ventral part of CN run from the medial part lateralward. This gives the impression that the efferent fibres avoid the area where the lemniscus enters and run caudal as well as rostral to this area. From the dorsal part many thin fibres still pass laterally to enter the bci. Some of them constitute the surface fibre layer of the IC, but others pass straight lateralward through the top of the ventral part.

Diagram 17: Medial to the ventral side of the bci tectopontine fibres occupy a small area, dorsal to which the lateral zone of grey matter is seen which does not take in endings from the ll. It is sharply separated from the ventral part of the CN by a concentration of fibres which originate in the medioventral part of the IC and run the rostral pathway to the bci. As mentioned before these fibres curve caudally before entering the bci in which action they are found in this section. The ventral part of the CN has a curved outline, its lateral side nearly reaches the top of the IC but its medial side does not reach dorsally beyond the level at which the central grey matter and the IC touch. The dorsal part occupies the mediodorsal area.

Diagram 18: Medial to the bci a zone of grey matter is found which corresponds to the parabrachial region of Moore and Goldberg (PB). This name could also be applied to the corresponding area in diagram 17 and 16 which also lies medial to the bci and from the IC receives a projection of the same type as the parabrachial region of diagram 18 as seen in degeneration experiments. It will, however, be less confusing to call the region rostral to the "recurving fibres" (see fig. 4) the PB, and the region caudal to them the lateral zone of the IC.

Medial to the PB in section 18 we find the recurving fibres which in diagram 17 form the sharp border between the ventral part of the CN and the lateral zone of the IC. Ventrally the fibres originating in the superior colliculus (SC) form the tectopontine bundle. Dorsomedially to this bundle the caudalmost cross-section of the processus rostroventralis is seen. It has the same cytoarchitecture as the ventral part of the CN.

Dorsal to this structure and separated by passing fibres (tectopontine and commissural fibres) one may observe a small area of grey matter still belonging to the ventral part of the CN and containing smaller cells than those found in the processus rostroventralis. The most dorsal area in this section is occupied by the rostral end of the dorsal CN.

Diagram 19: The PB is almost separated from the rostral pole of the processus rostroventralis by tectopontine fibres.

Dorsolaterally the fibres from the top of the IC, many of them commissural fibres, run rostralward.

DIAGRAM OF SAGITTAL SECTIONS (LATERAL TO MEDIAL, FIG. 8):

Diagram 14: In this section we find between the fibres of the bci a number of small cells and a few medium-sized ones forming part of the parabrachial region. Ventrocaudal to the bci and lateral to the ll small cells of the same type as those found caudal to the IC in section 15 may be observed. The larger cells of the nucleus parabigeminalis sue nucleus paralemniscalis (PL) are clearly distinguishable from the surrounding cells.

In diagram 15 the picture becomes more complicated. The PB is reduced to the triangle rostral to the IC and the fibres seen in front of this triangle do not belong to the bci but to the lateral tegmental tract described by Morest (1964). The border between the PB and the IC is formed by the transversally cut fibres coming from the medial part of the IC along its rostral site and recurving rostroventralward in its lateral part, but it is not sharp. Besides, the portion of the IC caudal to this border, corresponding to the "lateral zone of the IC", has the same appearance as the PB and can be distinguished in the same way from the central nucleus of the IC by the absence of terminations of the lateral lemniscus. At the caudal side of the IC a small fibre area is found. From the dorsal part of this area we can trace fibres running obliquely to the dorsal side of the IC, to join the bci at its dorsal and lateral side, whereas the fibres from the ventral part enter more ventrally and medially. Between the last-mentioned fibres very large cells are found. There are only a few of these but they are conspicuous because of their isolated position amidst the fibres.

Fig. 8. Sagittal sections demonstrating the subdivisions of the IC.

Caudal and dorsal to this fibre area the small cells and fibres of the surface extreme zone of the IC are seen. Some of these fibres turn ventrocaudally lateral to the ll, the others pass rostrally to form a component of the bci.

Diagram 16: The parabrachial triangle in this section is in part occupied by ventrocaudally directed tectopontine fibres. In small bundles transversally cut fibres from the IC penetrate these homolaterally descending tectal fibres. They inter-connect the PB and the processus rostroventralis.

Diagram 17: The triangle rostral to the IC is divided into two parts. The tectopontine fibres form a fairly sharply bordered area at its dorsorostral side. Its ventral part is formed by the lateral side of the processus rostroventralis, which cannot be sharply distinguished from the beginning of the deep layer of the IC also present here. The transversely sectioned fibres, which form the border between the parabrachial triangel and the IC are collected in a bundle, the "rostral collection of fibres". They originate partly in the homolateral IC and partly in the contralateral one. Caudal to this bundle the ventral part of the CN is seen in which the lemniscus lateralis ends. The dorsal part of the CN is distinguished by the oblique fibres and the absence of lemniscus lateralis endings.

Besides, its cells are smaller and more closely packed.

Caudally the central nucleus is sharply bordered by a "caudal collection of fibres", similarly destined to enter the bci. In the caudal part of the CN we find scattered fibres, which are going to join the "caudal collection". On the surface of the IC the thin-fibered layer is still found, attenuating medially.

Diagram 18: The processus rostroventralis can be differentiated from the grey substance dorsorostral to it, which has been called the deep grey matter of the SC (3g). The stratum lemnisci — the second white layer — becomes clearer (and farther separated from the IC).

The border between the rostral collection of fibres and the dorsal part of the CN is indistinct. The ventral part of the CN is situated between the rostral and the ventral collections of fibres. There are only few fibres running lateralward in the ventral part of the IC. It would seem, therefore, that before joining the bci the efferent fibres of the IC prefer either the rostral or the caudal collection of fibres, thus evading the central part of the IC where the lateral lemniscus enters.

Diagram 19: The processus rostroventralis which also receives afferents from the lateral lemniscus, is clearly visible as an area with large cells. The surface fibre layer which becomes thinner and hard to distinguish in this section is about to disappear.

Diagram 20: A remarkable feature in this and more medial sections is the change of place of the caudal fibre collection which now lies caudoventral to and in more medial sections comes to lie ventral to the CN, where it is responsible for the sharp ventral border of the IC.

Diagram 21: The processus rostroventralis becomes less protruding.

Diagram 22: For a good understanding of the structure it is necessary to keep in mind that the composition of the rostral collection of fibres changes from the lateral part to the medial part. In the lateral sections it is almost entirely composed of fibres from the IC of the same side, but medially the number of commissural fibres from the contralateral collicle increases. More medially the caudal collection of fibres, now located ventral to the IC, diminishes in size. The border line between the dorsal and the ventral part of the IC keeps its place.

Diagram 23-27: More medially the dorsal part is the last part to disappear.

DISCUSSION

The subdivision of the IC mentioned above and the one suggested by Cajal (1955) by means of Nissl, Weichert-Pal and Golgi-stained sections of adult and new-born mice, dogs and cats have certain points in common.

His "central nucleus" corresponds to my "ventral part of the central nucleus" (CNv) as far as its cytoarchitecture is concerned. The borders in his drawings and descriptions, however, are quite different.

The "lateral zone" is comparable in both subdivisions.

Cajal's "roof of the IC", however, differs entirely from my "dorsal part of the central nucleus" (CNd). Where he describes a lamination in 4 layers I find a homogeneous population of small cells. The ventral border of "the roof of the IC" [only one picture (Cajal 1955 fig. 110) indicates this subdivision fairly rostral in the mesencephalon] is not well-defined. Goldberg and Moore (1967) avoid to speak of this dubious "roof of the IC". Cajal does not distinguish the nucleus parabrachialis.

The main problem in subdividing the IC was not to distinguish a dorsal and a ventral part in the CN, but to delimit the lateral zone (LZ). The composition of this area changes continuously proceeding rostrally.

Bci fibres pass through it and collect in its lateral part. The lateral zone gradually merges with both the PB and the CNd. The borders between these structures have been determined arbitrarily.

The afferents of the inferior colliculus

4

A DESCRIPTION OF THE LOWER AUDITORY CENTRES AND THEIR ASCENDING AND RECURRENT FIBRE CONNECTIONS

INTRODUCTION

As is generally known the IC receives the majority of its afferents via the lateral lemniscus, a part of the classical auditory system, already studied by von Monakow (1890), Held (1891), Cajal (1952), Woollard and Harpman (1939), Rasmussen (1946), a.o. A detailed study of the components of the auditory system paying special attention to the tonotopic relations, however, is still lacking.

For practical reasons the cochlear nuclei will be described first, followed by the experiments with lesions of the cochlea. Subsequently the projection of the cochlear nuclei, and the connections and the structure of the corpus trapezoideum, the superior olive, the preolivary nuclei, the nucleus of the corpus trapezoideum and the lateral lemniscus with its nuclei will be considered. At the end of this chapter the other afferents of the IC, the fibres of spinal origin and those originating from the nuclei of Goll and Burdach will be discussed, but the descending afferents of the IC will be described in the next chapter.

To reveal the tonotopic organization of the ascending auditory system, the relation between the cochlea and the cochlear nuclei had to be studied first in this respect. As it is generally accepted that the successive tone frequencies have their own localization within the organ of Corti, small lesions of the spiral ganglion may confirm the tonotopic projection into the cochlear nuclei, electrophysiologically demonstrated by Rose (1963). Similarly the tonotopic organisation of the superior olive and the IC may be revealed with small lesions of the cochlear nuclei.

The cochlear nuclear complex

The classical two subdivisions of the cochlear nuclei, the dorsal (DC) and the ventral cochlear nucleus are morphologically well circumscribed. The latter is subdivided into the anterior and the posterior ventral cochlear nucleus (AVC, PVC) by the entering cochlear nerve (fig. 9). The dorsal nucleus can be easily distinguished by its laminated structure. Unfortunately at the meeting point of the DC, the AVC, the PVC and the cochlear nerve (VIII c) the picture is less clear, because of the entrance of recurrent fibres into the cochlear nuclear complex. Moreover the granular layer, which covers

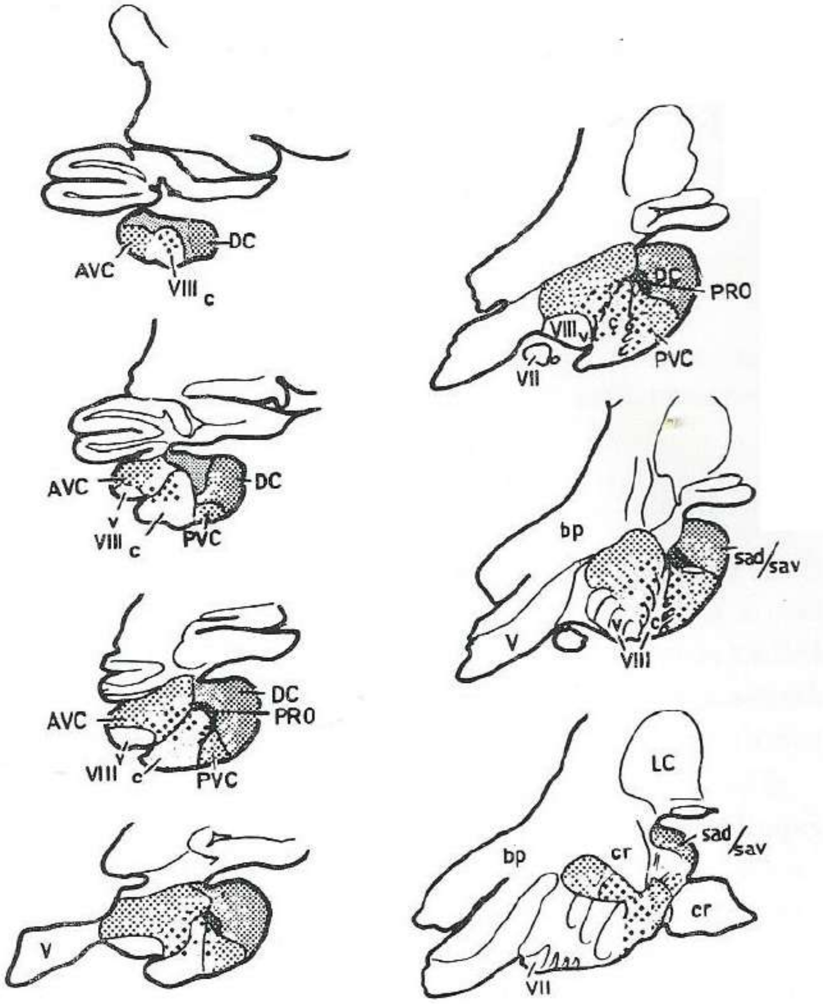


Fig. 9. Sagittal sections of the cochlear nuclear complex. Black dots indicate the different kinds of cells and their packing.

the free surface of the AVC and the PVC at this place, penetrates between the DC and the dorsal part of the PVC. At this level Winkler (1914) distinguished a nucleus proprius and Lorente de Nó (1933) a nucleus centralis.

According to Harrison and Irving (1965, 1966a, 1966b), in the rat neither their connections nor their fine structure (synaptic endings and dendrites) show the differentiation of a PVC and an AVC, as in both near the entering nerve identical areas are found.

In Häggqvist-stained material of normal nuclei the dendritic pattern, the arrangement and the sizes of their cells and the calibre of their efferent fibres can be studied, and in Glees- and Nauta-stained sections moreover the mode and place of termination of their afferents and efferents. In the present study, therefore, the subdivision of the cochlear nuclei will again be attempted with the help of these techniques.

THE SUBDIVISION OF THE COCHLEAR NUCLEAR COMPLEX (FIG. 9)

1. The rostral part of the AVC. Rostrally closely packed cells are found with small dendrites and myelinated fibres 4 mu in diameter, originating in them. In Glees-stained sections calices of Held are visible around the cell bodies and in Nauta-stains from series with cochlear nerve lesions degenerated preterminals.

2. The caudal part of the AVC and the rostral part of the PVC. In both large and middle-sized cells are found, in the latter with small dendrites, however. From both 8-12 mu fibres originate together with 4 mu fibres. Both areas are more or less connected by cells spreading mainly in the lateral part of the entering nerve, which ends on them by way of calices. Boutons in this region are very rare.

3. The caudal part of the PVC. In this part of the cochlear nuclei the cells have more and longer dendrites, mainly directed dorsomedially, and the cells are not closely packed. This type of cells is also described by Harrison and Irving in the rat.

In normal Häggqvist-stained material the stria acoustica ventralis of Held seems to originate from them. Sagittal sections Nauta-stained in lesions of the basal turn of the cochlea show a different preterminal pattern in this part of the PVC (fig. 10). The cells in the vicinity of the entering cochlear nerve receive their preterminals around their somata and the more caudal ones with the longer dendrites show preterminals running parallel to these dendrites. The fibres can be seen leaving the nerve at right angles; of these they are most probably collaterals.

In Glees-stained sections calices around these cells are not visible, but only boutons.

4. The DC. The laminated part of this nucleus consists of a surface granular layer, a layer of bipolar cells with a peripherally and a centrally directed dendrite, and a fibre layer through which the afferent and the efferent fibres run. In the surface layer small clusters of granular cells are found at different places, together with the outer dendrites of the bipolar cells, which enter this layer (fig. 339 of Cajal, 1952). The bipolar cells receive their afferents which form a terminal network around the inner dendrite and part of the soma, a.o. from the cochlear nerve.

The inner layer consisting of fibres with only a few cells spread between them, is formed mainly by the outgoing stria of von Monakow and the entering cochlear branches terminating on the bipolar cells.

5. The nucleus proprius. This nucleus belongs possibly to one of the other subgroups. Its cells are smaller than those around it and more closely packed, and there are no cochlear nerve fibres traversing it. Only cochlear fibres from the basal turn terminate in it (B 145L; B 162, fig. 10) and form a fine network around its cell bodies, but its efferents are unknown.

6. The granular layer, covering the AVC and the PVC. It largely resembles the granular layer of the DC, but both its afferents and its efferents are unknown, although Cajal supposed the thin fibres of the corpus trapezoideum to originate from it. In the granular layer of the DC on the contrary recurrent fibres certainly terminate, as will be shown later.

DISCUSSION

After Cajal, Lorente de Nó gave a detailed description of the cochlear complex of the cat using Golgi material. Thereafter only Harrison and Irving recently gave a description of the AVC and the PVC in the rat, but nobody else studied these nuclei in any other mammal.

Fig. 10. Section through the cochlear nuclear complex. Clearly visible are the tufts of preterminals rectangular to the deseending branch of the cochlear nerve in the region of the PVC. (B 162).

The subdivisions of the DC of Lorente de Nó could not be recognized, as the anatomical differences distinguished by him could not be observed. Moreover they interfere with the frequency-scale demonstrated by Rose (1963) electrophysiologically, to be confirmed anatomically in the present study.

According to Harrison and Irving fibres from the basal turn terminate in subdivisions that do not receive terminals from the apex cochleae. Besides this they found other parts receiving fibres from the cochleae but lacking a projection via the trapezoid body (ct). Apart from its consequences their intricate subdivision in the rat could not be confirmed in the cat in the present investigation.

The presence of the cells with the long dendrites in the PVC making contact with dorsally running fibres of the cochlear nerve may be explained by pointing to the triangular shape of this nucleus of which the narrow top restricts the numbers of cells finding a place within it. Probably a number of them had to move ventrally and consequently had to contact the cochlear nerve fibres by way of both a long dendrite and preterminals extending far ventrally.

The differentiation of a third group of cells in the PVC, analogous to the third group of Harrison and Irving was unsuccessful in the cat, but the nucleus proprius, not distinguished by them, may be its equivalent.

Outside the borders of the cochlear nucleus complex no cells were found between the fibres of the entering cochlear nerve.

THE TONOTOPIC ORGANIZATION IN THE COCHLEAR NUCLEAR COMPLEX

To investigate the tonotopic organization of the auditory centres, lesions had to be made step by step in the successive nuclei, beginning with the cochlea.

Therefore a number of partial cochlear lesions were effectuated (table 1), of which a part were controlled both macro- and microscopically.

Table 1. Lesions of the nervous VIII.

Series	Sectioned	Localisation of the lesion
B 63	transversal	almost totally
B 145	sagittal	basal turn
B 146	sagittal	lesion of the acoustic nerve immediately medially to the cochlea
B 159	transversal	middle turn + small part of apical turn
B 160	transversal	left side: almost totally right side: middle turn
B 206	sagittal	apical turn and part of middle turn
B 207	transversal	apical turn

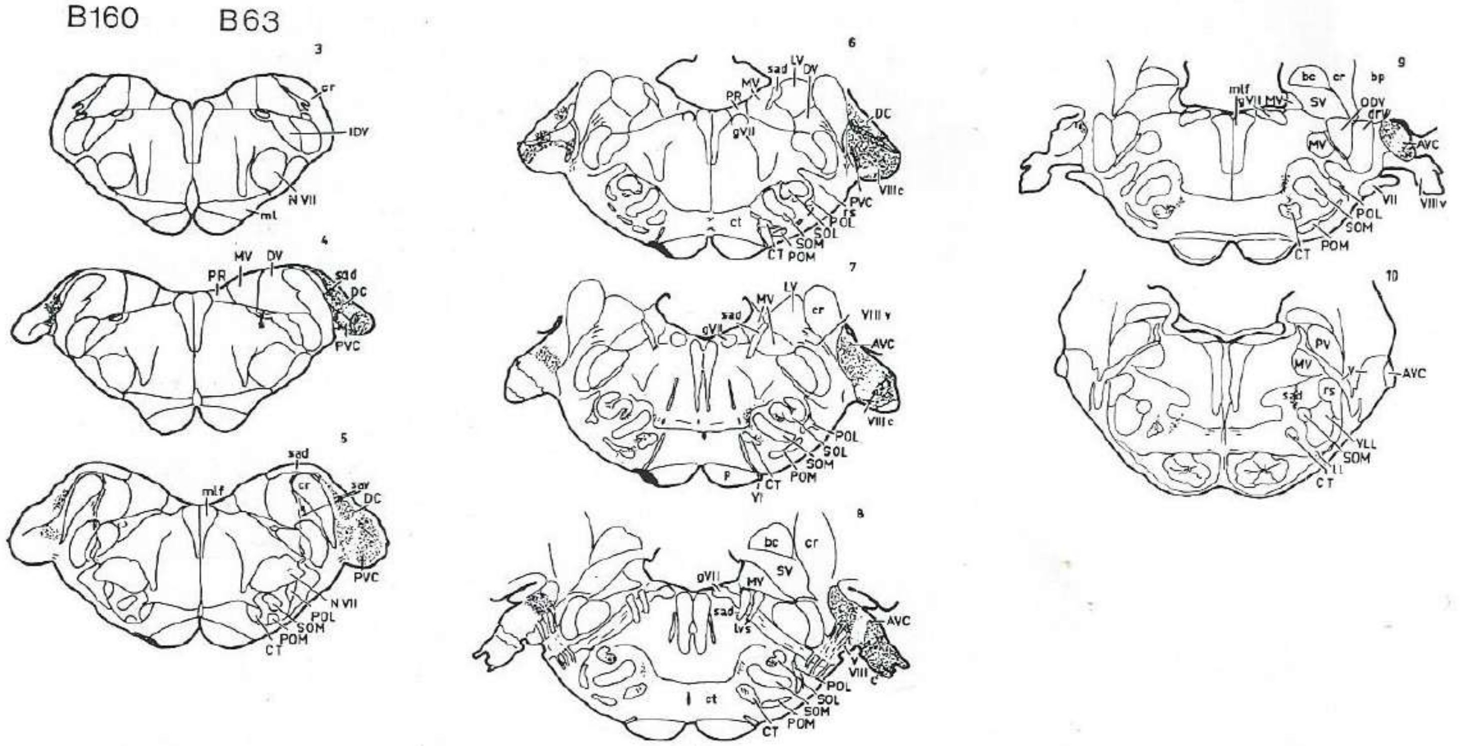


Fig. 11

Series B 160 with a lesion in the middle turn of the cochlea (fig. 11), shows that after their bifurcation the anterior branches distribute to the AVC and the posterior to the PVC and the DC. In each of these nuclei the degenerated preterminals form a band of degeneration within the sections. In the series B 63, with a lesion of the cochlea sparing part of the spiral ganglion, similar bands are seen at other places (fig. 11). A three-dimensional reconstruction of these sections demonstrates that the bands represent planes in each subdivision of the cochlear nucleus complex (fig. 12 and 13).

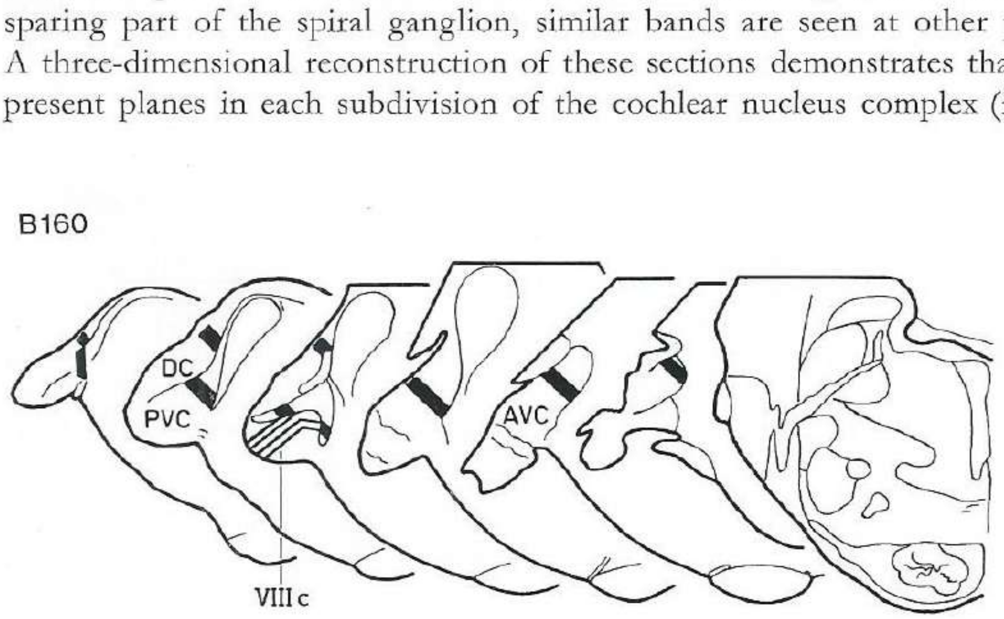
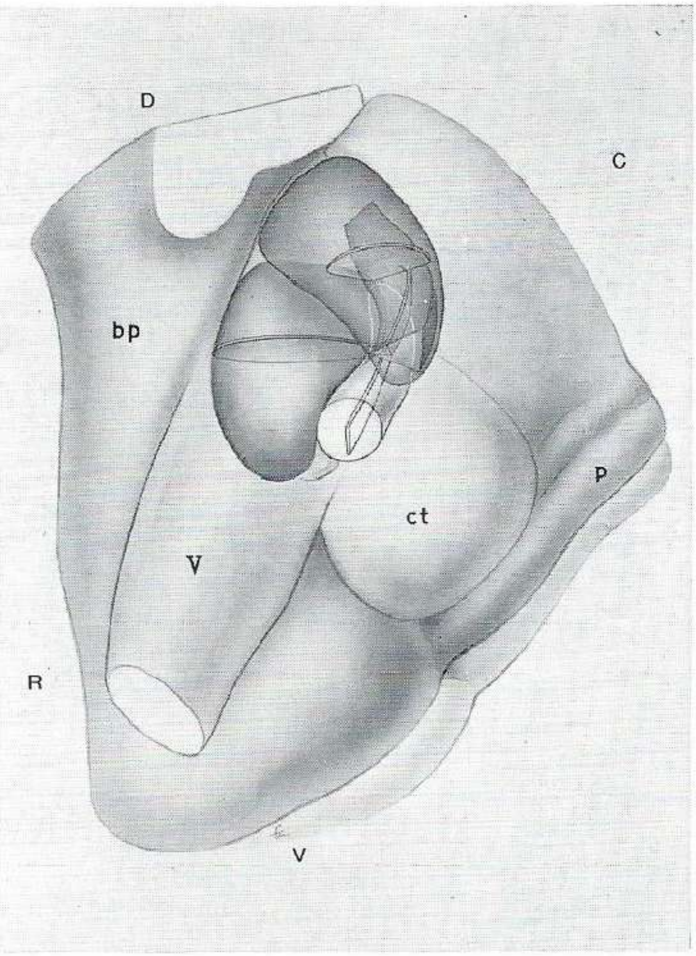


Fig. 12. Experiment B 160 R. Lesion of the spiral ganglion (middle turn). Orderly arrangement of sections of the medulla oblongata. Schematically the bands of degeneration are indicated.

Fig. 13. Semitransparant three-dimensional reconstruction of the isofrequency planes in the subdivisions of the cochlear nuclear complex.



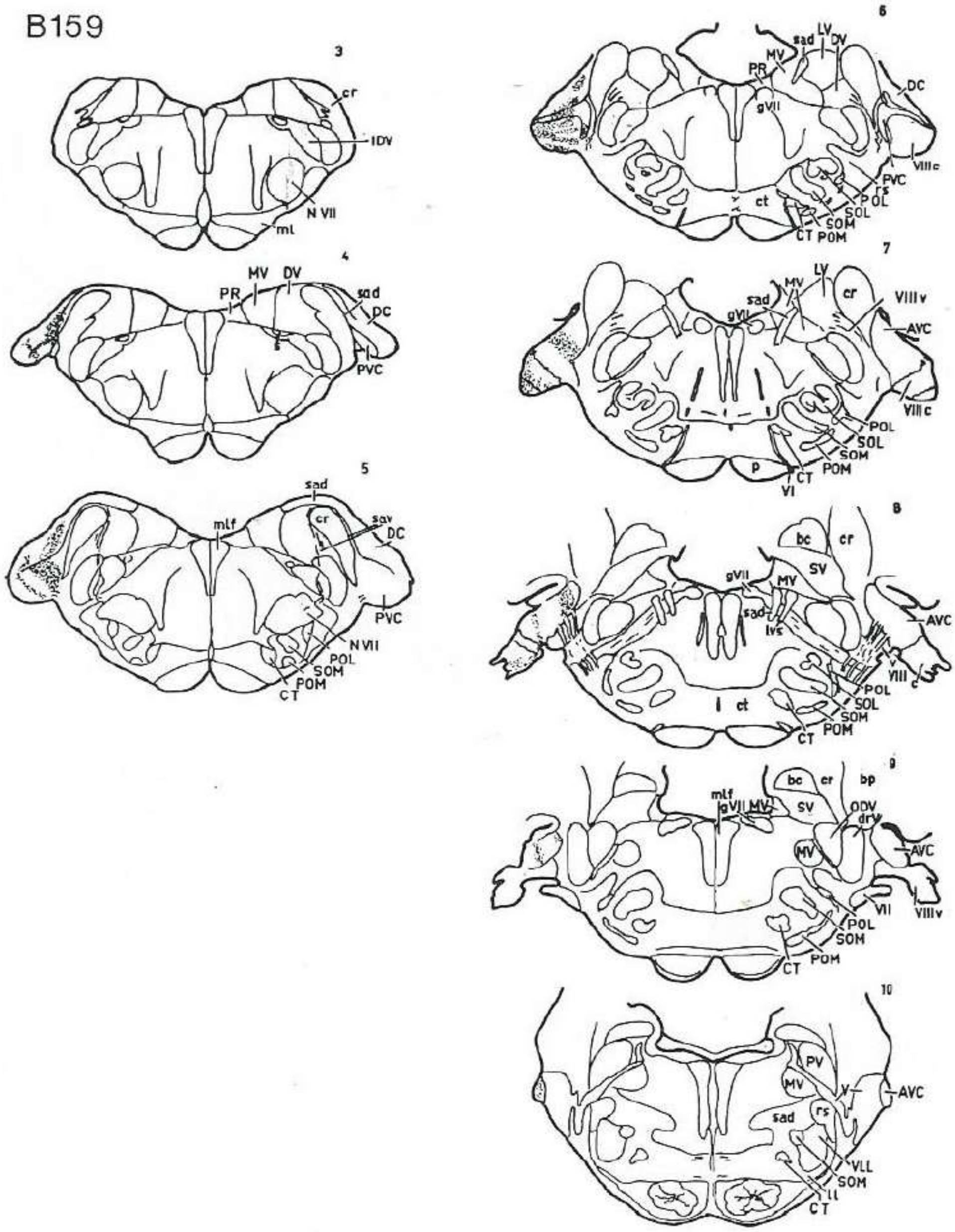
Their width seems to depend on the number of spiral ganglion cells destroyed and their place on the part of the cochlea involved, and it is obvious that they represent the areas activated by certain tone-frequencies and therefore may be called "isofrequency planes".

As soon as the branches of the cochlear nerve fibres enter one of the nuclei, preterminals are seen to fill every part of their plane, and the fact that planes in the sections are sharply bordered, corroborates the conclusion that every fibre forms a plane with its ramification. Otherwise either gaps in the surface of the plane or differences between its parts could be expected.

Series B 159 (fig. 14) in which the lesion involves not only a part of the basal turn but also destroys 10-20 ganglion cells of the middle turn demonstrates that these latter cells give rise to a complete plane of degeneration in every subdivision. The plane is thin due to the small number of cells destroyed, and the distance between the two planes corresponds to about one turn of the cochlea.

The experiments B 207 and 206 with microscopically controlled lesions of the apical part of the cochlea and B 146 R with a degeneration resembling that in fig. 14 show that the apex projects to the ventrolateral part of the nuclei, and experiment B 145 (fig. 15) with a lesion of the base of the cochlea that this part projects dorsomedially. The isofrequency planes therefore prove to be arranged from ventrolateral to dorsomedial, the latter representing the high frequencies.

Fig. 14.



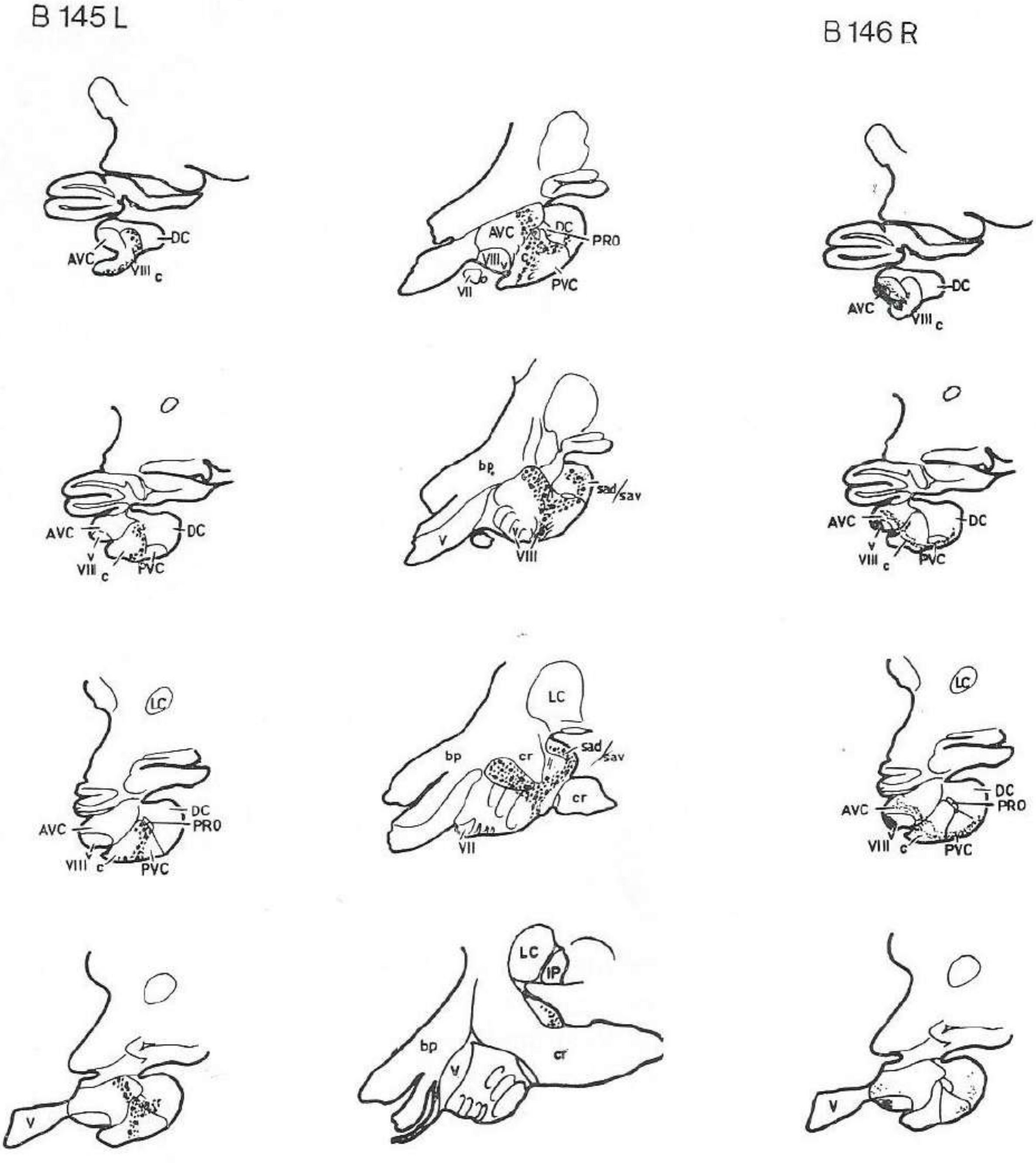
The bifurcation of the cochlear nerve fibres repeatedly described in Golgi material (Cajal, Lorente de Nó), is visible also in Häggqvist-stained sections when cut in an appropriate plane.

A node of Ranvier is usually also seen in both branches immediately proximal to the bifurcation (fig. 16).

DISCUSSION

The anatomical demonstration of the isofrequency planes is a crude representation of the way frequencies shift from ventrolaterally to dorsomedially in all subdivisions of the cochlear complex.

Fig. 15.



B 145 L

B 146 R

When this is the only way the information about frequency is conveyed to the neurons of the cochlear nuclei, those cells must be able to detect very small shifts in activity in the neuropyl.

To give an idea of the number of elements involved some data will be quoted from the work of Spoendlin 1966 and others. According to Spoendlin the internal haircells are arranged in one row, their number being slightly smaller than 3500 (p. 6). Each haircell activates about 20 spiral ganglion cells. The total number of spiral ganglion cells connected to the internal haircells is about 45000. Each spiral ganglioncell is connected with few probably only one internal haircell.

According to Schuknecht 1960 the number of fibres of the cochlear nerve activated

Fig. 16. Cochlear nerve fibres at their splitting point. Magn. 1300×.

by a tone of certain frequency depends both on this frequency and the intensity of the tone. This number at least amounts to 20 and is more likely to be 200 to 300. In the latter case 10 to 15 internal haircells around the locus of maximal excitation are activated.

The number of frequencies a cat can distinguish (Schuknecht, Spoendlin pag 68) is about 2000, a number of the same magnitude as the number of internal haircells. Because the total number of fibres in the cochlear nerve is estimated at 40,000-50,000 a shift to the next detectable frequency involves some 20 fibres. A shifting to the nearest distinguishable lower frequency activites ± 20 spiral ganglion cells on the side of the apex, while 20 spiral ganglion cells on the side of the basal turn stop being activated. In the cochlear subdivisions this change in frequency makes that 20 fibres are added to the plane on the ventrolateral side, while on the dorsomedially side it deminishes with the same number.

That this has to happen a 2000 times in the cochlear subdivisions along the ventrolaterally-dorsomedially axis in order to distinguish the whole frequency scale is amazing.

It is difficult to conceive of a neural apparatus capable of detecting differences in activity some microns apart. As yet our present knowledge of the structure and synaptology of the cells of the cochlear nuclei is insufficient to see how these difficulties are solved.

The projection of the cochlear nuclei

In normal Häggqvist-stained material three fibre systems connecting the cochlear nuclei with other structures within the central nervous system can be distinguished. The first, the dorsal acoustic stria of von Monakow (sad), consists of thin fibres and the second, the ventral stria of Held, consists of the coarse fibres located ventral to the former. The corpus trapezoideum (ct), the third system, falls apart into three components, already alluded to in the description of the cochlear nuclei.

The projection of the cochlear nuclei will be described in this order and the course and termination of the fibres originating from each subdivision will be depicted in a diagram of an imagninary horizontal plane through all auditory nuclei (fig. 20, 21, 23, 26 and 27). An impression of the total projection of the cochlear nuclei can be obtained from figure 17 (B 104) showing the degeneration resulting from a total destruction of these nuclei.

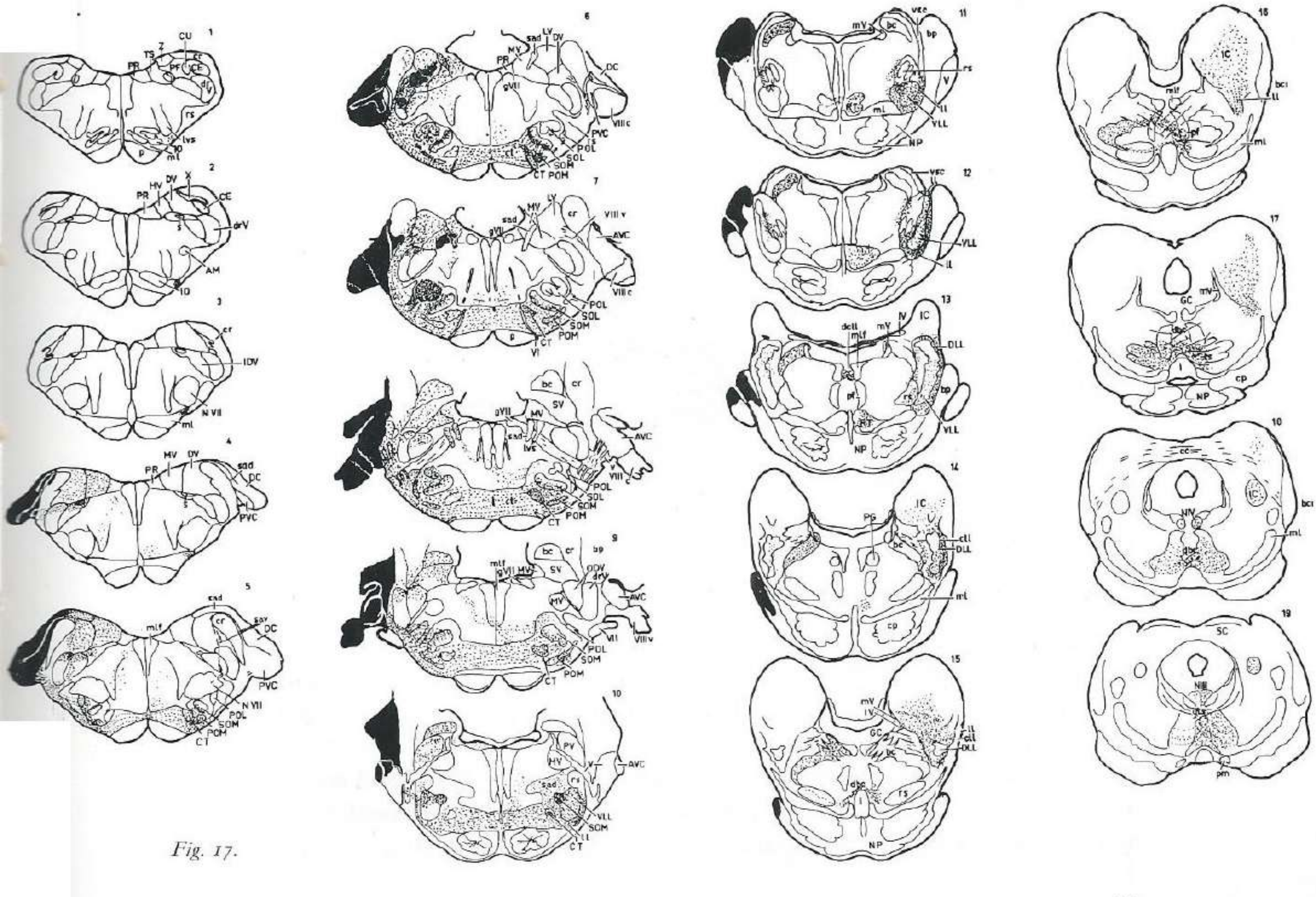
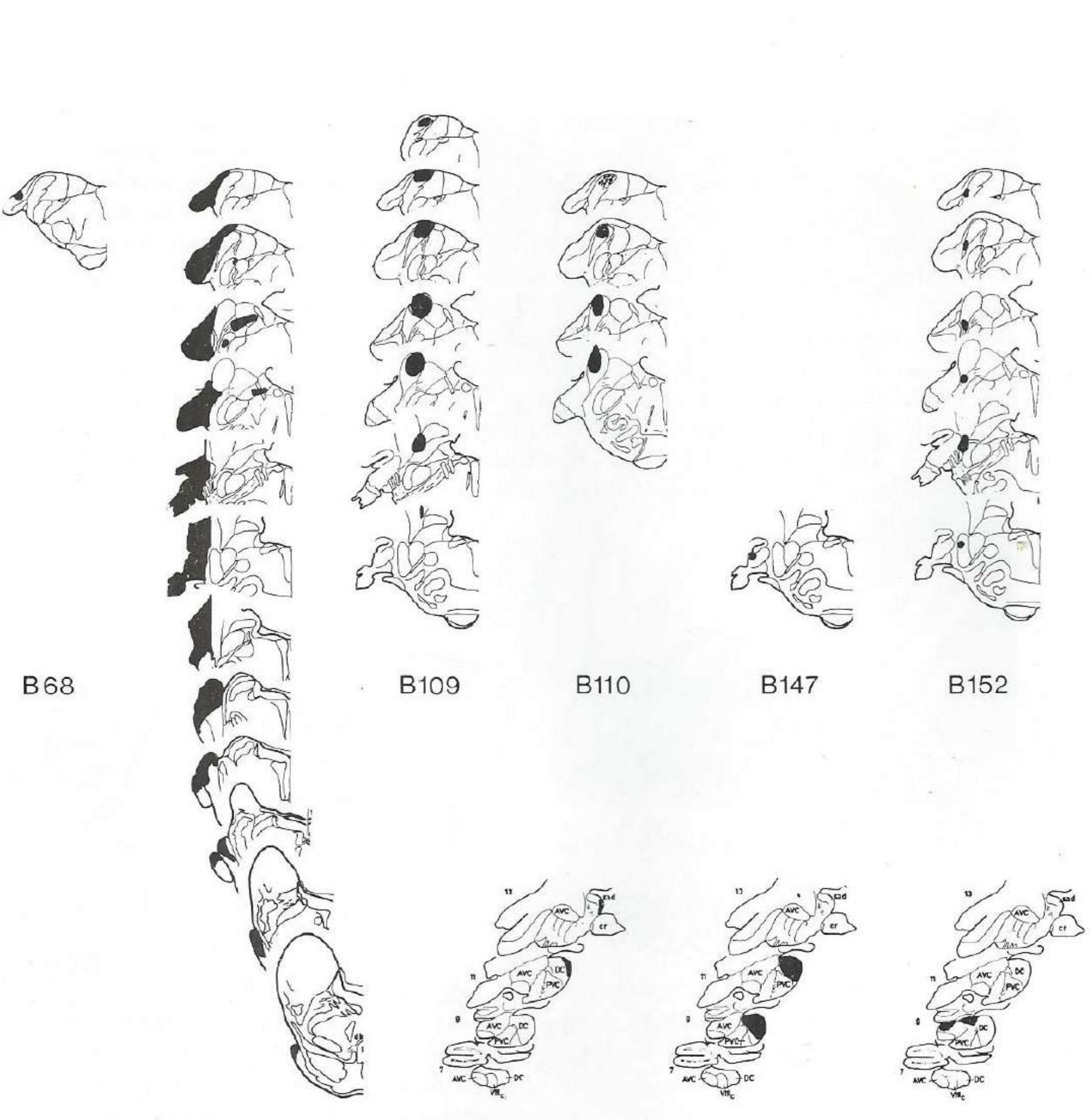


Fig. 17.

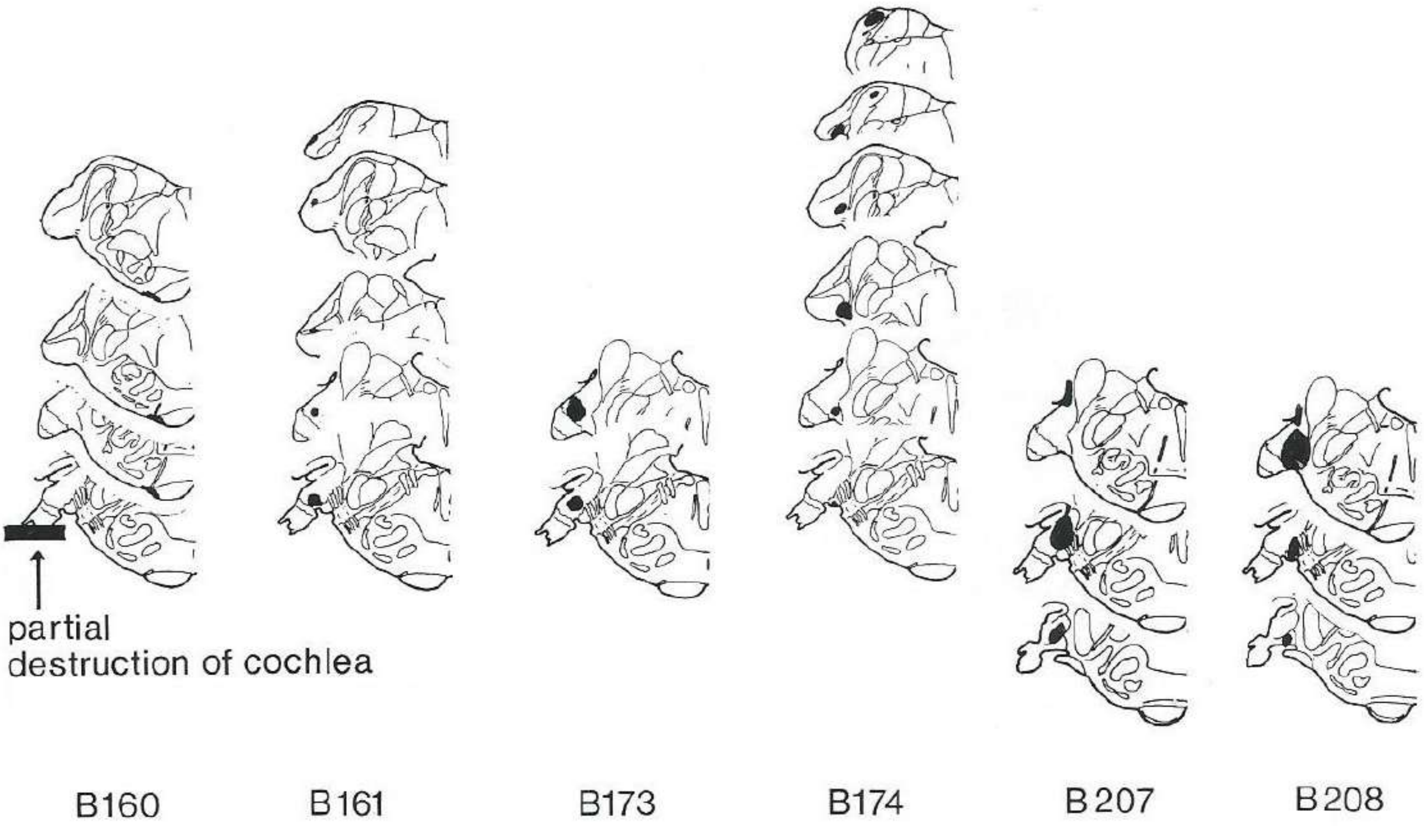


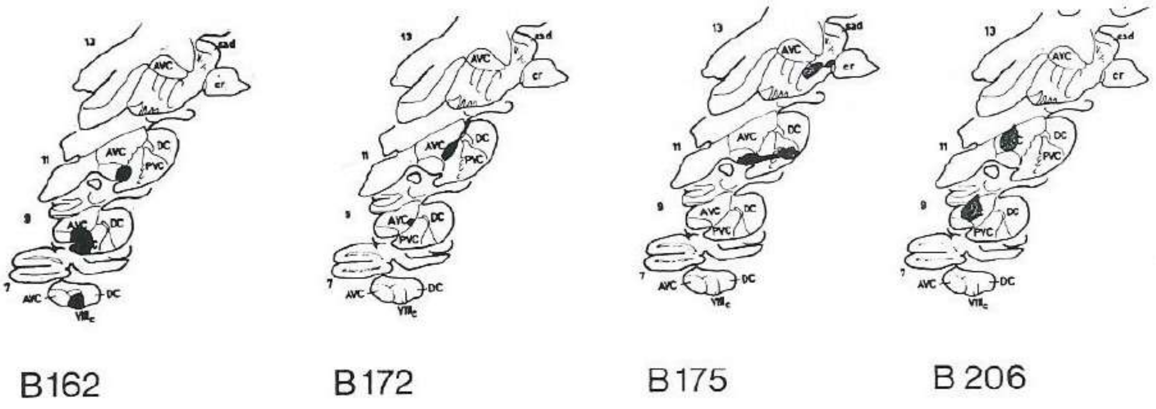
B68 B109 B110 B147 B152

Fig. 18 B104 H4746 H4763 H4832

As is generally known the superior olivary complex is located in an indentation of the dorsal margin of the ct, the fibres of the latter curving ventrally along it. It is composed of the following components:

the lateral and medial superior olives (SOL and SOM), the lateral and medial preolivary nuclei (POL and POM), the nucleus of the corpus trapezoideum (CT) and the cells located dorsomedially to the SOM.





THE STRIA DORSALIS OF VON MONAKOW, THE PROJECTION OF THE DC (FIG. 19 AND 20)

Exclusive lesions of the DC (B 68 and H 4746, fig. 18 and H 6813, fig. 28) show plainly that all its efferents run via the stria of von Monakow.

In other experiments (B 109, B 110, H 4763, fig. 18), one of which is illustrated in

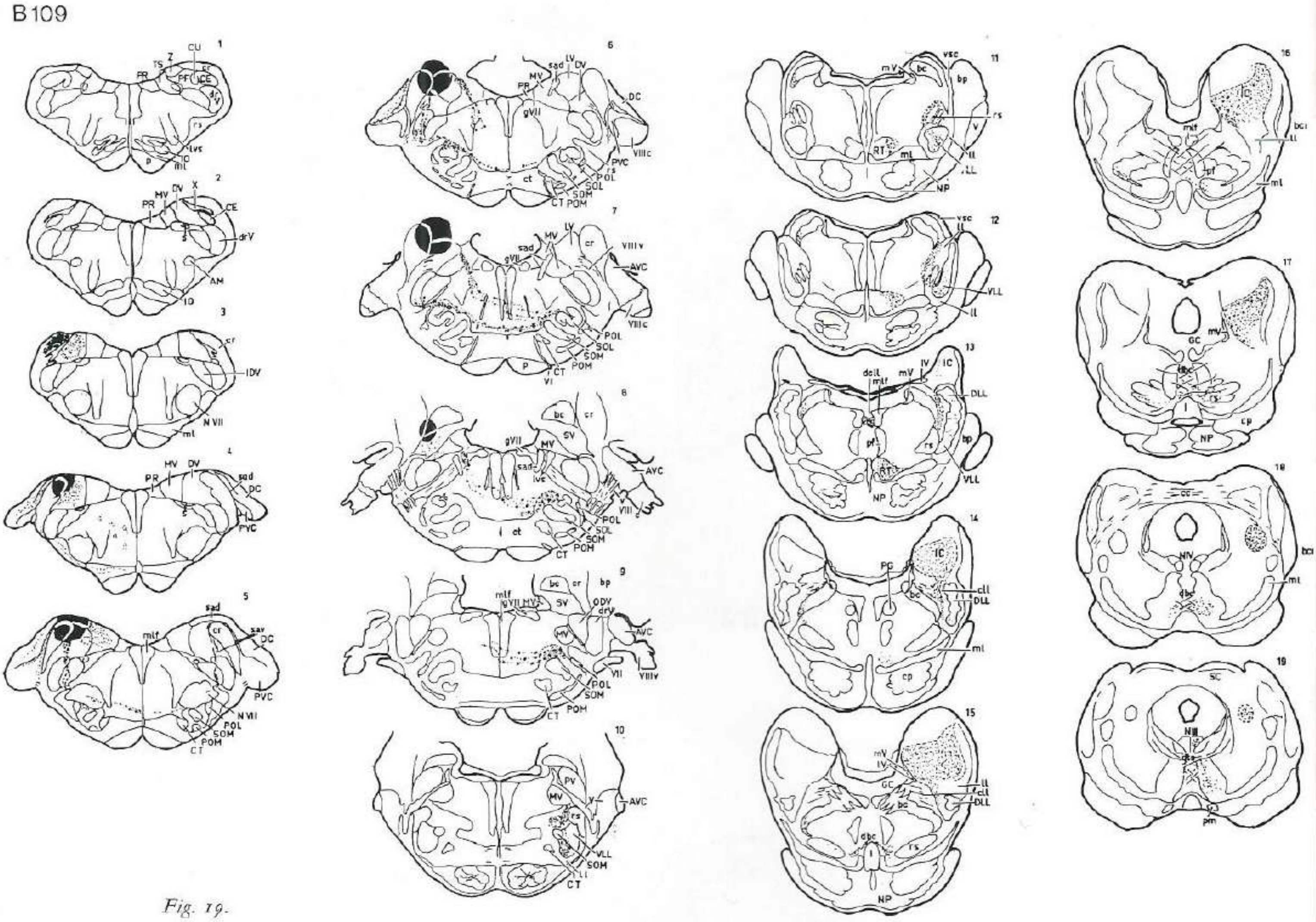
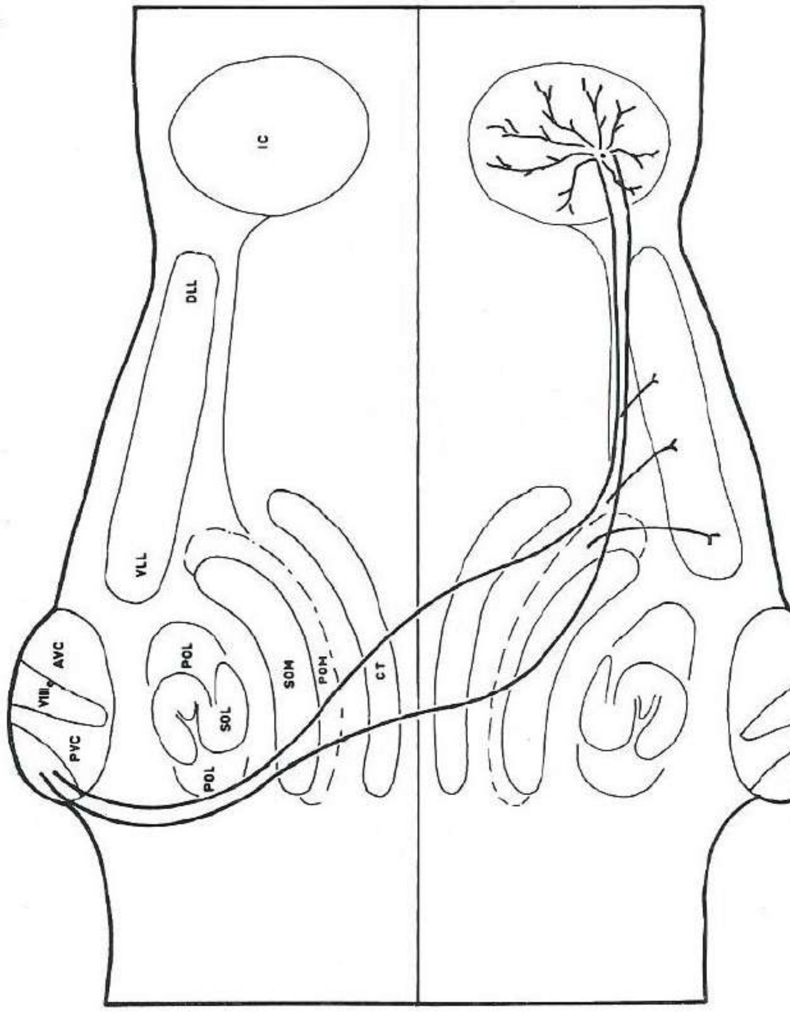


Fig. 19.

figure 19, a concomitant degeneration of the ventral stria is present due to a larger lesion. Reaching the midsagittal plane the sad bundles spread wide apart but reassemble at the medial side of the contralateral lateral lemniscus (ll), where they give off preterminals to most of the cell clusters lying between the latter's fibres. The dorsal nucleus of the ll (DLL), however, of which the border with the other lemniscal nuclei is vague, receives very few preterminals.

The remaining fibres terminate in the inferior colliculus (IC), of which the degeneration occupies the whole ventral part of the central nucleus in the cases H 4763 and B 109.

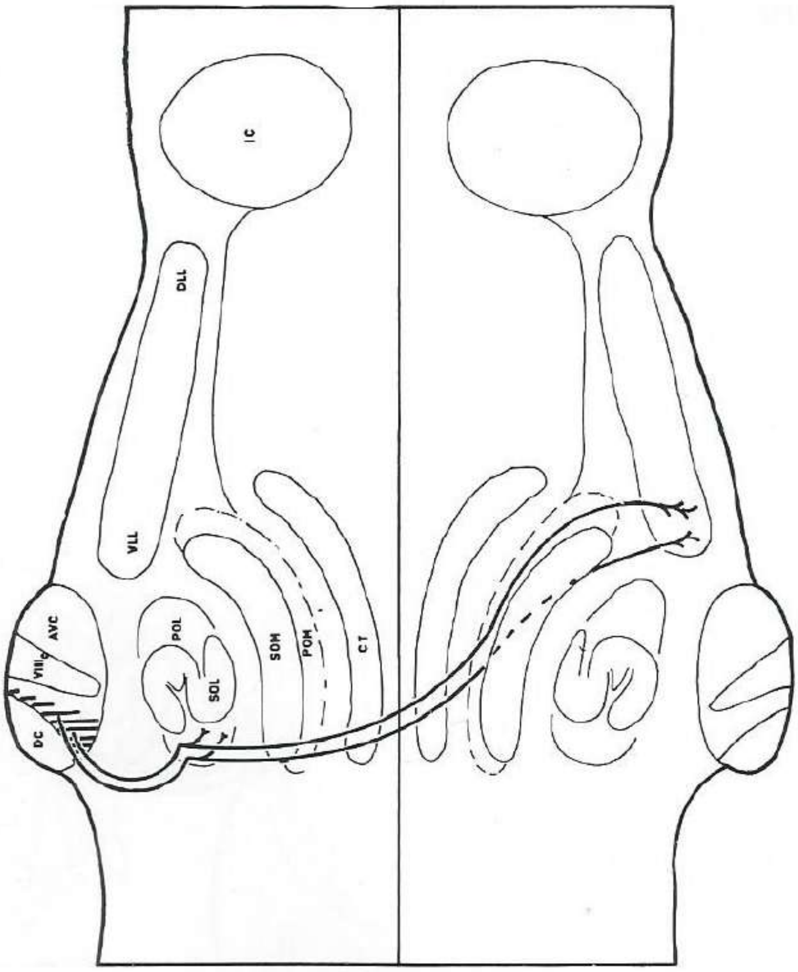
Fig. 20. Stria dorsalis of von Monakow.



THE STRIA VENTRALIS OF HELD. THE PROJECTION OF THE CAUDAL PART OF THE PVC (FIG. 19 AND 21)

In experiments B 165 (fig. 28), B 174 and B 175 (fig. 18) with lesions of the caudal part of the PVC a degeneration of the thick fibres of the ventral stria and part of the ct, but not of the sad, was obtained. Their further course and termination could be determined by a comparison of these series with those reported in the section of the sad, and of series in which the ventral stria itself was interrupted somewhere in its course (B 151, fig. 28, B 167, fig. 29). As is well known the ventral stria at once after passing along the restiform body turns ventrally. It runs along the caudodorsal side of the SOL, where it gives off a number of preterminals around the cells in its dorsal vicinity, which presumably belong to the preolivary nuclei. After passing dorsal to the SOL the fibres run along the SOM to the other side where they turn rostrally, partly along the ventral side of the SOM, partly remaining dorsal to it. They give rise to a coarse preterminal degeneration, possibly corresponding to calices, in the ventral nucleus of the ll (VLL), especially within its lateroventral part, but do not reach more rostral regions (and do not terminate in the IC either).

Fig. 21. Stria ventralis of Held.



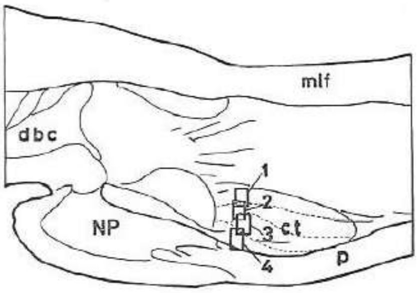
THE FIBRES TO THE CT. THE PROJECTION FROM THE AVC AND THE ANTERIOR PART OF THE PVC

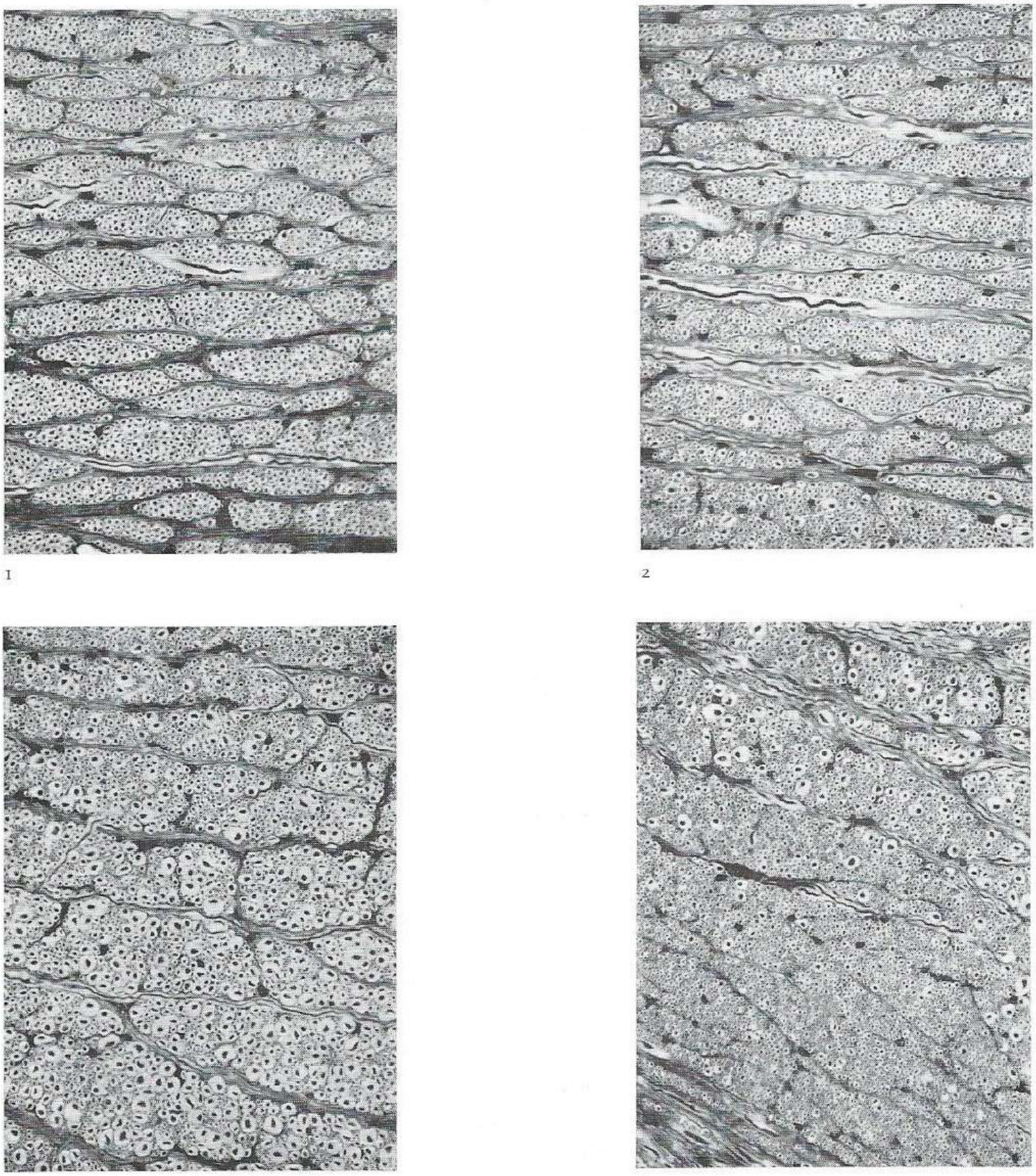
a. The fibre spectrum of the corpus trapezoideum

Except for a small number of thin recurrent fibres in the ventral surface region, all the fibres found in the ct at the midsagittal plane originate in the cochlear nuclei as will be proved presently. The different groups of fibres to be distinguished by their origin in the cochlear nuclei and their fibre pattern will be followed when shifting to their position at the midsagittal plane. Most of this shifting takes place in the lateral region of the corpus trapezoideum, close to where the ct is going to be formed. In the medial part of the cochlear nuclei middle-sized fibres (4 mu) derived from the rostral part of the AVC are located rostrally. Caudal to them coarse fibres (8-12 mu) are found, derived from the caudal part of the AVC and the rostral part of the PVC, and dorsally thin fibres (1-4 mu) some of which will prove to be recurrent ones.

The coarse fibres have a relatively uncomplicated course, as they run straight from their cells of origin to their termination in the contralateral CT. Immediately medial to the cochlear nuclei the 4 mu fibres within the ct shift to a more dorsal and caudal position relative to the coarse fibres. The thin fibres, moreover originally located

Fig. 22. Fibre spectrum in four parts of the ct.





dorsally, pass ventrally, traversing the bundles of the thicker fibres of the ct. These thin fibres thus form a surface layer over the whole caudorostral width of the ct. During their further course medially the greater part shifts to the more rostral position in which they are found midsagittally.

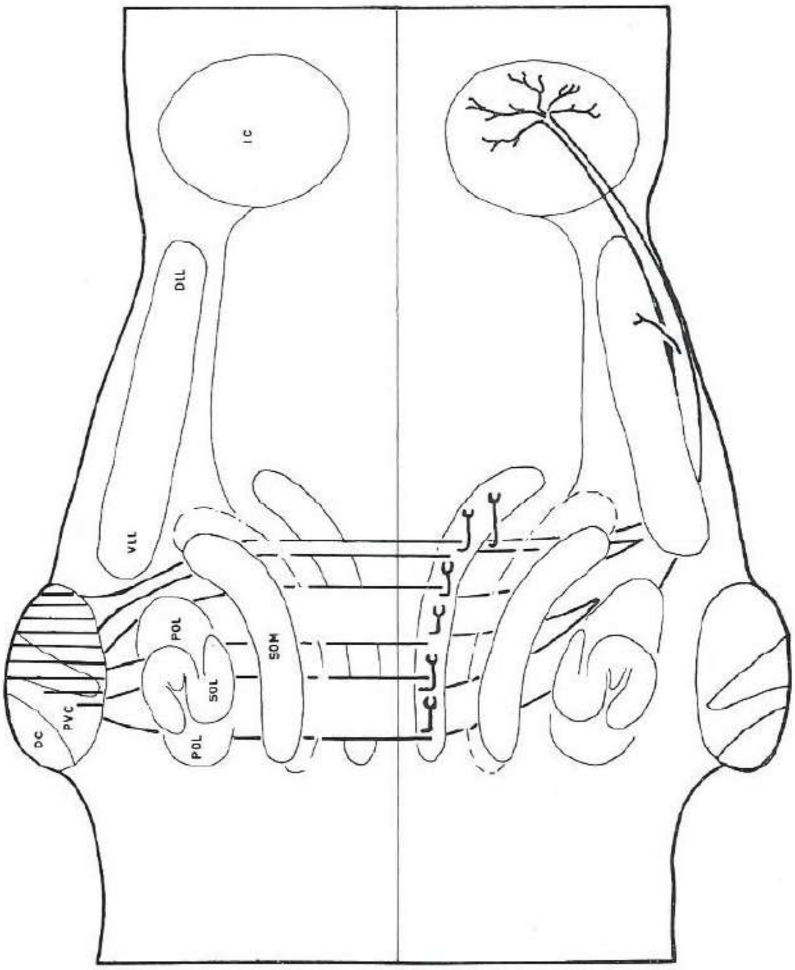
At the midsagittal plane (fig. 22), dorsally in the ct the middle-sized fibres are found. Contrary to what was observed directly medial to the cochlear nuclei, their area falls apart into a dorsal region of fibres of a very uniform calibre of 4 mu, which extends over the whole rostrocaudal surface of the ct with the greatest amount rostrally, and a more ventral layer with equally uniform but slightly smaller fibres ($\pm 3\frac{1}{2}$-4 mu) showing the same rostrocaudal extent and similarly the greatest amount rostrally. Ventral to these fibres an area with coarse fibres 8-12 mu in diameter is found, which has its greatest surface area in the caudal half of the ct, and only a few fibres in its rostral part. With these coarse fibres fine ones about 1-4 mu in diameter are mixed, which ventrally gradually increase in number and are the only ones present at the ventral surface of the brain stem. They are again most numerous in the rostral levels of the ct.

Near the cochlear nuclei the $3\frac{1}{2}$-4 mu fibres area cannot be distinguished from the 4 mu fibres area, but probably it comes into existence medial to the superior olive, by the 4 mu fibres giving off collaterals to the olive (see below), subsequently to decrease in size somewhat. In Glees-stained sections there are numerous collaterals visible ventral to the olivary complex, but the caliber of the parent fibres can be only approximately determined as around 4 mu. On the contrary collaterals of the 8-12 mu fibres could not be found, but the 1-3 mu fibres certainly give off collaterals, as is obvious in Nauta-, Häggqvist- and Glees-stained sections, although because of their tiny size the branching could not be seen.

The shifting of the fibres within the ct is shown in the following experiments. In B 172 (lesion in the caudal half of the AVC, see fig. 18), the servered medium-sized fibres causing preterminal degeneration in the caudal part of the olives, at the midsagittal plane are separated from the degenerated coarse and fine fibres. The latter shift to a more rostral position, whereas the medium-sized keep to their site in the dorsocaudal part of the ct. This shows that the rostral thick fibres originate directly rostral to the entering cochlear nerve, together with the most caudally located medium-sized ones. The most rostral medium-sized ones, spared in this experiment, originate in the rostral part of the AVC.

As is clear from the preceding description, within the ct three fibre systems can be distinguished by their fibre patterns. The efferents from the caudal part of the AVC and the rostral part of the PVC unfortunately cannot be readily distinguished, because they comprise all three calibres. The contribution of the rostral part of the AVC on the contrary consists entirely of 4 mm fibres and this contingent, quantitatively the most important, proved to be tonotopically organized (see below), but about such an organization in the other systems nothing is known as yet.

Fig. 23. Thick fibre component of the ct.



b. The coarse fibres of the corpus trapezoideum (fig. 23)

Both the anterior part of the PVC and the posterior part of the AVC send their coarse fibres directly into the ct, to terminate in the posterior and anterior halves of the contralateral CT respectively. They can be easily followed in normal Häggqvist-stained series, which show conclusively that ipsilaterally they terminate neither in the superior olive nor in the CT, but run to the contralateral side, where they curve rostro-dorsally ventral to the CT. Coarse fibres subsequently are seen entering this nucleus and terminating on its cells with a calix of Held. Series B 132 (Häggqvist-stained) and B 131, B 162, B 172 and B 55 (Nauta-stained fig. 18, 28) confirm this experimentally, although a degenerated calix could be seen neither in Häggqvist- and Nauta-stained nor in Glees-stained sections.

Unfortunately it proved unfeasible to sever the coarse fibres selectively, which precludes establishing their total termination on the CT, and leaves open the possibility that they give off collaterals and the main fibres reduced in caliber enter the ll.

Series B 161, B 162 and B 172 in which mainly coarse and thin fibres are severed (shown by the scarcity of preterminal degeneration in the SO, see section medium-sized fibres), not only shows abundant degeneration with coarse preterminals between the cells of the CT, but similarly in the ll laterally, with affected preterminals in the

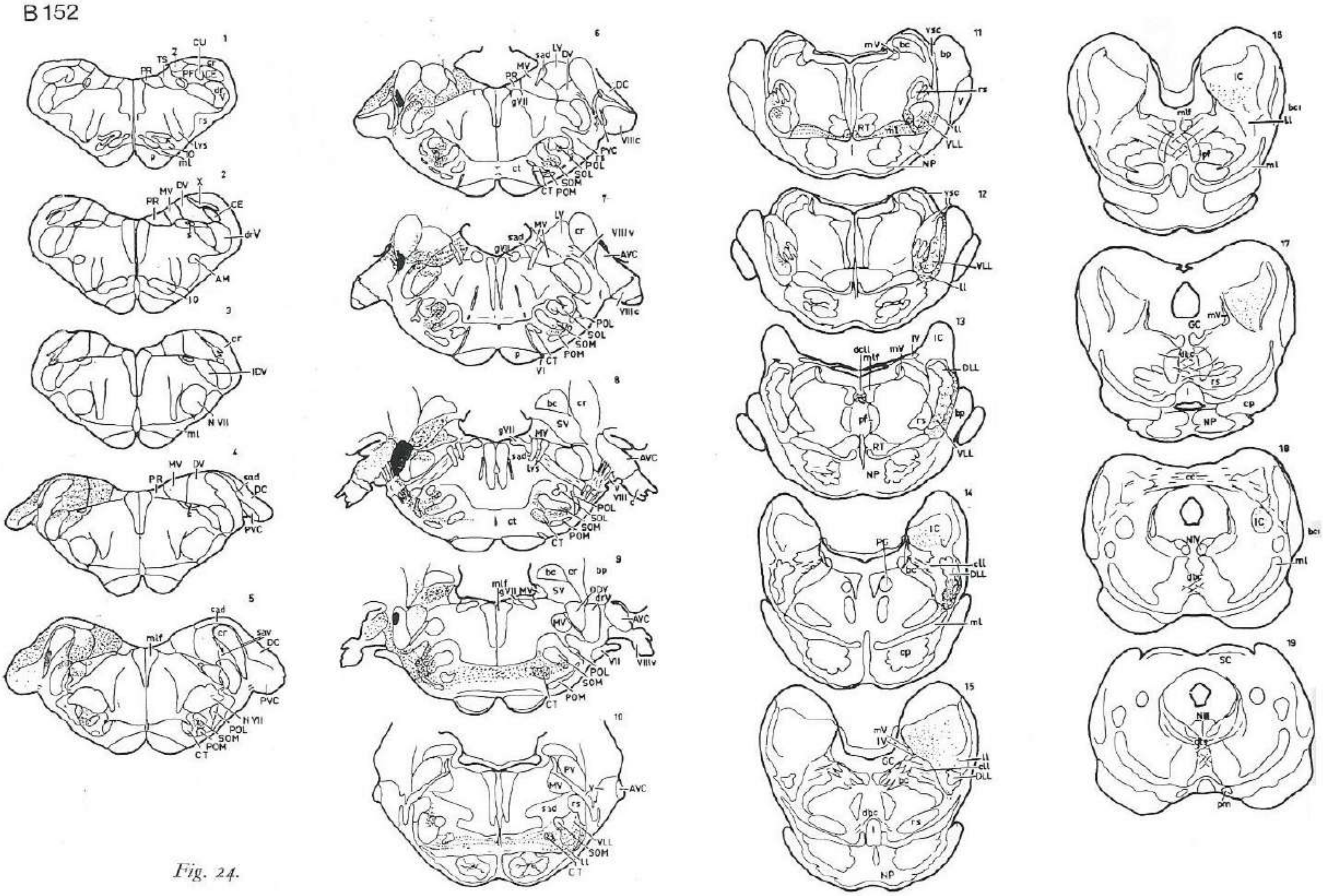


Fig. 24.

rostrodorsal part of the VLL and the rostroventral part of the central nucleus of the IC. These experiments therefore advocate the supposition, that coarse fibres give off collaterals to the CT and subsequently enter the ll, reduced in calibre.

Special attention in the present experiments was payed to degeneration within the homolateral POL, ascribed by Harrison and Irving to collaterals of the thick fibres. The fact that degeneration of the latter fibres of the ct are always accompanied by that of the superficial thin ones, makes determining the origin of the tufts of degenerated fibres, which at right angles to the fibres of the ct run to the ipsilateral POL, awkward. As most of the fibres of the tufts are derived from the surface region of the ct, they are likely to originate fromthe thin fibres.

B 147

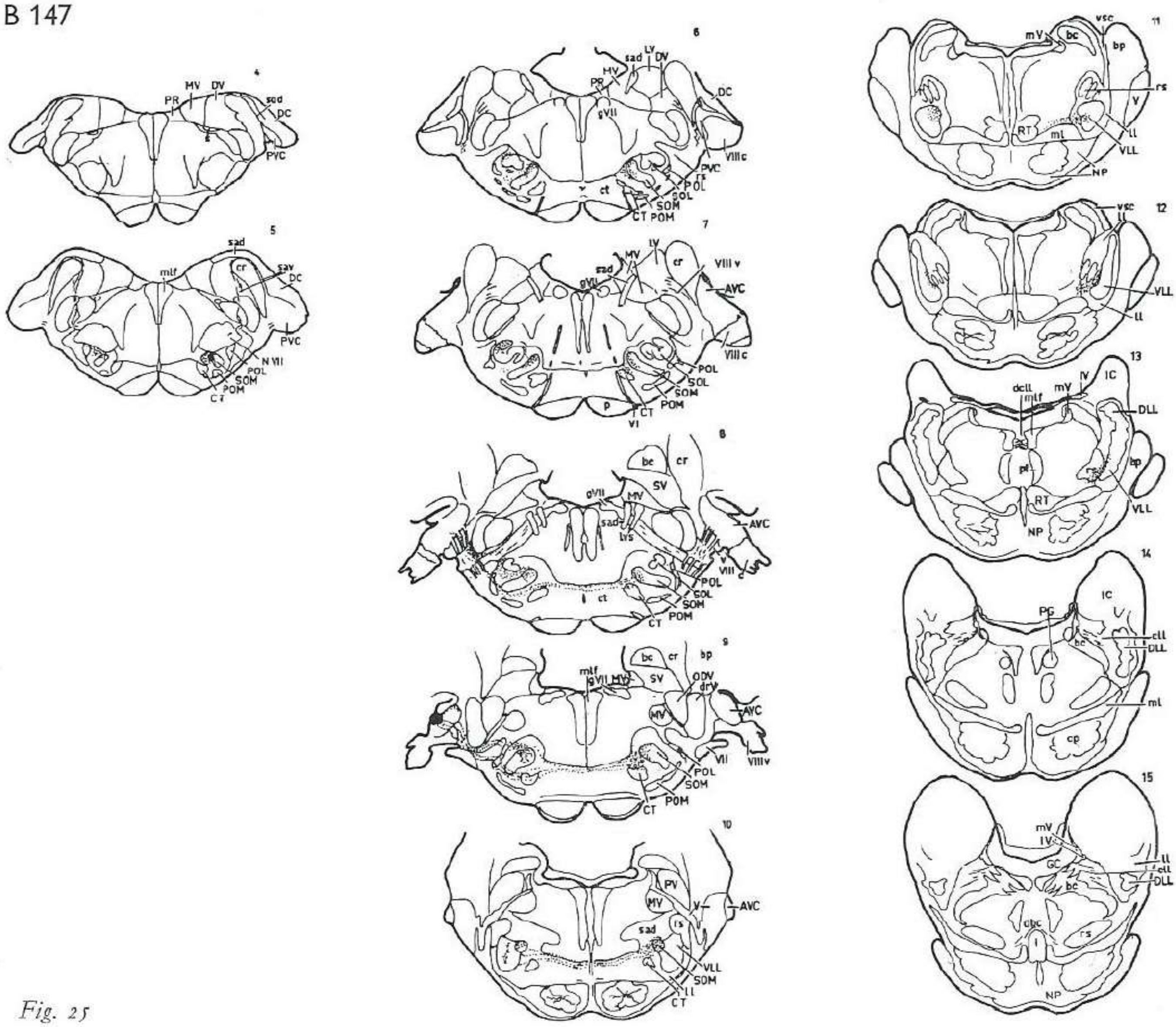


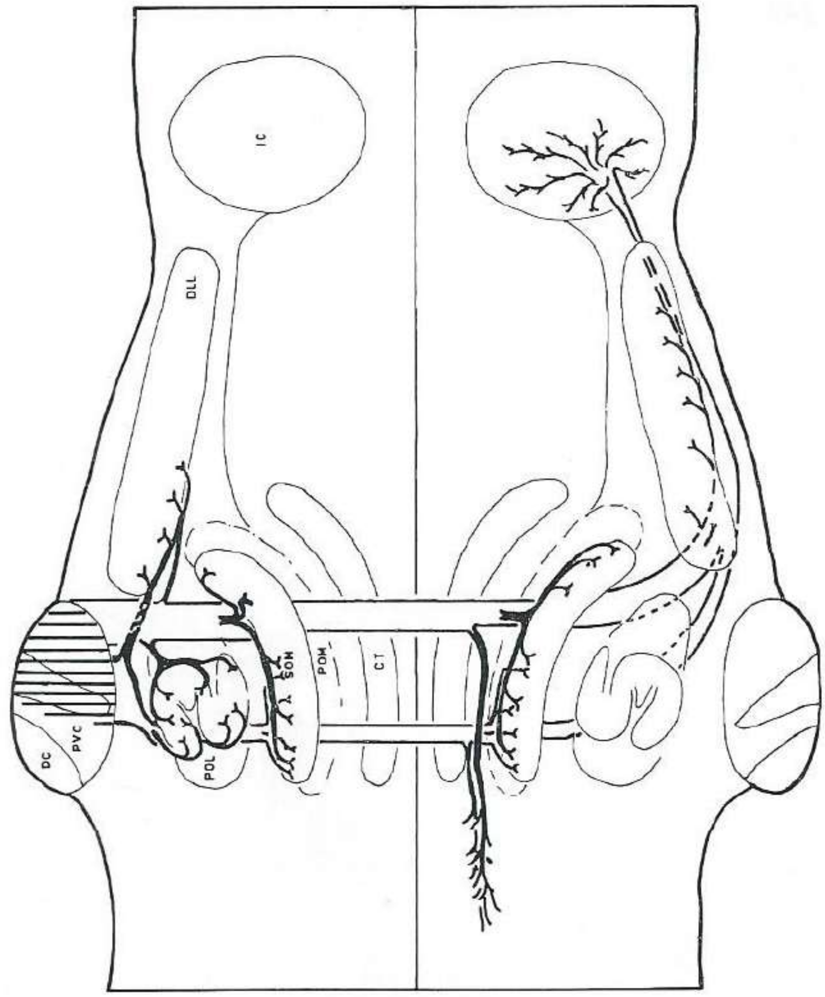
Fig. 25

c. The medium-sized fibres of the ct. The tonotopic projection to the SO and the IC (fig. 26 and fig. 17, 24 and 25).

Lesions of the PVC are followed by preterminal degeneration in the caudal part of the homolateral SOL and the SOM of both sides, whereas in lesions of the rostral part of the AVC abundant degeneration is found all over these nuclei. (Series B 152 and B 147, fig. 18, 24 and 25).

The degenerated fibres in the latter lesions run in the rostral part of the ct and differ in calibre from the majority of the fibres originating around the cochlear nerve. When reaching the homolateral SO, the fibres before entering the SOL run along it over a distance to form its fleece, as already described by Cajal. The fibres appertaining to its caudal part run along the outer side of the SOL to reach their termination, but the fibres from the rostral part of the AVC, although running in the rostral half of the ct, terminate over the whole caudorostral length of the SO.

Fig. 26. Medium-sized fibre component of the ct.



In the Nauta-stained preparations it is obvious that the dendrites of the SOM ganglion cells are directed both medially and laterally, as described by Stotler (1953). In the present experiments the fibres from the homolateral cochlear nuclei were seen ending on the lateral and those from the contralateral on the medial dendrites, every cell in this way receiving afferents from both sides. Degeneration therefore in the homolateral SOM actually was restricted to its lateral and in the contralateral SOM to its medial half. (Fig. 17, series B 104 and fig. 26). The contralateral SOL, however, did not show any preterminal degeneration.

Whether the fibres from the rostral half of the AVC terminate around the cells of the contralateral CT is hard to decide, because they run through this nucleus to reach the SOM.

Homolaterally they also traverse part of the CT, but it is clear that running in a transversal direction they have no contact with the cells. Contralaterally they curve to the caudal part of the SOM and come into close contact with a number of the cells of the CT, but even with a lesion of most of the rostral part of the AVC (experiments B 207, fig. 18) a number of medial CT cells remain free from degeneration.

The medium-sized fibres from the PVC and the AVC not ending in the SO enter the opposite ll to run at the lateral border of its nuclei, but some of them are found both caudal and rostral to the ventral nucleus. A small number of them enters the ll at its medial side, but rostrally shifts laterally.

Small tufts of fine fibres running perpendicular to the coarser ones of the ll enter the VLL at successive levels, where within the nucleus small concentrations of degenerated fibres are seen next to cell groups entirely free from them. This suggests that they are collaterals, branchig from their parent fibres within the ll.

The number of degenerated fibres entering the IC is only a fraction of those entering the ll (fig. 17), and it is clear that many end in its nuclei. The termination within the IC is again located in the ventral part of its central nucleus.

With regard to the medium-sized fibres from the rostral part of the AVC a distinct tonotopic relationship with both the SO and the IC could be revealed. In experiments B 147 and B 152 (fig. 24 and 25) it could be easily verified that the lesions are located in the different frequency planes of the AVC (series B 159, B 160, B 147 and B 152, fig. 11 and 14).

The lesion in the laterorostral part (the low frequency area) of the AVC is followed by preterminal degeneration only in the lateral part of the ipsilateral SOL, and in the dorsal part over their whole lengths in both SOM.

In experiment B 152 (fig. 24 and 25) with the lesion in the dorsomedial part the high frequency area of the AVC, the degeneration fills the medial part of the SOL and the ventral part of the SOM bilaterally. Therefore it is clear that the frequency scale from low to high in the SOL runs from lateral to medial, and in the SOM from dorsal to ventral.

In B 147 unfortunately staining of the mesencephalon was unsuccessful, but in series B 206 and B 207 degeneration could be localized at the lateral side of the IC, the medial remaining more or less free from it. The reverse was seen in B 152 where the lateral part of the IC is free from degeneration and the medial shows a high concentration of it. This demonstrates that the frequency shift from high to low in the central nucleus of the IC is directed from medial to lateral. This is in accordance with the electrophysiologically established data of Rose, Greenwood, Goldberg and Hind (1963).

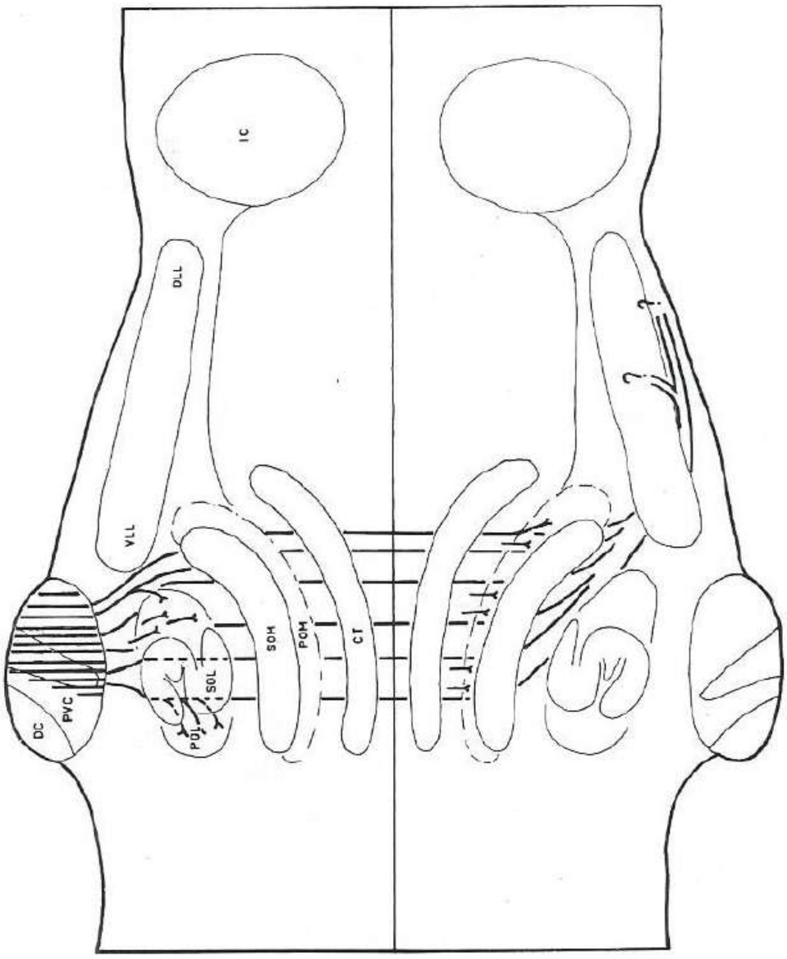
This is corroborated by the way the degenerated fibres from the entrance of the ll can be seen fanning out in the ventral part of the central nucleus in a transverse plane. Although there are a few branches, they do not give rize to a meshwork of preterminal fibres.

Within the nuclei of the ll and the CT no frequency tonotopy could be revealed, although especially the former receives preterminals in a way suggesting it.

Other areas of termination of the medium-sized fibres in the experiments with lesions in the AVC are:

a. The nucleus of the ipsilateral ll (fig. 26). A small strip of cells at the medial side of this nucleus in its ventral half receives preterminals, but contralaterally these cells remain free from degeneration. Neither is there any degeneration in more rostral structures of the auditory system at the homolateral side and it is notably absent in the IC.

Fig. 27. Thin fibre component of the ct.



b. A conspicuous bundle of degenerated fibres at the contralateral side runs from the CT caudally along the ventral surface of the medulla, between the medial lemniscus and the ventral spinocerebellar tract, where small cells are found on which preterminals are seen. The more caudally the fewer the fibres preserved, and at the rostral level of the inferior olive all fibres have terminated (fig. 26).

d. The thin fibres of the ct (fig. 27)

Lesions of the AVC and the rostral part of the PVC besides the coarse and medium-sized fibres, most probably also demonstrate a projection of the 1-4 mu fibres to the homolateral POL and the contralateral POM, apart from the fibres entering the contralateral ll, without reaching the IC. In the first part of their course the fibres are found between the coarse and medium-sized fibres as well as dorsal to them, but where the ct begins they shift to a more ventral position and mix with recurrent fibres of the same calibre. They remain in this ventral and surface part of the ct during their course to the other side. Ventral to the POL homolaterally, tufts of thin fibres are seen, running at right angles to the crossing fibres, entering the POL and terminating in it. Contralaterally a much smaller quantity of fibres terminate in the POM, whereas the remaining fibres join the ventrocaudal part of the ll.

In series B 161, B 162 and B 172 (fig. 18) with a degeneration of both the coarse and the thin fibres of the ct and a very few medium-sized ones, the area of the thin fibres can be traced into the contralateral ll. Before the IC is reached, however, they disappear, whereas the coarse ones terminate in the collicle. The most rostral place of termination of the thin fibres therefore remains dubious, but from these series one gets the impression that none reach the IC.

The majority of the 1-4 mu fibres originate in the caudal half of the PVC/AVC. The preterminals degenerated in the caudal part of the homolateral POL come from the caudal part of the PVC/AVC, those in its rostral portion from their middle part and only a small quantity of fibres from the rostral region of the AVC. Possibly the granular cells, found at the lateral border of the cochlear complex are their cells of origin, as already supposed by Cajal.

It remains uncertain whether the fibres that constitute the tufts found ventral to the homolateral POL all are collaterals of the 1-4 mu fibres, or partly their terminal branches. The microscopical picture strongly suggests them to be collaterals, as in Glees-stained sections a number of dichotomies are actually found in this region. The calibre of the dichotomies found, indicates that they belong to the system of medium-sized fibres, but the dichotomies of the 1-4 mu fibres may be more difficult to observe.

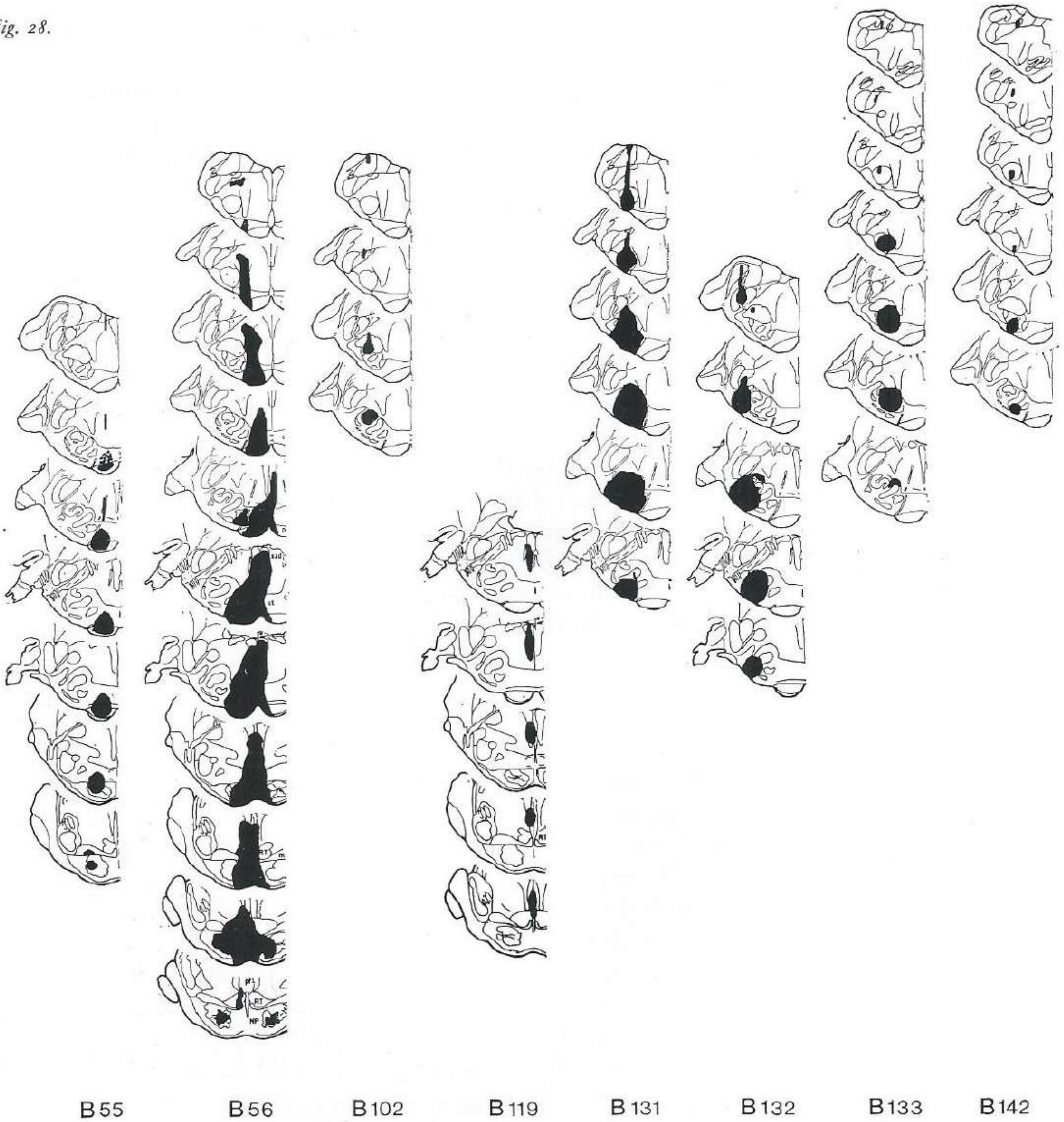
DISCUSSION

Only a few systems from the cochlear nuclei reach the IC directly, one of them as the stria dorsalis of von Monakow. Its origin, course and termination as became obvious in my investigations correspond to the description in the investigations of Barnes, Magoun and Ranson (1943) and Stotler (1949) but differs in many details from the recent ones of Fernandez and Karapaz (1967). The latter investigators found many areas of termination, which I could not confirm.

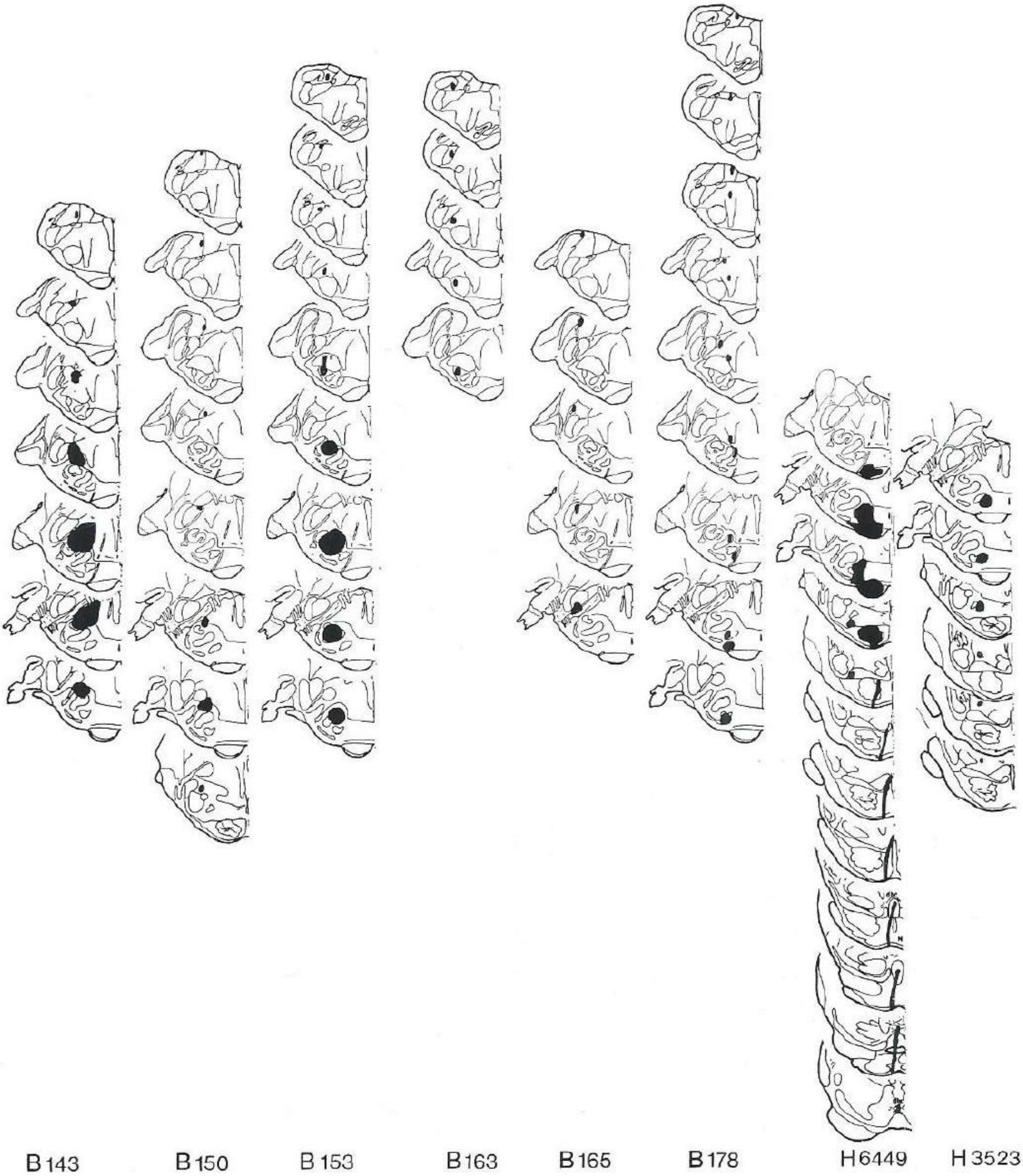
This also is the fact with the stria of Held. Fernandez and Karapaz demonstrate preterminals in the preolivary and retro-olivary nuclei (the latter nomenclature is not used in this thesis) but fail to establish both its exact origin and termination. By comparing the different experiments the origin and termination could be determined in this study.

Another group of fibres that reaches the IC, originating from the cochlear nuclei, is the component of the middle-sized fibres of the corpus trapezoideum. This is by far the most complicated part of the ct, with its numerous sites of termination and its tonotopic organization. This tonotopy is not new, as in 1963 Rose, Greenwood, Goldberg and Hind have found such a tonotopic organization in the IC electrophysiologically. Tsuchitani with Boudreau (1966) have done the same in the SOL, Warr (1965) found a topical projection from the AVC to the superior olives. The isofrequency planes in the cochlear nuclei justify the conclusion that the topical projection found

Fig. 28.

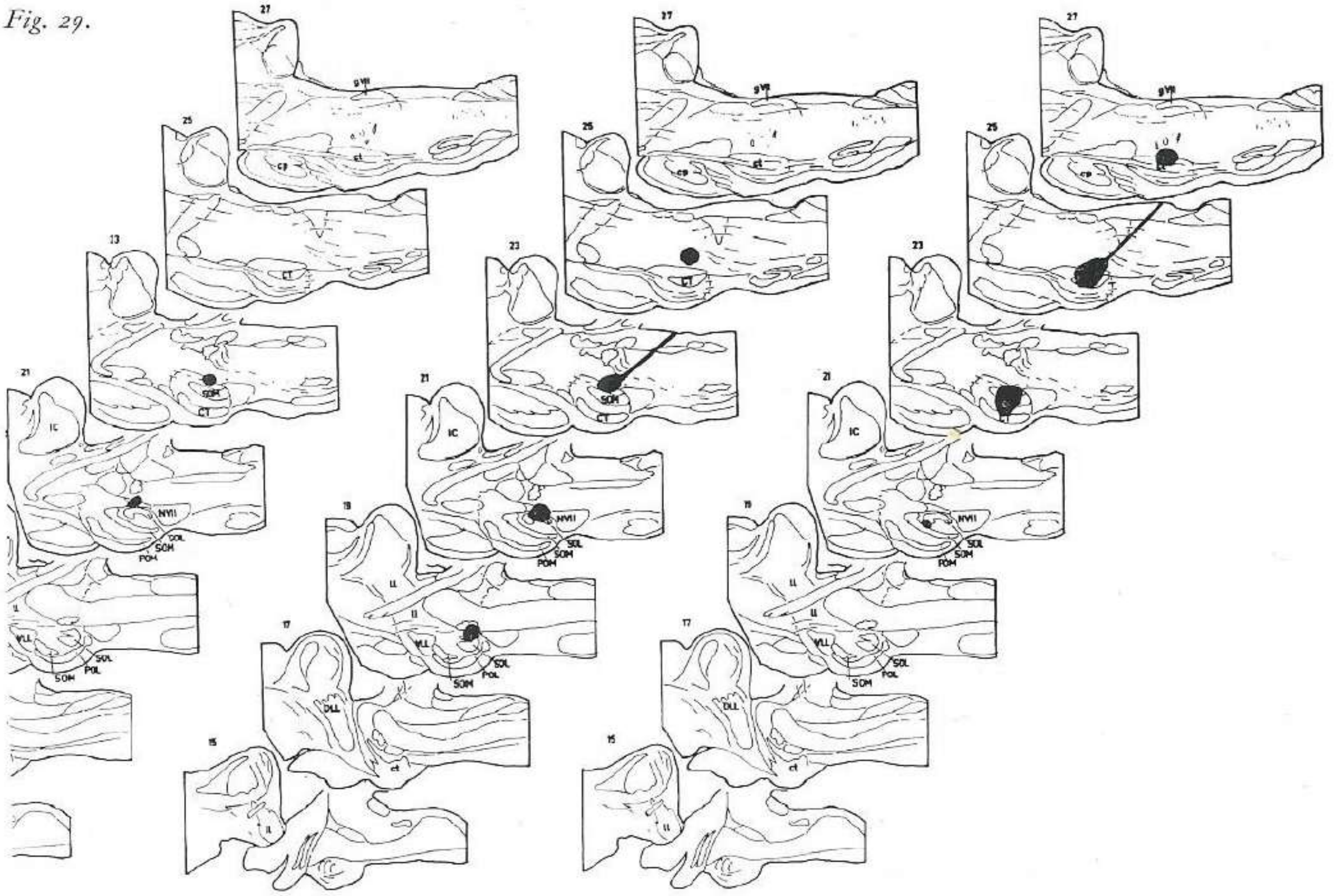


by Warr is indeed a tonotopical relation, and that the tonotopical organization of the SOL of Tsuchitani and Boudreau is found in the SOM and IC alike. The latter fact was already known from the publication of Rose, Greenwood, Goldberg and Hind. These investigators only used one electrode running more or less mediolaterally and leaving both the ventrodorsal and the caudorostral dimensions unexplored.



Undoubtedly the laminae described by Morest (1964) play an important part in frequency analysis, possibly each lamina representing one frequency. Warr (1965) has also found a homolateral projection to the VLL, which is in accordance with my experiments. The termination in the homolateral DLL and IC, as described by him, could not be confirmed, however.

Fig. 29.



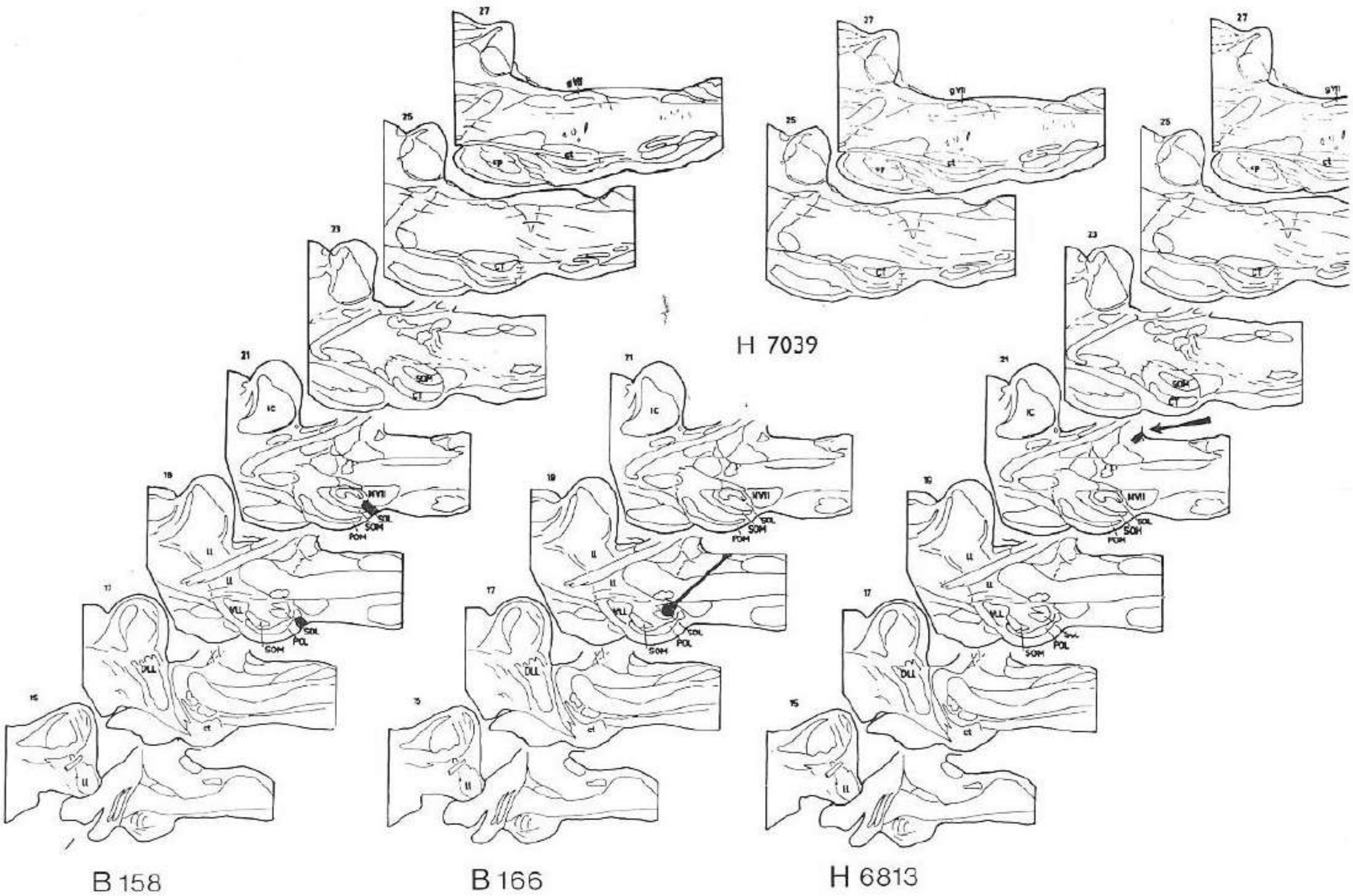
B 144 B 151 B 154

The projection of the middle-sized fibres contralaterally, ventral to the facial nucleus has nowhere been reported in the literature. It possibly influences the part of the facial nucleus that innervates the musculus stapedius.

The thick fibre component of the corpus trapezoideum.

Comparable investigations have been done in the rat by Irving and Harrison (1965) and by Harrison and Irving (1966). They find collateral preterminals from the thick fibres in the homolateral POL and the contralateral POM, which in my experiments appear to be collaterals from the thin fibre component. This has also been found by Warr (1965).

The problem "collateral or terminal branch" also concerns the medium-sized and the coarse fibres. The sections sometimes suggest collaterals, sometimes terminal branches, but probably both are present, and the fibre pattern of the ct confirms this supposition. In the ll we also find a configuration suggestive of collaterals, but terminal branches also have to be present because the degenerated fibres diminish in number on their way to the IC.



The superior olivary complex

The superior olivary complex is composed of the lateral and the medial superior olives (SOL and SOM), the lateral and the medial preolivary nuclei (POL and POM), the nucleus of the corpus trapezoideum (CT) and the cells located mediodorsal to the SOM. [The latter group is said to be the origin of the crossed olivocochlear bundle (Rasmussen, 1946)]. Systematically the projections of the different parts of the olivary complex will be described. For the lesions see figures 28 and 29.

a. The projection of the SOL and the SOM (fig. 28 and 30) with a lesion of the SOL and the SOM

Series B 153 (fig. 30) may be used to demonstrate the projection of both the lateral and the medial superior olive. In the first place it shows that all fibres crossing within the ct derived from the cochlear nuclei and none from the superior olive. The crossing fibres from this olive, consisting of about half those of the SOL with a few of the SOM,

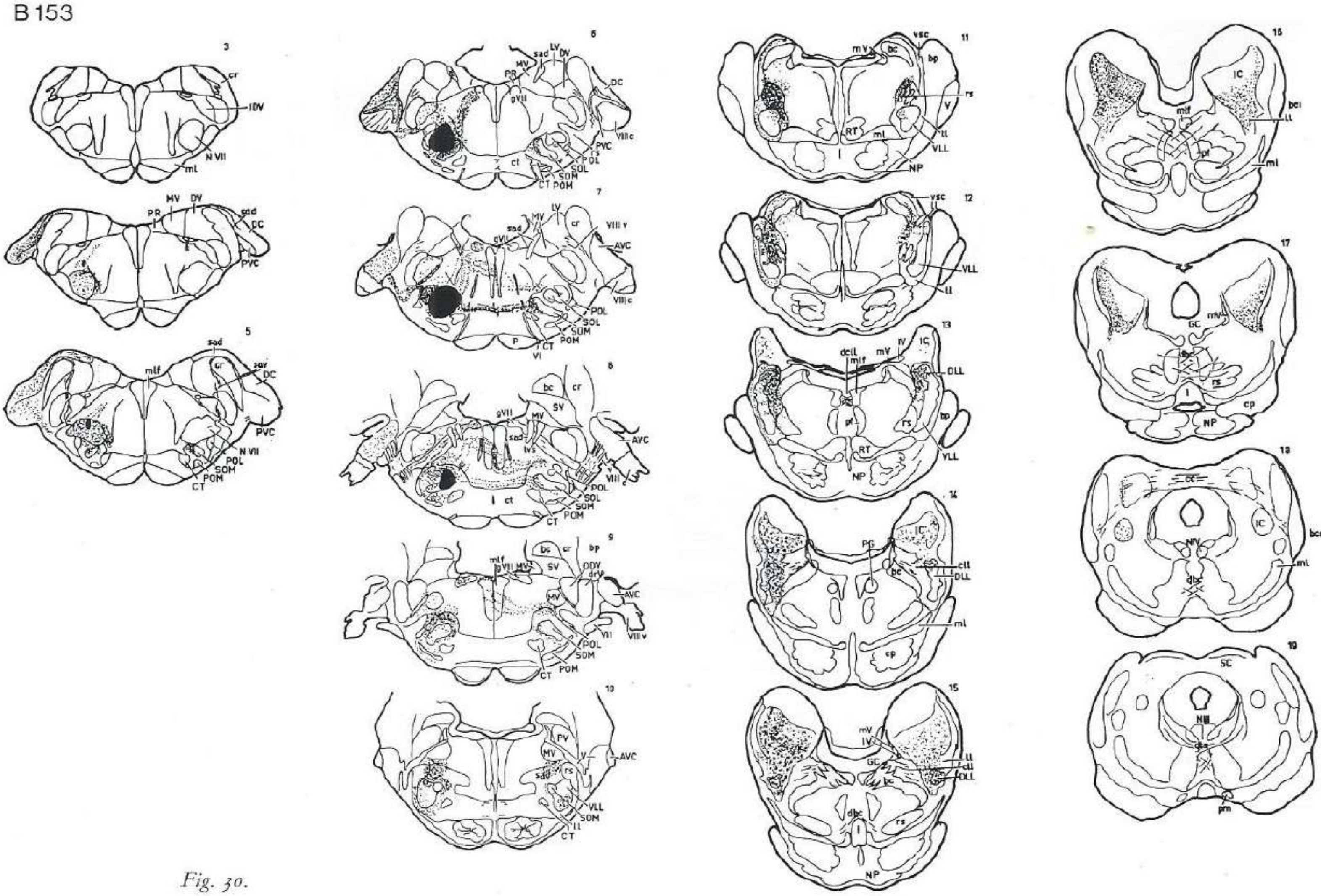


Fig. 30.

initially, similar to the facial nerve root fibres, run in the direction of the facial nerve knee. Closely ventral to it, however, they bend sharply medially to cross in a loose formation, subsequently to assemble again rostral to the contralateral superior olive and medial to the ll nuclei. They run to the IC in this position, giving off a number of preterminals to the dorsorostral part of the VLL and to the DLL. They have been called the olivary peduncle by earlier authors.

Ipsilaterally the fibres from the superior olive run more or less directly rostrodorsally in the medial part of the ll to the same areas of termination in the VLL, the DLL and the IC (fig. 31 and 32).

Both the crossed and the direct oliveray fibres terminate in the ll nuclei by way of small tufts of very fine fibres, directed perpendicularly to the ll fibres themselves, with between the tufst areas of little or no degeneration. (This way of terminating also was seen in the fibres from the cochlear nuclei, except for the stria of Held, which has much coarser preterminals in the VLL).

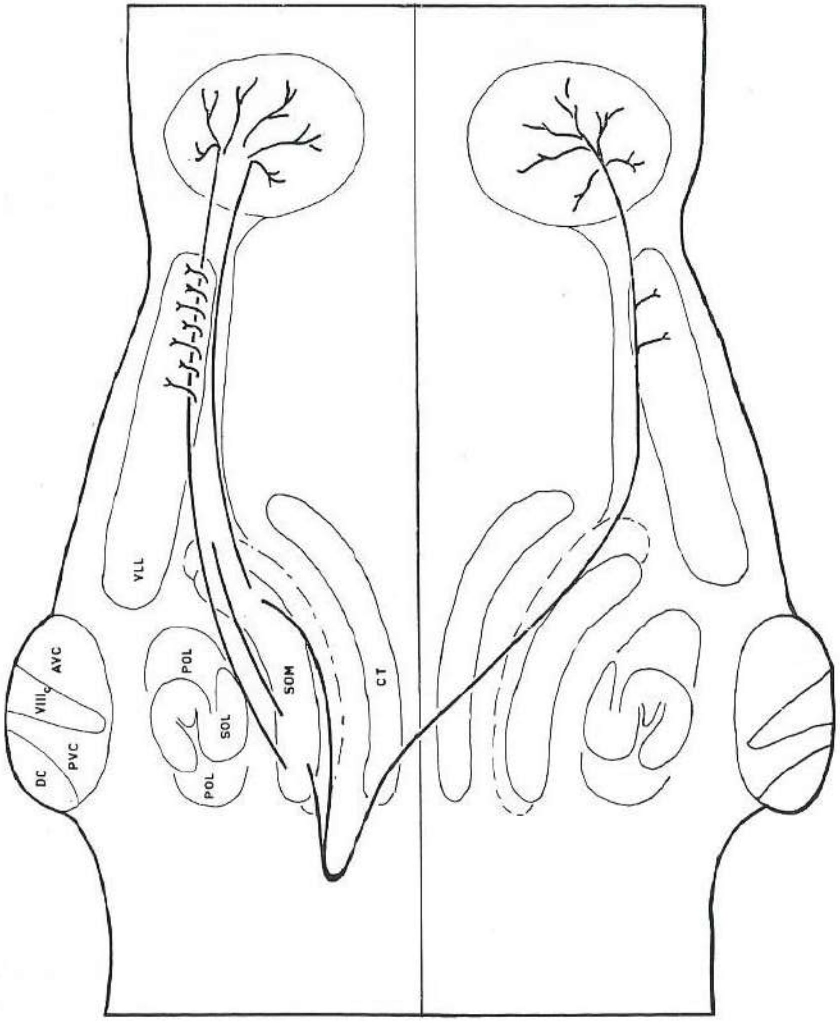


Fig. 32. Efferents of the SOM.

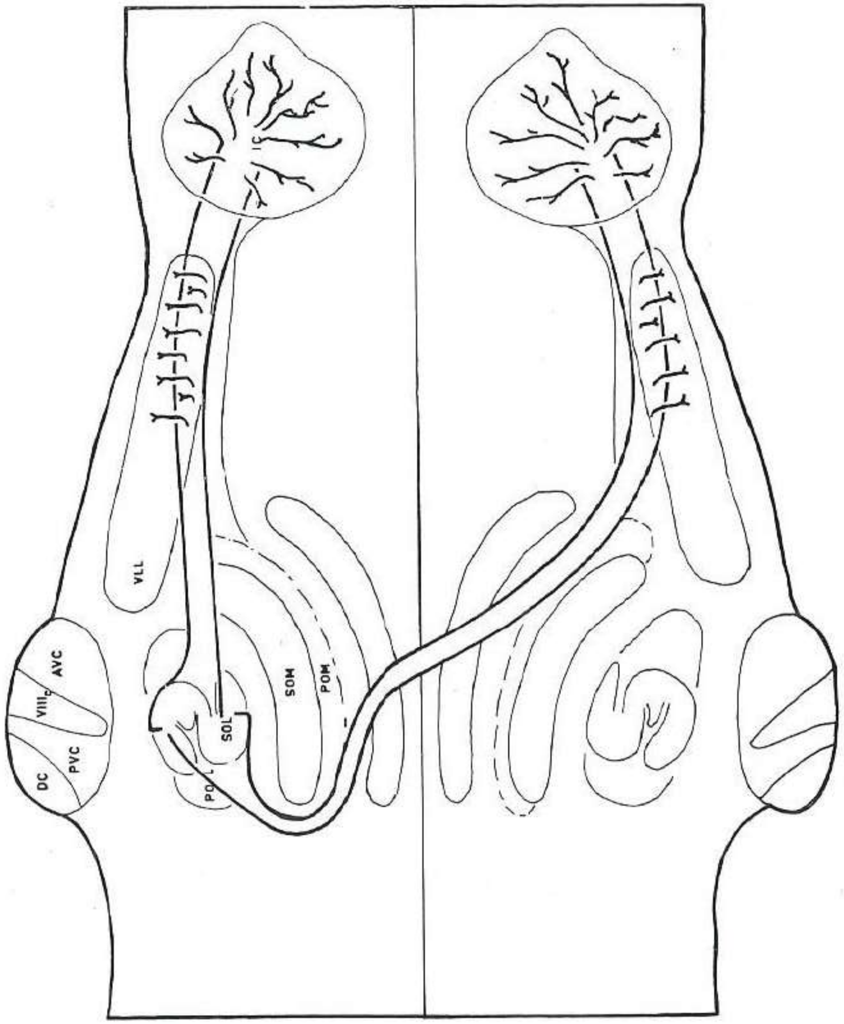
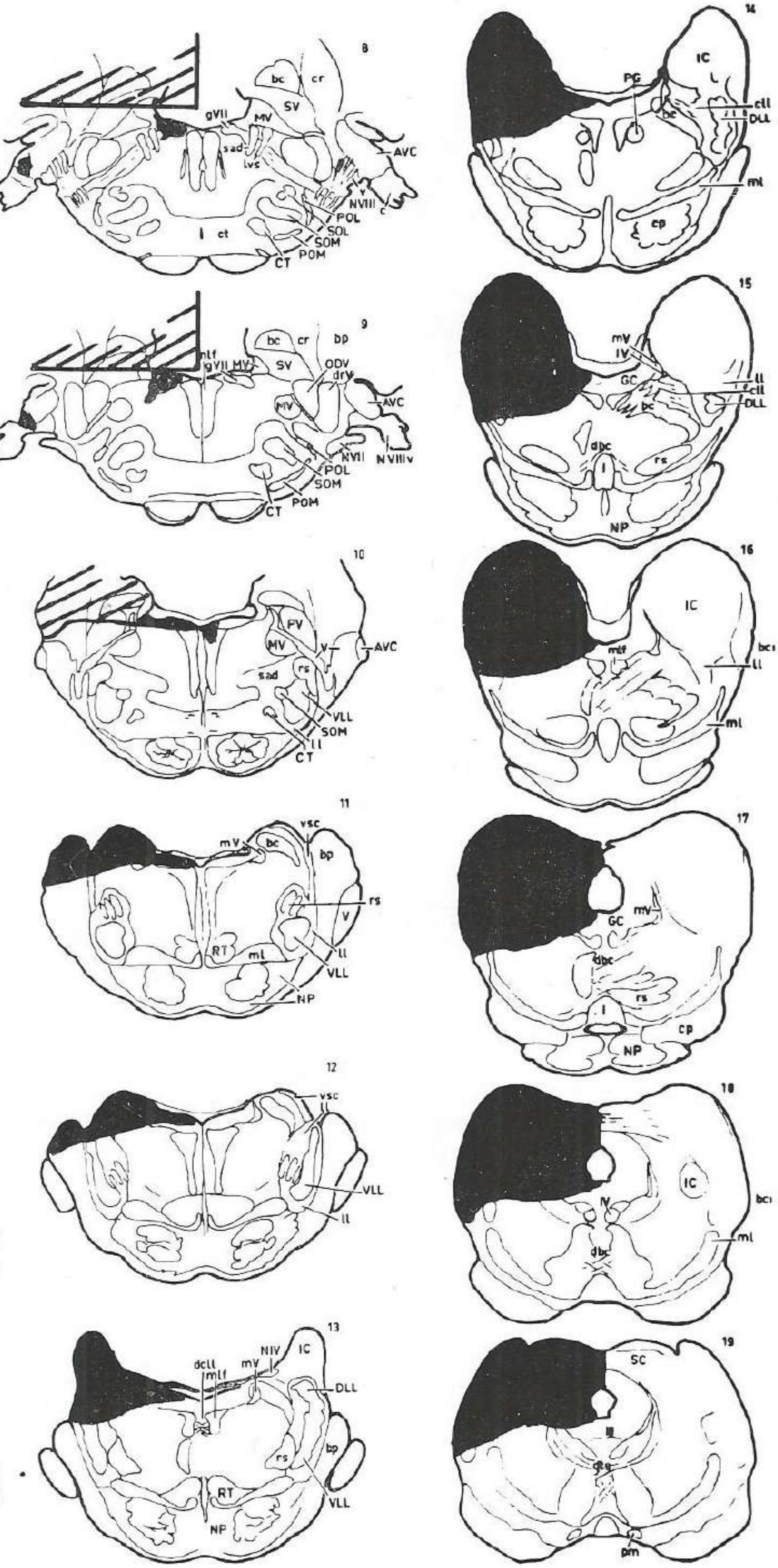
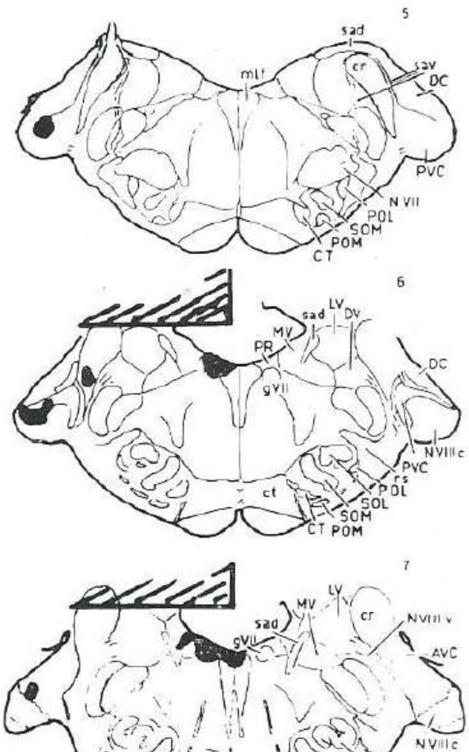


Fig. 31 Efferents of the SOL.

Fig. 33. Hemicerebellectomy and ablation of the inferior colliculus and the superior colliculus of the same side, with a survival time of 1½ year.

B 201





Within the IC termination is found in the ventral part of the central nucleus, where occasionally small areas with a higher density of preterminal degeneration are seen.

In differentiating between the fibres from the SOL and the SOM the series B 102, B 166, B 178 and B 201 can give valuable information. The most important is *B* 201 (fig. 33), an ablation of $1\frac{1}{2}$ year duration of an IC and the cerebellum. Following this ablation ipsilaterally the ll nuclei have disappeared and *the SOM has been reduced to a few cells*, whereas contralaterally it seems to be normal. The SOL of both sides contrarely contains an equal number of unaltered cells, which number may be somewhat reduced, but the POL, the POM and the CT are entirely unaltered. The contralateral cochlear nuclei similarly have a normal appearance, but the homolateral ones have been deformed in a second operation ten days before death. The conclusion can be drawn that the greater part of the SOM projects to the IC and possibly to the DLL of the same side. Why the SOL failed to develop distinct retograde changes may be due to its bilateral projection on the IC, as the orthograde degeneration experiments B 166 and B 102 conclusively demonstrate.

In the retrograde degeneration experiments the POL, POM and CT remain unchanged, according to expectation because orthograde degeneration experiments still to be reported demonstrate a recurrent projection of a number of preolivary neurones, whereas the CT will prove to project on the ipsilateral SOL.

b. The projection of the CT (fig. 34)

As has already been reported the SOL does not receive fibres from the contralateral cochlear nuclei, and midsagittal sections of the ct neither are followed by preterminal degeneration within it because the ct at its midsagittal plane only contains fibres from the cochlear nuclei. When the CT is included in the lesion, however, degeneration within the ipsilateral SOL is found. Once being aware of this connection between these two nuclei, its fibres in normal material can be traced from the CT to the SOL straight through the SOM. The rostral cells of the CT prove to project to the rostral part of the SOL and the more caudal ones to its more caudal parts (B 55, B 178, H 6449 and H 3523, fig. 28).

c. The projection of the preolivary nuclei (fig. 35)

Although the experiments do not allow concluding to all preolivary nuclei having a recurrent projection, there are many indications that this actually is the case, and a number of selective POL lesions especially show their recurrent projection (exp. B 102, B 142, B 158, B 163, B 176, fig. 28, 29).

a. The projection of the POL. In series B 102 and B 142 degenerated fibres in small bundles from the caudal cell groups of the POL can be seen to curve ventrally to traverse the rubrospinal tract in a ventrolateral direction. They subsequently between the fibres of the ct bend sharply laterally towards the cochlear nuclei; the fibres from

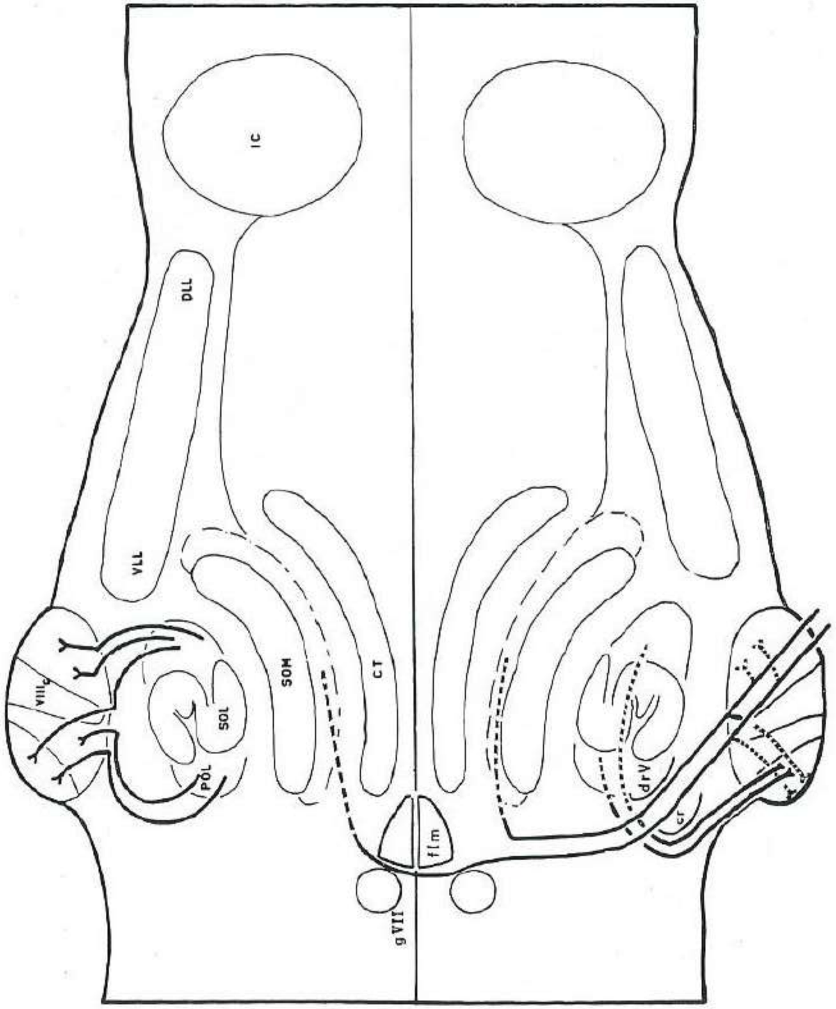


Fig. 35. Recurrent connections.

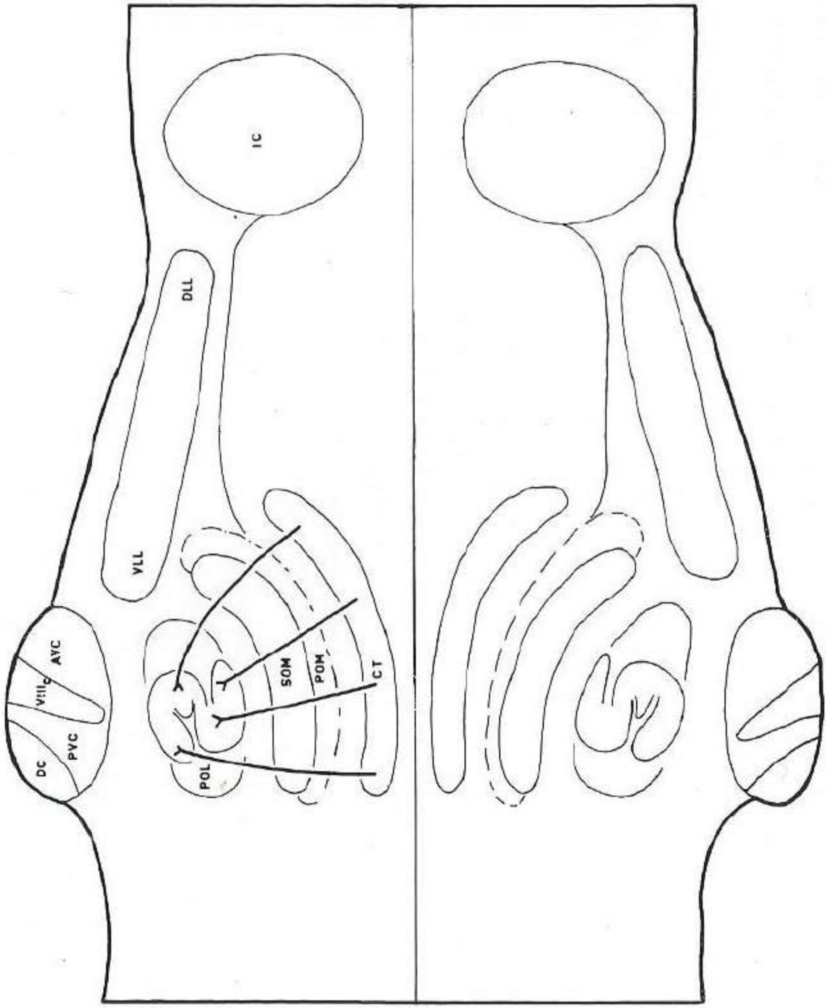


Fig. 34. Efferents of the CT.

the caudal group of the POL probably end in the rostral part of the PVC and the deep layers of the DC, but possibly in the whole PVC. The fibres running to the DC before entering it run between the PVC and the trigeminal nerve spinal tract, traversing the meeting point of the three main subdivisions of the cochlear nuclei.

The axons of the rostral cell group of the POL can be followed directly to the AVC (series B 176), covering its medial surface before entering it. Part of these axons can be traced into the DC where terminations are visible in its deep layers. They similarly enter the DC at the meeting point of the three cochlear nuclei.

b. The projection of the POM. In none of the experiments the POM was selectively lesioned and therefore they cannot provide any additional information about the origin of the crossed and uncrossed olivocochlear bundles, considered to originate from these nuclei. Degeneration of these systems was present in series with lesions including other auditory nuclei. In series B 154 in which the *crossed olivocochlear fibres* were the only ones degenerated at this side, especially in the superficial layer of the DC extensive terminal degeneration was visible. In the sagittally sectioned series the fibres connecting this degeneration with the olivocochlear bundle could not be found, but their existence cannot be doubted.

Collaterals of both the crossed and the direct olivocochlear bundles detach from them when passing along the AVC to terminate in it. This termination described by Rasmussen (1960), was also present in the series B 151, B 154, B 178 on both sides, in B 176, B 189 on the crossed side (and in B 131 in the DC at the crossed side). In all the series the number of collaterals and the amount of preterminal degeneration is small. Experimental evidence of the origin of the recurrent fibres travelling in the stria dorsalis and terminating in the DC is unsufficient. They were observed in the experiments.

They may originate in the grey matter surrounding the SOL, because a lesion dorsal to this nucleus made them degenerate (experiment B 189).

Rasmussen's description of recurrent degeneration within the stria dorsalis after lesioning the contralateral VLL could not be confirmed, however.

Summarizing it can be stated that the caudal part of the POL projects on the homolateral DC and PVC, its rostral part on the homolateral DC and AVC, whereas a number of neurones possibly belonging to these olivary nuclei project on the DC via the stria dorsalis. The olivocochlear bundle not only terminates in the organ of Corti, as described by Rasmussen, but most probably also in the DC and for a small part in the AVC.

DISCUSSION

Because the efferents of the cochlear nuclei run along the superior olives and do not traverse them, the olives can be lesioned selectively and their efferents studied (exp. B 153). The olivary peduncle, already mentioned, described by Bechterew (1885), Held (1891, 1893), Cajal (1896), a.o. undoubtedly is the first part of the crossing efferents of the superior olive. The crossed and direct olivocochlear bundles, which also run

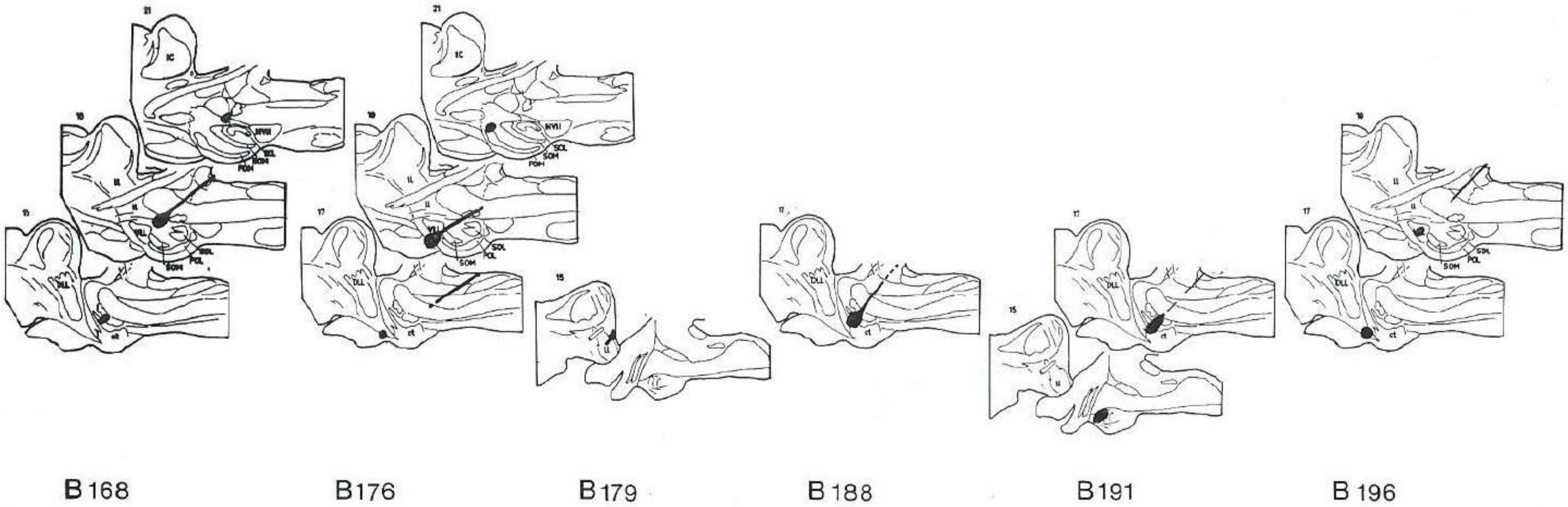
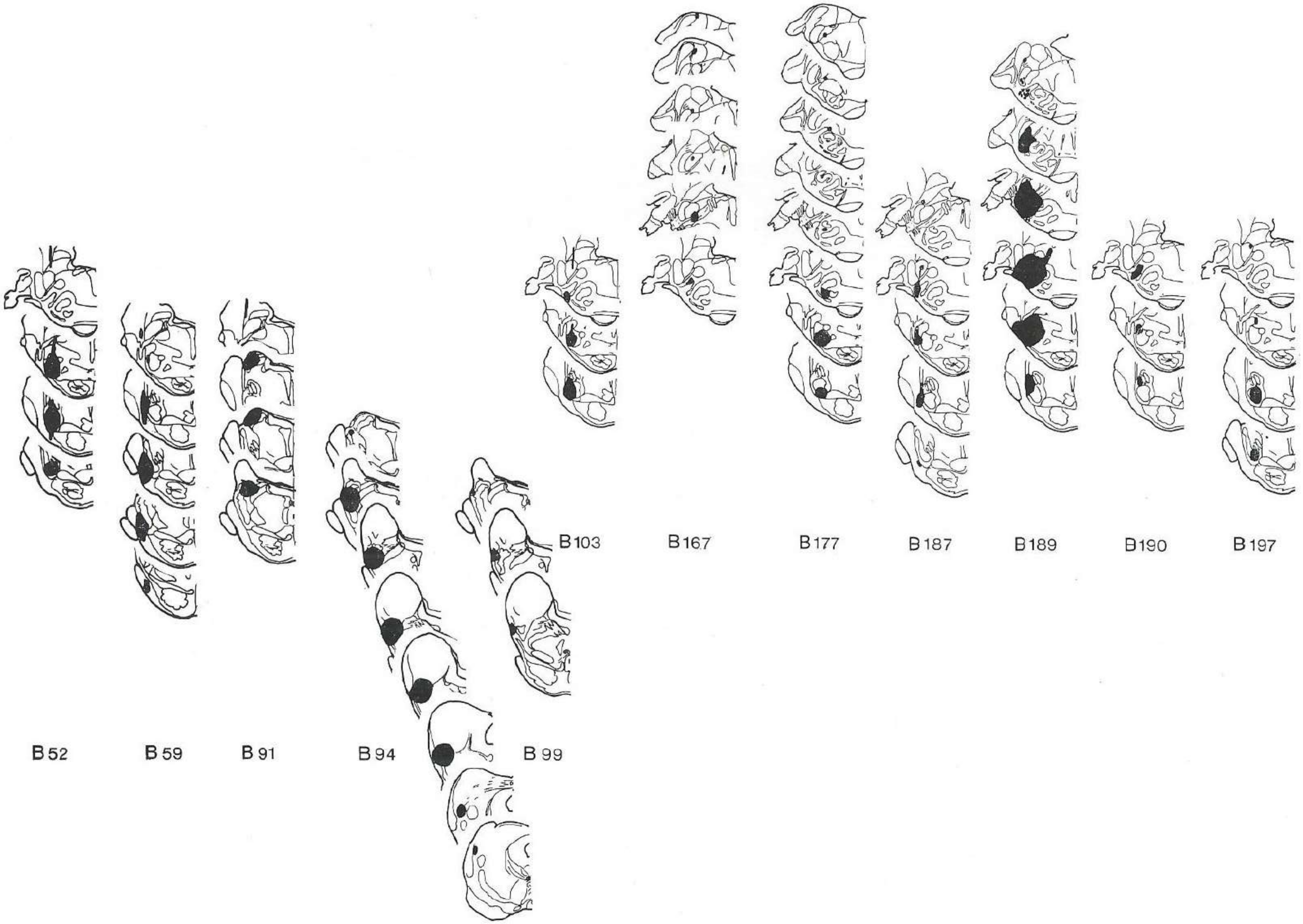

B 168
B176
B 179
B 188
B191
B 196
21
IC
NVII
SOL
SOM
POM
19
LL
DLL
POL
VII
17
15
ct

Fig. 36.


B52
B59
B91
B94
B99
B103
B167
B177
B187
B189
B190
B197

more or less parallel to the facial nerve root fibres, are only few compared to them. Rasmussen (1946) found that the SOL does not contribute to the olivary peduncle, which fibres according to him originate in the SOM, exactly contrary to the conclusions presently arrived at.

The SOL projects equally to both sides of the pontine and mesencephalic acoustic nuclei. The SOM for the greater part projects homolaterally, but when taking in account that the AVC projects bilaterally on it, both SOM's can be considered to provide each side with an equal amount of information from the cochlear nuclei.

Stotler's conclusion (1953), based on retrograde degeneration experiments, that the efferents of the CT do not pass beyond its immediate vicinity, and that of Harrison and Warr (1962), who from retrograde degeneration in the CT following lesions ventral to the SOL similarly supposed the CT to project on the homolateral SOL, are supported by the present experiments. The course of the recurrent fibres to the cochlear nuclei and the cochlea described by Rasmussen in 1960 cannot be much added to presently, as the origin and the termination a of number of recurrent fibres still have to be settled.

The investigations of Rossi and Cortesina (1960) about the origin of the olivocochlear bundles in the rabbit together with my experiments justify the supposition that the preolivary nuclei are especially engaged to the recurrent fibre systems.

The lateral lemniscus and its nuclei

The nuclei of the lateral lemniscus are divided into the dorsal nucleus (DLL) and the ventral nucleus of the ll (VLL).

The DLL can be differentiated from the VLL by its efferents, known as the commissure of Probst. Its cells moreover are slightly larger than those in the VLL. According to Stotler (1953), the DLL only contains boutons, whereas the VLL besides boutons shows calices and modified calices of Held.

The VLL is the column of cells reaching from the DLL rostrally to the medial superior olives and the preolivary nuclei caudally. The transition between the VLL and the preolivary nuclei is difficult to establish. This ventral part of the VLL moreover is the area of termination of the stria of Held, which fibres possibly are the ones terminating with calices and modified calices of Held. The dorsal part of the VLL is sometimes called the middle group of lateral lemniscus nuclei.

A typical feature in the greater part of both the VLL and the DLL is the way fibres terminate in them, as small tufts of very thin fibres, detaching from the ll at right angles. They look like collaterals, but can be the terminals of one fibre also, and possibly both are found. Only ventrolaterally in the VLL where the coarse fibres of the stria of Held terminate this mode of termination is not found.

a. The projection of the VLL

Lesions of the VLL (B 52, B 59, B 103, B 176, B 177, B 187, B 189, B 190, B 196, B 197, fig. 36) always accompanied by interruption of part of the fibres from the cochlear

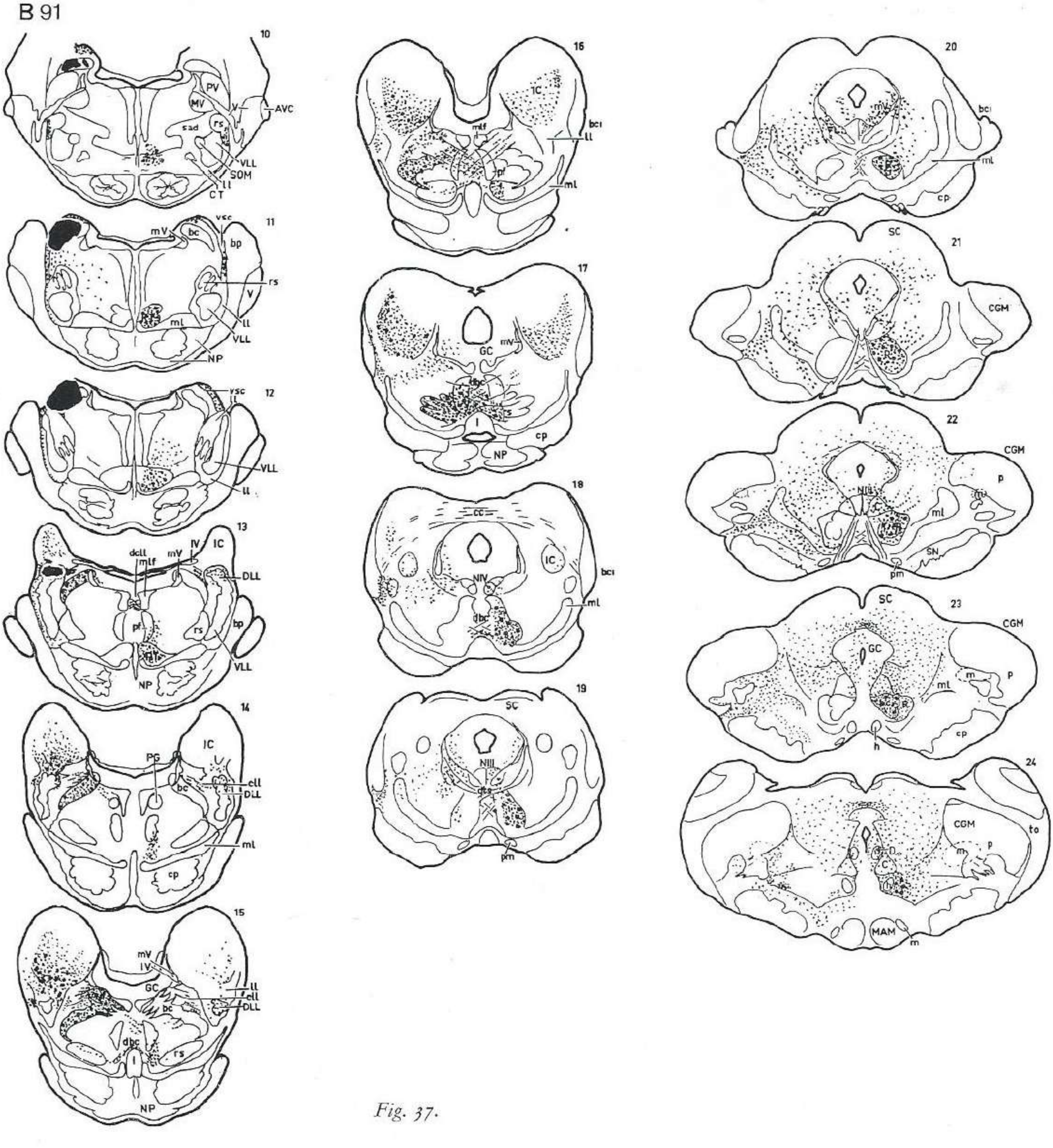


Fig. 37.

nuclei and/or the superior olives, give a more abundant degeneration in the nuclei of the ll and the IC than severance of the efferents of the cochlear nuclei and the superior olives alone. That makes it likely that the VLL projects to the more rostral nuclei of the ll and to the IC. That all cells of the homolateral VLL have vanished in the experiment with a chronic ablation of the IC (B 201) is in accordance with this supposition.

b. The projection of the DLL

Lesions of the DLL (B 91, B 94, B 99, B 179, fig. 36) do not give information about the projection of the DLL to the IC of the same side because of the number of interrupted fibres from lower auditory centres. Series B 201 with a chronic ablation of the IC neither does, because the DLL may be partially included in the lesion.

The commissure of Probst is clearly demonstrated in lesions in the DLL (fig. 37). In accordance with Woollard and Harpman (1939/40) and Goldberg and Moore (1967), it can be stated that its origin lies in the DLL and its termination in the contralateral IC, especially in the lateral zone of the ventral part of its central nucleus.

c. The isthmoperipeduncular bundle (fig. 37)

The efferents of the nuclei of the ll as well as those of the superior olives and the cohlear nuclei do not reach rostrally beyond the IC. There is, however, a small bundle of fibres originating in the neighbourhood of the DLL, probably non-auditory in function, which reaches to the level of the CGM, running close to the ll and the bci.

This bundle which is quite compact when curving ventrally around the lateral lemniscus, originates in the grey matter of the dorsal part of the pontine tegmentum dorsal to the brachium conjunctivum (the dorsal nucleus of the brachium conjunctivum). From this nucleus fibres course laterally and form a bundle before curving around the ll (series B 91, fig. 38; B 180, fig. 39), to pass laterally, caudal to the latter entering the

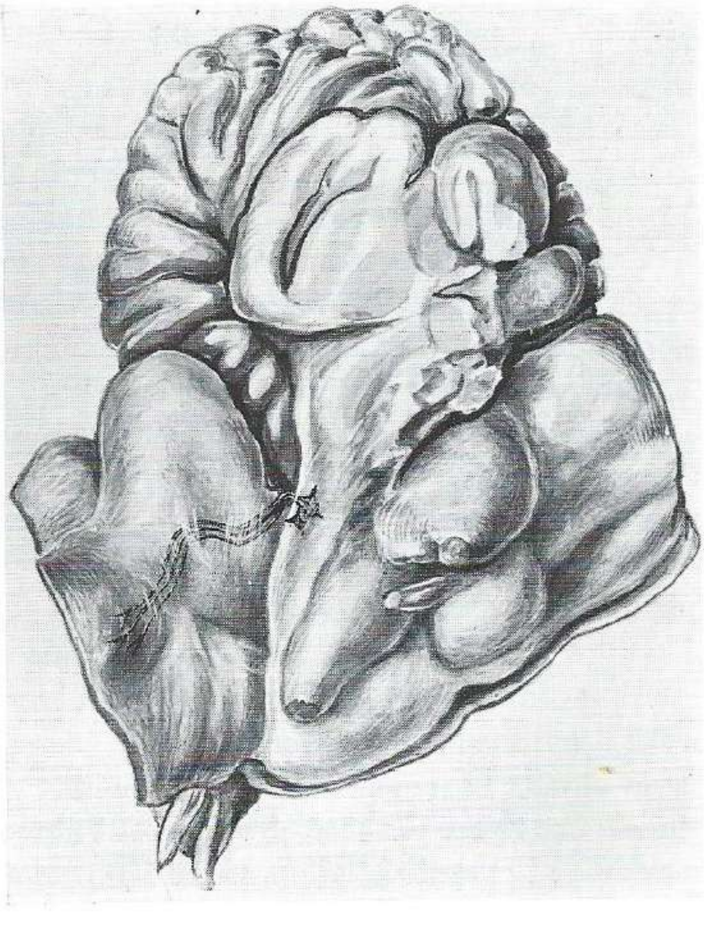


Fig. 38. Isthmoperipeduncular bundle.

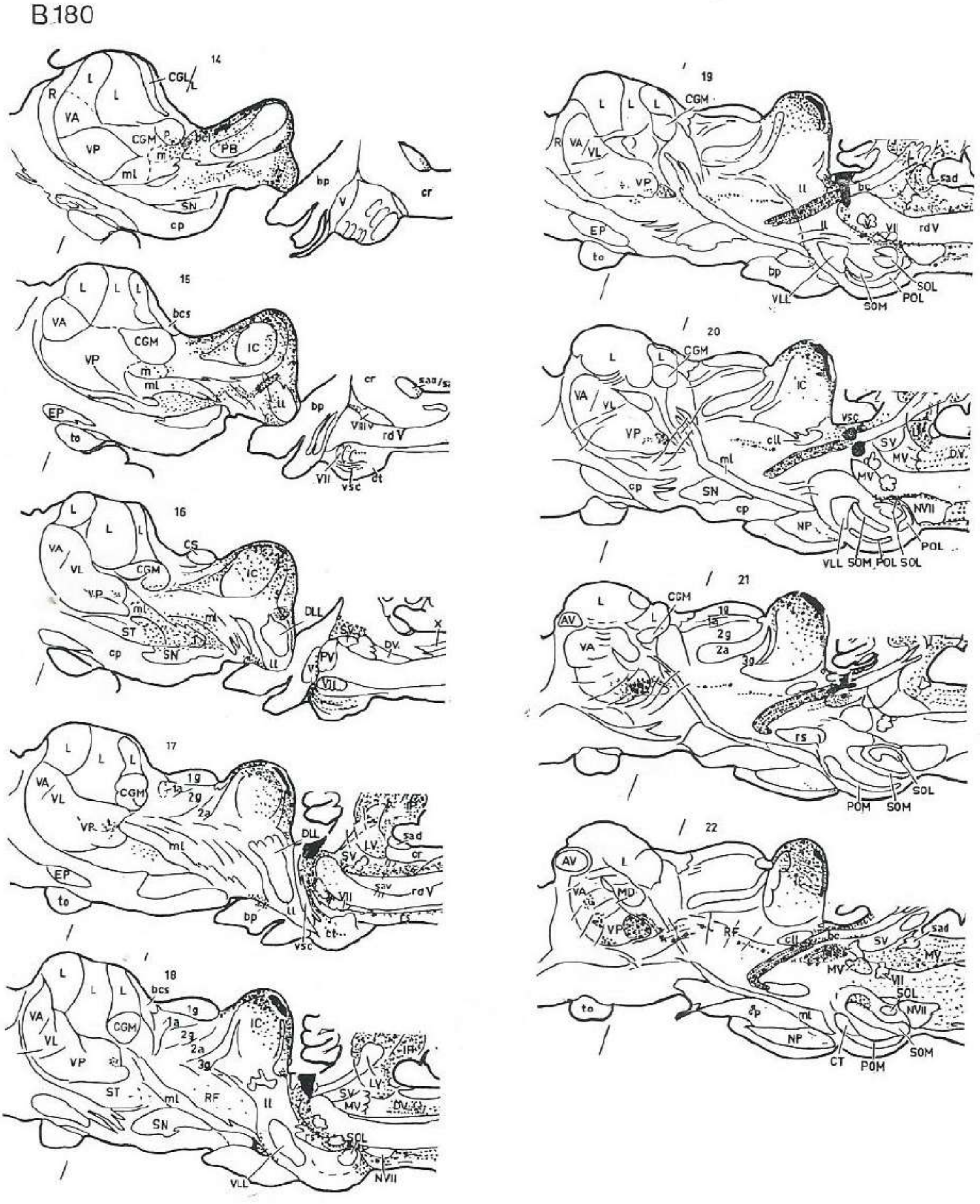


Fig. 39.

IC. At the lateral side of the ll the bundle turns rostrally to run parallel to the bci, curving dorsally around the nucleus parabigeminus (paralemniscalis). Rostrally it loses its compactness medial to the ventral part of the bci (fig. 39) and subsequently reaches the area between the CGM, the cerebral peduncle and the medial lemniscus, where it terminates.

Tracing it as far back as possible other possibilities being excluded by appropriate lesions [hemicerebellectomies (exp. Voogd), hemichordotomies (B 193, B 194 fig. 40, 41), lesions of the nuclei of the lateral lemniscus and of the IC] makes it likely that this

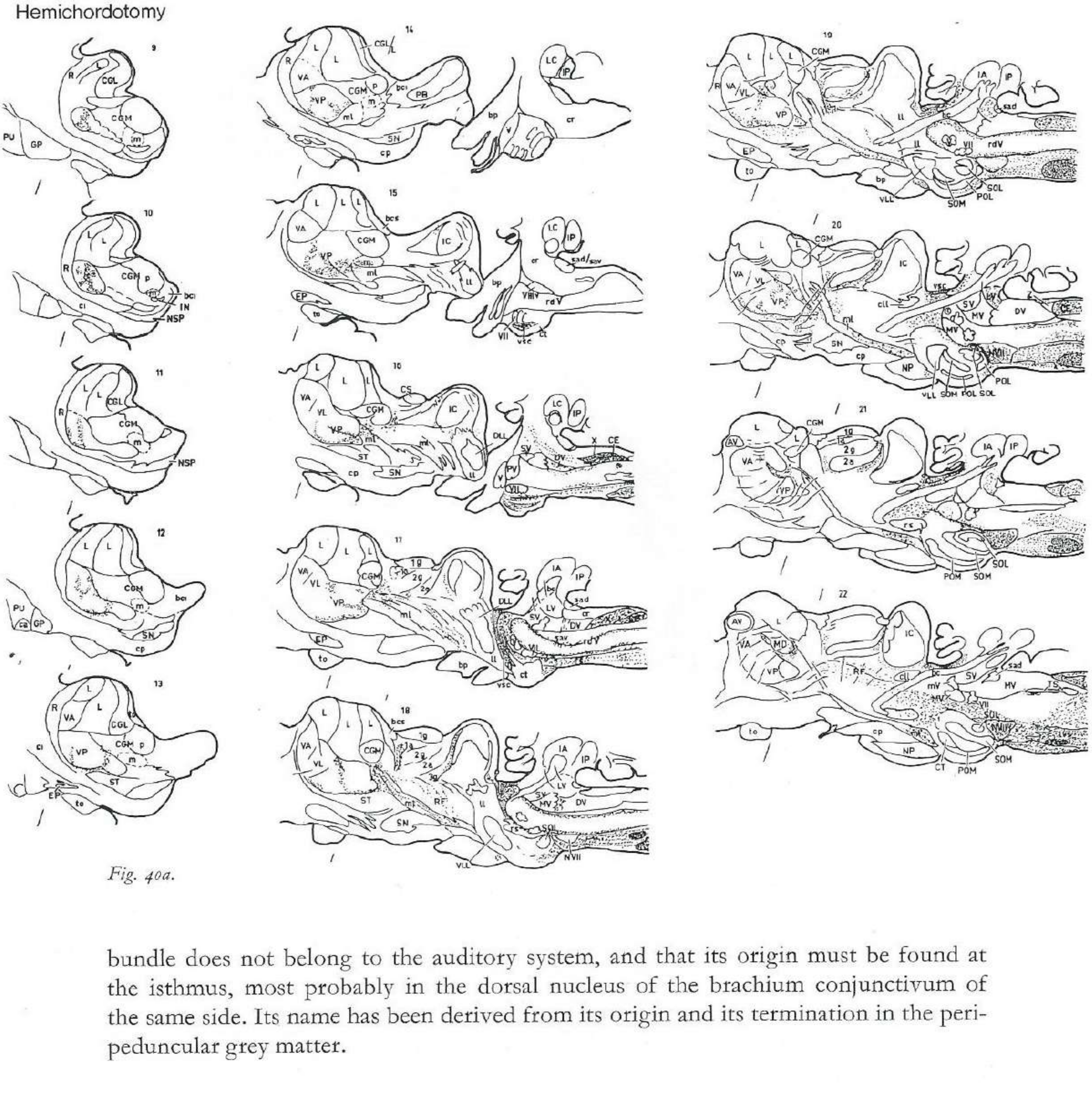


Fig. 40a.

bundle does not belong to the auditory system, and that its origin must be found at the isthmus, most probably in the dorsal nucleus of the brachium conjunctivum of the same side. Its name has been derived from its origin and its termination in the peripeduncular grey matter.

DISCUSSION

At the moment experimental evidence suffices, in the cat at least, to disprove the existence of Cajal's fibres of the ll running along the IC to more rostral structures, including the CGM (voie acoustique central). The so-called central acoustic tract of

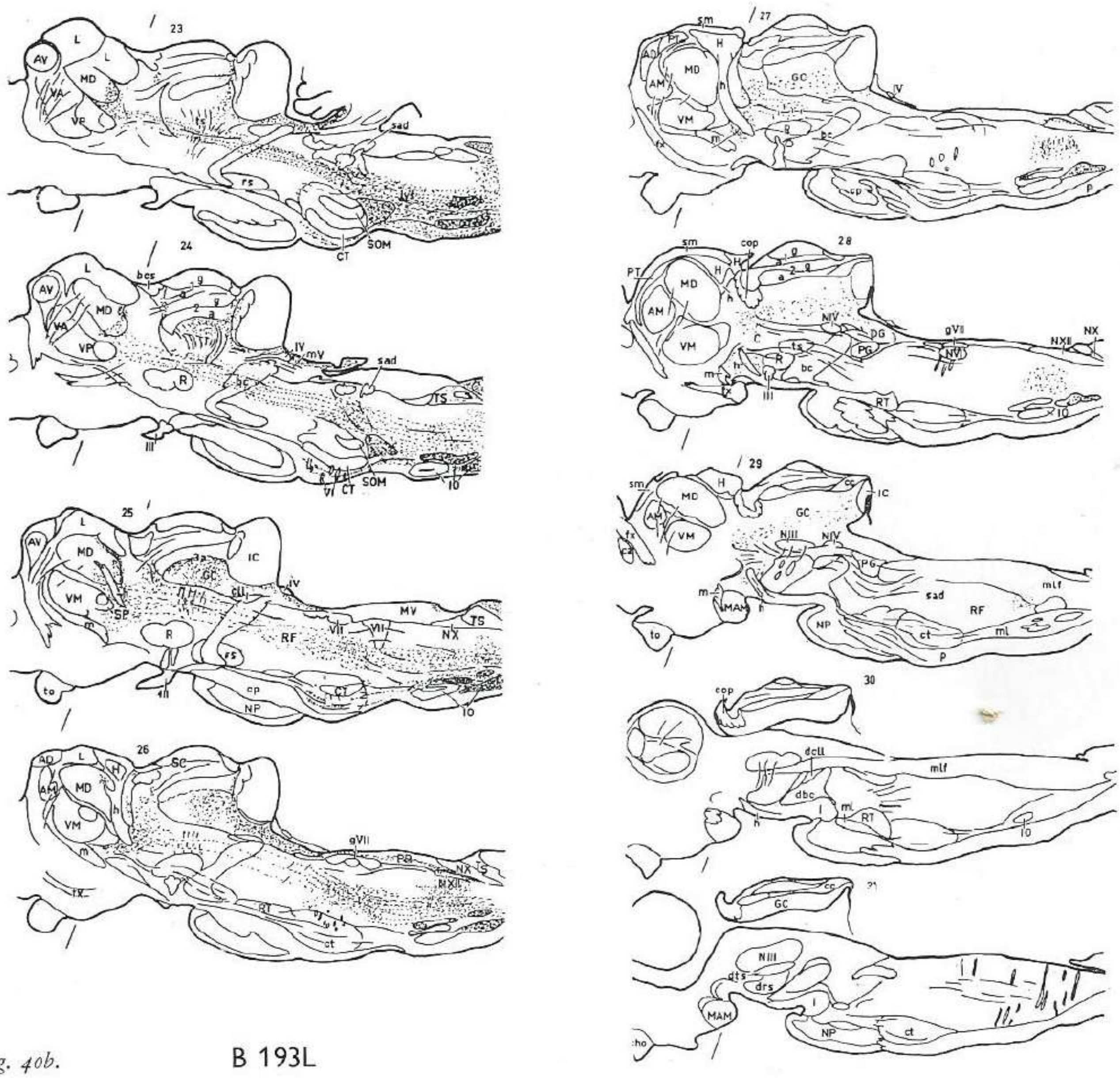


Fig. 40b. B 193L

Papez (1929), which was supposed to originate in the DLL to reach more rostral auditory structures, only described in a short abstract of a lecture, neither could be confirmed by my experiments. Morest (1966) in an extensive experimental study, concluded that at its site the so-called "lateral tegmental tract" is found which originates in the surroundings of the IC but not caudal to it. This tract which terminates in the dorsal part of the principal nucleus of the CGM, obviously belongs to the auditory system and differs from the central acoustic tract mainly in its origin.

Goldberg and Moore (1967) after lesions of the DLL found degeneration in the area of the lateral tegmental tract (sive the central acoustic tract of Papez), but they supposed it to consist of passing spinal fibres. This may be the case when their lesions

B 194
Hemichordotomy

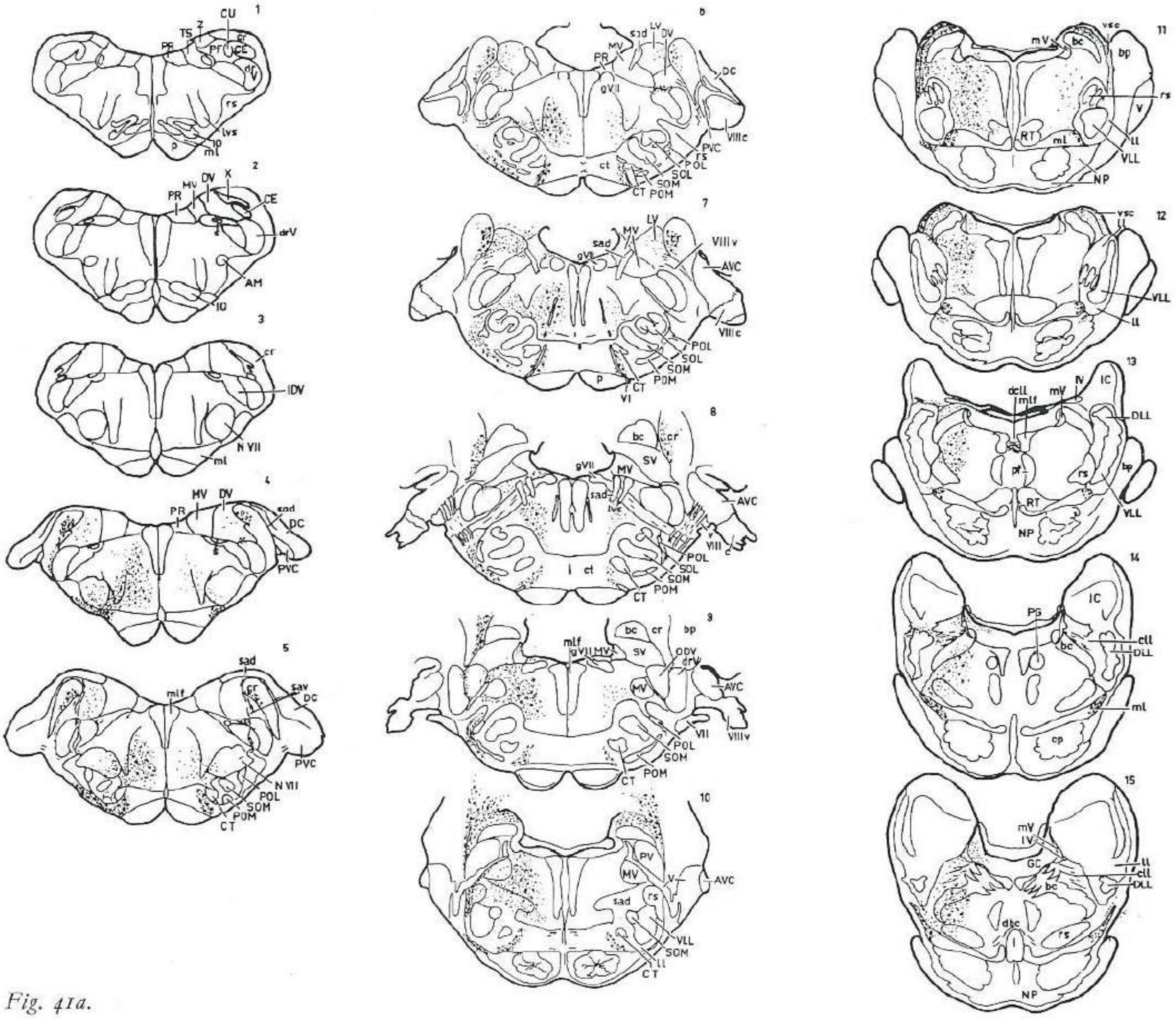
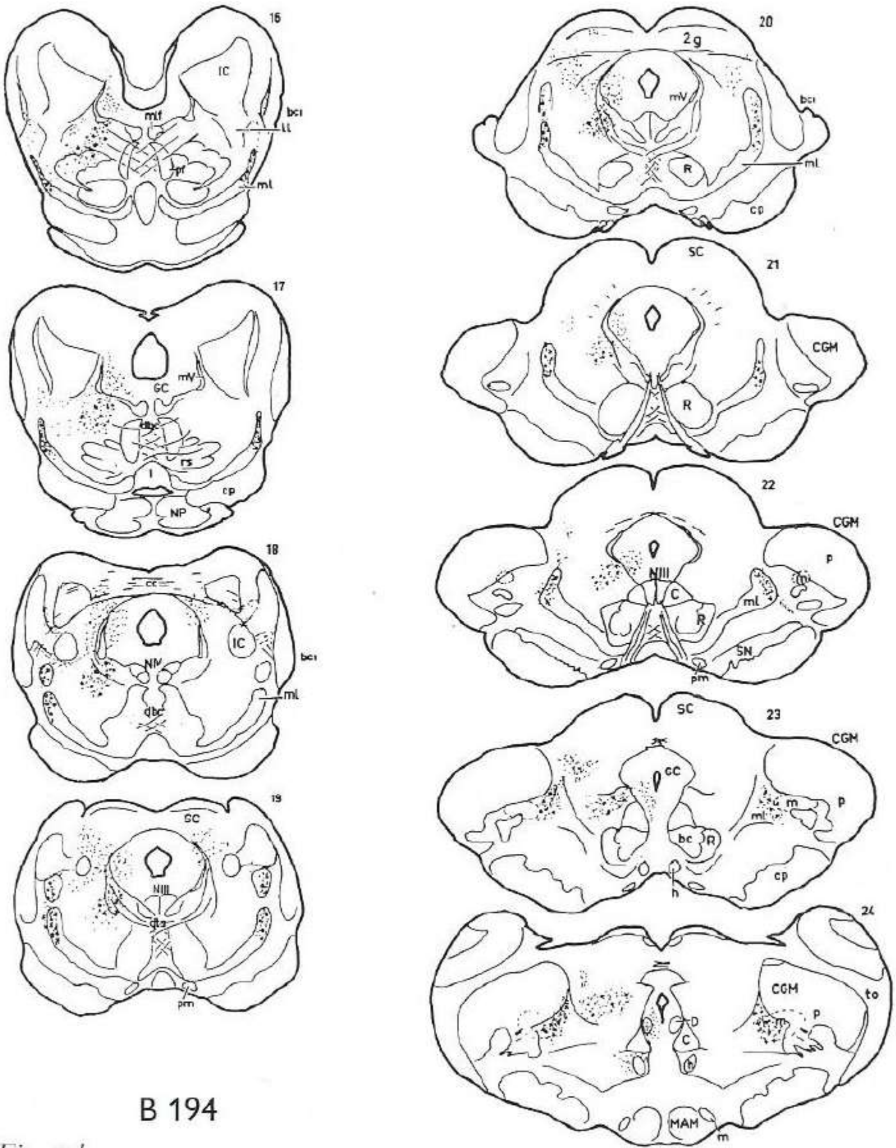


Fig. 41a.

interrupt fibres in the lateral part of the medial lemniscus which contains the cervicothalamic tract, but no fibres of spinal origin (compare series B 193, B 194, fig. 40, 41). Anderson and Berry (1959) in the cat did not find spinothalamic fibres concentrated in the area of the lateral tegmental tract. Mehler, Feferman and Nauta in the monkey (1960), however, located them at the site of the lateral tegmental tract, a small area at the level of the superior colliculus dorsal to the medial lemniscus. Glees (1953) and Sie (1956) in human material described a "thalamopetal bundle" in the same area. According to them and to Gebbink (1967) and Schoen (personal communication) part of this bundle consists of spinothalamic fibres, whereas at the level of the IC an other part comes into existence.



B 194

Fig. 41b.

Comparing these data we may conclude that the spinothalamic fibres, together with the lateral tegmental tract form a bundle, formerly called the central acoustic tract of Papez. Cajal's "voie acoustique centrale" is more widely spread and therefore does not exactly correspond to Papez' description. It is likely that Cajal was mislead by medial lemniscus and spinothalamic fibres which in sagittal sections follow the course depicted by him and of which a number terminate in the direct vicinity of the IC as will be described below.

The isthmoperipeduncular bundle lies too far laterally to be confused with the more medially located lateral tegmental tract and seems to have remained unobserved till now. Its origin in the dorsal nucleus of the brachium conjunctivum and its termination in the peripeduncular grey ventral to the CGM, indicate that this system does not subserve an auditory function. In this context it is interesting to note that in a hemichordotomy many fine fibres are supplied to the dorsal nucleus of the brachium conjunctivum of the same side (see fig. 40 and 41).

Other ascending projections to the IC and its direct vicinity

a. Spinal afferents. Hemichordotomies at a high cervical level show (series B 193, B 194, fig. 40 and 41) the tectum mesencephali to receive afferents from the spinal cord by way of the spino- and cervicothalamic systems. Within the lateral part of the medial lemniscus, fibres of the latter system pass dorsally rostral to the lateral lemniscus and terminate in a small area just rostral to the IC (see figures 40 and 41), exactly at the transitional zone of the inferior and the superior colliculi. Degeneration is also found in a similar position rostral to the superior colliculus.

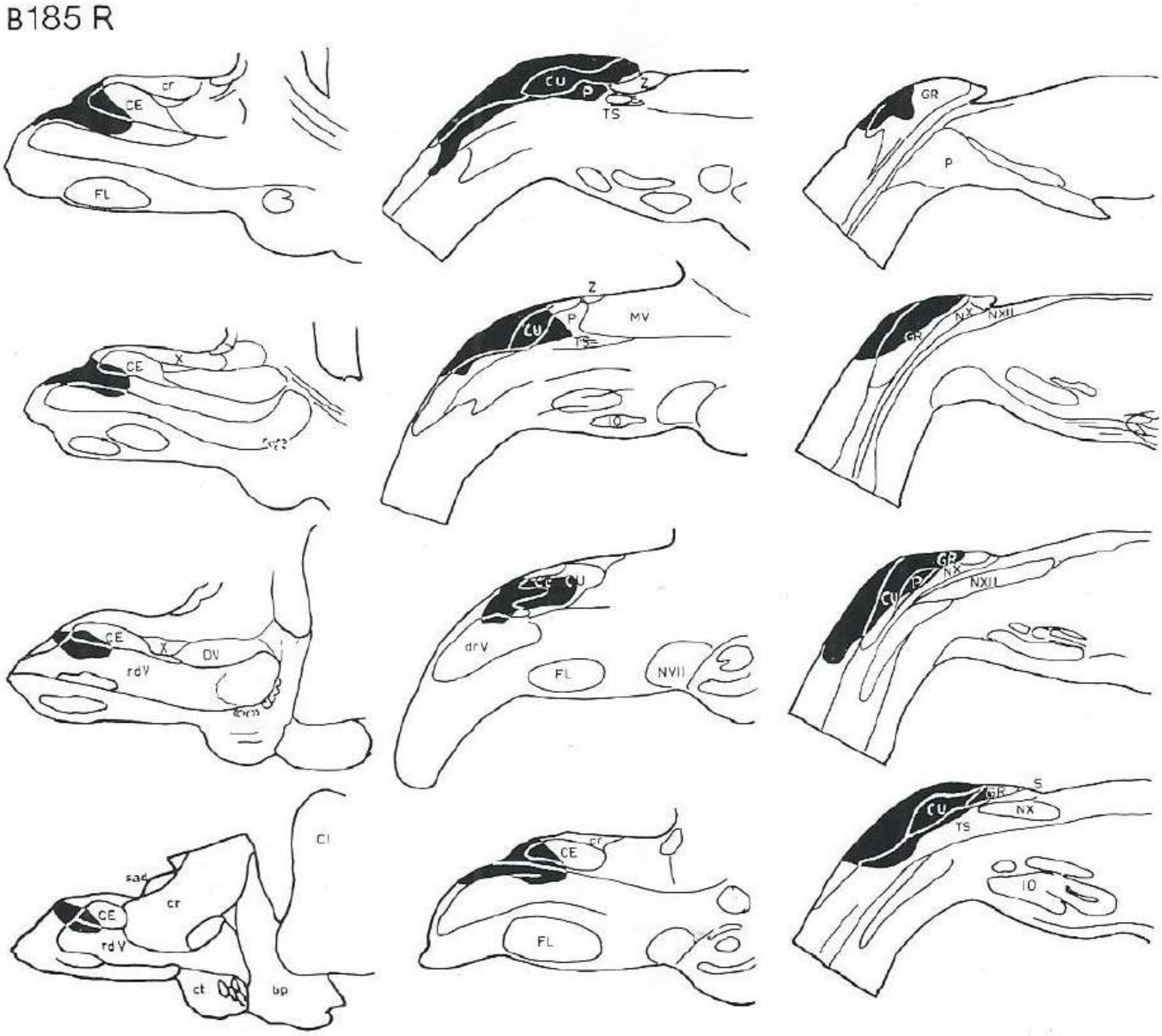


Fig. 42.

The spino-cervico-thalamic fibres can be followed farther rostrally running through the medial part of the magnocellular nucleus of the CGM, where termination is not obvious but neither improbable. More rostral terminations in the thalamus will not be described, but in general they confirm what was found by others (Anderson and Berry, 1959; Mehler et al., 1960).

From these series it also can be concluded that spinothalamic fibres are not interrupted by lesions restricted to the VLL and the DLL, but only when the lesion occupies the lateral part of the medial lemniscus, which is in contradiction to the opinion of Goldberg and Moore (1967).

b. The medial lemniscus. Especially the tectal terminations of the components orginating in the nucleus gracilis and cuneatus have been studied, but in the sagittal series the thalamic and other degeneration is also depicted (fig. 42 and 43, series B 185, B 195).

In the superior colliculus the degeneration is mainly found in the third grey layer, but laterally this layer is replaced by the parabrachial area, where the degeneration is found especially at its borders, and caudal to it in the lateral zone of the IC. Remarkable are the degenerated preterminals on the small cell clusters between the fibres of the bci, and the tiny concentrations of them on groups of cells in the central nucleus of the IC. Moreover degeneration is found just rostral to the IC and the SC, as was the case in the hemichordotomy series.

All together only a few cells of the central nucleus of the IC receive preterminals from the medial lemniscus, some fibres terminate in the lateral zone of the IC, but the majority terminate rostral to the IC. The parabrachial area remains almost free of degeneration.

At the level of the CGM degenerated fibres are found in the magnocellular part of the CGM, partially traversing it and partially to terminate there, in accordance with the findings of Morest (1965).

DISCUSSION

The termination of the medial lemniscus and spinotectal fibres in the tectum mesencephali partially overlaps. They have a common termination in the structures surrounding the colliculi, but the medial lemniscus moreover terminates on some small groups of cells in the central nucleus of the IC. The sharp borders between areas with and without degeneration in the parabrachial area once more justify the demarcation of this area as a separate nucleus.

SUMMARY

Summarizing we can state that the first order neurons all are interrupted in the cochlear nuclei, and the second, third and fourth order neurons in the inferior colliculus, which emphasises the latter's importance in the auditory pathway.

The second order neurons all are located in the cochlear nuclei. The third order neurons are located in the superior olives, the nucleus of the corpus trapezoideum

B185 R

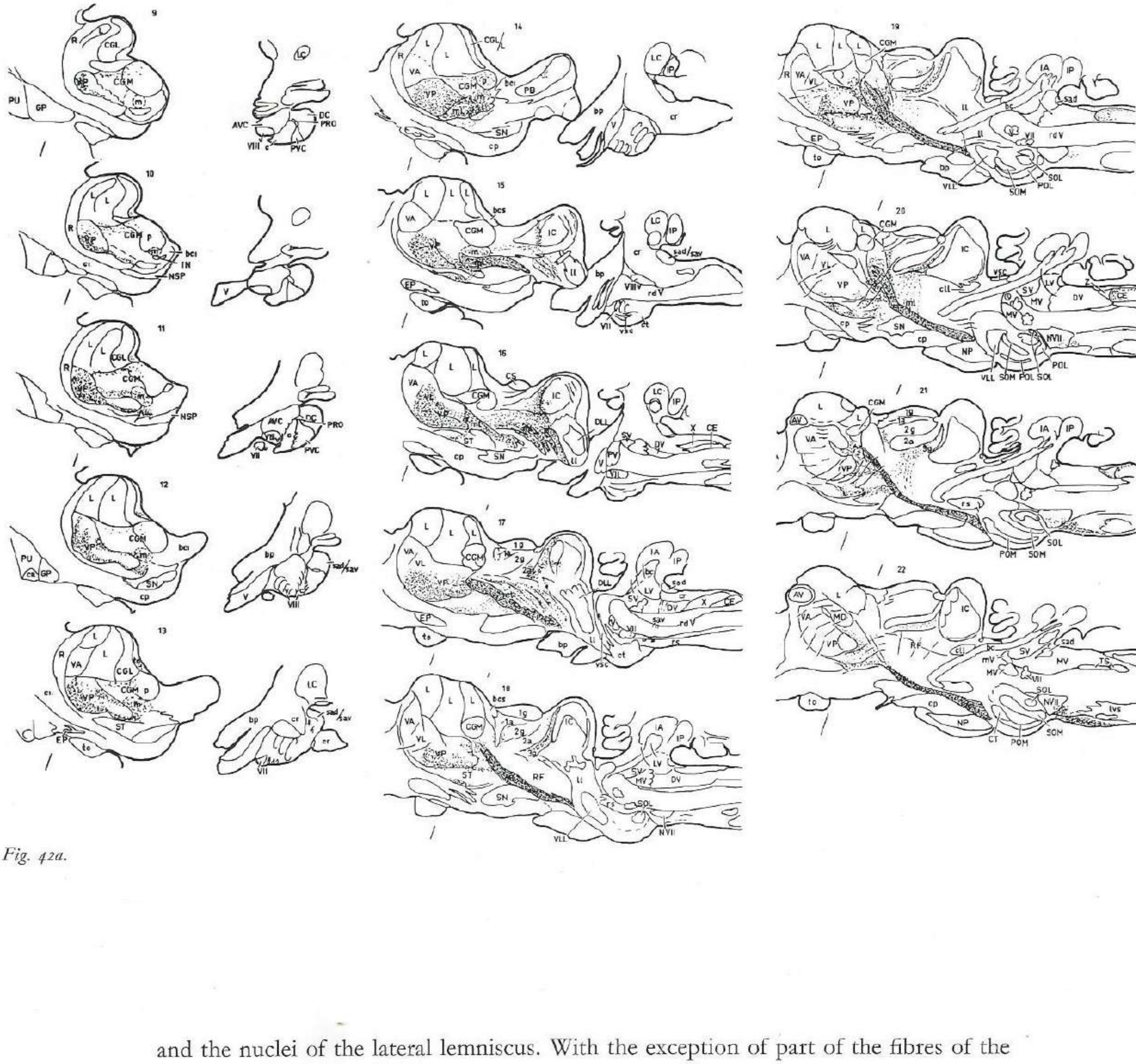


Fig. 42a.

and the nuclei of the lateral lemniscus. With the exception of part of the fibres of the CT which terminate in the SOL, their fibres terminate in the IC.

The fourth order neurons are located in the nuclei of the lateral lemniscus and the lateral superior olive, which also projecti on the IC, but part of those of the DLL after crossing in Probst's commissure.

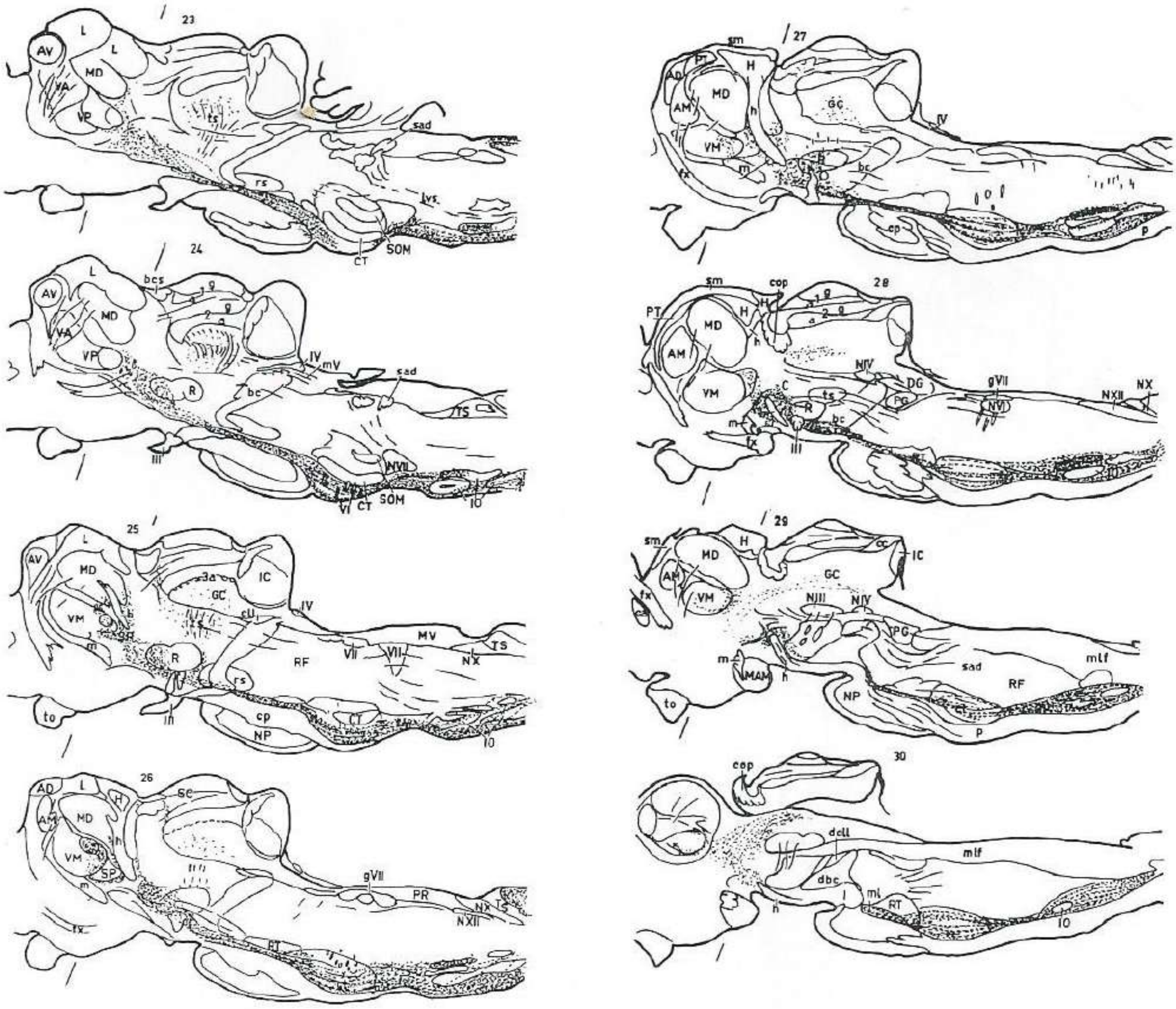


Fig. 42b. **B 185R**

Descending afferents to the inferior colliculus

Afferents from auditory cortex and corpus geniculatum mediale.

From the cortex: As is seen in series B 52 (fig. 44) where a temporal ablation is made, the degeneration runs for a part to the CGM where it ends in the ventral part as does the

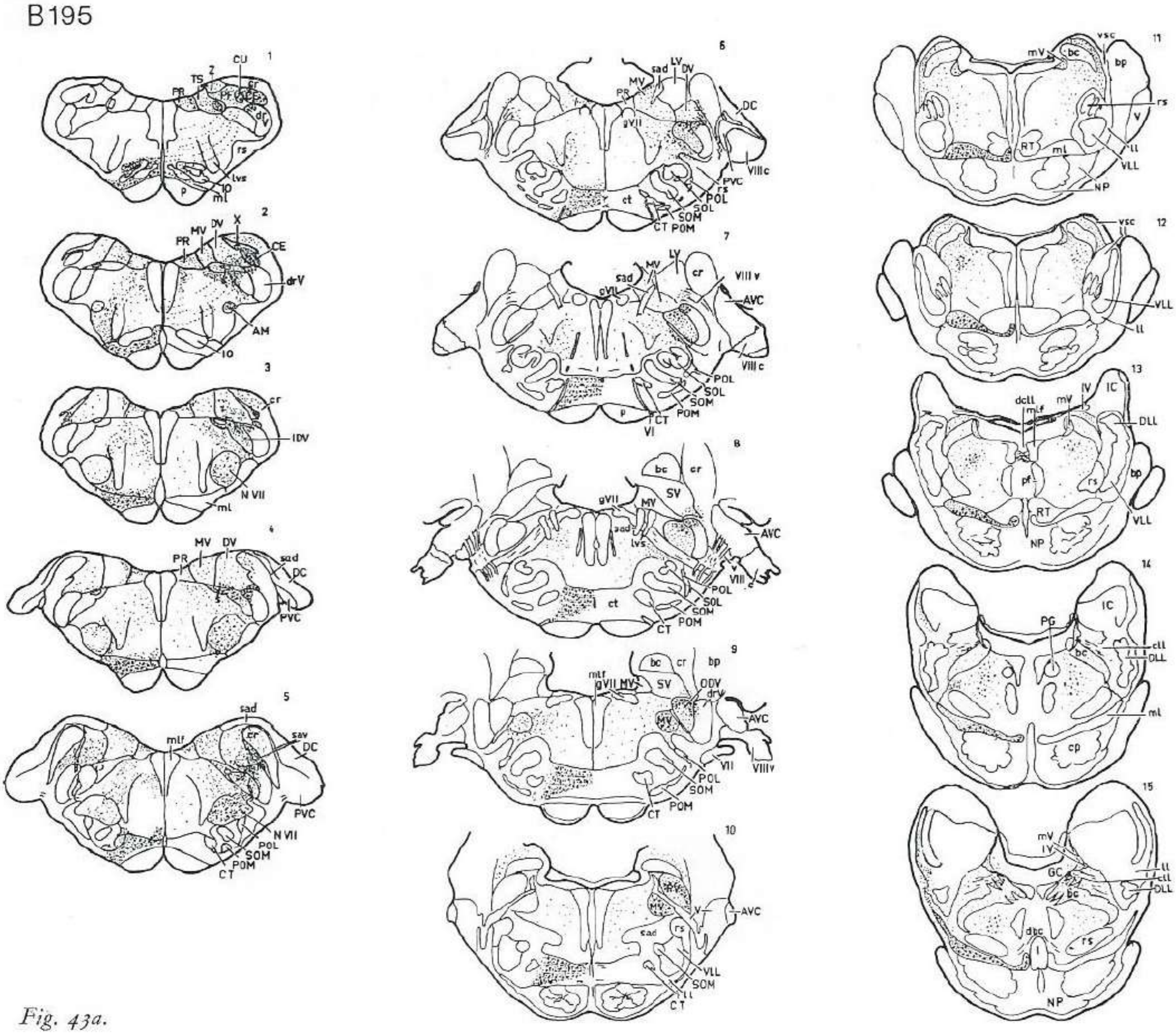


Fig. 43a.

projection from the IC. The magnocellular part does not receive preterminals distinctly. The inferior colliculus receives a noticeable quantity of fibres as is seen in figure 44, mainly ending in the dorsal part and the lateral zone. Originally lying in the lateral part of the pedunculus cerebri the degenerated fibres begin to turn dorsally at the level of the caudal CGM border. These fibres most probably enter the superior colliculus. At lower levels the degeneration is seen entering the inferior colliculus along the medial side of the bci. The PB and the top of the processus rostroventralis receive a number of degenerated fibres. More caudally the ventral nucleus seems to remain free from degeneration, while the dorsal part gets a distinct preterminal projection. Through the commissure of the IC a number of fibres reach the contralateral IC where they terminate mainly in the dorsal part of the central nucleus. It also remains doubtful whether the degeneration in the lateral zone is preterminal. The other cortex areas frontal, occipital and parietal fail to give degeneration in the IC.

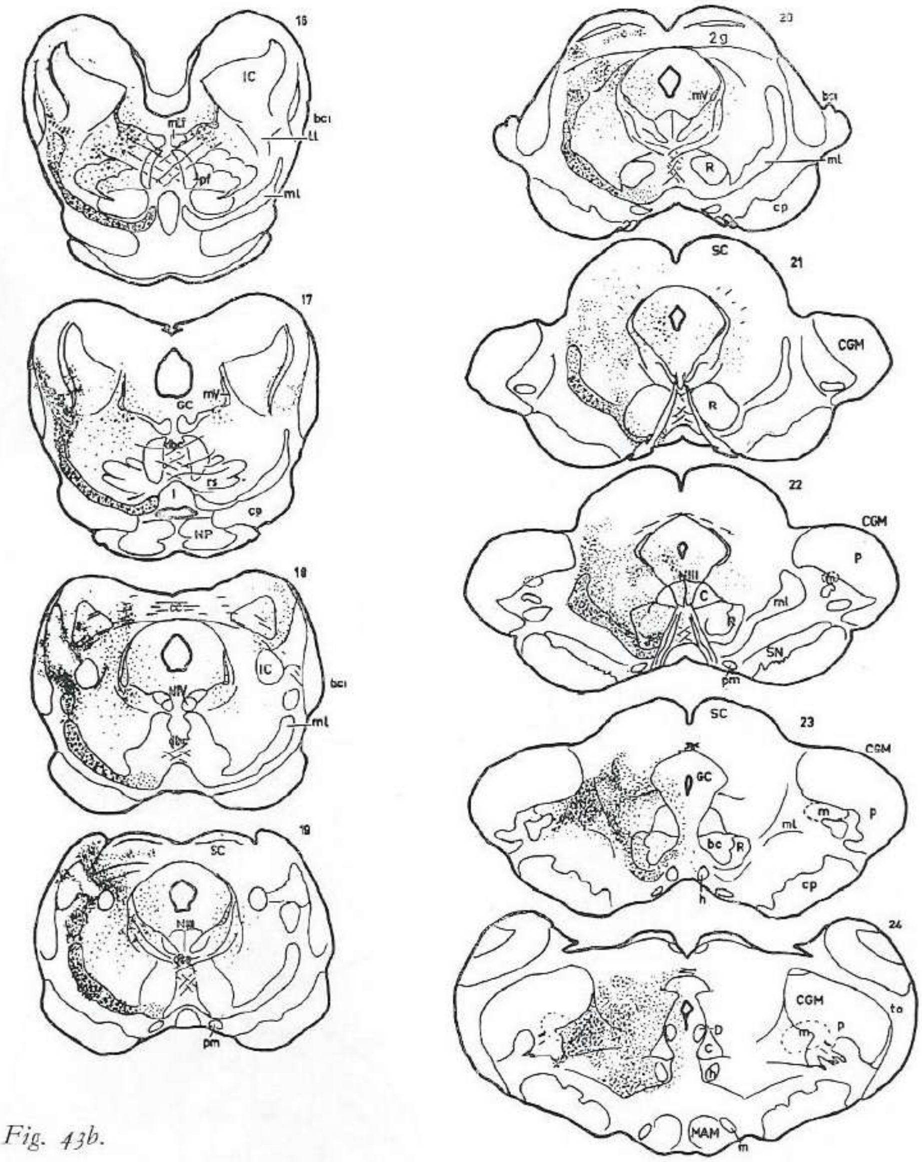
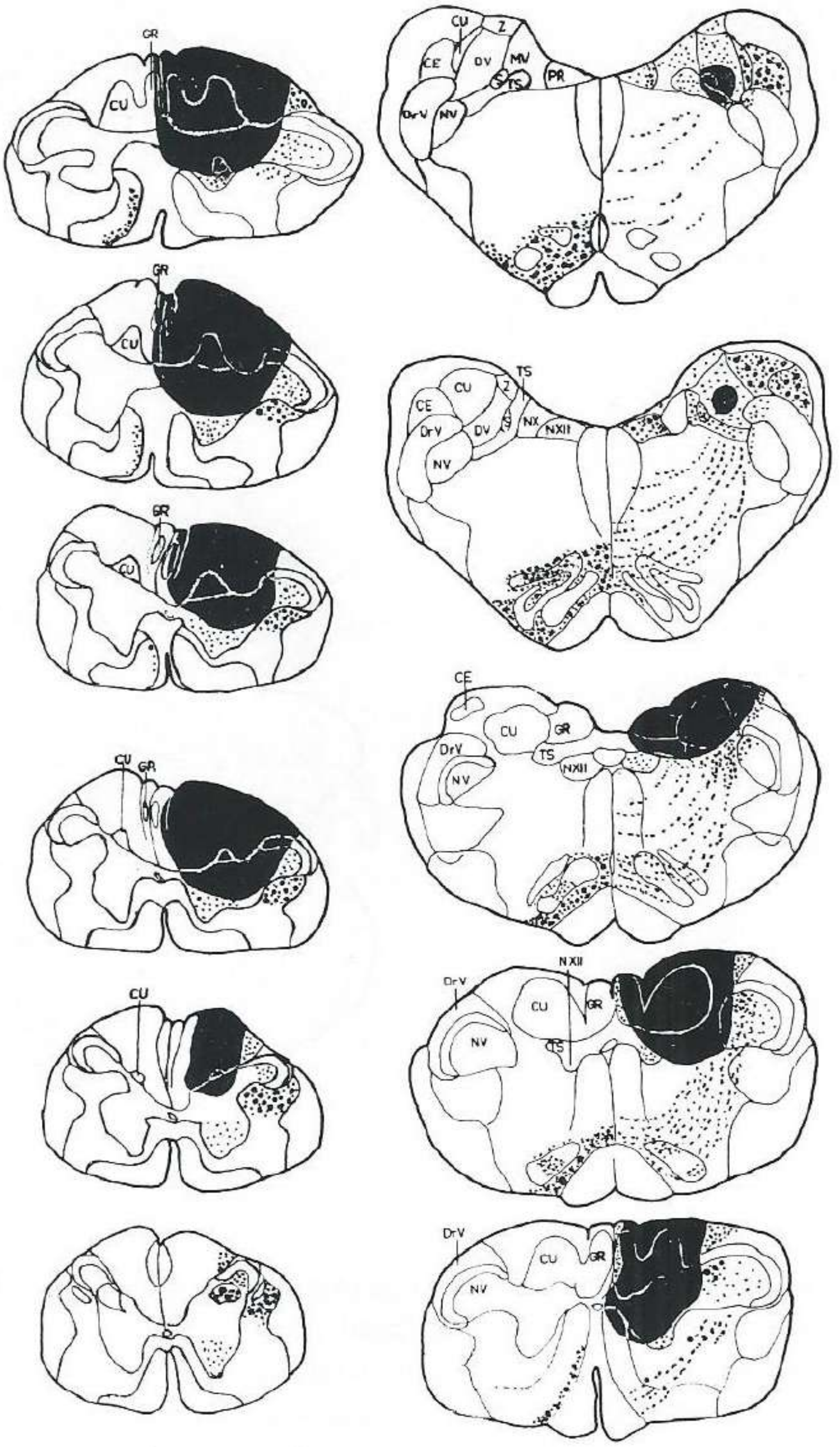


Fig. 43b.

From the CGM: In series H 6555 and B 203 (fig. 45 and 46) the lesion destroys part of the principal nucleus and small part of the magnocellular nuclei. The degeneration descending from this lesion assembles in the corner between CGM and colliculus superior, in which location it descends to where the bci occupies this region. It is then found in the dorsal part of the brachial area, while a smaller quantity of degenerated fibres intermingles with the ventral part of the bci. Where the parabrachial area begins, a clear preterminal degeneration is seen between the nuclei of this area, while a few fibres are traceable to a more medial location just dorsorostral to the processus rostroventralis of the IC.

In the rostral part of the IC the degenerated fibres are found in its outer zone at the lateral and dorsal side. Preterminals are seen directly medial to this outer zone. A number of degenerated fibres seem to run into the commissure of the IC. In the vicinity of the IC and caudally in its mediodorsal half a greater area of preterminal degene-

Fig. 43c. B 195



ration is seen. This corresponds fairly well with the dorsal part of the IC. In the lateral zone there is likewise preterminal degeneration.

The obvious preterminal degeneration ensures that we have to do with orthograde and not with retrograde degeneration here.

B 50


28
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MD
L
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VPL
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ZI
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26
L
CGL
to
CGM
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h
CM
VP
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CGM
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22
CGM
P
III
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R
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21
SC
CGM
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mV
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19
SC
III
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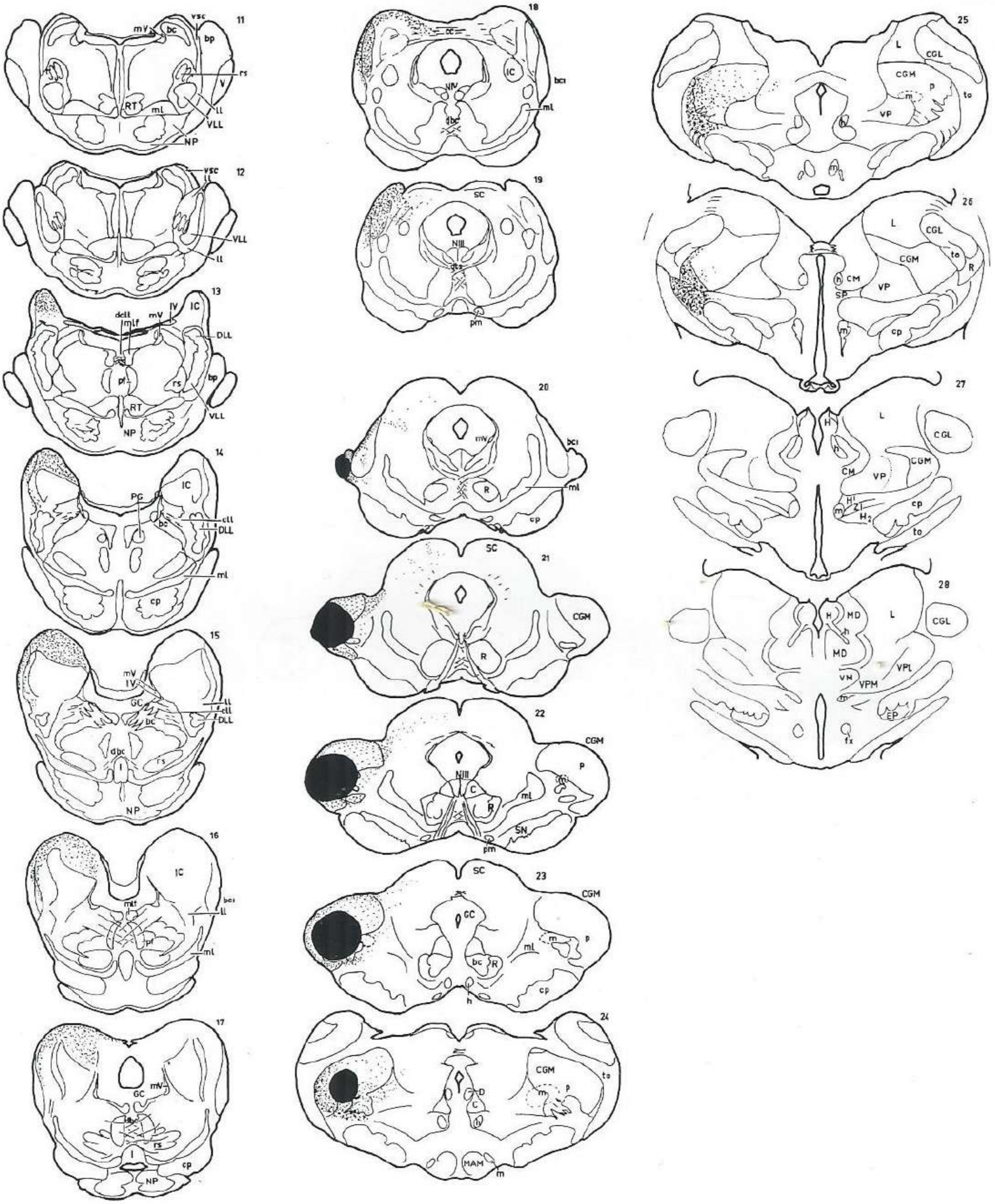
Fig. 44

H 6555



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VLL
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18
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IC
NIV
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Fig. 45.

As we have seen the projection from temporal cortex and CGM (which are possibly not the only structures rostral to the IC connected with it) is about equal. Both fibre systems reach the IC along its lateral side, the fibres from the cortex remaining laterally in the cerebral peduncle as far as the pons; the fibres of the CGM at once via the bci enter the IC, laterally. Both terminate mainly in the dorsal part of the central nucleus and in the lateral zone. The parabrachial nuclei in both series receive an intensive preterminal degeneration. In both series moreover the connection with the rostral tip of the processus rostroventralis of the IC is seen. Besides it is striking that the degeneration keeps so well to the borders between the different parts of the IC, which is a real support for the usefulness of its differentiation. Rasmussen (1964) described two different pathways from the cortex to the IC, which compared with my series show only a difference in degree. He also mentions the preterminal degeneration in the parabrachial area. His observation of preterminals in the lateral tegmental nuclei possibly corresponds with the degeneration I found dorsorostral to the processus rostroventralis.

To bring our anatomical data in accordance with the findings of the physiologists Buser et al. (1966) and Massopust and Ordy (1962) is quite possible, but leaves a number of questions unanswered. In their anatomical control Massopust and Ordy find a projection on the silent "rind" as they call it (which corresponds with Moore's brachial and capsular area) and on the central nucleus. It is not clear, however, whether the projection to the central nucleus is restricted to the dorsal part. This is essential, because the ascending fibres from a.o. cochlear nuclei do not end in its dorsal part, and this part of the central nucleus belongs to the silent area most probably. This could not be verified in the article of Massopust and Ordy either.

Buser and co-workers found the areas on which the auditory cortex project mainly to be located at the ventral and lateral side of the IC. Their pictures demonstrate that the area extends ventrally even into the entering lateral lemniscus. The lateral as well as the few dorsal locations may well correspond with the entering fibres from the cortex and the CGM. The ventral, however, cannot be explained with our experiments.

Kusama, Otani and Kawana's conclusions (1966) are partly in accordance with my results. They do not mention the dorsomedial concentration of degeneration in the IC especially, and they give a more detailed projection from the auditory cortex. According to them area I gives the most important projection.

B 203

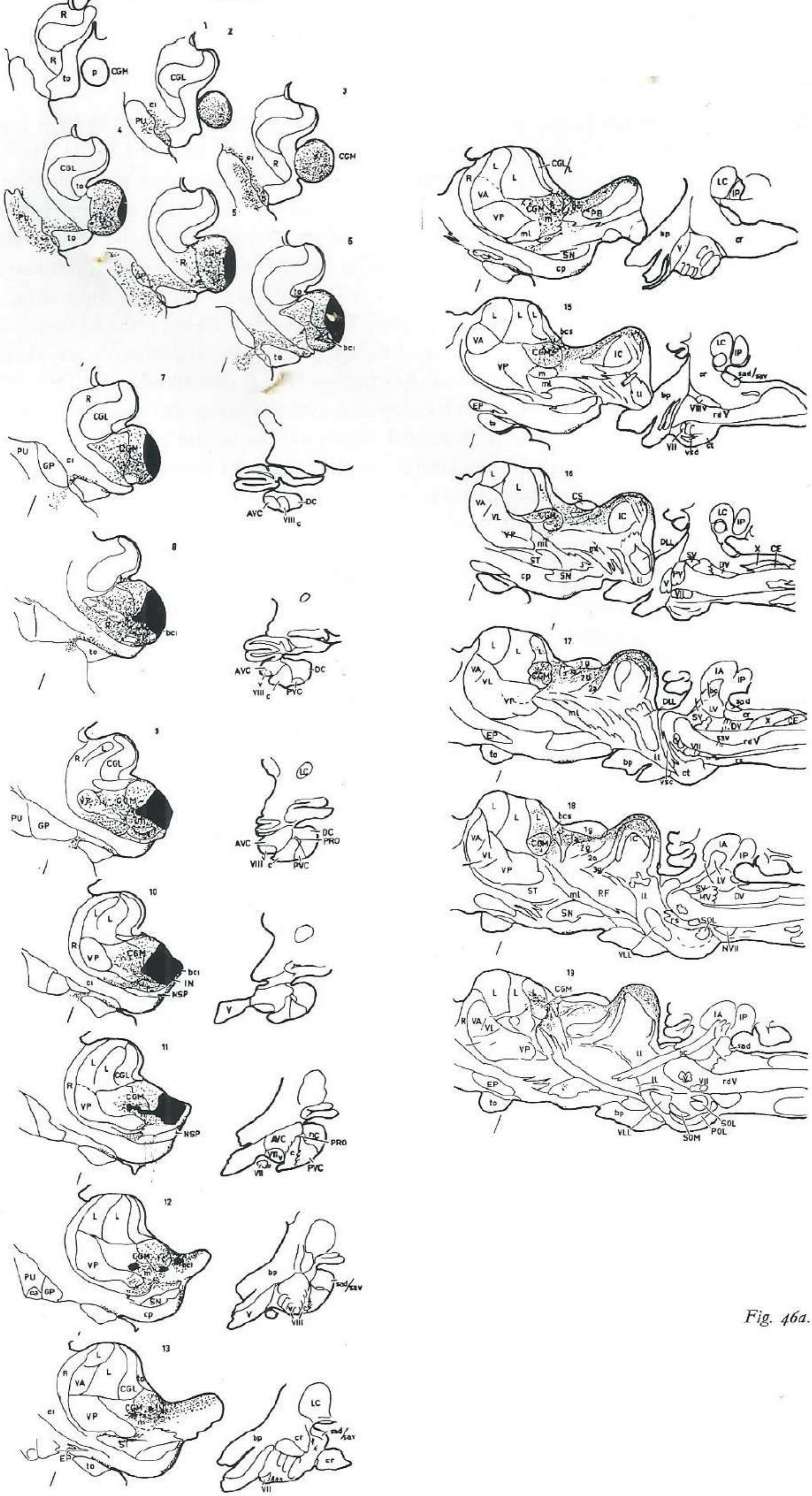
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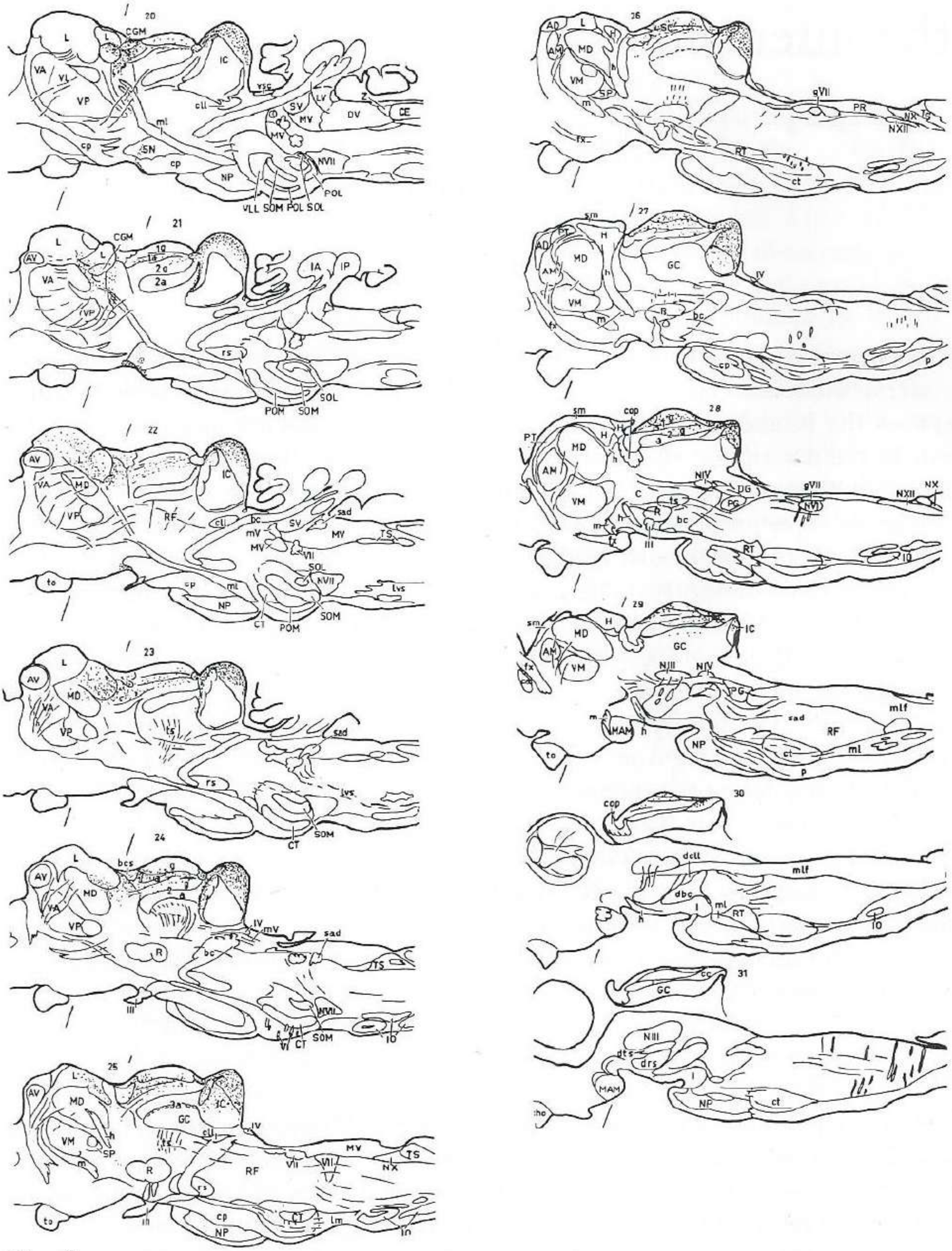
Fig. 46a.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NVII
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CT
SOM
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Fig. 46b.

Efferent connections of the inferior colliculus

5

The main efferent connection of the inferior colliculus (IC) is formed by the brachium of the inferior colliculus (bci), which terminates in the medial geniculate body (CGM), but between the IC and the CGM groups of cells are found which also play a role in audition. In the description of Moore and Goldberg (1963) they are called the parabrachial region (PB) and the nucleus interstitialis. According to them the PB is that part of the midbrain tegmentum which extends from the rostral pole of the IC to the caudal pole of the CGM and lies medial to the bci. It will be considered together with the intrinsic connections of the IC. The nucleus interstitialis is defined by them as the group of medium-sized cells which lies between the fibres of the bci at the caudal side of the CGM. It will be considered together with the termination of the bci. Special attention will be paid to a recurrent fibre system originating from the IC, which terminates in more caudal auditory nuclei, the colliculocochlear bundle. It will be described together with a system arising from the superior colliculus (SC): the tectopontine tract.

To facilitate the description of the efferents of the IC they will be subdivided into the following groups:

1. intrinsic connections of the IC
2. commissural connections of the IC: the commissure of the inferior colliculus
3. ascending connections from the IC: the bci
4. descending connections from the IC and the SC: the colliculocochlear bundle and the tectopontine tract.

a. *Intrinsict connections of the IC*

As may be expected most of the fibres originating in the IC run laterally to enter the bci, and laterally located lesions therefore interrupt most of these fibres, but medially located ones (B 149, B 157, B 106, B 139, B 156, see figures 47a and b, 48a and b) better demonstrate the efferents from certain cell groups in the IC.

From the medial lesions in series B 139 and B 156 (figures 49 and 51) we can trace the degenerated fibres laterally mainly along the rostral border of the central nucleus of the IC, and partly along its ventrocaudal side, but at the lateral side of the IC the two fibre concentrations fuse. Part of the rostral fibres directly enter the surface area of the bci, but others first run ventrocaudally and subsequently recurve in a ventrorostral direction. Together with the fibres passing along the ventrocaudal border of the central nucleus they join the medial part of the bci (see fig. 4 and 5, p. 7). The region in which the recurving fibres are found (the lateral zone of the IC) lies directly medial to the incipient bci and lateral to the central nucleus.

In all cases of medially located lesions of the IC preterminal degeneration is found in this part of the lateral zone, in its rostral prolongation (the PB), similarly located medial to the bci but lateral to the processus rostroventralis of the IC, and in the caudal surface zone of the IC which contains the laterally directed fibres. After partial lesions of the IC the central nucleus only contains passing degenerated fibres, and convincing preterminal degeneration is never present. The dorsal part of the central nucleus in particular does not receive preterminal degeneration from lesions of its ventral part. The processus rostroventralis, however, is undoubtedly the area where fibres originating in more caudal parts of the IC terminate (see fig. 53, scheme 18 and others).

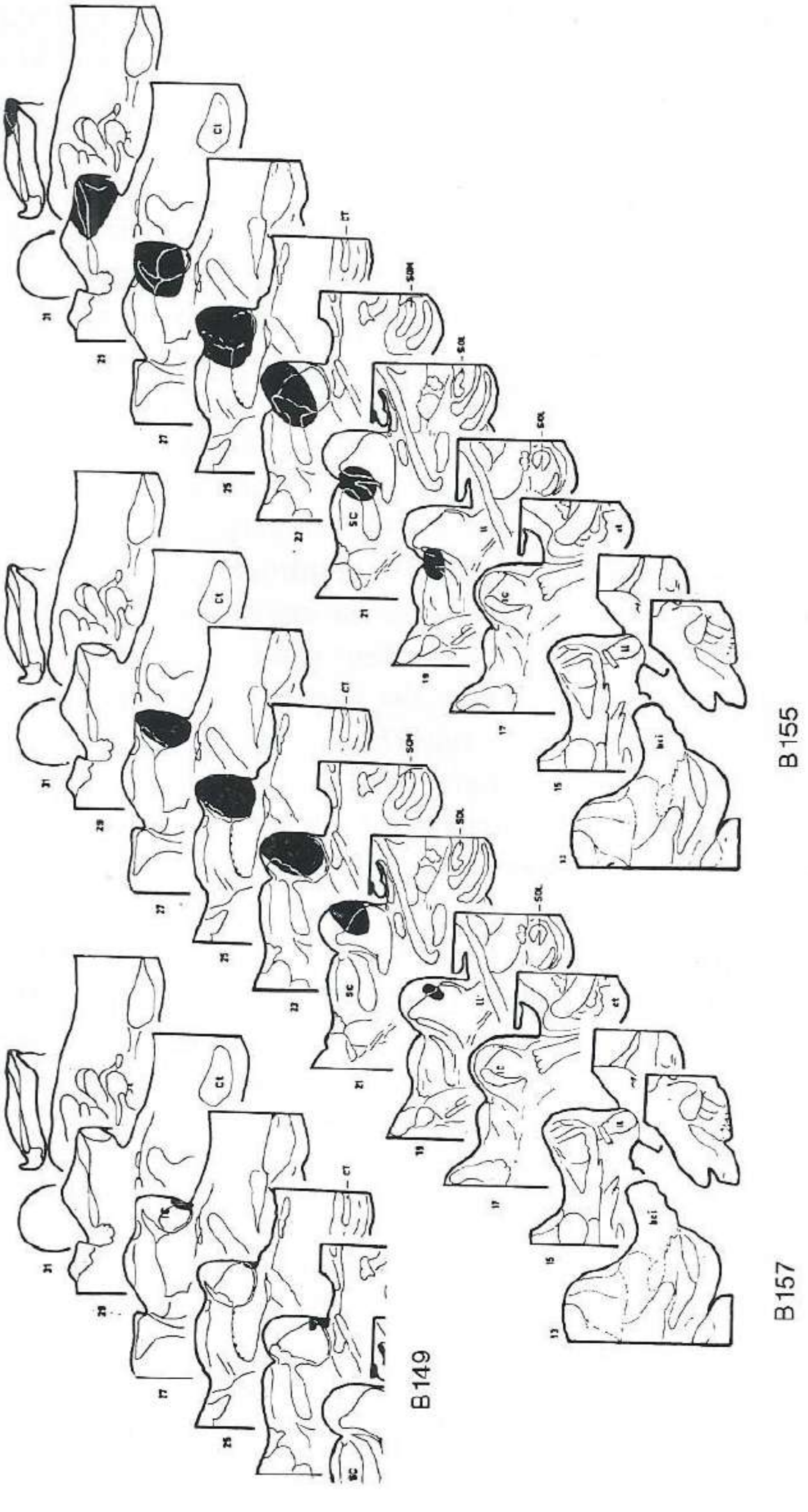
As pointed out the PB is the region medial to the bci and lateral to the processus rostroventralis, which contains preterminal degeneration after complete ablation of the IC. Demonstrated by the degeneration found in the series B 170 and B 171, with large lesions of the IC (figures 50, 54 and 55) this region comes into existence between the incipient bci and the recurving fibres on their way to it, lateral to the central nucleus (see fig. 5 and fig. 6, chapter 3). In certain areas the degeneration is unmistakably preterminal, but at other places the recurving fibres may cause confusion. More rostrally the PB laterally borders the processus rostroventralis, their border being indicated by bundles of normal, tectopontine fibres, which alternate with smal strands of fibres, cells and numerous dendrites which interconnect the two structures. These strands probably are extensions of the PB and have therefore been included in the PB of the diagrams. Like the PB and the processus rostroventralis the connecting strands contain preterminal degeneration. The most rostral part of the PB in these series is found in the region between the superior colliculus and the tegmentum mesencephali, medial to the dorsal edge of the bci. This area scarcely differs from the surrounding reticular formation, but it receives a circumscribed preterminal degeneration in most lesions of the IC (see fig. 49, 50 and 51, level 20, series B 171, B 139, B 156).

The preterminal degeneration in the PB is sometimes found in small concentrations corresponding to its small clusters of cells. In normal material the PB can be recognized by the slightly larger cells when compared with the surrounding reticular formation, which, however, are smaller than those in the processus rostroventralis.

Apart from terminating fibres the PB and the connecting strands also contain fibres passing between the bci and the processus rostroventralis. The preterminal degeneration in the latter abounds in series B 170 and B 171 (fig. 50, 54 and 55) and spreads all over the processus. The fine preterminals are confined within the borders of the processus, except for the dorsolateral region where they are connected with the degeneration in the PB by the above-mentioned strands.

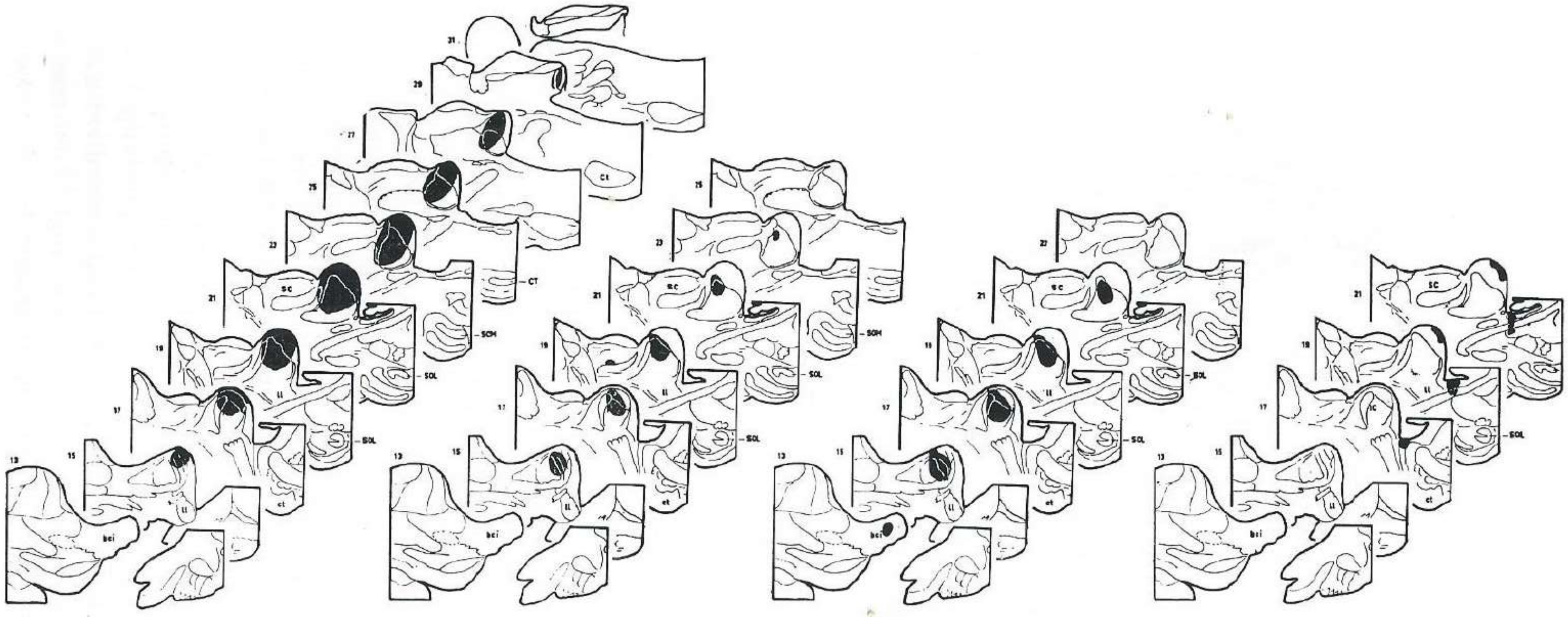
In series with lateral lesions (B 83, B 93 and B 192) the degeneration is found along the rostrodorsal side of the processus only, which the fibres reach from the bci

Fig. 47a.



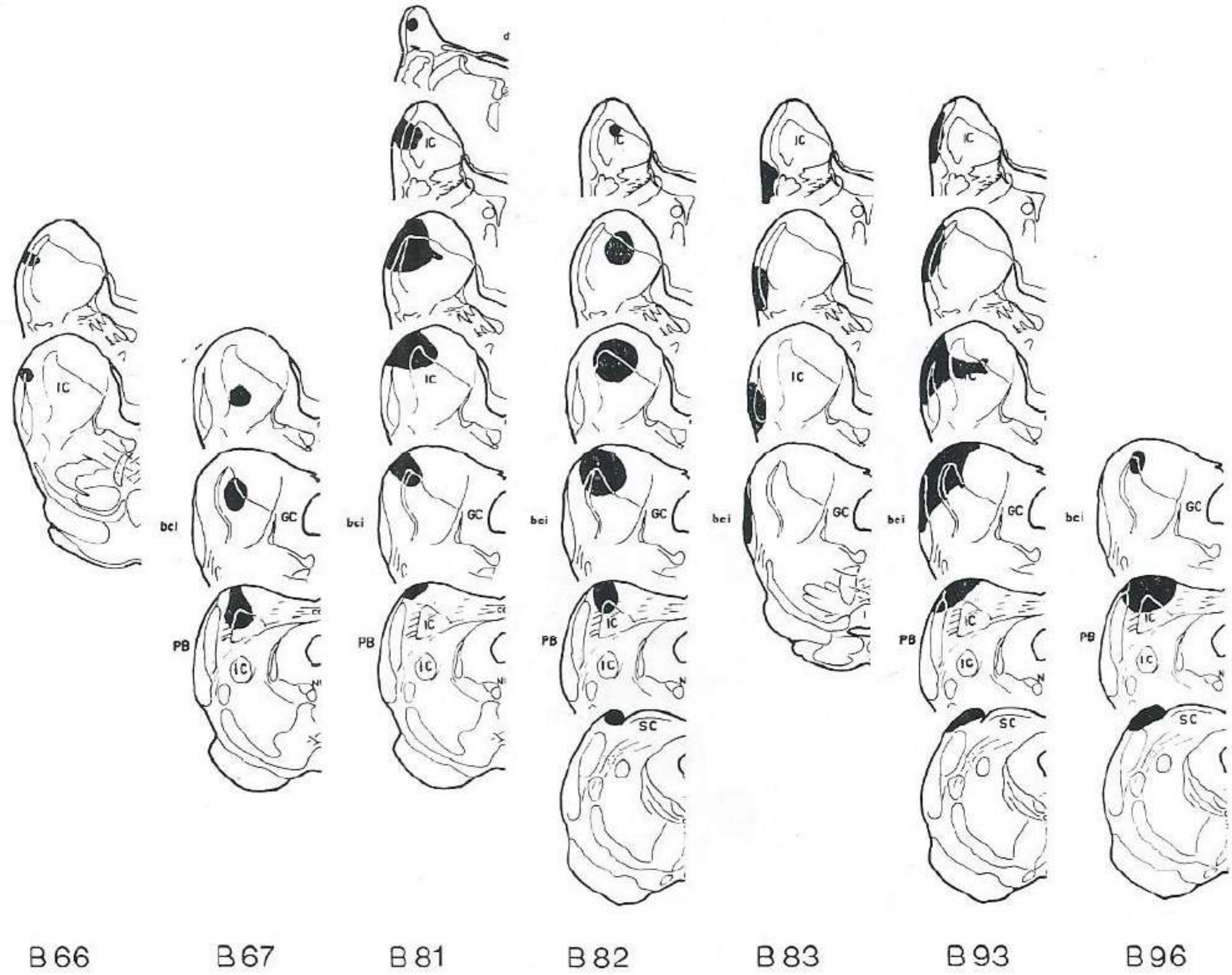
via the PB which similarly receives preterminals, and the tectopontine fibre fascicles. A similar course of the fibres to the processus is seen in series B 161, with an electrode track lesion within the bci.

Series with medial lesions, B 149 and B 156 (fig. 50, 53) produce a degeneration at the dorsal side of the processus. In series B 139 (fig. 51) with a similar lesion we find the preterminals concentrated in two areas, a lateral and a dorsomedial one, both areas



B170 B79 B80 B180

Fig. 47b.



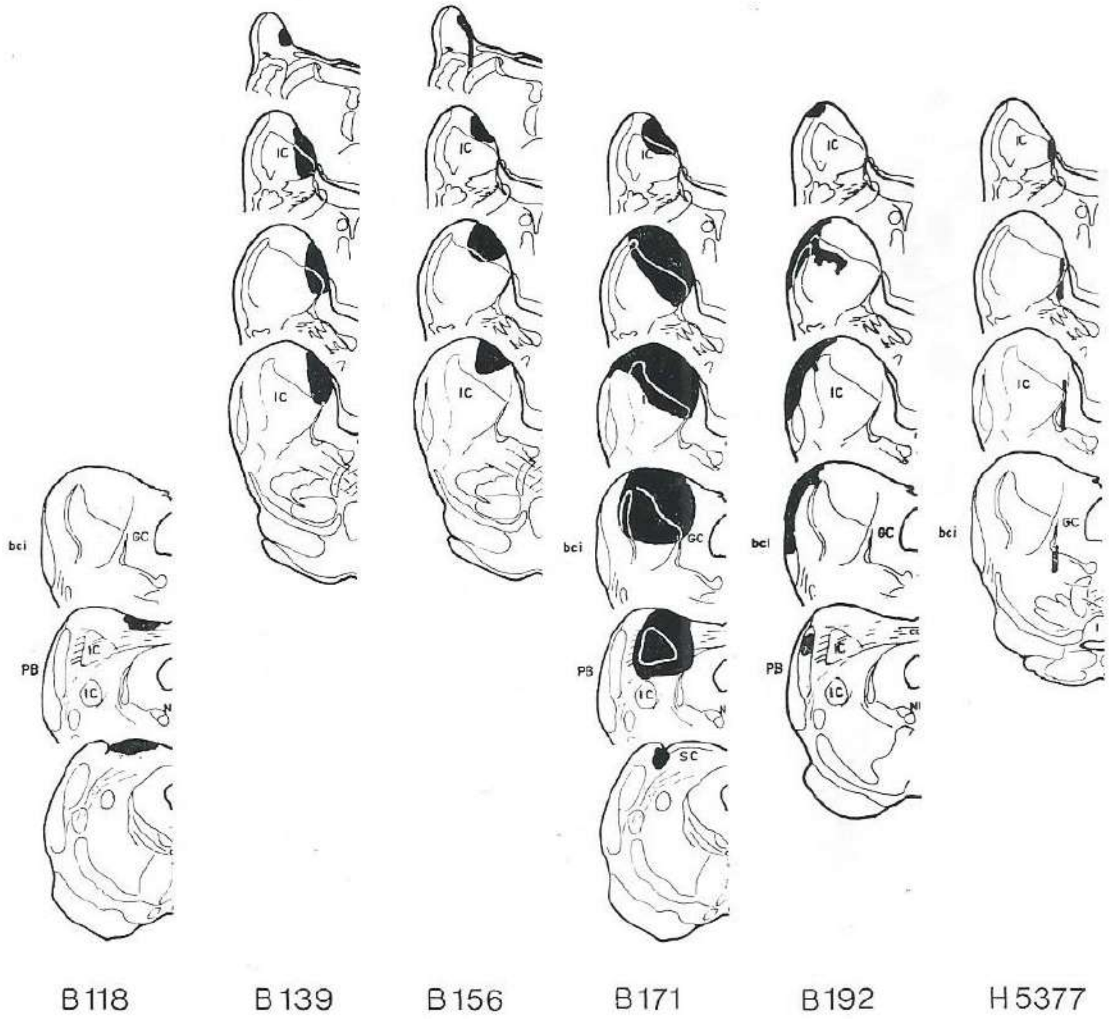
again connected with the degeneration in the PB and the bci. The greater part of the degeneration in the processus is caused by fibres which enter it along its mediodorsal side. Farther rostrally this dorsomedial area of degeneration occupies the whole processus still firmly connected with the PB and the bci.

The presence of fibres passing from the bci to the processus is therefore established, but that of fibres running in the reverse direction is difficult to ascertain, although it is suggested by the series with medially located lesions, B 139 and others. Only in B 180, with a superficial lesion of the IC, preterminal degeneration in the processus was absent.

When the lesions are restricted to the IC, a small quantity of preterminal degeneration is found in the central grey matter.

DISCUSSION

In the description of the normal structure of the IC (chapter 3) this was divided into a central nucleus and a lateral zone, the latter recognizable by its slightly different fibre architecture. Medially located lesions of the IC show that it receives a strong projection

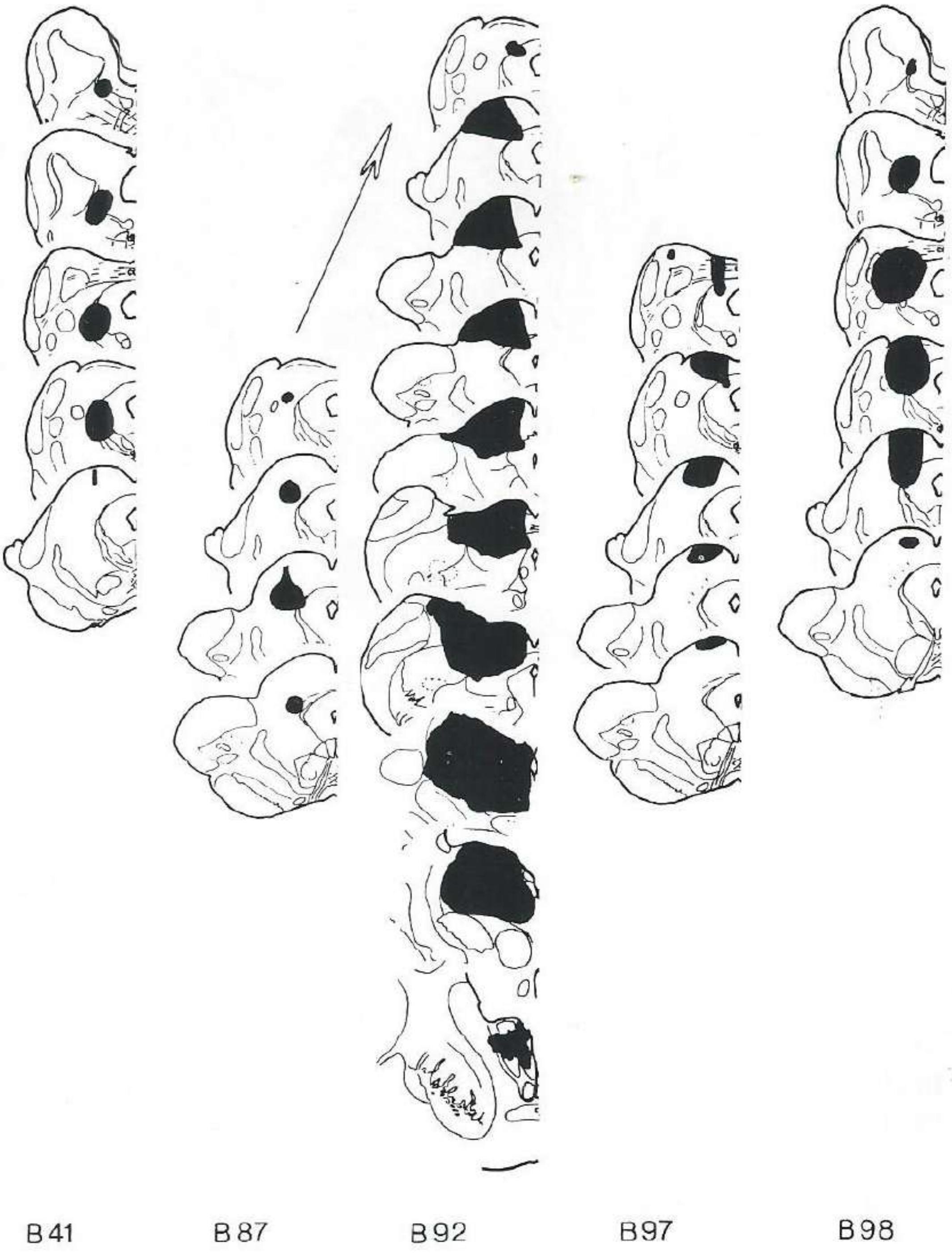


from the IC itself. In this respect it resembles the PB, located more rostrally between the bci and the processus rostroventralis. Moore and Goldberg (1963) who described the PB, did not bother about its caudal border, but schematically they depicted also the termination of IC efferents in the lateral zone. The rostral extremity of the PB can scarcely be distinguished from the reticular formation, hence this nucleus is defined by its afferent connections from the IC only.

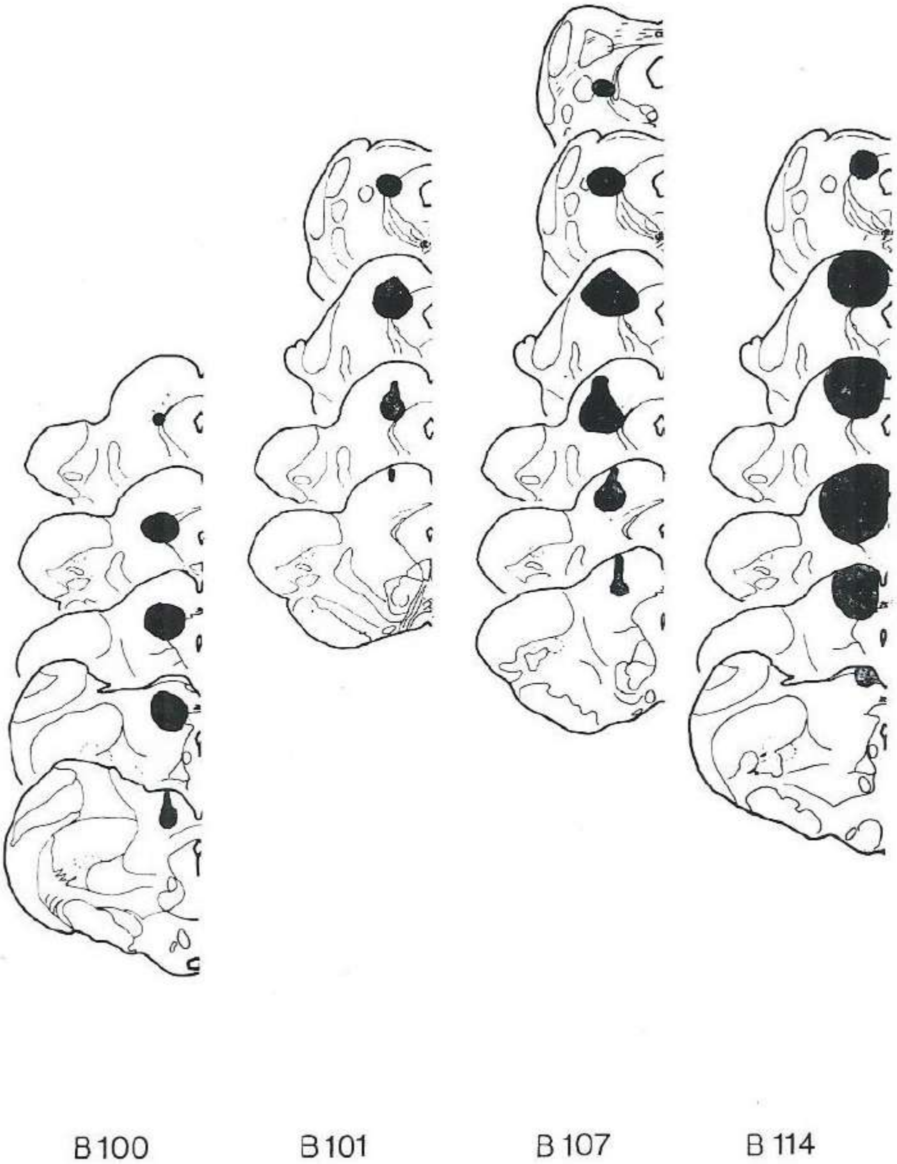
Intrinsic connections of the central nucleus appear to be absent, although the fact that the established termination of the lateral lemniscus in this region does not look like preterminal degeneration, indicates that such a statement should be considered with some caution. Many fibres of the IC, however, terminate in the processus rostroventralis. With respect to their afferent connections the lateral zone, the PB and the processus rostroventralis are therefore very similar. The region immediately rostral to the IC (probably including the PB, the processus rostroventralis and the lateral zone) projects on the dorsal part of the CGM (Morest, 1965), which has to be investigated in greater detail.

As far as a possible topical projection of the central nucleus en the processus and

Fig. 48a.



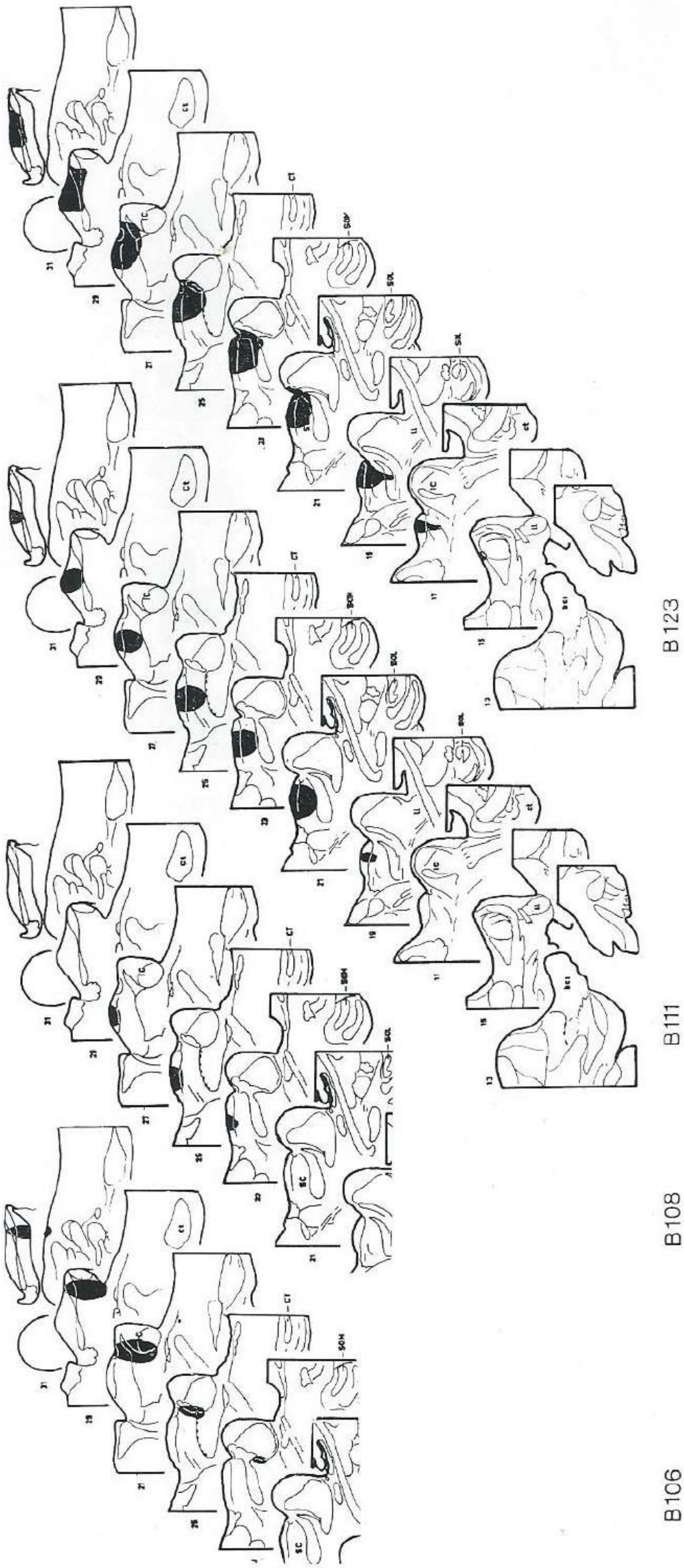
the PB is concerned, the material is inconclusive. Medial lesions generally produce degeneration in the dorsomedial and rostral parts of the processus, and lateral ones along its lateral side. No indications of a topical projection to the PB were found. In one small and superficial lesion of the IC (B 180) degeneration in the processus was absent, but in the PB it occupied the usual position.



b. Commissural connections: the commissure of the inferior colliculus

Part of the efferent fibres of the IC located in the layer rostral to the IC take a medial direction and enter the commissure of the IC, which similarly lies at the rostral side of the inferior colliculi. The fibres which end in the heterolateral IC have therefore to curve caudally to enter its nucleus (see B 170 and B 171, figures 50, 54 and 55).

Fig. 48b.



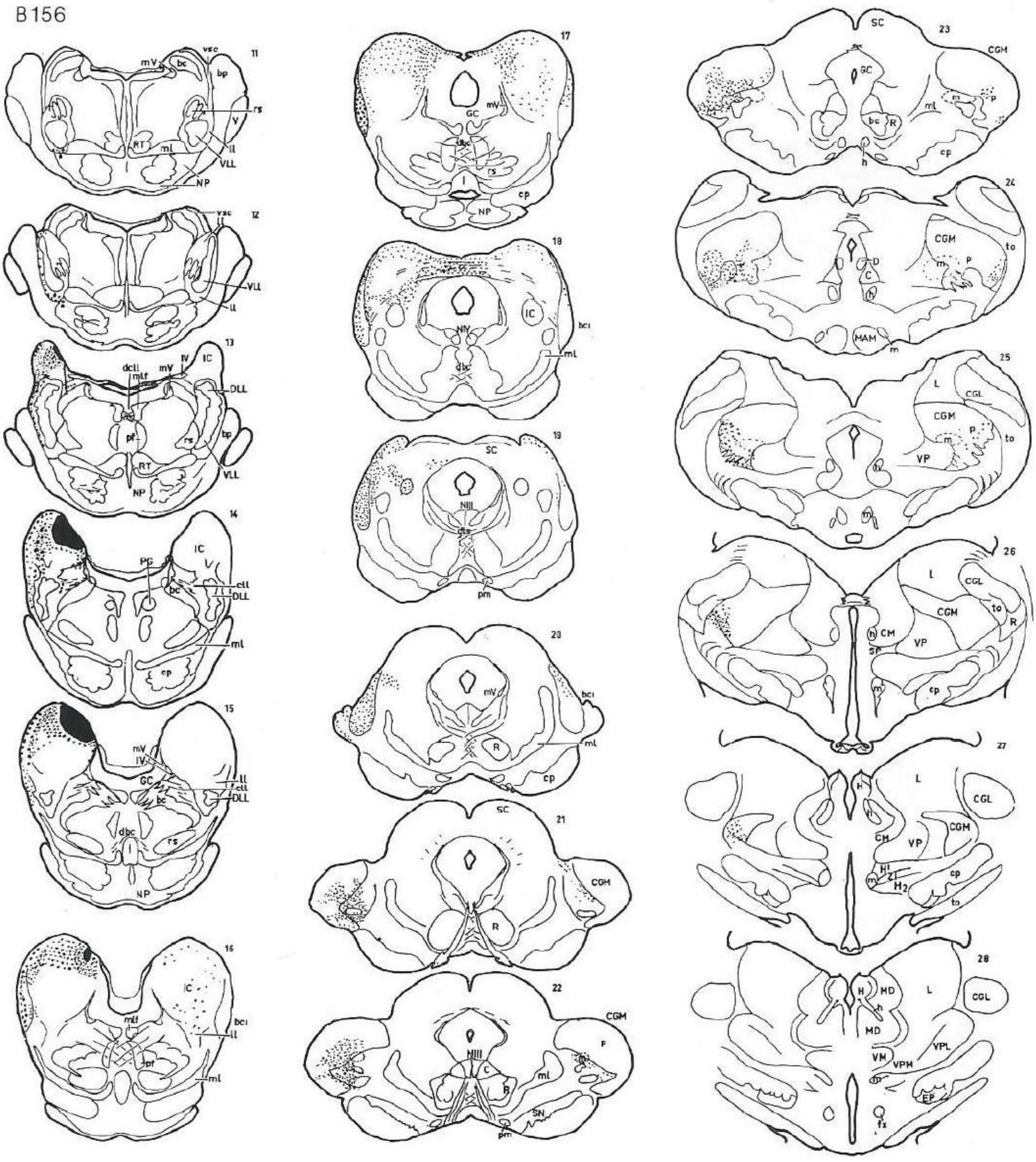


Fig. 49.

Other fibres after crossing proceed in a lateral direction along the rostral side of the IC and subsequently enter the bci. In the lateral zone some of them curve caudally before entering the brachium, as described on the homolateral side.

The localization of the preterminal degeneration in the heterolateral IC does not

B 171

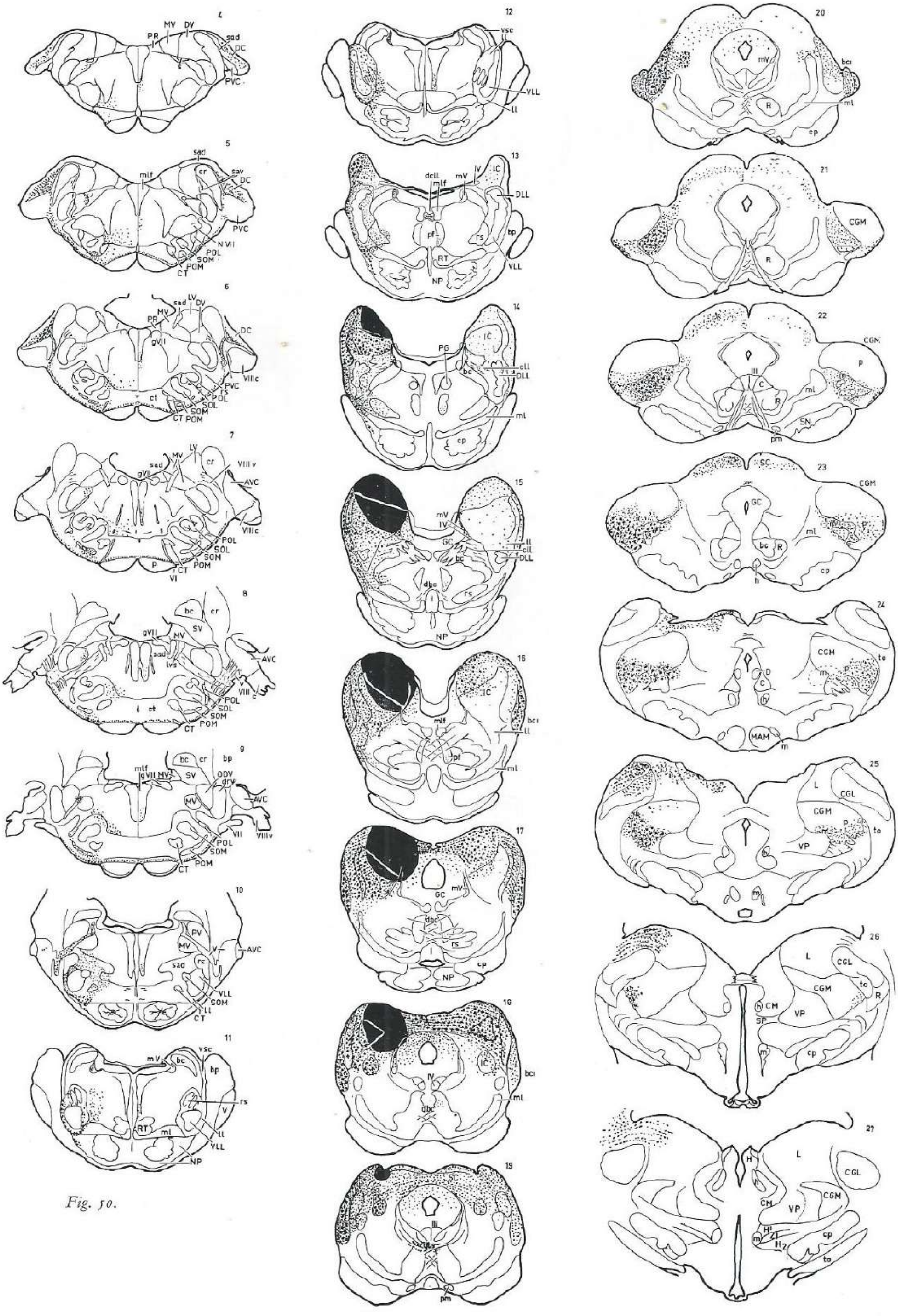

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Fig. 50.

B 139

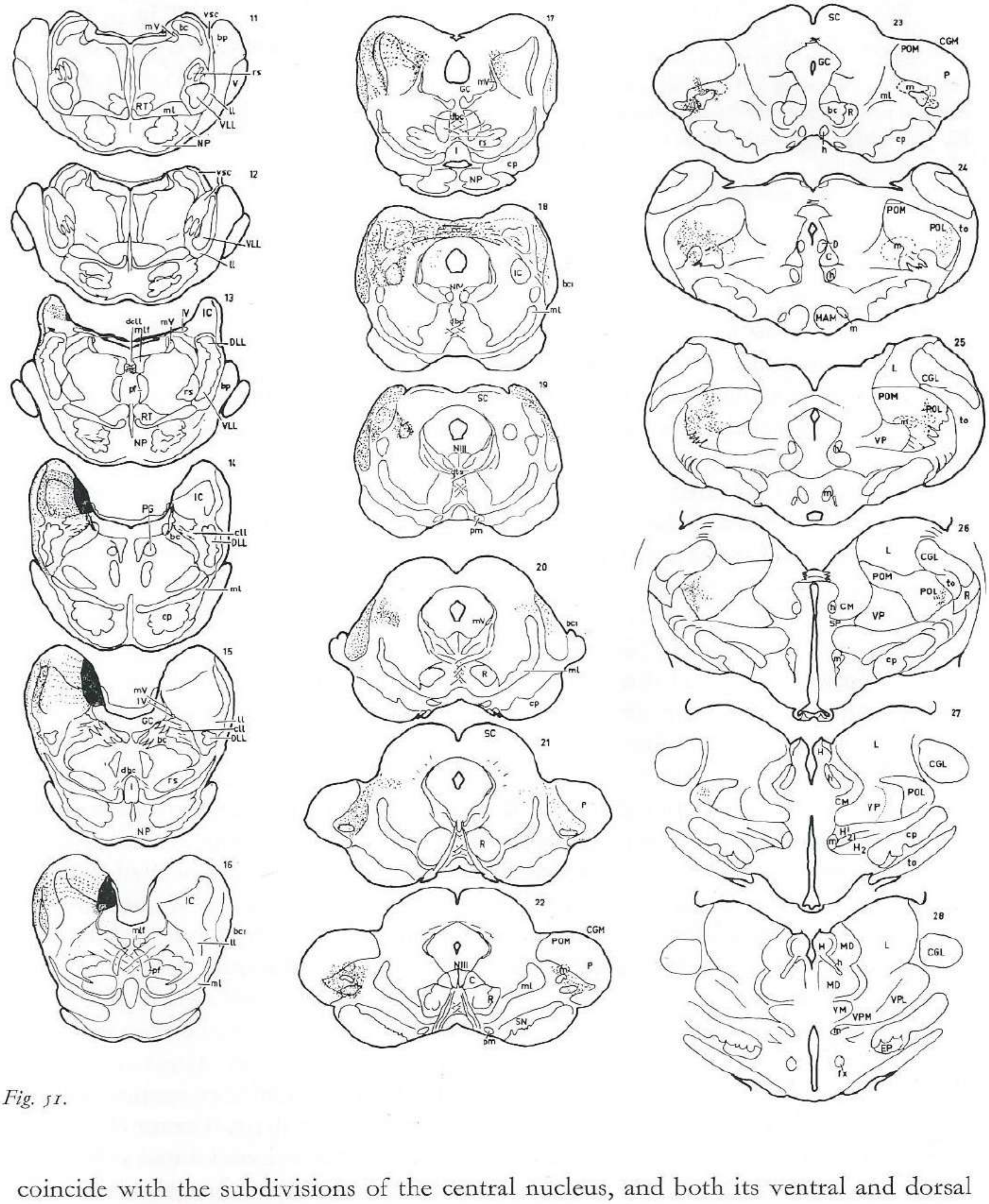

Fig. 51.

coincide with the subdivisions of the central nucleus, and both its ventral and dorsal part receive terminations. Immediatly lateroventral to the commissure concentration of preterminal degeneration is most dense, but in the ventral part of the central nucleus degeneration is largest in its dorsorostral portion, whereas the rest of it is almost free from degeneration. The processus rostroventralis receives a preterminal degeneration

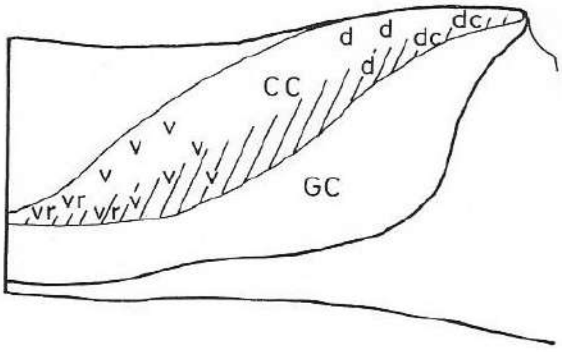

Fig. 52. Commissure of the IC.

vr = fibers originating in the ventrorostral part of the IC
v = fibers originating in the ventral part of the IC
d = fibers originating in the dorsal part of the IC
dc = fibers originating in the dorsocaudal part of the IC

Hatched part contains fibres from the medial half of the IC. The other part contains fibers from the lateral part of the IC.

similar to the homolateral, but of less intensity. In the series B 171 and others we find degenerated fibres between the rostral tip of the processus rostroventralis and the bci. Because at more caudal levels the processus does not contain much degenration, here again the degenerated fibres seem to come from the bci to terminate in the rostral tip with its direct surroundings.

All partial lesions of the IC are followed by degeneration into its commissure, but the distribution of the degeneration in the heterolateral IC usually is the same in all such experiments. Connections between the IC's of both sides therefore are not topically organizaed, but within the commissure a certain localization is present.

Lesions B 180 (fig. 39), located dorsally, causes degeneration in the caudal tip of the commissure, whereas B 149 (fig. 53), a ventromedial lesion, leaves this area free and shows more degeneration halfway the commissura than B 180. In a more rostral lesion the highest concentration of degeneration will probably be seen in its rostral end.

It may be expected that fibres arising from the medial part of the IC cross in a more ventral position than those from its lateral part, although my series do not always support this statement. Series B 192 and B 139 (fig. 51) e.g., with a lateral and a medial lesion respectively, both reveal a degeneration in the whole dorsoventral range of the commissure. B 66, however, with a dorsolateral lesion, shows degenerated fibres in the dorsal part only, whereas in B 149 (fig. 53), with a ventromedial lesion, the greatest number of degenerated fibres is located in the ventral part of the commissure. Simplified a distribution as illustrated in figure 52, can be depicted diagramatically.

DISCUSSION

All lesions of the IC give rise to a degeneration in the commissure, even the small laterally located lesions of B 83 and the ventromedial one of B 149. Contrarely Moore and Goldberg (1963) found no contralateral degeneration in lesions located either very laterally or ventrally. The relative number of cells in the lateral zone is smaller than more medially, because this area contains the fibres running to the bci. For this reason and because no fibres passing to the commissure, from more lateral regions are interrupted, degenerated fibres entering the commissure may be few and remain unnoticed in such lesions.

The termination of the commissural fibres in the IC is mainly found in the central nucleus, and the PB and the lateral zone do not receive their preterminals, except perhaps for a few cells in the direct vicinity of the bci. Moreover fibres detaching from the bci terminate near the rostral tip of the processus rostroventralis. No evidence was found of a topical organization in the crossed projection of the IC.

c. The ascending connections of the IC: the brachium of the inferior colliculus

The bci connects the IC with the CGM. In the literature on the CGM many different opinions are expressed on its demarcation and subdivision (for a detailed report on the relevant literature see Moore and Goldberg, 1963, and Morest, 1964).

The outlines of the CGM given in the diagrams were drawn from Häggqvist-stained series, but some borders certainly are arbitrary and the main purpose of the diagram is only to show the termination of the bci. The simple nomenclature first introduced by von Monakow (1895) and revised by McK. Rioch (1929) was used for this purpose. The latter distinguishes a magnocellular part (fig. 56 and 57) and a principal part with smaller cells. As the cells lie wide apart it is difficult to border the group, and a dotted line was therefore drawn around them in my diagrams.

The pars principalis in my diagrams includes the nucleus suprageniculatus, as distinguished by several authors (Münzer and Wiener, 1902; Ingram, Hannet and Ranson, 1932; Jimenez-Castellanos, 1949; Jasper and Ajmone-Marsan, 1954; Snider and Niemer, 1961; Morest, 1964). The posterior thalamic group of Rose and Woolsey (1949), in which the nucleus suprageniculatus is included, should be similarly located in the pars principalis of my diagrams. In figures 56 and 57 the different opinions on the subdivision of the CGM are given, adapted to my diagrams.

Because no important differences were noticed between the crossed and uncrossed fibres in the bci, they can be considered together. Where the bci enters the CGM the nucleus interstitialis is found between its fibres. When all the fibres of the bci are degenerated, as in the experiments B 170 and B 171 (fig. 50, 54, 55) the cells of the nucleus interstitialis still stand out clearly against the surrounding degeneration. With high power magnification small degenerated fibres are seen in the direct vicinity of the cells, but termination is certainly not abundant. A little more rostrally the bundles of the bci form a meshwork of degenerated fibres spreading to different directions. This marks the rostral border of the nucleus interstitialis and indicates the beginning of termination within the CGM.

Lateral to the bci entering the nucleus interstitialis the caudal end of the CGM is found, but in this part no degeneration is visible. The majority of the fibres of the bci are directed toward the rostroventral side of the CGM, giving off preterminals laterally and ventrolaterally. The magnocellular part seems to receive few preterminals, and it only contains a small number of fibres passing to more rostral levels. In the rostral half of the CGM the degeneration, still concentrated ventrally, intermingles with the geniculocortical fibres, and the ventral part of the CGM therefore has no longer a

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VII
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CGL/L
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VA
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CGM
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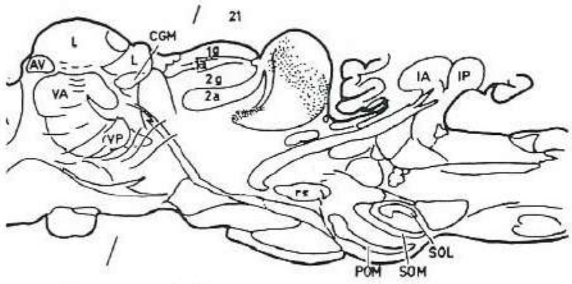
Fig. 53.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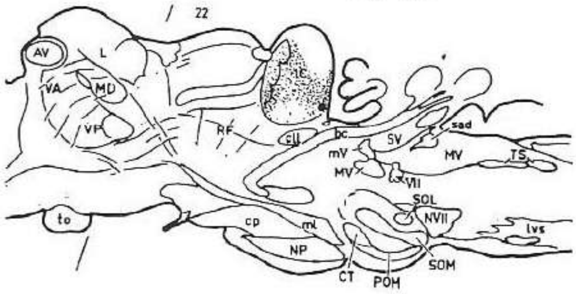
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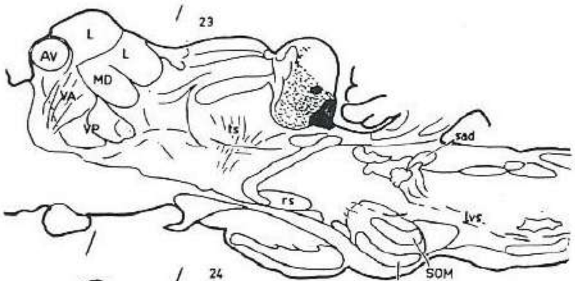
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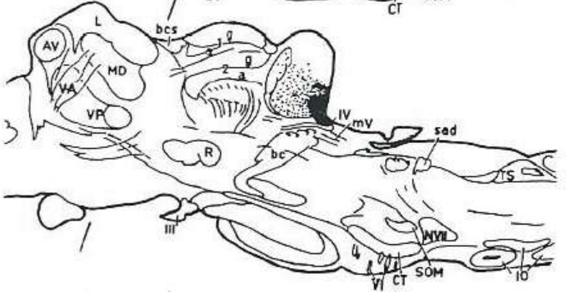
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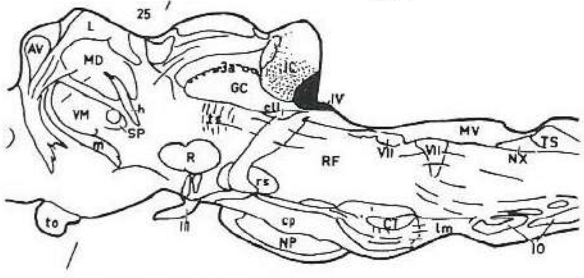
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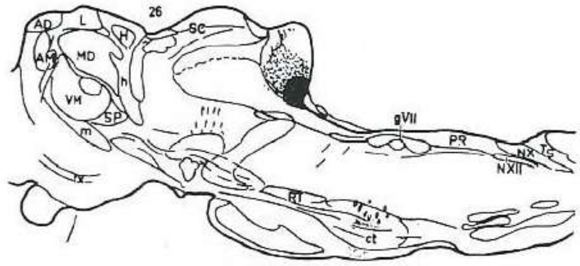
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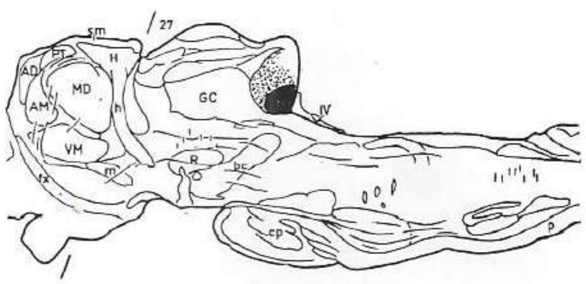
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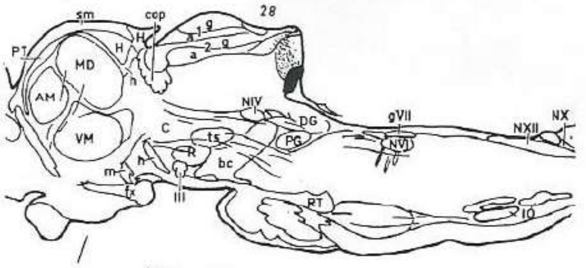
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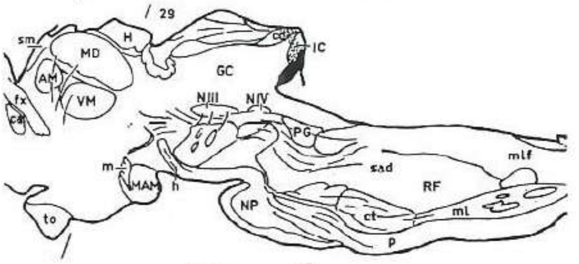
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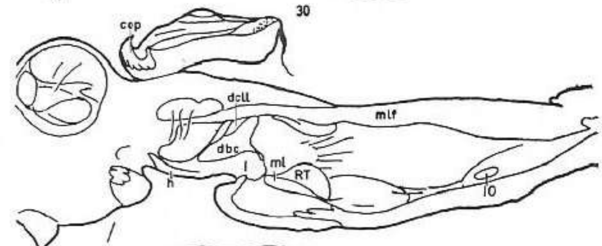
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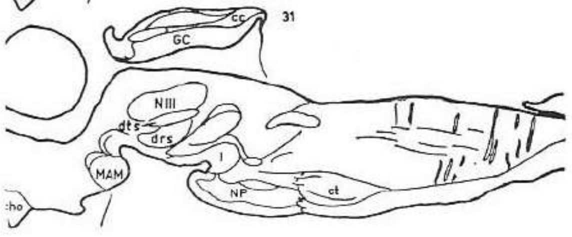
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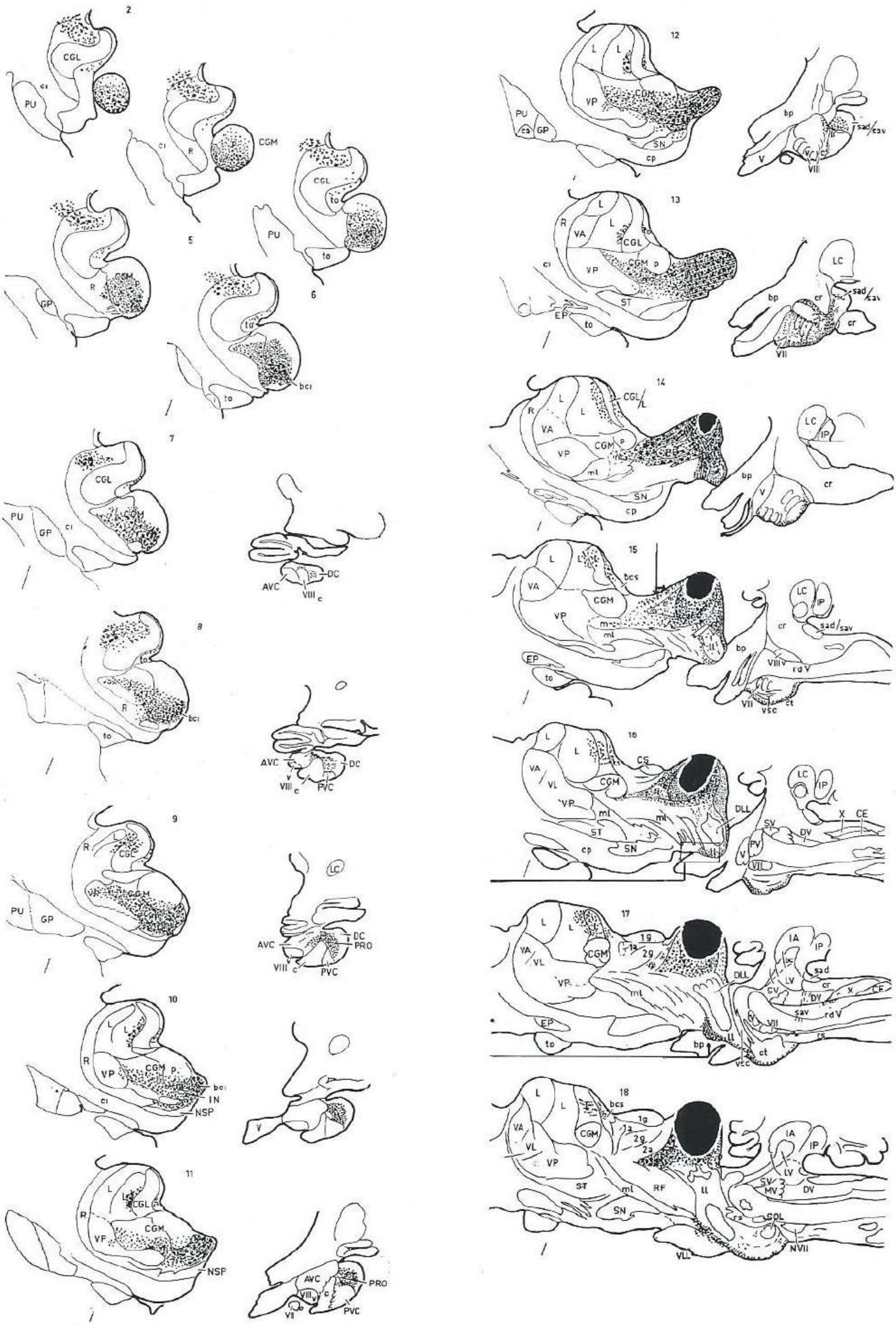
B 170 L

Fig. 54.



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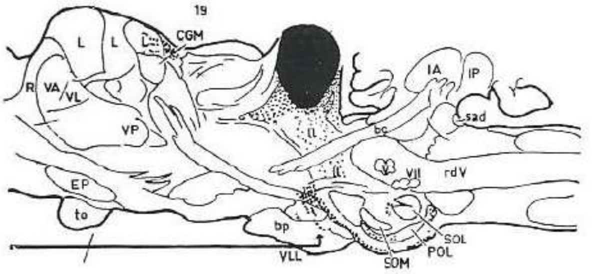

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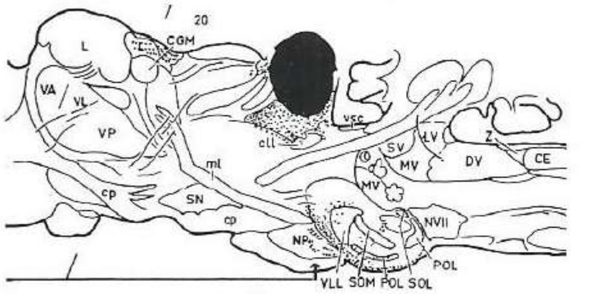

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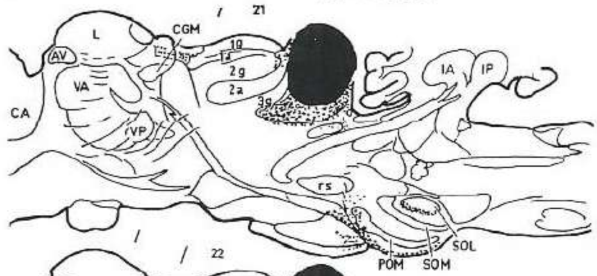

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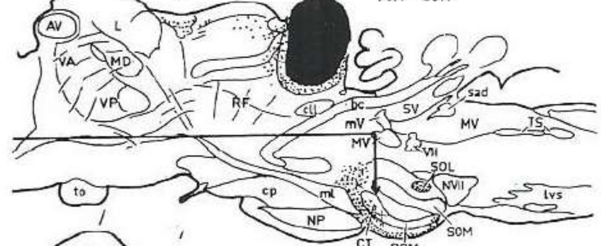

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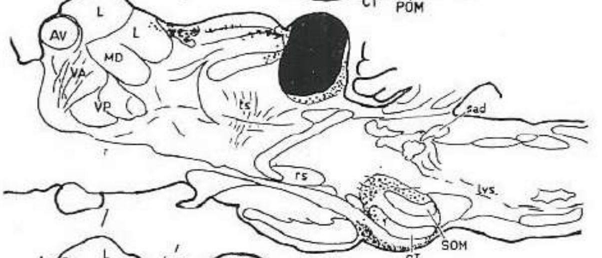

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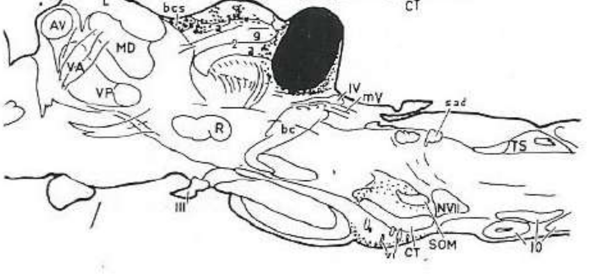

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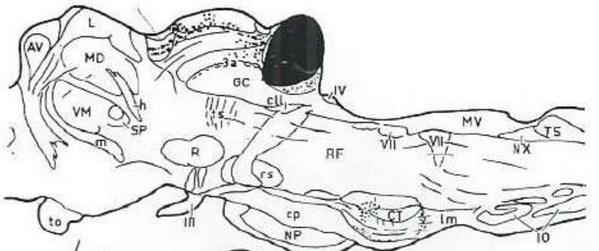

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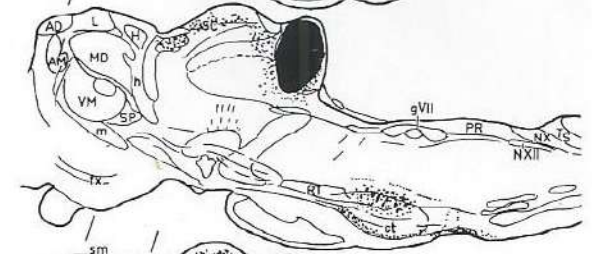

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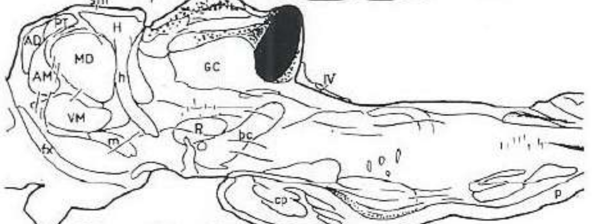

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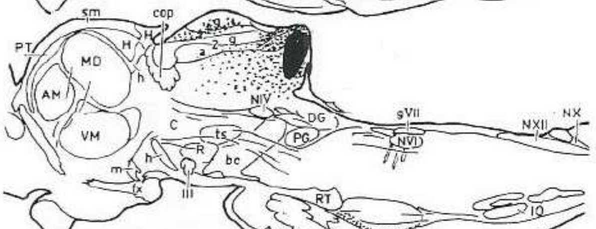

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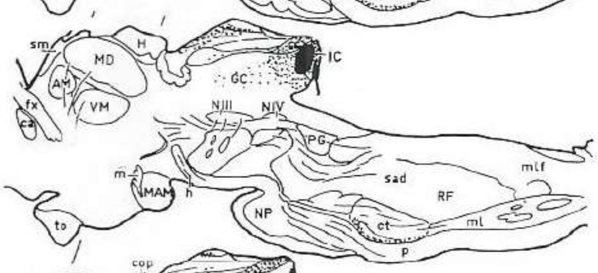

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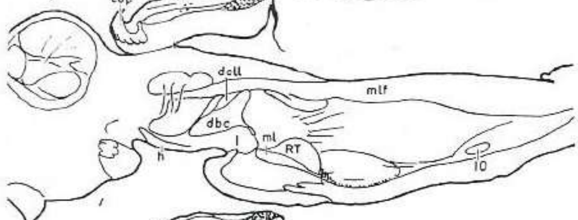

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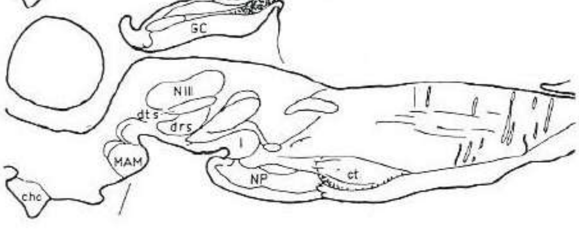

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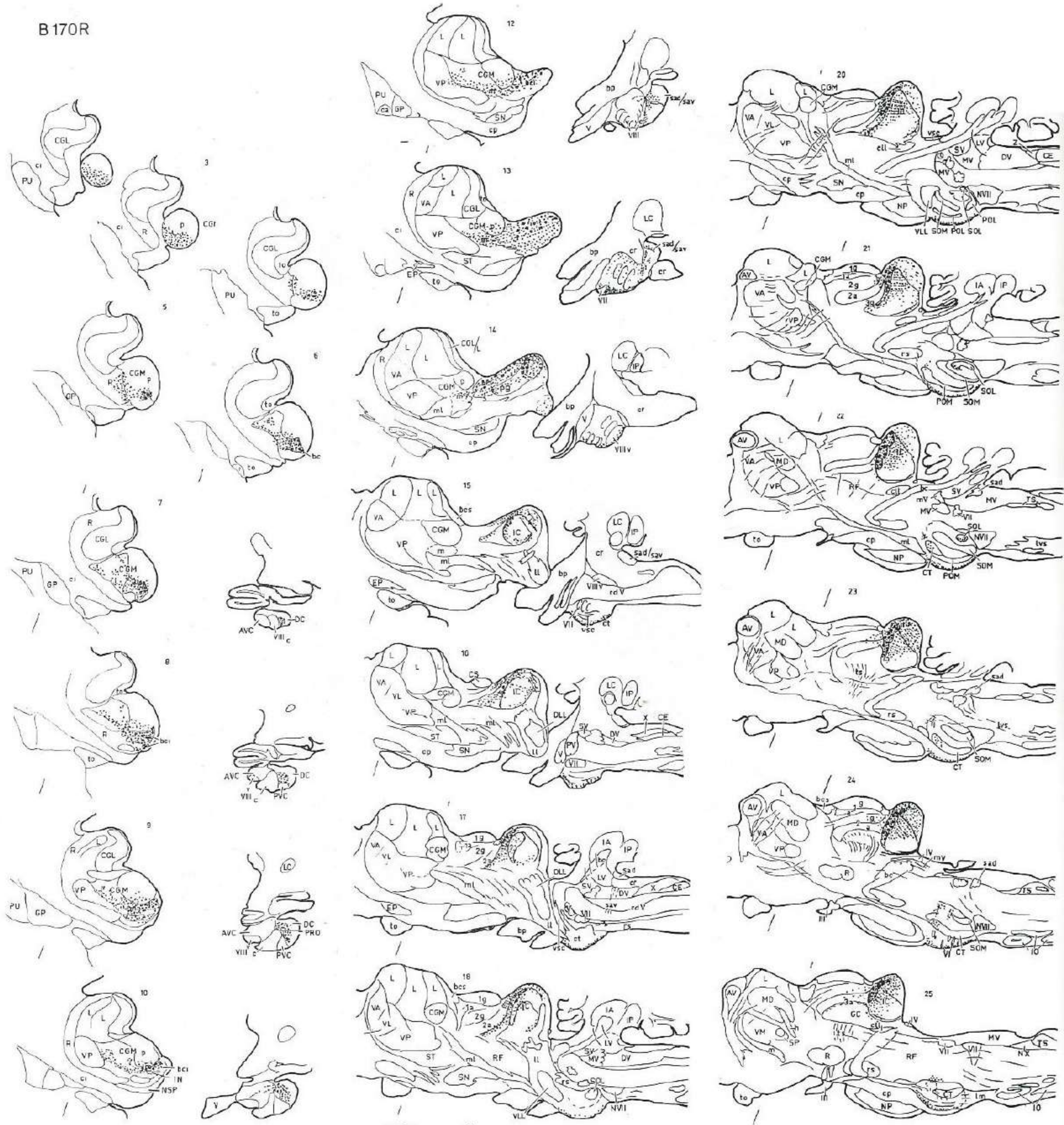

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Fig. 55.

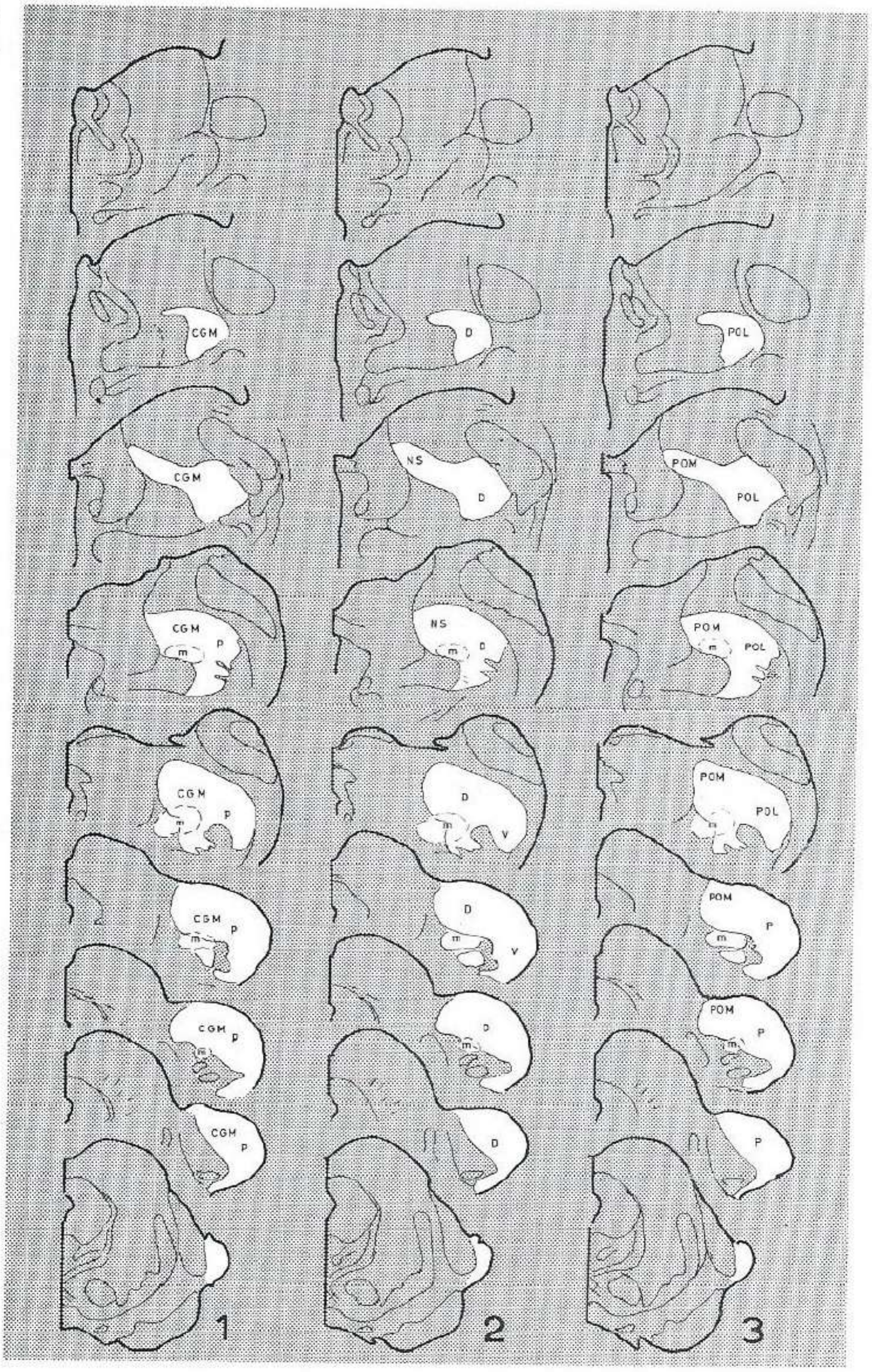


Fig. 56. Different opinions on the subdivisions of the CGM.

compact appearance. Where the geniculocortical fibres turn laterally to enter the hemisphere, the rostral pole of the CGM still contains preterminal degeneration.

The dorsal part of the CGM does not contain degenerated fibres; it is continuous with the caudal pole of the CGM in which no degeneration is seen either, but the transition between the ventral part provided with degeneration and the caudal and dorsal parts without is not sharp. Another region without degenerated fibres is found in

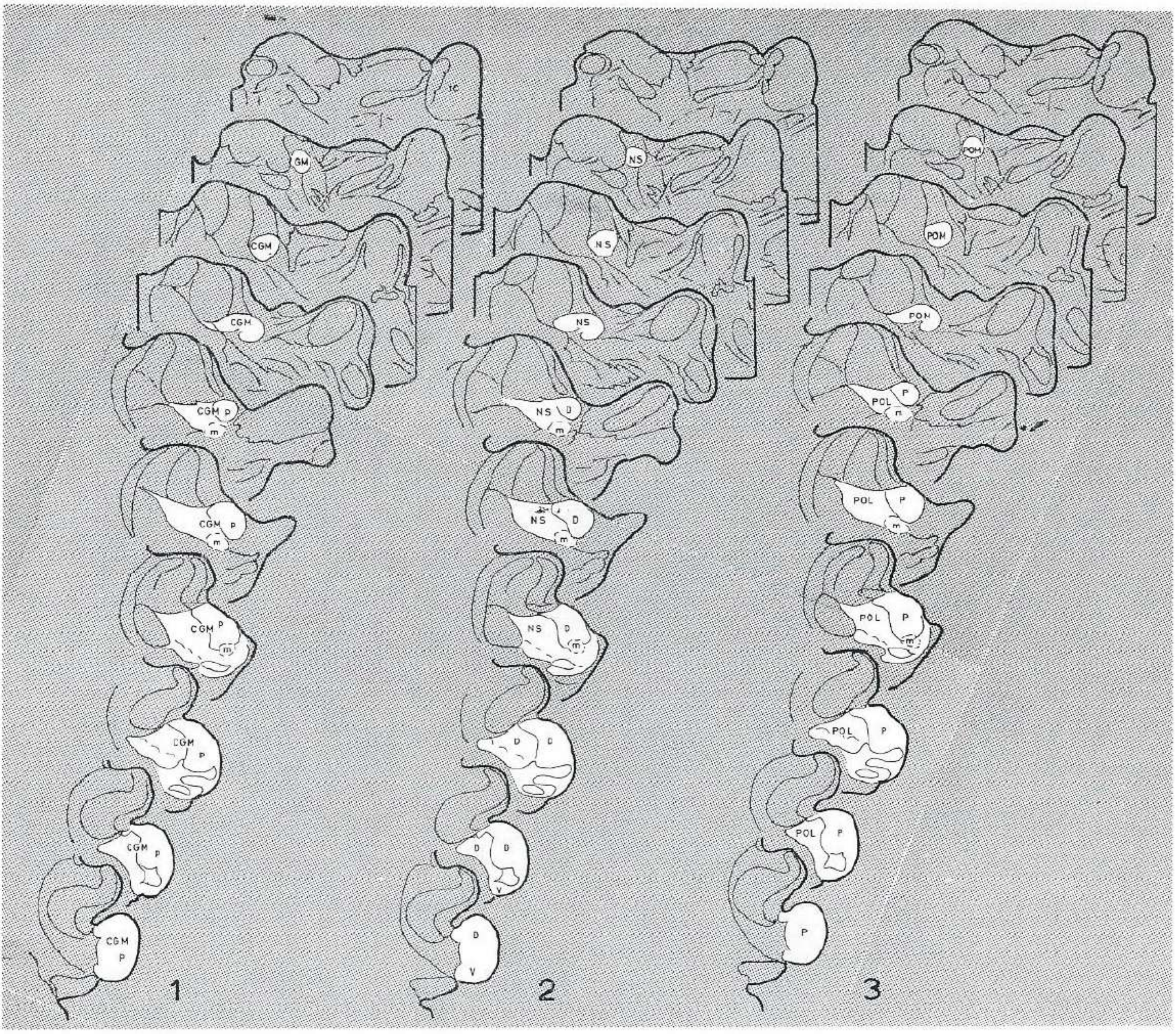


Fig. 57. Different opinions on the subdivisions of the CGM.

the ventromedial part of the CGM, caudal to the area in which the efferent geniculo-cortical fibres collect. It is located between the main mass of bci fibres and the ventral surface of the CGM, and laterally it is bordered by the laterally directed fibres which leave the bci. A number of degenerated fibres running through and along this area reach the superficial layer of the CGM to enter a fibre capsule in which they run to the rostral portion of the CGM, mainly its lateral region.

In my experiments with partial lesions of the IC no important differences were noted in the projection on the CGM of the two parts of the central nucleus and the lateral zone of the IC. Neither was it possible to demonstrate a difference in termination between the fibres of the medial and those of the lateral parts of the central nucleus. The termination of the crossed fibres of the bci in the CGM showed the same peculiarities as that of the uncrossed ones, but their number was less and the distinction between the interstitial nucleus and the CGM is therefore less conspicuous.

Within the bci the fibres of the different parts of the IC only show a slight degree of topical arrangement. The lesions in B 66 and B 96, located in the dorsolateral part of the IC, cause degeneration in the lateral part of the bci, and the degeneration from the heterolateral IC is located in its dorsal part, but the other lesions give rise to a homolateral degeneration all over its area. In transverse Häggqvist-stained sections the bci presents a homogeneous fibre pattern, with some thick fibres (8-10 micron) scattered all over its area, but small fibres forming its bulk.

DISCUSSION

Most of our observations on the projection to the CGM have been made before by Moore and Goldberg (1963). The nucleus interstitialis of the bci was originally distinguished from the CGM in experiments on its retrograde degeneration.

Its distinction is supported by the experiments reported above, which show that its lack of afferents from the IC distinguishes it from the CGM. Moore and Goldberg do not mention this difference and describe preterminals from the IC in this nucleus.

The fibres of the bci do not terminate in the whole CGM nucleus. In the first place the whole dorsal part does not receive preterminals although the transition to the ventral part is vague and at places some fibres may be seen reaching far dorsally. Morest (1965) found the lateral tegmental tract, which originates in the gray matter directly rostral to the IC to terminate in this region. The caudal margin of the CGM, lateral to the entering bci, does not receive fibres from it either and consequently has to be considered as an extension of its dorsal part (Rasmussen, 1961). The other part free from degeneration lies more ventromedially, and besides it the magnocellular portion is also almost devoid of afferents from the IC. In experiments described in chapter 4 fibres from the medial lemniscus and the spinothalamic tract could be traced into it (fig. 40-44; see also Morest, 1964).

The fibres of the bci, which pass rostrally along the ventrolateral surface of the CGM, described by Moore and Goldberg (1963) were also seen in my experiments. They take this remarkable course to end in the same parts as the fibres that take the normal course through the CGM.

In the experiments on the efferents of the IC I could not find a difference in ascending projection between the three parts of the IC, the ventral and the dorsal part of the central nucleus, and the lateral zone. Experiments which might throw light on the efferent projection of the processus rostroventralis are unfortunately lacking in the present material, which is the more unfortunate since the intrinsic connections of the IC indicate that this region differs from the ventral part of the central nucleus.

The tonotopic relation described by Moore and Goldberg (1963) and Tarlov and Moore (1966) do not contradict my conclusions about the projection on the CGM.

I could demonstrate neither a lateromedial organization in the bci, nor a relation with the lateromedial tonotopic organization, as found in the central nucleus of the IC.

d. The descending connections of the inferior and superior colliculus: the colliculocochlear bundle and the tectopontine tract

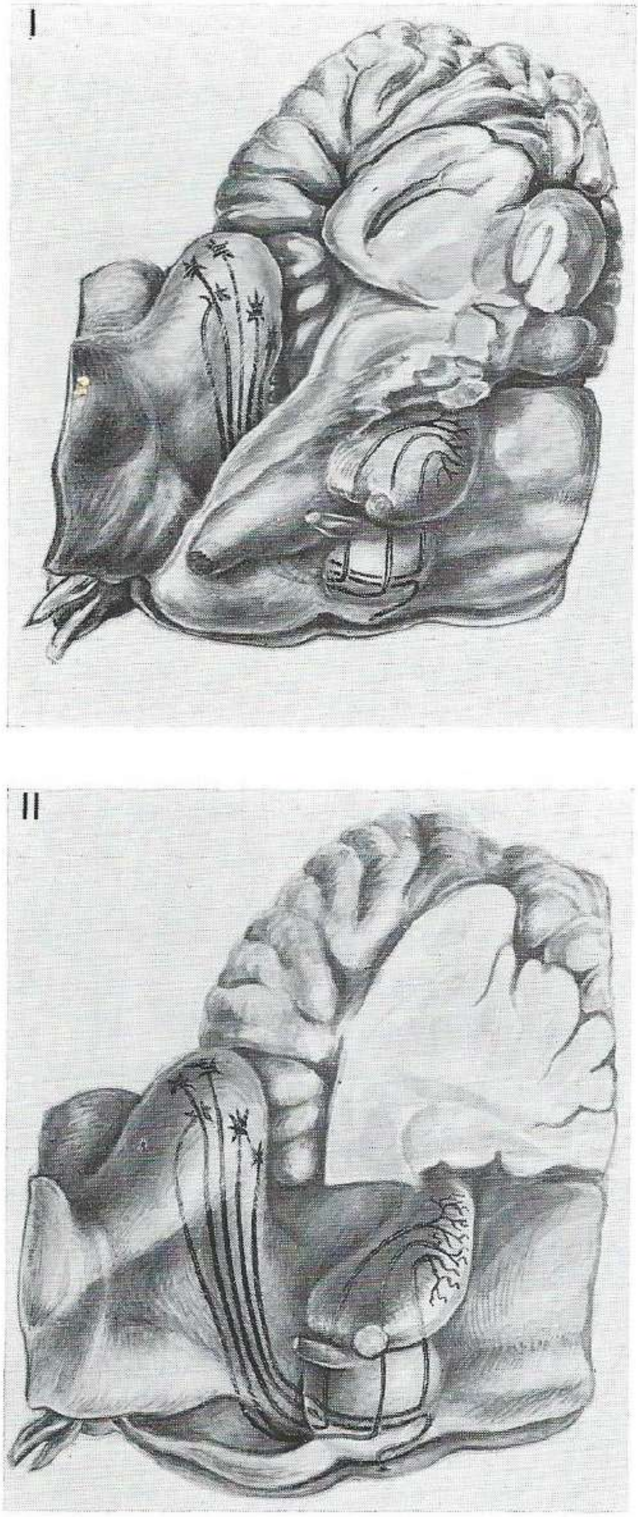
A thin-fibered system from the IC runs ventrally and becomes located between the brachium pontis and the lateral lemniscus, where it curves caudally. Partly lying dorsal to the lateral basal pontine nuclei, partly running through them in small bundles the fibres reach the corpus trapezoideum, where the bundle divides and spreads to both sides along the surface of the corpus trapezoideum. The fibres end in the dorsal cochlear nuclei of both sides, taking their course between the descending root of the trigeminal nerve and the anteroventral cochlear nucleus (see fig. 58 and 59 and series B 170 and B 171, fig. 50, 54 and 55). Preterminals are also found in the preolivary nuclei, around the cells of origin of the homolateral olivocochlear bundle and especially in the medial part of the lateral superior olive at both sides.

Rostral to this colliculocochlear bundle are found the fibres of the tectopontine tract originating in the SC. They descend in the lateral tegmentum and enter the lateral pontine nuclei rostral to the colliculocochlear bundle. After having traversed them they are located lateral to the pyramid, where they descend as far as the level of the inferior olives.

A detailed description of both systems follows. From the caudal side of the IC preponderantly thin fibres descend ventrally. During their course caudally the fibres from more rostral and ventral cells of the IC join the descending bundle (see B 170 and B 171, fig. 50, 54 and 55). They concentrate at the ventrorostral side of the lateral lemniscus, directly medial to the brachium pontis. In small bundles we can follow them through and just dorsal to the lateral pontine nuclei, and where they enter the lateral pontine nuclei a small concentration of preterminal degeneration is found. At the caudal side of the basal pons the bundle reaches the corpus trapezoides (ct) at its ventral side immediately lateral to the pyramidal tract. Subsequently the fibres pass in all directions but mainly along the surface of the medulla bilaterally and cross the pyramids at their dorsal margins mainly in the rostral half of the ct. Part of the fibres are going to terminate in the dorsal cochlear nuclei of both sides, but the others end in the following nuclei.

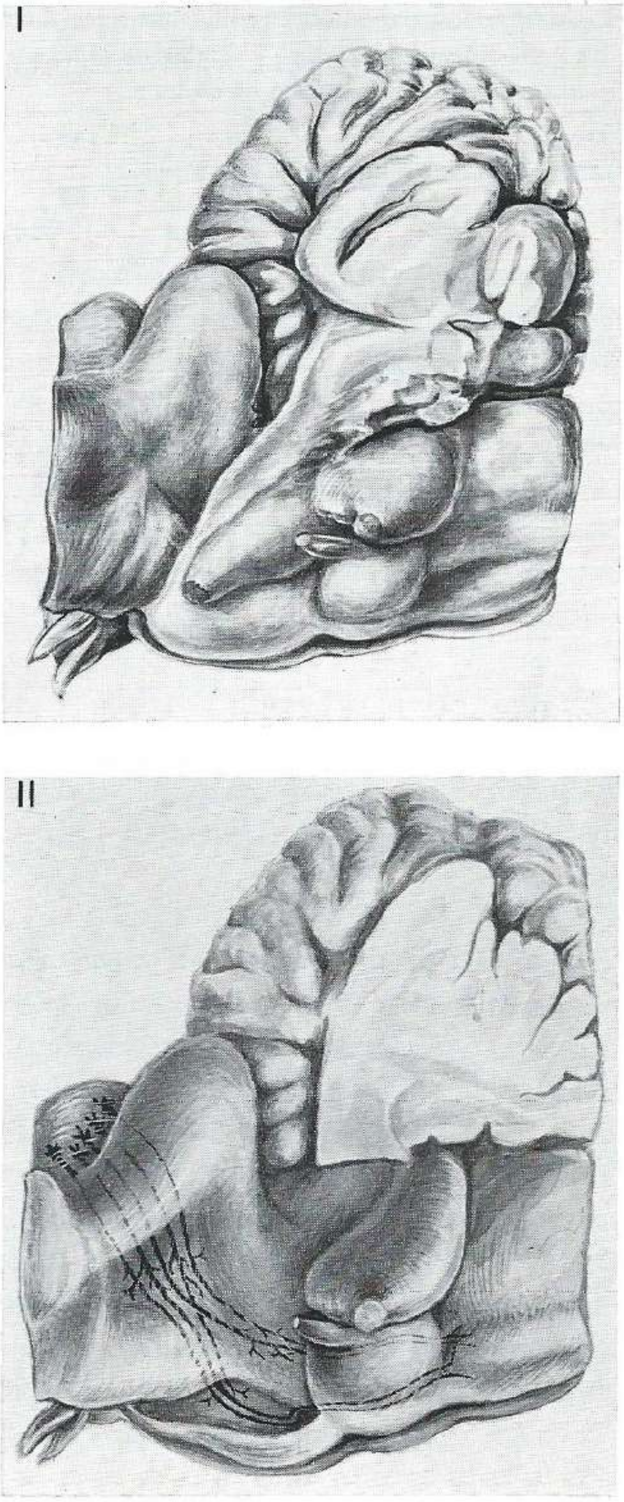
The *medial preolivary nuclei* (and in some series the nucleus of the corpus trapezoides as well) receive degenerated fibres although not everywhere, but in some areas. Very significant is the degeneration in the *medial part of the lateral superior olive* (SOL), where a network of rather coarse degenerated fibres is found caused by a few afferent fibres only that cannot even be recognized. The corresponding part of the contralateral SOL receiving the same amount of degeneration, similarly without afferents being noticeable, suggests that the afferents of this special area of the SOL follow the colliculocochlear pathway as far as the close proximity of the SOL to branch off and enter it. In series

Fig. 58. Demonstration of the colliculocochlear bundle in a three-dimensional picture. In II the brachium pontis is removed with part of the cerebellum.



H 5377 a few degenerated fibres can actually be seen running between the medial preolivary nucleus and the medial part of the SOL. Another strong argument for this course is found in series B 160 (fig. 18), in which besides the partial destruction of the cochlear nerve there is a small superficial lesion lateral to the pyramidal tract, exactly at the site of the descending colliculocochlear bundle. The terminal degeneration in the medial parts of the SOL on both sides in this series proves that the afferents

Fig. 59. Demonstration of the tectopontine tract in a three-dimensional picture. In II the brachium pontis has been removed with part of the cerebellum.



run in this colliculocochlear bundle. However, B 144, with a lesion dorsal to the medial superior olive (fig. 29) similarly shows degeneration in the medial part of the contralateral SOL. In this case other known sources for terminal degeneration in the SOL can be excluded and one of its main afferent systems, the fibres from the cochlear nuclei, only terminate in the homolateral SOL. So it can be concluded that the colliculocochlear bundle is not the only pathway of the recurrant fibres to the medial part of the SOL.

Table 2

	TERMINATION IN				
Series No.	DC	POM (+CT)	SOL	Dorsomed. of SOM	See scheme at page
cs — B 41	–	c	c	c	78
B 66	–	h	h	–	76
B 67	b	h	h	h	76
B 79	b	h	–	–	75
B 80	b	h	–	h	75
B 81	b	h	h	–	76
B 82	b	–	–	–	76
B 83	b	h	h	h	76
cs — B 87	–	–	b	h	78
B 93	b	h	h	–	76
B 94	b	–	–	–	51
B 95	b	–	–	–	
B 96	–	–	–	–	76
cs – B 97	–	h	b (h > c)	h	78
					no sign of coll. cochl. bundle
H 5377	–	b	b	b	77
cs — B 98	–	–	–	–	78
cs — B 106	–	–	–	–	80
cs — B 107	–	–	c (few)	–	79
B 118	–	–	–	–	77
B 139	–	–	–	–	77 and 83
B 149	–	–	–	–	74 and 86 + 87
B 155	–	–	–	–	74
B 156	–	–	–	–	77 and 81
B 157	b	–	h	–	74
B 170	b	h	b	h	75 and 88 + 89 and 90
B 171	b	h	h	h	77 and 82
B 180	–	–	–	–	(deg. is present in the SOM) 55 and 75
B 192	b	h (few)	–	–	77

h = homolat. b = bilat. c = contralat.

In the series indicated with cs there are lesions mainly in the SC.

The fibres to the dorsal cochlear nuclei take their course laterally along the ventral surface of the ct, rostrally more so than caudally. On reaching the ventral cochlear nucleus the fibres turn dorsally, between the descending root of the trigeminal nerve and the anterior ventral cochlear nucleus, to reach the dorsal cochlear nucleus where they end, leaving free its surface zone. A few fibres take their course directly through the anterior ventral cochlear nucleus, to reach the dorsal nucleus.

Table 2 shows the termination of the descending degeneration in the auditory nuclei after partial lesions of the IC. This table shows that:

1. The degeneration in the dorsal cochlear nuclei is always found on both sides.
2. In four cases, B 41, B 66, B 97 and H 5377 there are no preterminals in the dorsal cochlear nucleus, whereas the olivary complex (the SOL, the preolivary nuclei and the cells of origin of the olivocochlear bundle) receives a distinct termination. In B 97 and H 5377 it was not possible to trace degeneration from the lesion to the olivary complex.
3. Comparing the lesions with a homolateral degeneration in the SOL, as seen in most cases, with the ones with a bilateral or contralateral one as even seen with a small lesion in H 5377, there is a tendency apparent in the former to be located laterally in the IC, and in the latter to a more medial location.

A number of lesions, which cause degeneration in the SOL, affect part of the SC. In order to exclude the SC as a possible origin of these fibres and to demonstrate that the tectopontine tract originates in the SC only a number of lesions were made in this collicle. These experiments proved to exclude it as an origin of the fibres to the lower auditory nuclei, and it must be concluded that in fact the SC has very little to do with the auditory system. In the experiments B 114 and B 111 (fig. 60 and 61) we could trace some degenerated fibres to the dorsal part of the CGM, and the cells on which they end do not differ from the surrounding cells. Moreover, a few fibres can be traced from the SC to the IC.

The lesions in the SC produce much degeneration of which I shall only describe the uncrossed descending bundle, known as the tectopontine tract, or the tractus tectobulbaris superficialis noncruciatus of Münzer (1895; Münzer and Wiener, 1902). Its fibres collect ventrolateral to the SC and lateral to the processus rostroventralis of the IC, traverse the PB, which they demarcate from this processus (see fig. 61). The fibres not ending in the lateral tegmental reticular formation run through the lateral basal pontine nuclei at a somewhat more rostral level than the colliculocochlear bundle, and they lie more ventromedially, between the fibres of the lateral part of the cerebral peduncle. At the caudal side of the pes pontis they are found within the lateral triangle of the pyramid. The number of degenerated fibres diminishes imperceptably and at the level of the inferior olive no more degenerated fibres are found (fig. 59). Termination of the tectopontine tract begins already in the nucleus paralemniscalis (Jasper and Ajmone-Marsan, 1954; sive nucleus aparabigeminus: Emmers and Akert, 1963, squirrel monkey), a group of cells which at the lateral surface lie in the triangle formed by the bci, the lateral lemniscus and the cerebral peduncle, where it causes a small elevation. The tectopontine fibres which collect at the caudolateral side of the SC run along and through the medial part of the nucleus parabigeminus and give rise to a clear preterminal network within it. Following the tectopontine fibres to the lateral pontine nuclei a fairly large quantity of preterminals is seen in the lateral reticular formation medial to the bundles. Dorsal to the medial lemniscus and directly rostral to the ct the preterminal degeneration in the reticular formation extends to more medial levels. Preterminal degeneration is also found dorsal to the ct and even caudal to it, medial to the facial nerve nucleus. This region also receives degenerated fibres which run through the lateral pontine nuclei (see fig. 60).

The termination on the basal pontine nuclei is slight, although a pericellular network is found where the fibres enter the lateral nuclei. After entering, however, very soon only smooth bundles of degenerated fibres are found which run caudally without giving off preterminals to the pontine nuclei.

DISCUSSION

The colliculocochlear bundle is a homolaterally descending system, distributed to the auditory nuclei of both sides. Since my demonstration of the colliculocochlear bundle in 1960 only Rasmussen (1961) gave a fragmentary description of a connection of the IC with the superior olivary complex and the dorsal cochlear nucleus. Not before 1964 Rasmussen gave a clear description of a colliculocochlear tract, which, however, differs in many details from the one described here. Other investigators saw only the beginning of the tract. Cajal (1955) describes fibres from the IC entering the region of the ct, where he lost sight of them. Woollard and Harpman (1939/1940) and others (for literature see Woollard and Harpman) find a tectopontine tract from the IC, whereas Münzer and Wiener (1902) who described the tectopontine tract for the first time, also mention endings in the trapezoid nuclei. Lorente de Nó (1931) saw the end of the tract where it now is known as the "centrifugal fibres of Lorente de Nó".

Differences between the observations of Rasmussen and the present ones are:

1. The termination in the contralateral preolivary nuclei seen by Rasmussen and not by me.
2. The termination in the medial part of the SOL, seen by me and not by Rasmussen.

My material, summarized in table 2 does not allow conclusions on the exact origin of the different fibre contingents, which can be distinguished in the colliculocochlear bundle; the one terminating in the dorsal cochlear nuclei of both sides, the other in the nuclei of the olivary complex. It may be concluded, however, that lesions which cause degeneration in the homolateral SOL are located more laterally than those giving rise to degeneration in the crossed SOL or in both. Other differences in the localization of the preterminal degeneration in the auditory nuclei of the series may be caused by the capriciousness of the silver-impregnation methods.

The course of the tectopontine fibres is similar to that of the colliculocochlear bundle. In the lateral sections of the sagittal series they form one system of fibres running to the lateral pontine nuclei (fig. 54 and 60) and even within them. This explains why earlier investigators thought the origin of the tectopontine fibres to be the whole tectum (Tsai, 1925). The termination of the tectopontine fibres mainly in the reticular formation, as seen by Münzer and Wiener (1902), who first described the tract, however, makes it possible to differentiate it from the colliculocochlear bundle, which has its endings in auditory centres.

Only in series B 170 degeneration was found at the medial side of the lateral lemniscus (fig. 50, level 8-17) and rostral to the ct. It is not likely that these fibres originate

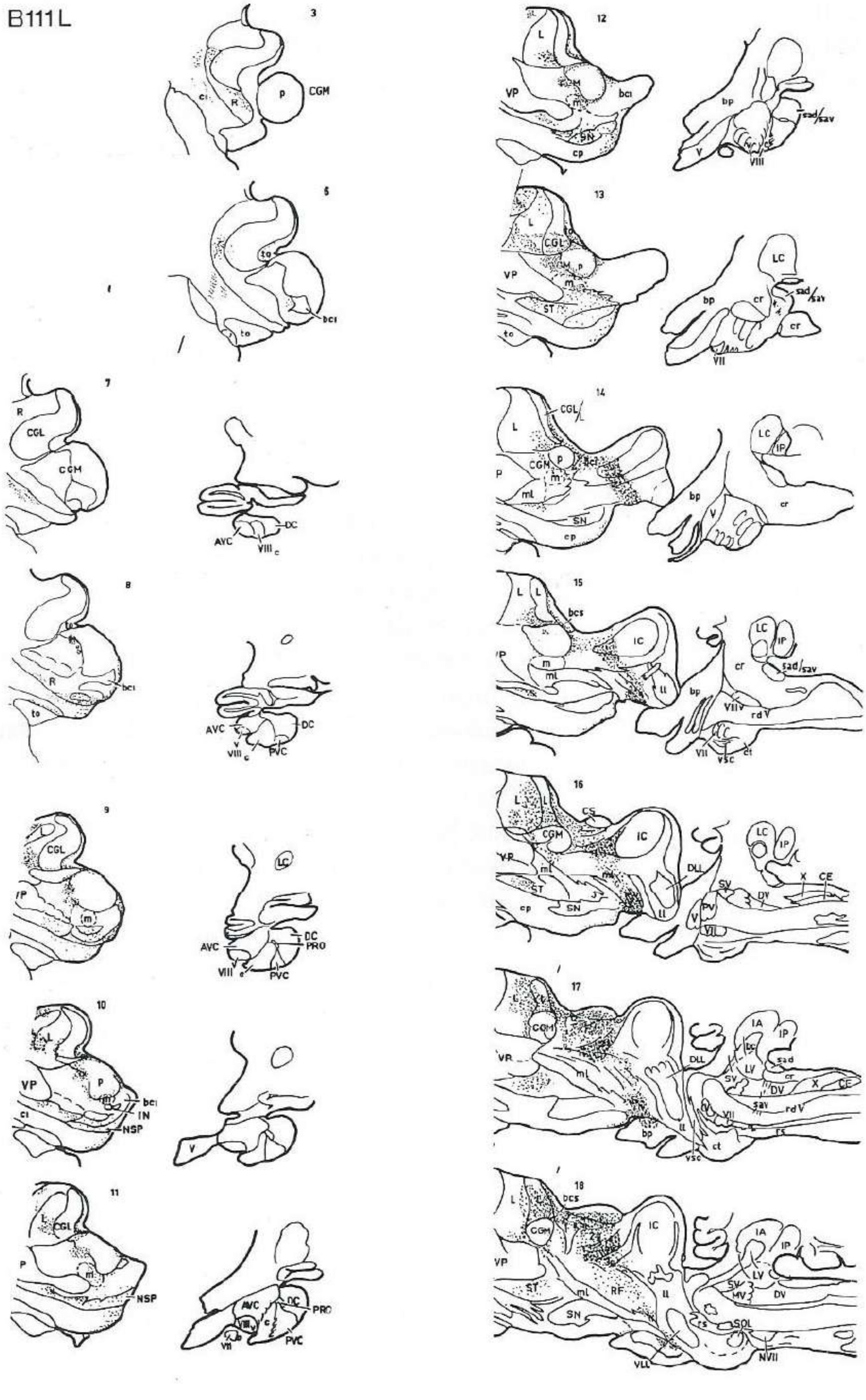

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Fig. 60.

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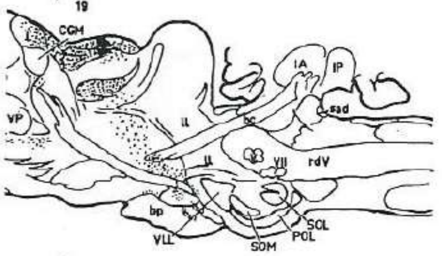

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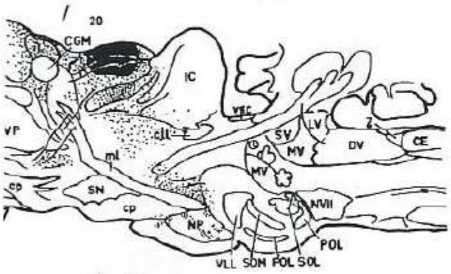

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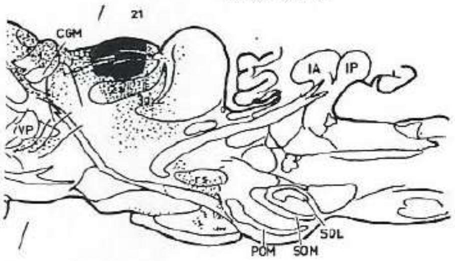

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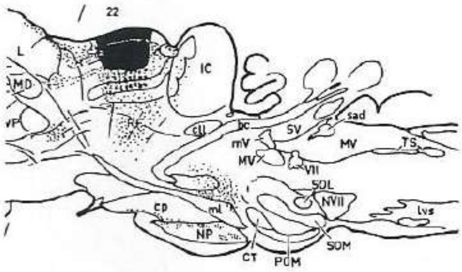

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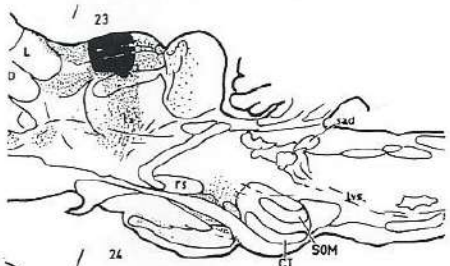

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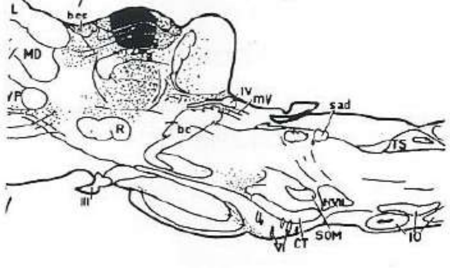

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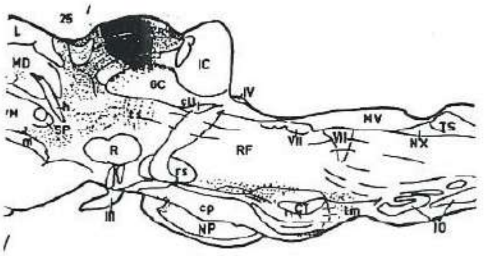

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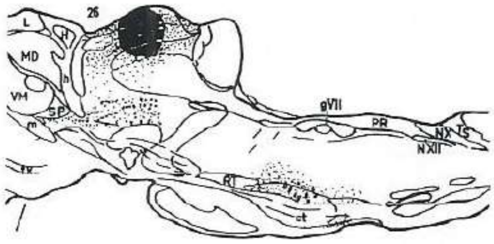

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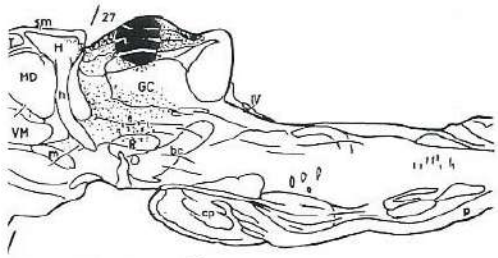

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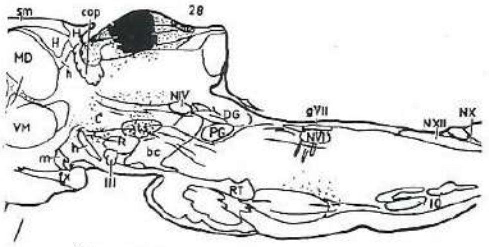

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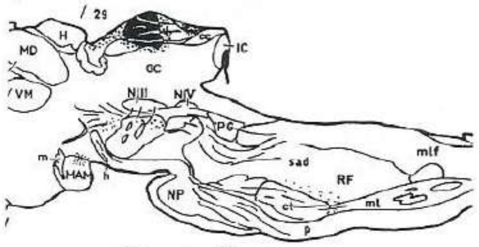

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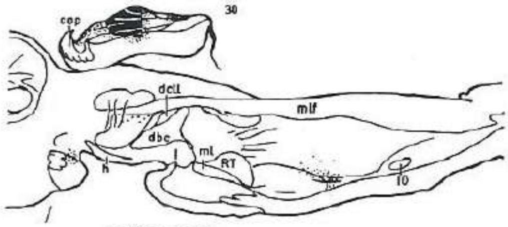

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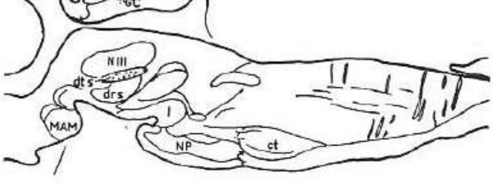


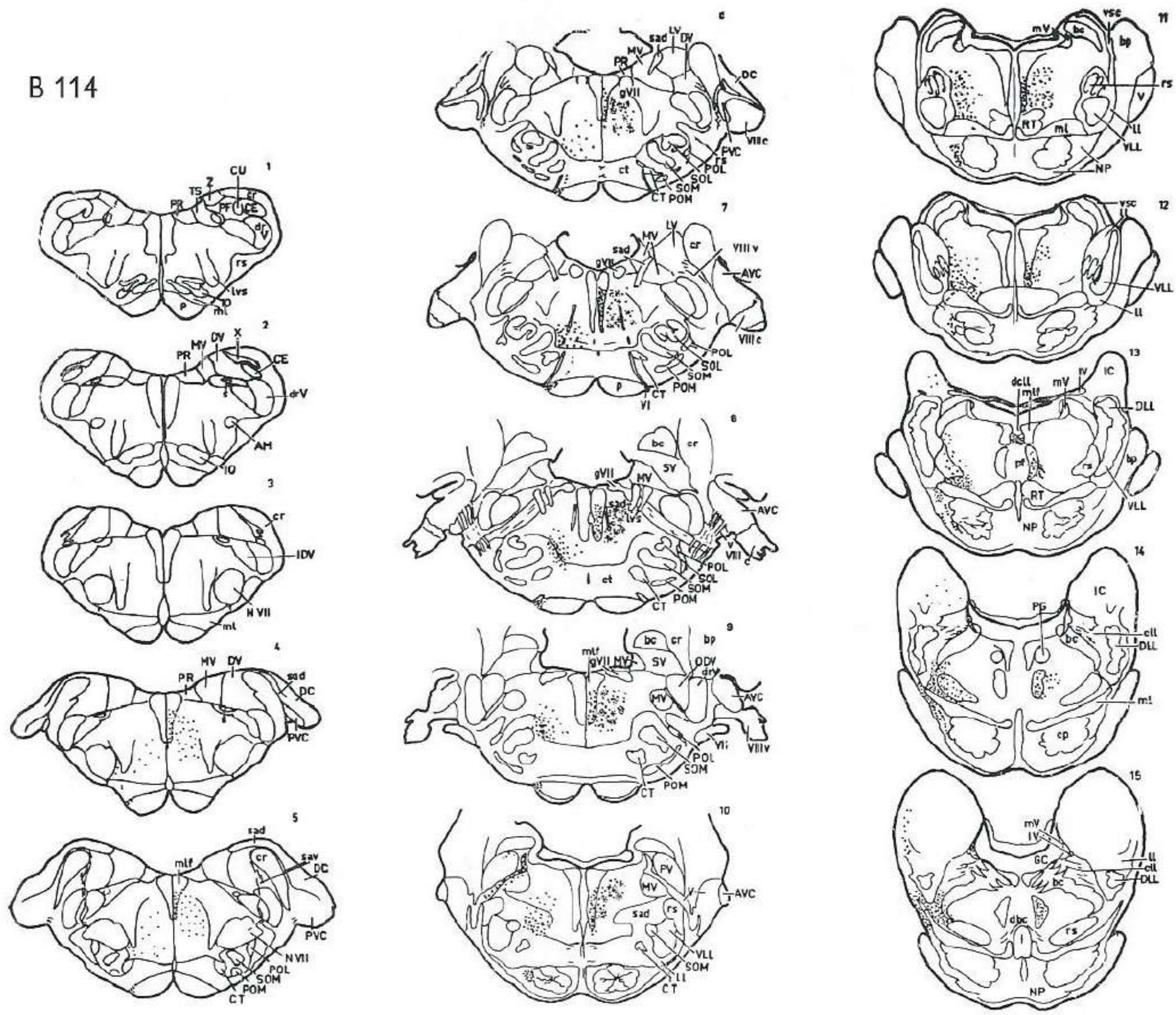


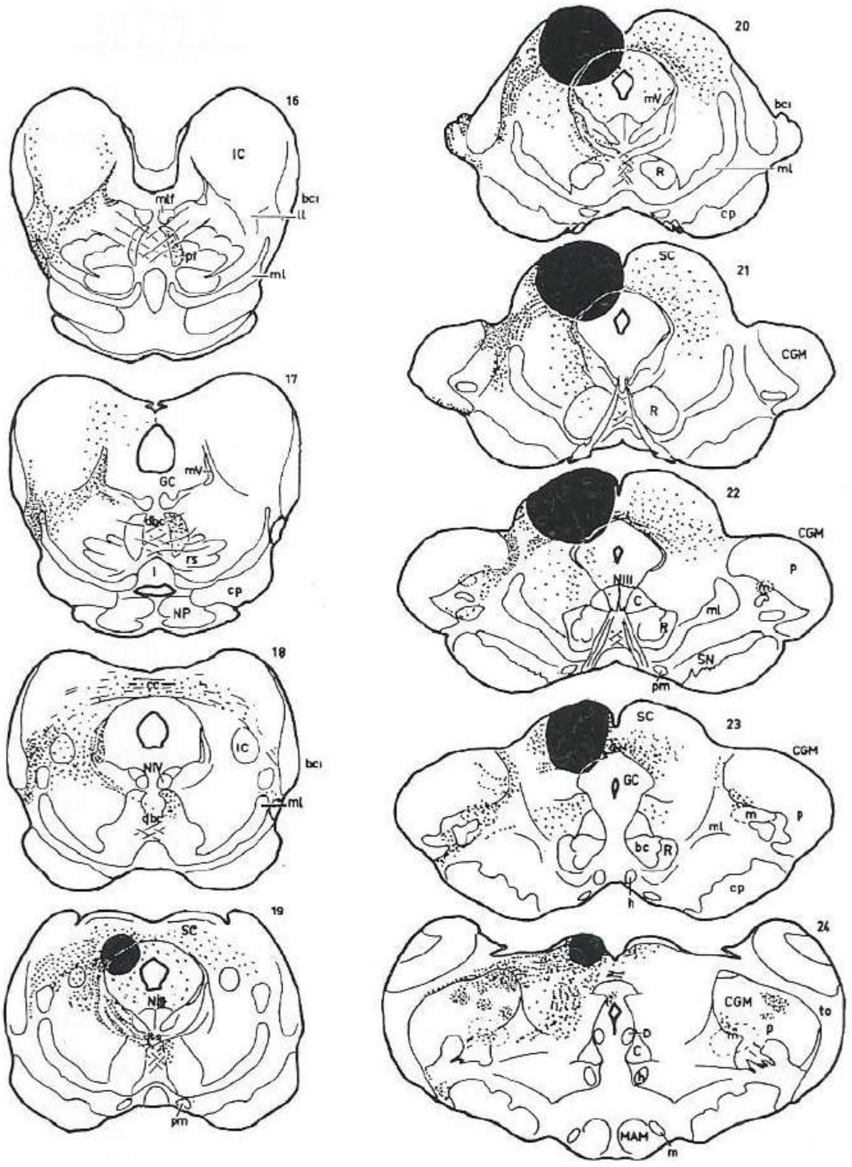
Fig. 61.

in the IC, otherwise they would also have been found in the other series. They are possibly fibres from more rostrally located regions such as the SC.

Whether the tectopontine tract originates in one layer of the SC or in several is difficult to say. Experiment B 108 with a surface lesion yields a lot of degenerated tectopontine fibres, which means that at least the surface layers give rise to the tectopontine tract.

CONCLUDING REMARKS

The IC has intrinsic connections with its lateral zone, the PB and the processus rostroventralis, and crossed connections mainly with the central nucleus. The bci connects the IC with the homolateral and to a lesser degree with the heterolateral CGM, the



distribution in both CGM nuclei being identical. The interstitial nucleus and large portions of the CGM do not receive afferents from the IC. The colliculocochlear bundle is a homolaterally descending system, which fibres pass through the lateral pontine nuclei together with the tectopontine tract. Its origin in the IC and its termination in lower auditory nuclei of both sides distinguishes it from the latter.

Although topical projections, which may subserve the tonotopic organization, are present in these systems, the material was unsuitable to demonstrate them clearly. Neither was it possible to find differences between the efferent projections of the various subdivisions of the IC, distinguished on account of their normal structure and their afferent fibre connections.

The tectocerebellar connection as described by Cupédo (1963) in the rat could not be found in my series. Although I must admit that they were not especially prepared for the search for this tract, the cerebellum always being removed before staining, the portion of the velum medullare anterius, which remained intact, never contained any degenerated fibre.

Snider and Stowell's (1944) electrophysiological information of tectocerebellar connections can be explained by part of the brachium pontis (the spinal system), which contains the fibres of the lateral pontine nuclei, projecting to the cerebellar lobules (Voogd, 1964), which Snider and Stowell found to receive auditory and visual impulses from the IC and SC respectively. The IC and the SC both project on a number of cells of the lateral pontine nuclei, and this may possibly be the route along which the auditory and visual impulses reach the cerebellar cortex.

Summary

6

Described were:

1. The structure of the IC.
2. a. The ascending auditory connections with their nuclei and other ascending afferents of the IC.
   b. The isthmoperipeduncular bundle.
3. The descending auditory connections.
4. The efferents of the IC and their terminal nuclei: parabrachial area, interstitial nuclei, CGM.

Ad. 1. The IC is subdivided into a central nucleus and a lateral zone. The former consists of a dorsal and a ventral part. The borders were described. The ventral part of the central nucleus has a processus protruding rostrally (the processus rostroventralis). The border between lateral zone and parabrachial area is vague.

Ad. 2. The cochlear nuclear complex is subdivided into a dorsal (DC) and a ventral (VC) part, and the latter again into an anterior (AVC) and posterior (PVC) part. The cochlear nerve separates both parts of the VC. The cochlear nerve terminal areas spread out in a special plane for each different frequency in all three subdivisions of the cochlear nuclear complex (its frequency planes).

A tonotopic projection was found in the cochlear nuclei, and this could also be established for the superior olives and inferior colliculi.

The efferents of the cochlear nuclei are differentiated in:

1. The stria dorsalis, originating in the DC and terminating in the controlateral ventral nucleus of the lateral lemniscus (VLL) and the inferior colliculus.
2. The stria ventralis originating in the caudal part of the PVC and terminating in the lateroventral part of the VLL.
3. The corpus trapezoideum, differentiated in
   a. thick
   b. middle-sized and
   c. thin fibres.

3a. The thick fibres originate from the cells lying around the entering nervus VIII (rostral part of the PVC and caudal part of the AVC), and terminate contralaterally in the nucleus of the corpus trapezoideum (CT) and probably also in the lateral lemniscal nuclei and the IC.

3b. The middle-sized fibres originate in the AVC and the rostral part of the PVC. They terminate in the superior olives (except the lateral superior olive contralaterally), the contralateral nuclei of the lateral lemniscus and the contralateral IC. In the homolateral ventral nucleus of the lateral lemniscus preterminals are also found. Contralaterally a small bundle can be traced from the region of the nucleus of the corpus trapezoideum to the level of the inferior olive. It is located in between the medial lemniscus and the ventral spinocerebellar tract.

The preterminals are tonotopically arranged in the superior olives and the IC.

3c. The thin fibres originate from cells lying in the neighbourhood of the entering nervus VIII. They terminate in the lateral preolivary nuclei homolaterally, and the medial preolivary nuclei contralaterally. They vanish during their course in the lateral lemnisucus.

The fibre spectrum of the corpus trapezoideum (ct) was studied both directly medial to the cochlear nuclei and midsagittally. It appeared that only fibres from cochlear nuclear origin cross in the ct.

The efferents of the superior olives were studied. The efferents of the lateral superior olive for about 50 percent run in the homolateral lateral lemniscus, to terminate in its nuclei and in the IC. The other half crosses in a typical way to the lateral lemniscus and IC of the other side, similarly terminating there.

The efferents of the medial superior olive terminate for the greater part in the homolateral lateral lemniscus and the IC, and a small part runs to the contralateral lateral lemniscal nuclei and IC, to terminate there.

The efferents of the superior olives cross dorsally in the medulla oblongate.

The efferents of the nucleus of the corpus trapezoideum terminate in the lateral superior olive of the same side.

The ventral nucleus of the lateral lemniscus sends its efferents to the homolateral IC, but probably a number of these fibres terminate already in the dorsal nucleus of the lateral lemniscus.

The dorsal nucleus of the lateral lemniscus projects to the DLL and the IC of the contralateral side by way of the commissure of Probst. Some projection to the homolateral IC could not be excluded.

The above-mentioned connections are schematically depicted in the figures 20, 21, 23, 26, 27, 31, 32, 34 and 35.

A preterminal degeneration is found within as well as in the direct vicinity of the IC, when the nuclei of Goll and Burdach are lesioned. This degeneration is also found in a high hemichordotomy.

The isthmoperipeduncular bundle connects the dorsal nucleus of the brachium conjunctivum with the peripeduncular grey matter of the level of the CGM. The problems concerning the central acoustic tract of Papez are discussed.

Ad. 3. The descending auditory connections

The course of the descending fibres from the auditory cortex and the CGM and the localization of their preterminals in the IC were investigated.

The preterminals are exclusively found in the lateral zone and dorsal part of the central nucleus. Preterminals are also found in the parabrachial area.

From the IC a fibre system to the dorsal cochlear nuclei of both sides has been described. In its course preterminals are seen in the homolateral medial preolivary nucleus, and in the lateral superior olive either homolaterally or heterolaterally and sometimes on both sides, more or less related to the site of the lesion in the IC.

Recurrent fibres from the lateral preolivary nuclei to the cochlear nuclear complex were investigated.

The termination of these olivocochlear bundle in the cochlear nuclei is described briefly.

Recurrent fibres are also found in the stria dorsalis. Origin and sites of termination could not be determined.

Ad. 4. Efferents of the IC

These are subdivided into

a. intrinsic efferents
b. uncrossed efferents
c. crossed efferents.

Ad. a. Lesions in the IC give rise to preterminal degeneration in the rostral part of the central nucleus and in the lateral zone. The degenerating axons partly run straight to these areas, partly they first run over some distance in the brachium of the IC. The course of the fibres to the brachium of the IC is described.

Ad. b. The efferents of the IC reach the parabrachial area where termination is found, the interstitial nucleus where few terminals are found, and chiefly the CGM by way of the brachium of the IC.

In the CGM terminals are mainly found in the ventral part and the surface layer. The dorsal part of the CGM is almost free of degenerated axons.

Ad c. The crossed fibres partly terminate in the IC of the other side. The areas of termination are the same as homolaterally. Quantitatively, however, they are fewer.

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ADDENDUM

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Abbreviations

8

AD	Anterodorsal thalamic nucleus
AM	Anteriomedial thalamic nucleus
AM	Ambiguus nucleus
AV	Anteroventral thalamic nucleus
AVC	Anteroventral cochlear nucleus
bc	Brachium conjunctivum
bci	Brachium of the colliculus inferior
bcs	Brachium of the colliculus superior
bp	Brachium pontis
C	Interstitial nucleus of Cajal
CA	Caudate nucleus
ca	Anterior commissure
cc	Commissure of the colliculus inferior
CE	External cuneate nucleus
CGL	Lateral geniculate body
CGM	Medial geniculate body
cho	Optic chiasm
ci	Internal capsule
CL	Centrolateral thalamic nucleus
cll	Commissure of the lateral lemniscus
CM	Nucleus of the centrum medianum
CN	Central nucleus of the inferior colliculus
CNd	Dorsal part of the central nucleus
CNv	Ventral part of the central nucleus
CO	Cochlear complex = dorsal and ventral cochlear nuclei
cop	Posterior commissure
cp	Cerebral peduncle
cr	Restiform body
CT	Nucleus of the trapezoid body
ct	Trapezoid body
CU	Cuneate nucleus
D	Nucleus of Darkschewitsch
dbc	Decussation of the brachium conjunctivum
DC	Dorsal cochlear nucleus
dcll	Decussation of the commissure of the lateral lemniscus (Probst)
DG	Dorsal tegmental nucleus of Von Gudden
DLL	Dorsal nucleus of the lateral lemniscus
drs	Decussation of the rubrospinal tract
drV	Descending root of the trigeminal nerve and its nucleus
dts	Decussation of the tectospinal tract
DV	Descending vestibular nucleus
EP	Entopeduncular nucleus
FL	Lateral funicular nucleus
fx	Fornix
GC	Central grey matter
GP	Globus pallidus
GR	Nucleus gracilis
gVII	Genu of the facial nerve
H	Habenula nucleus
h	Fasciculus retroflexus of Meynert
H 1	Field H 1 of Forel
H 2	Field H 2 of Forel
I	Interpeduncular nucleus
IA	Interpositus anterior nucleus
IC	Inferior colliculus
IDV	Pars interpolaris of the descending trigeminus nucleus
IN	Interstitial nucleus of the brachium of the colliculus inferior
IO	Inferior olive
IP	Interpositus posterior nucleus
ip	Isthmoperipeduncular tract

L	Lateral thalamic nucleus
LC	Lateral cerebellar nucleus
LD	Laterodorsal thalamic nucleus
ll	Lateral lemniscus
lt	Lateral tegmental tract of Morest
LV	Lateroventral thalamic nucleus
lvs	Lateral vestibulospinal tract
LZ	Lateral zone of the inferior colliculus
m	Mammillothalamic fasciculus of Vicq d'Azyr
m (CGM)	Magnocellular part of the CGM
MAM	Mammillary body
ml	Medial lemniscus
mlf	Medial longitudinal fasciculus
MV	Medial vestibular nucleus
MV	Masticator nucleus
mV	Mesencephalic root of the trigeminal nerve
N	Substantia nigra
NCM	Centromedial thalamic nucleus
NP	Grey matter of the pes pontis
NSP	Suprapeduncular nucleus
ODV	Oral part of the descending trigeminal nucleus
P	Para solitary nucleus
p	Pyramid
p (CGM)	Principal part of the CGM
PB	Parabrachial region of the brachium of the colliculus inferior
PC	Paracentral nucleus
pf	Predorsal fascicle
PG	Deep dorsal tegmental nucleus of von Gudden
PL	Nucleus paralemniscalis sue parabigeminalis
pm	Mammillary peduncle
POL	Lateral preolivary nuclei
POM	Medial preolivary nuclei
PR	Nucleus prepositus hypoglossi
PRO	Nucleus proprius of the cochlear nuclear complex
PT	Parataenial thalamic nucleus
PU	Putamen
PV	Princeps nucleus of the trigeminal nerve
PVC	Posteroventral cochlear nucleus
R	Red nucleus
RF	Reticular formation
rs	Rubrospinal tract
RT	Nucleus reticularis tegmenti pontis of Von Bechterew
s	Tractus solitarius
sad	Dorsal acoustic stria or stria of von Monakow
sav	Ventral acoustic stria or stria of Held
SC	Superior colliculus
SM	Submedial nucleus
sm	Medullary striae
SOL	Lateral superior olive
SOM	Medial superior olive
SP	Subparafascicular thalamic nucleus
ST	Subthalamus
SV	Superior vestibular nucleus of Von Bechterew
to	Optic tract
ts	Tectospinal fibres
TS	Nucleus of the tractus solitarius
V	Trigeminal nerve
VIII C	Cochlear nerve
VIII V	Vestibular nerve
VA	Ventral anterior thalamic nucleus
VL	Ventrolateral thalamic nucleus
VLL	Ventral nucleus of the lateral lemniscus
VM	Ventromedial thalamic nucleus
VP	Ventroposteral thalamic nucleus
VPL	Ventroposterolateral thalamic nucleus
VPM	Ventroposteromedial thalamic nucleus
vsc	Ventral spinocerebellar tract
X	Cellgroup X of Brodal and Pompeiano
Z	Cellgroup Z of Brodal and Pompeiano
ZI	Zona incerta
1g	Superficial cell layer of the colliculus superior
1a	Superficial fibre layer of the colliculus superior
2g	Intermedial cell layer
2a	Intermedial fibre layer
3g	Deep cell layer
3a	Deep fibre layer

The roman numerals indicate the cranial nerves. An N before them indicates the cranial nuclei.

Capitals indicate the nuclei, the small letters indicate the fibre systems.

Samenvatting

9

Beschreven werden:

1. De structuur van de colliculus inferior.
2. a. De ascenderende auditieve verbindingen met de daarin liggende auditieve kerngroepen en andere ascenderende afferentia van de colliculus inferior.
   b. De isthmo-peripedunculaire bundel.
3. De descenderende auditieve verbindingen.
4. De efferenten van de colliculus inferior met de eindigingsgebieden (parabrachiale area, nucleus interstitialis, CGM).

Ad 1. De colliculus inferior wordt onderverdeeld in een centrale kern met een dorsaal en ventraal gedeelte en een laterale zone. Hun grenzen werden bepaald. Het ventrale deel van de centrale kern blijkt een uitsteeksel naar rostraal te bezitten (processus rostroventralis). De overgang van laterale zone in parabrachiale area is vaag.

Ad 2. Het cochleaire kerncomplex wordt onderverdeeld in een dorsaal (DC) en een ventraal gedeelte (VC), het laatste nogmaals in een anterior (AVC) en een posterior (PVC) gedeelte (pars anterior en pars posterior). De nervus cochlearis vormt de scheiding tussen deze twee delen van de ventrale kern. De nervus cochlearis blijkt zich voor iedere frequentie vlakvormig uit te breiden in ieder van de onderafdelingen (iso-frequentie vlakken). Een tonotopische projectie kon worden vastgesteld in de cochleaire kernen, en eveneens in de olivae superiores en de colliculus inferior.

De efferenten van de cochleaire kerngroepen zijn te onderscheiden in:

1. Stria dorsalis, komend uit de DC en eindigend in de contralaterale ventrale kern van de lemniscus lateralis en de colliculus inferior.
2. Stria ventralis, komend uit het caudale deel van de PVC en gaande naar de contralaterale ventrale kern van de lemniscus lateralis.
3. De corpus trapezoideum vezels onder te verdelen in
   a. dikke
   b. middeldikke en
   c. dunne vezels.

3a. De dikke vezels komen uit de gebieden om de intredende nucleus cochlearis heen en gaan naar de contralaterale kern van het corpus trapezoideum en waarschijnlijk ook contralateraal naar de laterale lemnsicus kernen en de colliculus inferior.

3b. De middeldikke vezels komen uit de AVC en het rostrale deel van de PVC. Ze eindigen in de olivae superiores (uitgezonderd de contralaterale oliva superior lateralis), de contralaterale lemniscus lateralis kernen en de contralaterale colliculus inferior. In de homolaterale ventrale lemniscus lateralis-kern wordt ook wat terminatie waargenomen. Contralateraal blijkt zich een klein bundeltje af te splitsen ter hoogte van de nucleus van het corpus trapezoideum, dat te vervolgen is naar caudaal tot het niveau van de oliva inferior.

De terminaties van deze middeldikke vezels blijken in de olivae superiores en de colliculi inferiores tonotopisch gerangschikt te zijn.

3c. De dunne vezels komend uit de gebieden rondom de uittredende nervus cochlearis eindigen in de laterale preolivaire kernen homolateraal, de mediale preolivaire kernen contralatraal en verdwijnen tenslotte tijdens hun loop in de lemniscus lateralis.

Het vezelspectrum van het corpus trapezoideum werd bestudeerd direct mediaal van de cochleaire kernen en midsagittaal. Opgemerkt werd dat uitsluitend vezels van de cochleaire kernen in het corpus trapezoideum kruisen.

De efferenten van de olivae superiores werden onderzocht. De efferenten van de laterale oliva superior gaan voor de helft naar de homolaterale laterale lemniscus kernen en de colliculus inferior. De andere helft gaat naar de contralaterale laterale lemniscus kernen en de colliculus inferior.

De efferenten van de mediale olive superior gaan voor het grootste gedeelte naar de homolaterale laterale lemniscus kernen. Een klein deel kruist naar de contralaterale laterale lemniscus kernen en de colliculus inferior.

De gekruiste efferenten van de olivae superiores kruisen dorsaal in de medulla oblongata.

De efferenten van de nucleus van het corpus trapezoideum blijken te eindigen in de homolaterale oliva superior lateralis.

De ventrale kern van de lemniscus lateralis stuurt zijn efferenten naar de homolaterale colliculus inferior, en waarschijnlijk ook naar de dorsale kern van de lemniscus lateralis homolateraal.

De dorsale kern van de lemniscus lateralis stuurt zijn efferenten via de commissura van Probst naar de contralaterale dorsale kern van de laterale lemniscus en naar de contralaterale colliculus inferior. Een projectie naar de homolaterale colliculus inferior kon niet worden uitgesloten.

In de schema's 20, 21, 23, 26, 27, 31, 34 en 35 wordt het beloop van deze verbindingen schematisch weergegeven.

Een hoge hemichordotomie en een achterstrengkern-laesie blijken beide terminale degeneratie te geven zowel in als in de directe omgeving van de colliculus inferior.

De isthmo-peripedunculaire bundel is een verbinding tussen de dorsale kern van het brachium conjunctivum en de peripedunculaire grijze stof ter hoogte van het CGM. Hij wordt beschreven in verband met de veronderstelde centrale acoustische baan van Papez, die waarschijnlijk niet bestaat.

Ad 3. De descenderende auditieve verbinding

Het verloop van de vezels uit het auditieve cortex areaal en uit het CGM en de localisatie van de preterminatie in de colliculi inferiores werden nagegaan. De eindiging in de colliculus blijkt uitsluitend aanwezig te zijn in de laterale zone en het dorsale deel van de centrale kern. Tevens is er wat terminatie in de parabrachiale area.

Een descenderende verbinding van de colliculus inferior naar de beide dorsale cochleaire kernen werd beschreven. In het verloop van deze bundel wordt ook preterminatie gezien in de mediale preolivaire kern homolateraal en in de oliva superior lateralis homolateraal, of heterolateraal, en soms beiderzijds, misschien afhankelijk van de localisatie van de lesies.

Descenderende of beter gezegd teruglopende verbindingen van de laterale preolivaire kernen naar het cochleaire kerncomplex werden bestudeerd. De terminatie van de olivocochleaire bundel in de cochleaire kernen werd kort beschreven.

Er blijken ook vezels terug te lopen via de striae dorsalis. Oorsprong en terminatie werden niet vastgesteld.

Ad 4. Efferenten van de colliculus inferior

Deze worden onderverdeeld in

a. intrinsieke efferenten
b. ongekruiste efferenten
c. gekruiste efferenten.

Ad a. Lesies in de colliculus inferior veroorzaken een preterminale degeneratie in het rostrale deel van de centrale kern en in de laterale zone. Gedeeltelijk trekken de degenererende axonen direct naar deze gebieden, gedeeltelijk verlaten de degenererende axonen de colliculus inferior via het brachium van de colliculus inferior. De loop van de vezels naar het brachium van de colliculus inferior wordt beschreven.

Ad b. Via het brachium van de colliculus inferior bereiken de efferenten de parabrachiale area, waar terminatie wordt gezien, de nucleus interstitialis waar weinig terminatie wordt gevonden en naar het CGM.

In het CGM termineren de axonen voornamelijk in het ventrale deel en de oppervlakkige zone. Het dorsale deel van het CGM krijgt weinig terminatie.

Ad c. De gekruiste vezels termineren gedeeltelijk in de colliculus inferior van de andere zijde, waar het eindigingsgebied gelijk is aan dat van de homolaterale zijde, ofschoon quantitatief minder.

STELLINGEN

I

Bij de indeling van het C.Z.S. in kerngroeperingen dient men zo mogelijk meer dan één criterium in overweging te nemen, in het bijzonder de afferente en efferente verbindingen.

II

De cellen, die in het cochleaire kerncomplex, de olivae superiores en de colliculus inferior door één frequentie geactiveerd worden, liggen in vlakken gerangschikt.

III

De kruisende vezels in het corpus trapezoïdes zijn uitsluitend afkomstig van het cochleaire kerncomplex.

IV

De twee-mans huisartsen-groepspraktijk verdient de voorkeur boven de groepspraktijk met meer leden.

V

De opvatting, dat een éénmaal doorgemaakte toxoplasmose-infectie een volledige bescherming biedt bij volgende zwangerschappen, is onjuist.

VI

Er zijn geen auditieve neuronen, die de colliculus inferior ononderbroken passeren.

VII

De naam "central acoustic tract" van Papez dient uit de literatuur te verdwijnen en de "laterotegmental tract" van Morest trede hiervoor in de plaats.

J. W. Papez: Anat. Rec., 42: 60, 1929.
D. K. Morest: J. Anat. London, 99: 611-634, 1965.

VIII

Aan een electroshock dient een narcose vooraf te gaan.

IX

Een geslaagd beeldend kunstwerk openbaart het wezen en de bedoelingen van de maker door zijn expressieve vorm, zonder een verbale toelichting nodig te hebben.

Mr. W. C. Feltkamp: „Zien en verstaan", van Mantgem en de Does, Amsterdam.

X

De door Lowry beschreven ultramicrochemische analyse-methoden verdienen een breder toepassingsgebied in de medische biologie.

A. H. Lowry: Bull. New York Acad. Med., 38: 789, 1962.

XI

Het verdient aanbeveling om bij de colleges anatomie een gedeelte van de tijd te besteden aan het klinische belang van de behandelde stof. Men zou dit de klinische- of toegepaste anatomie kunnen noemen.

Stellingen behorende bij het proefschrift van J. van Noort,
The structure and connections of the inferior colliculus,
Leiden 1969