THE VESTIBULAR NUCLEI IN THE CAT

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INTRODUCTION

Some confusion exists in the literature with regard to the delimitation and nomenclature of the vestibular nuclei, making comparisons between results of studies by different workers difficult. A precise chart of the normal topography of the nuclei is essential for an unequivocal presentation of experimental findings. When undertaking studies on the connexions of the vestibular nuclei, we deemed it necessary, therefore, to perform as a first step a thorough mapping of the vestibular complex in the experimental animal employed.

While the basis for any subdivision of a nuclear complex will always have to be the cytoarchitectonic features of its component groups, experimental data on fibre connexions may give additional information. The results of our studies of the connexions of the vestibular nuclei, published separately (Brodal & Pompeiano, 1957; Brodal & Torvik, 1957; Pompeiano & Brodal, 1957*a*, *b*) have, therefore, been taken into account in our analysis. For practical reasons the relevant literature will be dealt with in the Discussion.

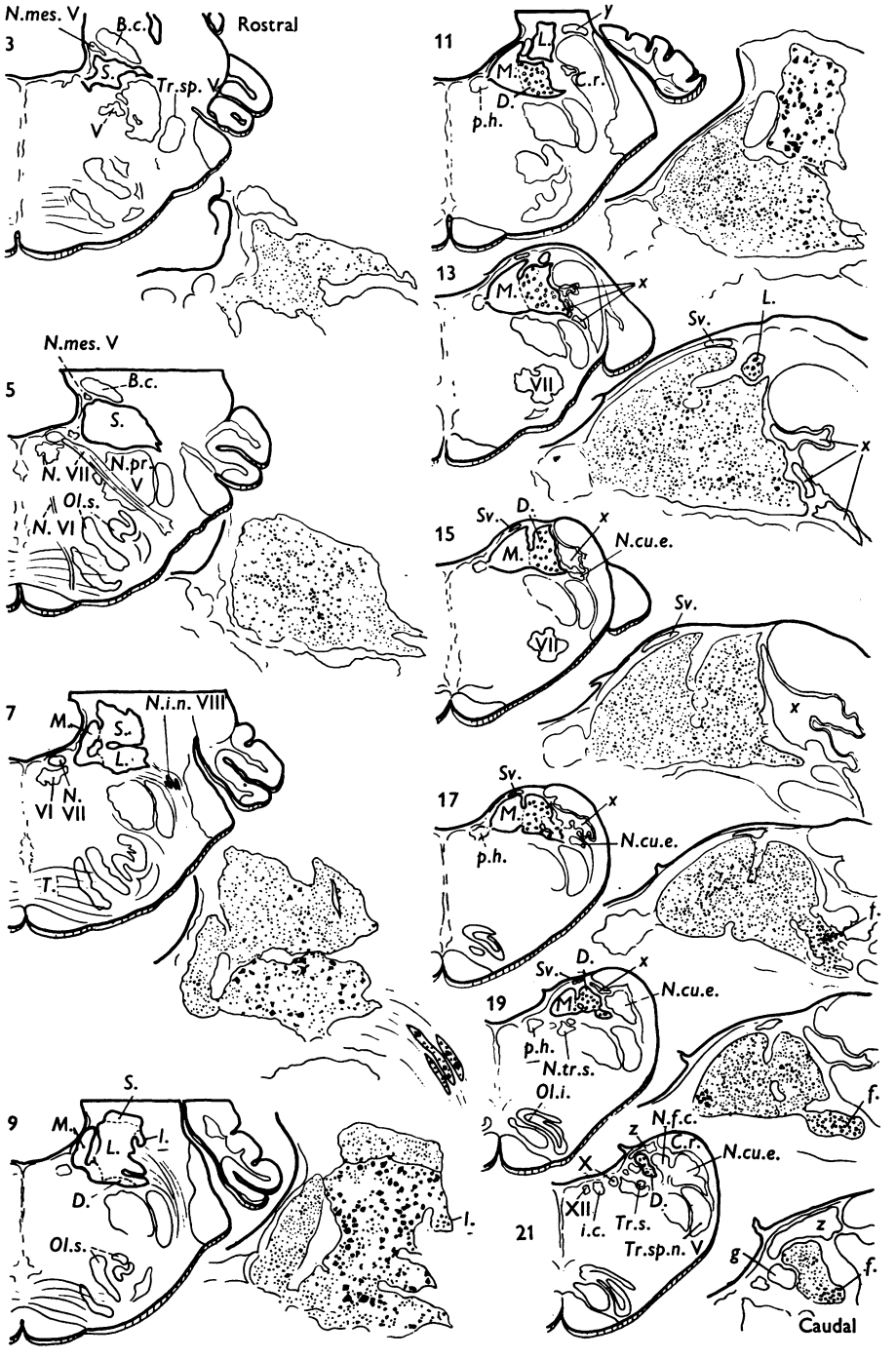
MATERIAL AND METHODS

The animals used in some of our experimental studies (Brodal & Pompeiano, 1957; Pompeiano & Brodal, 1957*a*) were young kittens 2–3 weeks old. The cytoarchitecture of the vestibular nuclei was, therefore, studied chiefly in such animals. Since, however, the chief difference between these young animals and adult ones is a denser packing of the cells, the map applies to adult animals as well.

The maps shown in Text-figs. 1 and 2 were made from serial Nissl-stained transverse sections through the brain stem of a normal kitten $2\frac{1}{2}$ weeks old. The brain was fixed in 96 % alcohol, embedded in paraffin and cut serially at 15 μ. Every fifth section was mounted and stained with Thionine. Drawings were made of sections at equal intervals by means of a projection apparatus, under low magnification. The more detailed drawings of the vestibular complex shown in Text-fig. 1 were made in the same way using a higher magnification, which permitted the marking of individual cells. The drawings were subsequently carefully controlled under the microscope. Photomicrographs were taken from different nuclear groups.

The maps shown in Text-figs. 1 and 2 are true reproductions of the topography of the vestibular nuclear complex in one particular animal. A study of several other, similarly treated, brains from other normal animals as well as from experimental

* This work was done while Dr Pompeiano, Physiological Institute, University of Bologna, Italy, was staying in the Anatomical Institute, University of Oslo, with a grant from the Rockefeller Foundation.



Text-fig. 1. A map showing the topography and cytoarchitecture of the vestibular nuclei in the cat as seen in transverse sections. The numbers of the sections reproduced correspond to those employed in Text-fig. 2. The rings in the descending nucleus represent the fibre bundles of the spinal (descending) root of the vestibular nerve. For particulars see text.

animals makes clear, however, that the series selected may be considered representative. There are only minor variations between different animals.

In addition to Nissl-stained sections series of fibre stained preparations were studied. One of these series was stained according to the Weil method, another according to the Bodian method. Several brains treated according to the method of Glees (1946) were also examined. From one of these the map of Text-fig. 3, showing the nuclei in horizontal sections, was prepared.

Cytoarchitecture and topography of the vestibular nuclei

The vestibular complex is here subdivided, according to common usage, into four principal nuclei, the superior nucleus of Bechterew, the medial (dorsal or triangular) nucleus of Schwalbe, the lateral nucleus of Deiters, and the inferior (or spinal) nucleus or nucleus of the descending root of the vestibular nerve, here referred to as the descending nucleus. In addition some minor groups may be distinguished.

The superior vestibular nucleus is easily outlined, except most rostrally. It is composed of rather loosely scattered, chiefly medium-sized and small cells (Pl. 1, fig. 4). In Nissl-stained sections the medium-sized cells are multipolar or more frequently round or spindle- or pear-shaped with rather fine Nissl granules. The nucleus in young animals sometimes has a somewhat excentric position. The smallest cells appear rounded, stellate, or spindle shaped. In the central portion of the nucleus there are some clusters of somewhat larger multipolar cells. Like the other

Abbreviations used in Text-figs. 1–3

B.c.	Brachium conjunctivum
C.r.	Corpus restiforme
D.	Descending (spinal) vestibular nucleus
f	Cell group *f* in descending vestibular nucleus
g	Group rich in glia cells, caudal to the caudal end of the medial vestibular nucleus
i.c.	Nucleus intercalatus of Staderini
L.	Lateral vestibular nucleus of Deiters
l.	Small-celled lateral group of lateral nucleus
M.	Medial (triangular or dorsal) vestibular nucleus
N.cu.e.	Nucleus cuneatus externus
N.f.c.	Nucleus funiculi cuneati
N.i.n. VIII	Nucleus interstitialis nervi vestibuli
N.mes. V	Nucleus mesencephalicus *n.* V
N.pr. V	Nucleus sensibilis principalis *n.* V
N.tr.s.	Nucleus tractus solitarii
N.tr.sp. V	Nucleus tractus spinalis nervi V
N. VI, VII, VIII	Cranial nerves VI, VII and VIII
Ol.i.	Oliva inferior
Ol.s.	Oliva superior
p.h.	Nucleus praepositus hypoglossi
S.	Superior vestibular nucleus of Bechterew
Sv.	Cell group probably representing the nucleus supra-vestibularis
Tr.s.	Tractus solitarius
Tr.sp.n. V	Tractus spinalis *n.* V
V, VI, VII, XII	Cranial motor nerve nuclei
X	Dorsal motor (parasympathetic) vagus nucleus
x	Small-celled group *x*, lateral to the descending vestibular nucleus
y	Small-celled group, lateral to the nucleus of Deiters
z	Cell group dorsal to the caudal part of the descending vestibular nucleus

cells the largest elements in transverse sections tend to be arranged in elongated groups from dorsomedial to ventrolateral (see drawing 5 in Text-fig. 1), due to the presence of fibre bundles with this course.

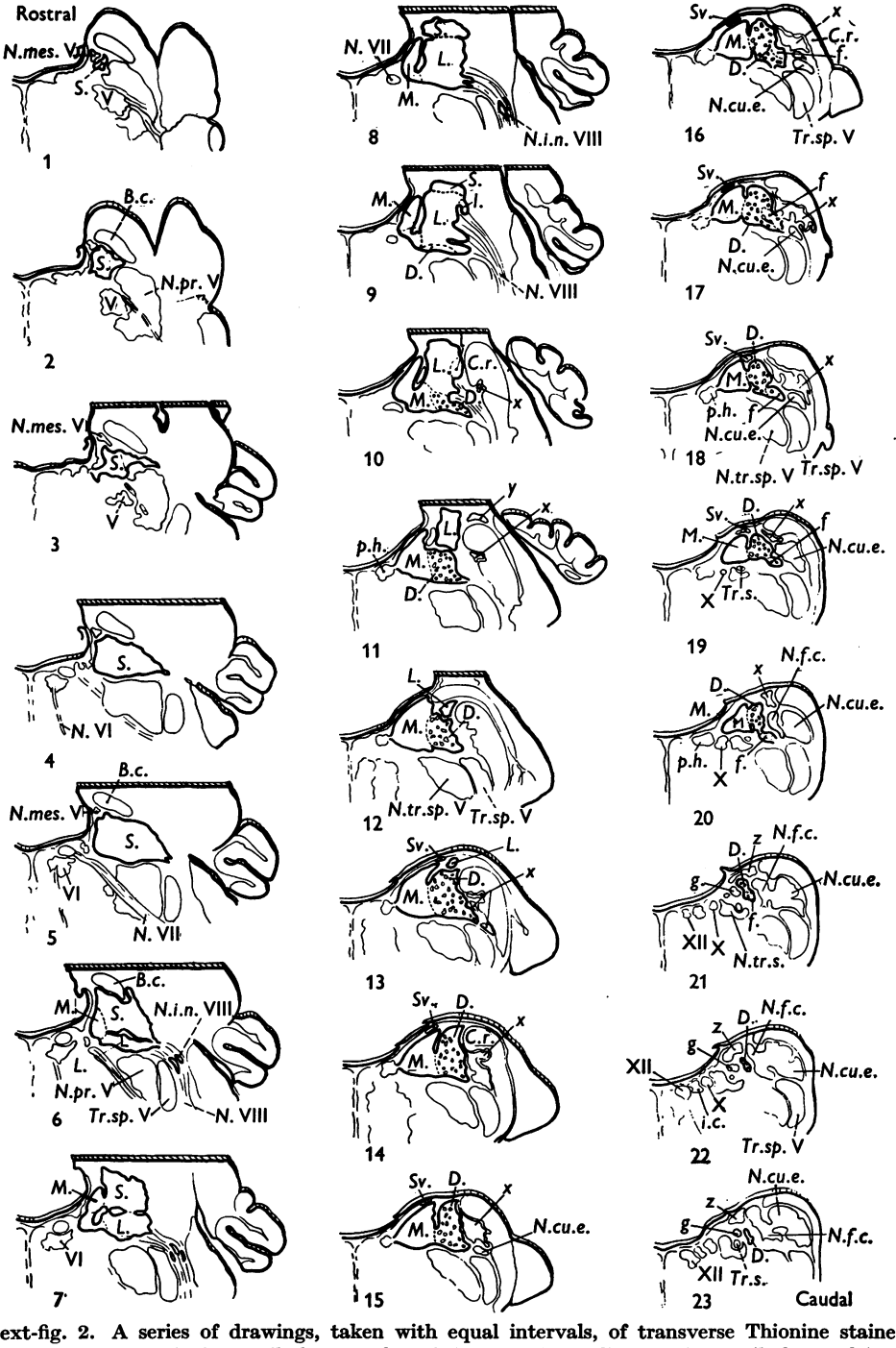
The superior nucleus extends from a level a little rostral to the caudal pole of the motor trigeminal nucleus (drawings 1–3 in Text-figs. 1, 2) to a level slightly caudal to the nucleus of the abducent nerve (drawing 9). In its middle part the nucleus has a triangular shape.

Along its entire rostro-caudal extent the superior vestibular nucleus is capped dorsally by the superior cerebellar peduncle. Medially the nucleus comes close to the floor of the fourth ventricle, except most caudally where the medial nucleus is interposed between it and the ventricle (drawings, 6, 7 in Text-figs. 1, 2). Here the two nuclei fuse. Dorsomedial to the rostral part of the superior nucleus is the mesencephalic trigeminal nucleus (drawings 1–5 in Text-figs. 1, 2). Ventrally to the caudal half of the superior nucleus is the lateral nucleus of Deiters. Their different cytoarchitecture makes the border between the two nuclei fairly distinct (most caudally they are separated by fibre bundles) except rostrally, because there are relatively few giant cells in the rostralmost part of the lateral nucleus. The rostral half of the superior nucleus is indistinctly separated from the principal trigeminal nucleus, which comes into contact with its ventral border. The lateral border of the superior nucleus is well defined by the presence of the fibre masses of the restiform body.

In fibre preparations the fibre bundles referred to above, coursing in a direction from ventro-lateral to dorso-medial, are distinct, and many of these fibres are myelinated. Otherwise the fibre texture of the superior nucleus shows no particular pattern.

The lateral vestibular nucleus of Deiters. This term is here taken to denote that part of the vestibular nuclear complex which is characterized by containing the giant cells of Deiters. These are multipolar, have coarse Nissl-granules, arranged concentrically around the nucleus, which is most commonly fairly centrally placed (Pl. 1, figs. 1, 2). They show considerable variations in size, having in 2–3 weeks old kittens a largest diameter across their perikaryon varying between some 30 to about 45 μ. The lateral nucleus also contains smaller cells of varying types. Some are fairly large, usually multipolar, others are medium-sized, frequently oval or spindle shaped, while still others are very small (Pl. 1, fig. 1). The giant cells are relatively more numerous and in general somewhat larger in the caudal part of the nucleus than in its rostral part (Pl. 1, figs. 1, 2, and drawings 7–11 in Text-fig. 1). The number of smaller cells, however, is definitely less in the former part. The two regions of the nucleus fuse imperceptibly with each other. At the lateral border of the nucleus a small group consisting of medium-sized cells only can easily be distinguished in most animals (Pl. 1, fig. 3, and drawings 9–10 in Text-figs. 1, 2). This group is here labelled *l*.

The lateral vestibular nucleus begins rostrally at the level of the middle of the superior nucleus (drawing 6 in Text-fig. 2). Its caudal end is found caudal to the nucleus of the abducent nerve (drawing 13 in Text-figs. 1, 2). Fibres of the striae medullares may separate the caudalmost part of the nucleus into two, a dorsal group, apparently situated in the base of the cerebellum, and a ventral group,



Text-fig. 2. A series of drawings, taken with equal intervals, of transverse Thionine stained sections through the vestibular complex of the cat. The outlines of the vestibular nuclei are shown as heavy lines. Abbreviations as in Text-fig. 1.

situated in the angle between the medial and descending nucleus and the restiform body.

The border between the lateral nucleus and the superior nucleus, dorsal to it, was considered above. The lateral nucleus extends further caudally than the superior. Its caudalmost part, therefore, borders dorsally on the white matter of the cerebellum ventral to the nucleus interpositus. Ventro-laterally the rostral part of the lateral nucleus approaches the trigeminal principal sensory nucleus and the spinal tract. Ventral to the caudal third of the lateral nucleus the descending nucleus is interposed between it and the spinal trigeminal nucleus (drawings 9–11 in Text-figs. 1, 2). The fibres of the facial nerve are found ventro-medial to the rostralmost part of the lateral nucleus. Caudally it borders medially on the medial vestibular nucleus. It can clearly be distinguished from this on account of its content of giant cells, and more dorsally by a narrow zone of fibres, almost free from nerve cells. Lateral to the lateral nucleus is the restiform body.

In fibre preparations the vestibular root fibres, which enter the lateral nucleus from its lateral aspect (drawings 6–10 in Text-figs. 1, 2) are seen to radiate fanlike within the territory of the nucleus, frequently producing a separation of its cells into minor aggregations. Other fairly heavy bundles of myelinated fibres enter the lateral nucleus from its dorsal aspect. Most of these are certainly cerebello-vestibular fibres.

The medial vestibular nucleus is clearly recognized as a particular entity in its medial part. At caudal levels its lateral borders are less clear. It is made up of cells of different sizes (Pl. 1, figs. 5, 6), the majority being medium-sized, triangular, multiform or more rounded, with a fairly centrally placed nucleus and rather fine Nissl granules. The smaller cells in the nucleus usually are round or pear-shaped in Nissl-stained sections, and their cytoplasm is scanty. The cells of the medial nucleus lie rather close together. At its middle levels, particularly dorso-laterally towards the descending nucleus, there are some more of the largest elements (Pl. 1, fig. 6) than further rostrally and caudally (Pl. 1, fig. 5). In many animals a tiny group of larger cells may be seen in the medialmost corner of the nucleus dorsal to the dorsal motor vagal nucleus (drawing 19 in Text-fig. 1).

The rostral end of the medial vestibular nucleus is found approximately at the same level as the rostral pole of the lateral nucleus (drawing 6 in Text-fig. 2) and is situated just underneath the floor of the fourth ventricle. Throughout its extent to its caudal extremity, at the level of the rostral pole of the hypoglossal nucleus, the nucleus retains its characteristic relation to the ventricle. The caudal end of the nucleus (see also Text-fig. 3) is found a little rostral to the caudal disappearance of the descending nucleus.*

Near its rostral end the medial nucleus is not clearly separated dorso-laterally from the superior nucleus (drawings 6 and 7 in Text-figs. 1 and 2). Ventrally it is continuous with the reticular formation, and medially it is connected by cell

* Below the caudal end of the medial nucleus is a dense accumulation of glia cells with a few nerve cells (*g* in Text-figs. 1–3), which continues caudally between the nucleus of the solitary tract, the descending vestibular nucleus and our group *z*, to be described below. Medial to the group *g* there is a slender column of relatively big multipolar cells. These cells may perhaps represent a caudal prolongation of the medial vestibular nucleus, which, as noted above, frequently contains some larger cells medially in its caudalmost part.

strands with the nucleus praepositus hypoglossi (drawings 11–18 in Text-figs. 1, 2). Ventral to the caudal extremity of the medial nucleus is the solitary tract and its nucleus and the dorsal motor vagal nucleus (drawings 19–20 in Text-figs. 1, 2). The lateral border of the medial vestibular nucleus is easily recognized at rostral levels, where a fibre bundle separates it from the lateral vestibular nucleus. More caudally the ventral part of the nucleus fuses laterally with the descending nucleus (drawings 9–20 in Text-figs. 1, 2) while its dorsal part is separated by a narrow cell-free zone from the latter. This zone may occasionally be identified even to the caudal end of the medial nucleus.

In myelin-sheath stained preparations finer fibres are seen coursing in all directions within the medial nucleus. More compact strands of fibres are seen only in its lateral-most region. These fibres run in a ventral direction to the ventro-lateral angle of the nucleus, where they turn medially and course closely ventral to the nucleus and to the nucleus praepositus hypoglossi. They appear to enter the area of the medial longitudinal fasciculus. The border between the medial and the descending nucleus is clearly seen in fibre preparations, particularly with myelin-sheath staining (Pl. 1, fig. 9).

The descending (spinal) vestibular nucleus is the most difficult part of the vestibular complex to outline. As defined by us (Text-figs. 1, 2) it is a rather large nuclear group.

Its cytoarchitecture is not quite uniform throughout. In addition to small and medium-sized cells, resembling those of the medial nucleus, the descending nucleus contains a certain number of larger cells (Pl. 1, fig. 7, and drawings 11–15 in Text-fig. 1). Some of these are multipolar and almost approach the giant cells of the lateral nucleus in size.* Such large cells occur throughout the nucleus, but are particularly abundant in its rostral part (drawings 11–13 in Text-fig. 1). Ventro-laterally in its caudalmost part (drawings 17–21 in Text-fig. 1) numerous fairly large cells are so densely packed (Pl. 1, fig. 8) that it appears justified to consider this region as a particular subdivision. Since it appears to be the same group which is labelled *f* by Meessen & Olszewski (1949, their Pl. VII) in the rabbit we have employed the same designation. The group *f* ventro-laterally approaches the spinal trigeminal tract and its nucleus (drawings 17–21 in Text-fig. 1). It shows some variations in shape between different animals and frequently forms a longitudinal column which may, however, be interrupted. Apart from the region of the group *f* the descending nucleus is characterized by the scattering of its cells due to the presence within it of large numbers of longitudinally running fibres (shown as rings in the drawings in Text-figs. 1, 2).

The descending nucleus begins rostrally at the level where the caudal vestibular root fibres enter the vestibular complex (drawing 9 in Text-fig. 2) as a transversely extended zone of cells immediately ventral to the lateral nucleus. A little further caudally (drawing 11 in Text-figs. 1, 2) bundles of longitudinally running fibres, presumably belonging to the spinal vestibular root, intrude between the two nuclei. The delimitation of the nucleus medially, where it more or less fuses with the

* Occasionally a characteristic giant cell of the type present in the lateral nucleus may be seen in the rostral part of the descending nucleus. These cells are probably to be considered as displaced Deiters' cells.

medial nucleus, was described above. At caudal levels the cytoarchitectonic differences between these two nuclei are less distinct than more rostrally (see drawings 11–19 in Text-fig. 1). Lateral to the descending nucleus is rostrally the restiform body, more caudally the group labelled *x* in our map, the external cuneate and the cuneate nucleus. At some places the nucleus almost fuses with the group *x*. Its caudal extremity lies immediately ventral to the group here labelled *z* (drawings 21–23 in Text-figs. 1, 2). On its medial side is the group of glia cells referred to above. It should be noticed that the descending nucleus dorsally extends to the surface of the rhombencephalon along its rostrocaudal extent, except for its caudal extremity and its rostralmost part.

In fibre preparations the descending nucleus is characterized by numerous longitudinally running fibre bundles (Pl. 1, fig. 9).

Some smaller cellular groups. Between the root fibres of the vestibular nerve there are some strands of cells, not very numerous, which represent the *noyaux interstitiels du nerf vestibulaire* of Cajal (1909). These cells (drawings 6–8 in Text-figs. 1, 2) are medium-sized and commonly elongated, with their long axis oriented along the vestibular root fibres. In some animals the nucleus contains scattered giant cells like those in the nucleus of Deiters, which may be connected with the interstitial nucleus by a strand of cells. Other strands may form a connexion with the descending nucleus, and scattered cells may extend towards the superior nucleus.

Dorsal to the vestibular nuclei there are some rather loosely structured *strands of cells which extend into the white matter of the cerebellum*, where they approach the central cerebellar nuclei and form a connexion between the superior and lateral nucleus with the nucleus fastigii and the ventro-lateral part of the nucleus interpositus.

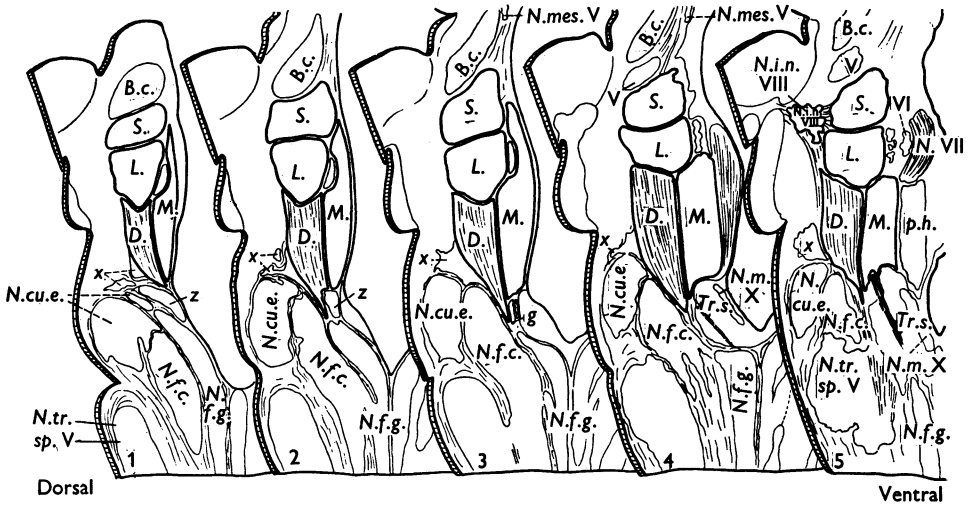
A small *group of cells*, here labelled *Sv*, is found *immediately beneath the dorsal surface of the medulla oblongata* at levels between the caudal end of the nucleus of Deiters and the level of the rostral pole of the external cuneate nucleus (drawings 13–19 in Text-figs. 1, 2). It is separated ventrally from the lateralmost part of the medial vestibular nucleus by some transversely running fibres. It may consist of a rostral and a caudal portion, and has more or less spindle-shaped cells, with their longitudinal axis oriented along the surface of the medulla. We believe this group to correspond to Olszewski & Baxter's (1954) nucleus supravestibularis in man.

A *small-celled group, here called y, is situated dorsocaudal to the restiform body* where this begins to fan out into the cerebellar white matter (Text-figs. 1, 2). In transverse sections it is seen to cap the restiform body dorsally. It is situated immediately lateral to the caudal part of the nucleus of Deiters, and is ventro-laterally practically in contact with the dorsal cochlear nucleus. From the dorsal aspect of this group, scattered cells form strands extending to the ventralmost part of the dentate nucleus.

Between the caudal half of the descending vestibular nucleus and the rostral pole of the external cuneate nucleus is a zone of cells, here called x, which differs from these nuclei with regard to its cytoarchitecture (Text-figs. 1–3). It contains scattered small cells of somewhat varying shape. It can best be distinguished from the adjoining nuclei in horizontal silver impregnated sections (see Text-fig. 3). The zone begins caudally a little below the rostral pole of the external cuneate nucleus and

increases in size more rostrally, its upper, broadest part covering the top of the external cuneate nucleus. Here it has the restiform body on its lateral side.

The small cell group, here labelled *z*, is found *immediately rostral to the rostral end of the nucleus gracilis* (drawings 21–23 in Text-figs. 1, 2, see also Text-fig. 3). It is situated closely underneath the dorsal surface of the medulla oblongata, dorsal to the caudal end of the descending vestibular nucleus and the group *g*. In Nissl-sections its cells are medium-sized, ovoid to polygonal, and on the whole rather pale. Caudally this group is usually separated from the rostral end of the nucleus gracilis by a narrow cell-free interval. Its cytology resembles somewhat that of the latter nucleus, a fact which makes it difficult to keep the two apart in Nissl-stained sections. However, in horizontal silver-stained sections (see drawings 1–2 in Text-fig. 3) the group *z* clearly differs from the gracilis nucleus in its fibre pattern. It is also unlike the group *x* (cf. above).



Text-fig. 3. A series of drawings, taken with equal intervals, of horizontal silver impregnated sections through the vestibular complex of an adult cat. This diagram is included especially in order to make clear the topographical relations of the small cell groups *x* and *z*, which may be mistaken to be parts of the descending vestibular nucleus. Abbreviations as in Text-fig. 1.

DISCUSSION

The subdivision of the vestibular nuclear complex shown in our maps (Text-figs. 1, 2) in general agrees with those made by several other students of these nuclei in mammals, including man. Since there are, however, conflicting views concerning some points, it may be appropriate to give our reasons for choosing the delimitation employed.

The name *lateral vestibular nucleus of Deiters* has been used very inconsistently. While von Monakow (1883, and later) considered as the nucleus of Deiters the part of the vestibular nuclear complex in which the giant nerve cells undergo chromatolysis following lesions at rostral levels of the cord, other anatomists define the nucleus of Deiters as comprising extensive parts of the entire vestibular complex.

We have employed the term lateral nucleus of Deiters (also called 'grosszelliger Vestibulariskern' or 'noyau à grandes cellules de l'acoustique') for that part of the vestibular complex in which the multipolar giant cells of Deiters form a characteristic cytoarchitectonic element. It should be emphasized, however, that there are at least as many cells of other types within its territory (cf. description and Text-fig. 1). This restricted use of the term is in agreement with the usage of authors such as Sabin (1897), Cajal (1896, 1909) and Kappers, Huber & Crosby (1936).

A few large cells, some of them attaining the size of the giant cells of Deiters, commonly occur in what is here called the descending nucleus, and occasionally in the regions of the medial nucleus bordering on the lateral nucleus. However, the architecture of the lateral nucleus proper (see Text-fig. 1 and Pl. 1, figs. 1, 2) is characteristic enough to justify its distinction as a separate nucleus, and the scattered giant cells found elsewhere are probably to be considered as displaced specimens. Support for this view is derived from the results of experimental studies, since following lesions of the spinal cord at high cervical levels not only the giant cells, but the other cells of the lateral nucleus (as defined here) as well, are affected with retrograde cellular changes (Pompeiano & Brodal, 1957*a*), while no changes occur in other vestibular nuclei. Furthermore, all descending fibres from the lateral nucleus appear to course in the vestibulo-spinal tract. Such findings indicate that the nucleus of Deiters as outlined here forms a particular unit of the entire vestibular complex, even if it, like other vestibular nuclei contributes fibres to the ascending medial longitudinal fasciculus (Brodal & Pompeiano, 1957).

The uniform efferent fibre connexions of the nucleus of Deiters as outlined on a cytoarchitectonic basis are of interest with regard to the question of its subdivision into minor groups. As mentioned above, there are some differences in architecture between various regions of the lateral vestibular nucleus as noticed also by some previous authors, for example Sabin (1897), who in man found differences which appear to be similar to those described here. Lewy (1910) (in the rabbit) comments on the fact that the shape of the giant cells is not the same throughout the nucleus. However, apart from the little group of medium-sized cells, here called *l* (Text-figs. 1, 2, Pl. 1, fig. 3), the other differences are slight, and in view of the uniform efferent fibre connexions may not be significant. The fact that the vestibulo-spinal fibres coursing to different levels of the cord show a somatotopical arrangement with regard to their site of origin within the nucleus (Pompeiano & Brodal, 1957*a*) may have some bearing, not yet capable for explanation, on the regional differences in architecture.

The group *l* probably should be considered a particular part of the lateral nucleus, even if its efferent fibres course in the vestibulo-spinal tract, since at least three-quarters of its cells send fibres to levels of the cord below Th_1 (Pompeiano & Brodal, 1957*a*).

Other data support the delimitation of the nucleus of Deiters as made in this study, for example the observation of Vraa-Jensen (1956) that in the chicken the cells of the nucleus of Deiters are derived from the medial part of the matrix in the basal lamina, and not, like the other vestibular nuclei, from the dorsal part of the alar lamina.

There are thus good reasons for delimiting the nucleus of Deiters as done here,

and to consider this as a particular unit of the vestibular complex. Mention should, however, be made of some papers in which another delimitation is chosen. Fuse (1912) distinguishes seven subgroups of the Deiters' nucleus basing, it appears, this extensive use of the name on the occurrence of large cells. His 'Triangularis-Anteil' obviously is part of what is here considered the medial vestibular nucleus, which at some levels contains large cells (see Text-fig. 1), and his medioventral group is clearly the rostral part of the descending nucleus as outlined here, in which there are a certain number of large cells, and even scattered (presumably displaced) Deiters' cells may occur. The interstitial nucleus of the vestibular nerve is called by Fuse the intravestibular group of the nucleus of Deiters. His other subdivisions: the dorsal, the mediodorsal, the central and the dorso-lateral group appear to be parts of what we have defined as the nucleus of Deiters. Also Lewy (1910) distinguishes different regions of the nucleus of Deiters, his 'ventrale Abteilung' according to his illustrations being the rostral part of the descending nucleus. Muskens (1914) speaks of the medial nucleus as part of the nucleus of Deiters. Winkler & Potter (1914) in their atlas of the cat's brain (their Pl. XXVII) label as ND (Deiters' nucleus) part of what is here considered as the descending nucleus.

In their atlas of the rhombencephalon of the rabbit Meessen & Olszewski (1949) label various groups as parts of the nucleus of Deiters. As judged from their cytoarchitecture and from their position only groups (subnuclei) Dtγ on Pls. IX and X, and Dtα on Pls. X and XI belong to the nucleus of Deiters proper. On Pls. VIII and IX the group labelled Dtα differs clearly cytoarchitectonically from the group carrying the same name on Pls. X–XI. There is little doubt that the group Dtα on Pls. VIII and IX as well as the group Dtβ on Pl. IX belong to the descending nucleus. It is seen from the photographs that, contrary to what is said in the text, the group Dtγ does not consist exclusively of giant cells. The reasons for its separation are not entirely clear.

The *superior vestibular nucleus* (angular nucleus, nucleus of Bechterew) by virtue of its uniform cytoarchitecture and relatively distinct borders is fairly unanimously delimited as done here by most authors (Cajal, 1909, in the mouse; Meessen & Olszewski, 1949, in the rabbit; Winkler & Potter, 1914, in the cat; Sabin, 1897, Jacobsohn, 1909, Marburg, 1910, and Olszewski & Baxter, 1954, in man). In the literature references are found to some cell groups, usually labelled as nuclei, which have been distinguished at levels where the superior nucleus is present. Thus Lewandowsky (1904) in the cat refers to a cell group which he calls '*nucleus supremus acustici*'. His short description and his figure 11, showing the nucleus in a Marchi preparation, do not enable one to get a clear impression of its extension. Like Fuse (1912) we have not been able to convince ourselves of the existence of this nucleus of Lewandowsky. It may be part of what we have outlined as the superior nucleus, but we do not feel that the regional cytoarchitectonic differences within the superior nucleus are sufficiently clear to warrant a subdivision of this nucleus into minor groups, the more so since the ascending fibres from the superior nucleus appear to take origin from all parts of it (Brodal & Pompeiano, 1957). Similar considerations as made above with regard to the 'nucleus supremus acustici' apply to what Fuse calls the 'nucleus of Onufrowicz' (1885) and the 'nucleus of Kohnstamm' (1910). Until further studies may reveal that the superior vestibular

nucleus is not an entity with regard to fibre connexions and intrinsic organization (arrangements of axons and dendrites, etc.), it seems advisable to consider it as one unit of the vestibular nuclear complex.

The *medial vestibular nucleus* (dorsal vestibular nucleus, triangular nucleus, principal vestibular nucleus, nucleus of Schwalbe) as outlined here corresponds to the nucleus as described and pictured for example by Sabin (1897), Cajal (1909), Ferraro *et al.* (1940) and Meessen & Olszewski (1949). Concerning the medial delimitation of the medial nucleus the descriptions in the literature largely conform. Likewise is there general agreement on the fact that the medial nucleus is situated beneath the floor of the fourth ventricle. Concerning the lateral borders of the nucleus there are, however, conflicting views. Reference was made above to the erroneous inclusion of part of the medial nucleus in the concept of the lateral nucleus. Some authors include into the medial nucleus part of what we have here delimited as the descending nucleus, namely its dorsocaudal portion. This is the case, for example, with Winkler & Potter (1914). In their atlas of the cat's brain (their Pl. XXVII) these authors distinguish four-cell groups within the medial nucleus. However, the medial part of their group *a* is the nucleus praepositus hypoglossi (cf. Brodal, 1952), while group *c* and part of *d* (and probably also the region labelled ND, Deiters' nucleus) appear to be cellular areas which belong to the descending nucleus. Thus, only group *b* and the lateral part of group *a* represent the medial vestibular nucleus proper. The ventral border of the medial vestibular nucleus may be difficult to define exactly in Nissl preparations since it fuses with the reticular formation.*

The area identified as the *descending vestibular nucleus* has a cytoarchitecture which, particularly in its rostral part, differs from that of the medial nucleus (cp. Pl. 1, figs. 5, 7), even if there are similarities in Nissl-stained sections, and the border between the two nuclei at some levels is indistinct. However, when the presence of the longitudinally running fibre bundles (shown in Text-fig. 2, see also Pl. 1, fig. 9) is used as a criterion, the descending nucleus can be unequivocally outlined. The delimitation of the descending (spinal) vestibular nucleus as given here largely agrees with that given by Cajal (1909) in the mouse and by Sabin (1897) in man.

It is worthy of notice that as judged by its cytoarchitecture as well as by the presence of descending vestibular root fibres the descending nucleus begins rostrally where the bulk of the vestibular root fibres enter the vestibular complex, namely, ventral to the caudal third of the nucleus of Deiters. Quantitatively it is thus an important part of the vestibular complex.† As mentioned above, some authors have considered the rostral part of the descending nucleus as belonging to what they call the nucleus of Deiters. In some descriptions the dorsal and medial regions of the nucleus as outlined here are taken to belong to the medial nucleus, probably because these parts of it extend dorsally to the surface of the rhombencephalon, and the

* It appears from studies of the distribution of primary vestibular fibres (unpublished) that the ventralmost strip of what in Nissl-preparations appears as the medial nucleus, is devoid of vestibular afferents, and thus should not be included in this nucleus.

† It is remarkable that the spinal afferents to the descending nucleus are limited to its extreme caudal ventro-lateral part only (Pompeiano & Brodal, 1957*b*), while this region of it appears to be poor in primary vestibular afferents (unpublished observations).

cytoarchitecture of the medial and descending nucleus at these levels is rather similar. For example, Winkler & Potter (1914), as mentioned above, include parts of what is here interpreted as the descending nucleus into the medial nucleus, considering apparently only the ventro-lateralmost region (composed of somewhat larger, densely packed cells) as the descending nucleus. Authors erroneously outlining the medial nucleus in this way are then left with a descending nucleus of modest dimensions, which to a large extent is made up of the rather compact cell group *f*, described above (drawings 16–21 in Text-figs. 1, 2, and Pl. 1, fig. 8). It may be discussed whether this part of the vestibular complex should be considered a particular nucleus. Experimental studies (Brodal & Torvik, 1957) show that many of its cells project on to the cerebellum, while others give off fibres ascending in the medial longitudinal fasciculus (Brodal & Pompeiano, 1957). However, cells belonging to the surrounding parts of the descending nucleus behave in the same manner. The group *f*, thus, cannot be separated from the adjoining areas of the descending nucleus by virtue of its efferent connexions, and until future studies may show that it owes its peculiarities to other features in the organization of the vestibular nuclei, it appears reasonable to consider it as a particular group of the descending nucleus only. As mentioned in the description it may frequently be interrupted into minor cell groups. The groups *b* and *c* of Meessen & Olszewski (1949, their pls. V, VI) are probably such minor groups of the larger collection of compactly placed larger cells, called here collectively group *f*.

It is of some importance to be aware of the fact that the medial part of the external cuneate nucleus is frequently broken up into minor clusters of cells which are very close to the lateral border of the descending nucleus. The presence between these two nuclei of the small-celled zone *x* (see Text-figs. 1–3) may facilitate the distinction between the descending vestibular nucleus and the external cuneate nucleus.

The *noyaux interstitiels du nerf vestibulaire* of Cajal (1909) have been observed by several authors (Fuse, 1912; Klossowsky, 1933; and others). In our experimental studies we have observed that some of its cells are affected by retrograde changes following lesions of the medial longitudinal fasciculus (Brodal & Pompeiano, 1957) or of the spinal cord (Pompeiano & Brodal, 1957 *a*), while lesions of the cerebellum do not produce changes in the nucleus (Brodal & Torvik, 1957). According to Cajal (1909) primary afferent vestibular fibres establish synaptical contact with its cells. The fact that the interstitial nucleus frequently contains some giant cells of the type found in the lateral nucleus, and the fact that its fibre connexions are similar to those of the latter suggest that it is possibly an aberrant part of Deiters' nucleus. This opinion was held also by Cajal (1909) and Fuse (1912).

The *small-celled zone x* (Text-figs. 1–3), lateral to the caudal part of the descending nucleus, might, on account of its close contact with this, be considered as part of it, and probably has by some authors been interpreted in this way. However, following lesions of the eighth nerve, terminal degeneration is not found in the zone *x* (Glees method, unpublished observations), while the descending nucleus is full of degenerating particles. Nor does the zone belong to the external cuneate nucleus, since lesions of the dorsal funiculi do not produce degeneration in it (Pompeiano & Brodal, 1957 *b*) while degeneration is abundant in the external cuneate nucleus. On the other hand, the zone *x* receives spinal afferents ascending in the lateral funiculus of

the cord (presumably collaterals of the dorsal spino-cerebellar tract). These findings on the afferents to this zone make it appear likely that our zone *x* represents a particular 'nucleus', even if its efferent connexions appear to be similar to those of the adjoining regions of the descending vestibular nucleus, since it sends fibres to the 'vestibular' areas of the cerebellum (Brodal & Torvik, 1957) and to higher levels of the brain stem (Brodal & Pompeiano, 1957). The fact that the external cuneate nucleus projects on to other regions of the cerebellum (Brodal, 1941) than the zone *x* furnishes additional evidence that this zone is not related to the external cuneate nucleus.

We have not been able to locate specific references to this zone *x* in the literature. It is interesting to notice, however, that it appears to be present also in the rabbit. From Pl. VII in Meessen & Olszewski's (1949) atlas it is seen that the lateralmost part of the area outlined as the *N.Rd.* VIII (descending nucleus) has smaller and less densely packed cells than the medial part. (Maybe the zone is present also on Pl. VI.) It is possible that the zone *x* is what has by some authors been referred to as the nucleus (proprius) corporis restiformis. Frequently, cell strands can be followed laterally from this zone into the area of the restiform body, which is also attached to the lateral part of the zone rostrally. Much confusion exists in the literature with regard to the so-called nucleus corporis restiformis (which sometimes has been confused even with the external cuneate nucleus). It is considered to be beyond the scope of the present paper to discuss this subject further.

The *small-celled group y*, lateral to the caudal part of the lateral vestibular nucleus, is difficult to evaluate. It is drawn but not labelled by Winkler & Potter (1914, their Pl. XXV), and it has been noticed by Fuse (1912) who shows it in his figure 27, corresponding precisely to our findings. Fuse considers this cell group to be related to the dentate nucleus, with which, as mentioned above, it is connected. It is not possible to decide whether it may correspond to what Cajal called the nucleus cerebello-acusticus (1896, p. 66). The group Dtθ on Pl. X in Meessen & Olszewski's (1949) atlas, according to its position, may be our group *y* in the rabbit, but if so, its cytoarchitecture appears to be somewhat different from that in the cat. (Certainly their group Dtθ does not belong to the nucleus of Deiters, however.) Contrary to Fuse (1912) we have not found convincing changes in this group following lesions of the cerebellum (Brodal & Torvik, 1957). Nor have we observed altered cells in it following lesions of the upper brain stem (Brodal & Pompeiano, 1957) or of the spinal cord (Pompeiano & Brodal, 1957*a*). On the whole it appears probable that our group *y* does not form part of the vestibular complex.

A nucleus *supra-vestibularis* has been described by some authors (for example Olszewski & Baxter, 1954, in man). We are inclined to believe that the group *Sv* (see Text-figs. 1, 2) might correspond to the supra-vestibular nucleus in man, since its topography and cytology appear to be similar. We have not been able to trace primary vestibular fibres to this group.

The small *cell group z*, situated immediately rostral to the rostral end of the nucleus gracilis is difficult to distinguish from the latter in Nissl-stained sections. It was only when studying horizontal silver-impregnated sections (see Text-fig. 3) that we became aware of the individuality of this small group. Like our group *x* the cell group *z* appears to be a particular nucleus. We have not been able to trace primary vestibular fibres to it (unpublished observations), and it thus does not appear to

belong to the vestibular nuclear complex. Unlike the adjoining part of the descending nucleus, it does not send fibres to the cerebellum (Brodal & Torvik, 1957). It receives fibres from the spinal cord (Pompeiano & Brodal, 1957*b*). Since these fibres ascend in the lateral funiculus the group *z* should probably not be considered a particular part of the nucleus gracilis.*

The small cell groups discussed here have been dealt with in some details, because if they are not kept apart from the vestibular nuclei proper, erroneous conclusions of experimental anatomical and physiological studies are apt to occur.

General comments. While our subdivision of the vestibular complex is based primarily on studies of the cytoarchitecture of the nuclei, experimental data on afferent and efferent fibre connexions have made it possible to clarify doubts as to the delimitation of particular cell groups. Such information on the whole supports the delimitations arrived at from studies of the cytoarchitecture, for example, with regard to the nucleus of Deiters and our zone *x*. On other points, however, the fibre connexions furnish evidence that a nucleus which has so far been considered a particular unit might deserve a finer subdivision into minor parts, as is the case with the descending and medial vestibular nuclei. Further studies of the fibre connexions of the vestibular complex are needed to clarify the questions. It will be important also to have more detailed information of the type and course of dendrites and collaterals of axons of the cells of the vestibular complex, obtainable only by means of the Golgi method, not least in order to make clear the possibilities of interaction between the various vestibular nuclei and the relations between these and the reticular formation of the brain stem. Even if some data of this kind are known, chiefly thanks to the studies of Cajal (1896, 1909) and Lorente de Nó (1924, 1931, 1933), it is essential that such features as well as the fibre connexions are studied with particular reference to the topographical subdivisions which can be distinguished within the vestibular nuclear complex.

In physiological studies of the vestibular nuclei it is equally important to pay due respect to topographical features in their organization. The disregard of this requirement by many physiologists has certainly hampered progress in our knowledge of the functional organization of the vestibular nuclei. The anatomical data known so far make it appear likely that these nuclei are mutually rather dissimilar also in a functional respect.

SUMMARY

The cytology and topography of the vestibular nuclei have been studied in serial Nissl-stained transverse sections through the brain stem of young cats. The subdivision of the nuclear complex arrived at from cytoarchitectonic studies is considered in the light of experimental studies of the fibre connexions of the vestibular nuclei, which have given important clues as to a rational subdivision. The subdivision employed is shown in Text-figs. 1–3, and in general agrees with that of most previous students.

The term *lateral vestibular nucleus of Deiters* should be restricted to that part of the vestibular complex which harbours the characteristic giant cells. The nucleus

* It is possible that our group *z* is represented by the dorsalmost part of what is labelled '*Gr.*+*Cu.m*' in Pl. IV in Meessen & Olszewski's (1949) atlas. In the plates of Winkler & Potter's (1914) atlas it is not possible to define a corresponding cell group.

contains also many smaller cells, some of which form a particular group *l*. The cells of this, as well as the other cells of the nucleus, send their fibres to the cord in the vestibulo-spinal tract in a somatotopically arranged pattern.

The *superior vestibular nucleus* is fairly easily outlined. No reasons for subdividing this nucleus further have been found.

The *medial vestibular nucleus*, in spite of its containing some large cells, should not be considered as belonging to the nucleus of Deiters, as has been done by some authors. It should also be clearly kept apart from the *descending vestibular nucleus*, which is characterized by the presence of longitudinally running fibre bundles. Within the descending nucleus a more compact group of medium-sized cells, here called group *f*, is present in its ventro-lateral caudal part. The connexions of this group are discussed.

The *interstitial nucleus of the vestibular nerve* of Cajal appears to be an aberrant part of the nucleus of Deiters.

Some smaller cell groups, topographically related to the vestibular nuclei, but not belonging to them, are described.

The findings made are compared with those reported by other authors. Points of disagreement are discussed and the importance of detailed references to the topography in anatomical and physiological studies is stressed.

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EXPLANATION OF PLATE

Photomicrographs (×125) of transverse Thionine stained sections (Figs. 1–8) through the vestibular nuclei of the cat to show the characteristic architecture in the various nuclei. Fig. 9, a photomicrograph of a transverse Weil stained section (×70).

Fig. 1. From the rostral part of the lateral vestibular nucleus (cp. drawing 7 in Text-fig. 1). Giant cells interspersed with many medium-sized and small cells.

Fig. 2. From the caudal part of the lateral vestibular nucleus (cp. drawing 11 in Text-fig. 1). Chiefly giant cells, most of them larger than those present in the rostral part of the nucleus.

Fig. 3. The group '*l*' of medium-sized cells (within the broken line) on the lateral aspect of the lateral vestibular nucleus (cp. drawings 9–10 in Text-figs. 1 and 2). Lateral to the nucleus the fibres of the restiform body (*C.r.*) are seen.

Fig. 4. From the superior vestibular nucleus (cp. drawing 7 in Text-fig. 1).

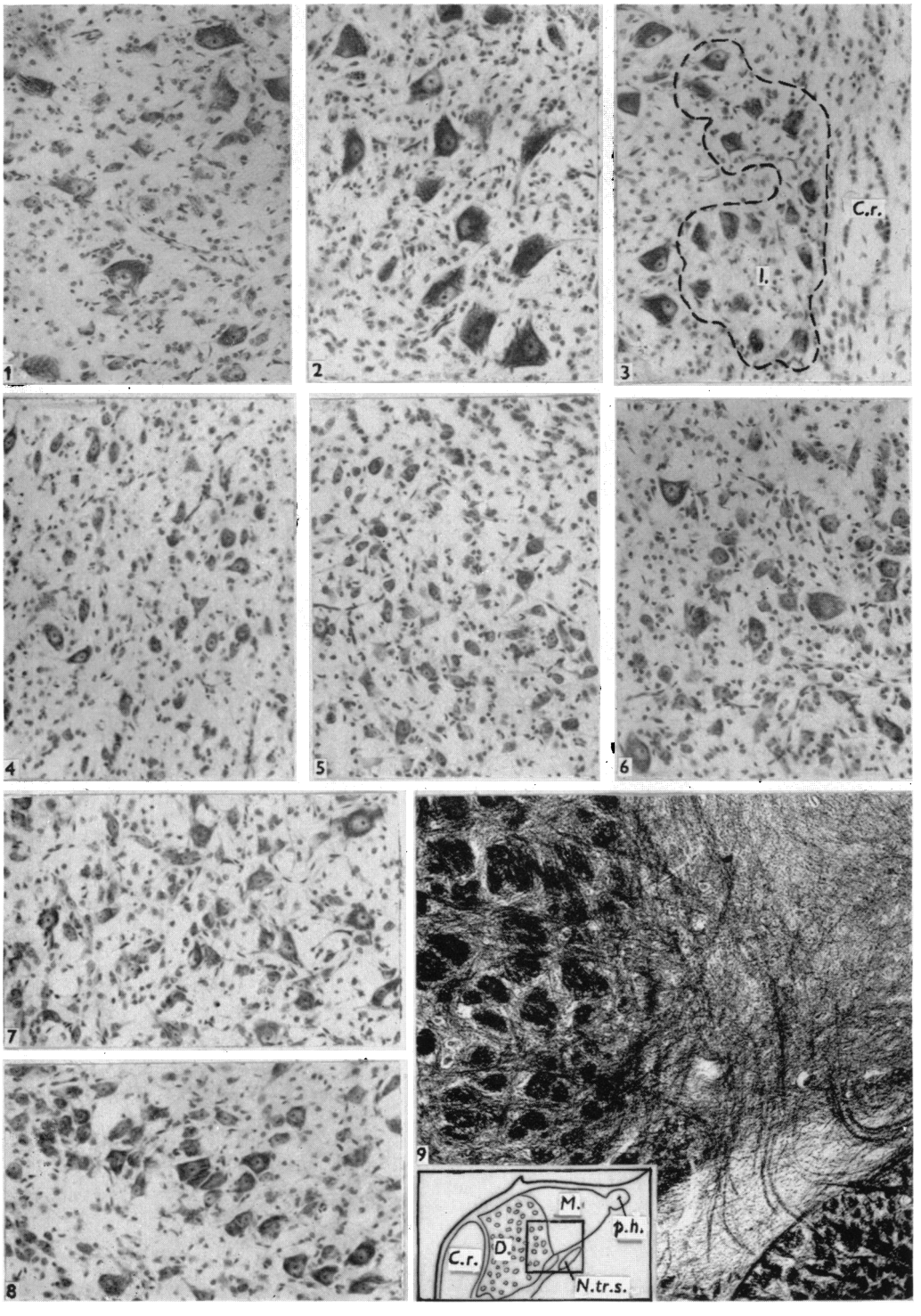
Fig. 5. From the rostral part of the medial vestibular nucleus (cp. drawings 7–9 in Text-fig. 1).

Fig. 6. From the middle levels of the medial vestibular nucleus (cp. drawings 11–13 in Text-fig. 1). Some large cells in addition to cell types present in the rest of the nucleus.

Fig. 7. From the descending vestibular nucleus (cp. drawings 11–15 in Text-fig. 1). Cells of different sizes, rather loosely arranged between the descending vestibular root fibres. One of the scattered larger cells is seen.

Fig. 8. Part of the fairly compact group, labelled '*f*', ventro-laterally in the caudal part of the descending nucleus (cp. drawings 16–21 in Text-fig. 1).

Fig. 9. In Weil stained sections the difference between the medial and descending nucleus is conspicuous. Abbreviations as in Text-fig. 1. Section from an adult cat (×70).



BRODAL AND POMPEIANO—VESTIBULAR NUCLEI

(*Facing p.* 454)