UCLEI AND THEIR
OMY AND FUNCTIONAL CORRELATIONS

BRODAL
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The Vestibular Nuclei and their Connections
Anatomy and Functional Correlations

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With 49 Illustrations (including 7 Plates)

Published for
THE WILLIAM RAMSAY HENDERSON TRUST
BY
OLIVER AND BOYD
EDINBURGH: TWEEDDALE COURT
LONDON: 39A WELBECK STREET, W.1.
1962

FIRST PUBLISHED 1962

PRINTED IN GREAT BRITAIN FOR OLIVER AND BOYD LIMITED, EDINBURGH AND LONDON
BY ROBERT CUNNINGHAM AND SONS LIMITED, ALVA

ACKNOWLEDGMENTS

THE authors are indebted to a number of persons for assistance of various kinds in the preparation of this text.

Our sincere thanks are due to several colleagues for informing us of results of studies not yet published and for permission to refer to their work: Dr D. Bowsher, Liverpool; Dr R. R. Gacek, Bethesda, U.S.A.; Drs Mehler, Feferman and Nauta, Washington, D.C.; Dr J. Szentágothai, Pecs, Hungary. For permission to reproduce illustrations from their papers we are indebted to Lord Adrian, London, Dr Gacek, Bethesda, Dr Gernandt, Bethesda, Drs Ruwaldt and Snider, Chicago, and Dr Wersäll, Stockholm.

Professor G. J. Romanes, Edinburgh, has read the manuscript and revised the English. For this and for supervision of the editorial work we would like to express our gratitude.

The late Miss S. Mörch and her successor Mrs I. Eggum have made the original drawings, Mr E. Risnes has been responsible for the original photomicrographs, and Miss O. Gorset has taken care of typewriting and secretarial work connected with the preparation of the manuscript. Our sincere thanks are due to these workers in the Anatomical Institute, University of Oslo, for their expert assistance, and to Mrs K. Nicotra and Miss M. Orsini in the Physiological Institute, University of Pisa, who have taken care of the typewriting and preparation of the illustrations, respectively, for the physiological section of this monograph.

Acknowledgment is made to the Editors of the following journals for permission to reproduce illustrations from our own previous papers and those of others: *Acta Morph. Neerl.-Scand., Acta oto-laryng. Stockh., Arch. ital. Biol., Arch. Sci. biol., Exp. Neurol., J. Anat.* (Lond.), *J. Physiol.* (Lond.), *J. Comp. Neurol., Arch. Psychiat. Z. ges. Neurol.* and to the Editors of *Neural Mechanisms of the Auditory and Vestibular Systems.*

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Oslo and Pisa, June 1960.

CONTENTS

PAGE

Introduction 1

Anatomy of the vestibular nuclei 3

1. Methods employed in anatomical studies of the vestibular nuclei 3
2. Normal topography and cytoarchitecture of the vestibular nuclei 6
3. Primary vestibular fibres with notes on the vestibular receptors. The cochleovestibular anastomosis 16
4. Efferent connections of the vestibular nuclei 27
   a. Vestibulospinal projections 27
   b. Vestibulocerebellar connections 37
   c. Fibres ascending from the vestibular nuclei to "higher" levels of the brain 42
   d. Other efferent connections of the vestibular nuclei. Centrifugal fibres in the vestibular nerve 51
5. Afferent connections of the vestibular nuclei 54
   a. Spinovestibular connections 55
   b. Afferents to the vestibular nuclei from "higher" levels 59
   c. Cerebellovestibular connections 64
      α. Afferents from the cerebellar cortex 64
      β. Afferents from the intracerebellar nuclei 72
   d. Other afferent connections to the vestibular nuclei 85
6. Intrinsic organization of the vestibular nuclei 86
7. Synopsis of anatomical data on the vestibular nuclei 90

Some physiological data on the vestibular nuclei and anatomico-physiological correlations 100

1. The vestibular receptors 100
2. Labyrinthine influences on the vestibular nuclei 103
3. Efferent connections 109
   a. Vestibular influences on the spinal cord 109
   b. Vestibular control of ocular movements: nystagmus 126
   c. Vestibular influences on the cerebral cortex 129
   d. Vestibular influences on the cerebellum 134
   e. Vestibular influences on vegetative functions 138

4. Afferent connections 138
a. Spinal influences on the vestibular nuclei 138
b. Descending influences on the vestibular nuclei 145
c. Cerebellar influences on the vestibular nuclei 149

Concluding remarks 168

References 171

Subject index 191

INTRODUCTION

THE authors would like to express their gratitude to the William Ramsay Henderson Trust and particularly to Professor G. J. Romanes, the Chairman of the trust, for providing this opportunity to bring together in a synthetic fashion the more important data now available on the vestibular nuclei. The rapid advances in recent times in the field of neurological sciences—as in other branches of medicine—have made the need for up-to-date surveys of particular subjects more urgent than ever before. It is our hope that the present little monograph may be of use to investigators working on the same and related items. The essence of this book was presented as three lectures in Edinburgh, on June 7th, 8th and 9th, 1960.

The following presentation is concerned primarily with investigations performed by the authors and their collaborators, with due consideration of the relevant literature. However, no complete historical review of the many questions dealt with is attempted, and the references in the text are not complete, since more extensive lists can be found in the original publications.

The investigations on the vestibular nuclei which are reported were originally prompted by anatomical studies on the fibre connections of the cerebellum performed in the Anatomical Institute, University of Oslo, and by physiological investigations into the cerebellum undertaken in the Physiological Institute, University of Pisa. With both approaches it had become evident by 1955 that there were still important gaps in our knowledge of the vestibular nuclei, which had for some time received relatively little attention from research workers. In particular it was felt in both laboratories that the importance of the relations between the cerebellum and the reticular formation of the brain stem might have been somewhat overemphasized to the neglect of the cerebellovestibular relations. A fruitful exchange of ideas, as well as the planning and in part the execution of a joint research programme was made possible during Dr Pompeiano's stay at the Anatomical Institute in Oslo on a Rockefeller Fellowship. Some of the studies to be reported here of partial problems related to the vestibular nuclei and their connections have been performed by the authors, others are the outcome of collaboration of one or more of us with the following colleagues: Professor Jan Jansen and Dr Ansgar Torvik, Anatomical Institute, University of Oslo; Dr D. Bowsher, Department of Anatomy, University of Liverpool; Professor G. Moruzzi and Dr C. Batini, Physiological Institute, University of Pisa.

As will be seen, our studies of the vestibular nuclei have revealed some details of their anatomical organization which are of interest for functional interpretations; but in spite of recent studies by means of microelectrodes and other physiological methods it is not yet possible to achieve a complete correlation between the anatomical and the physiological observations. Nevertheless, even if many conclusions of necessity will be provisional, we have found it useful to devote some space to an attempt to correlate the findings from the two spheres of research. A brief survey of some major points treated in the present monograph has been given previously (Brodal, 1960). Clinical aspects will not be considered except for occasional references to some relevant data.

ANATOMY OF THE VESTIBULAR NUCLEI

As mentioned in the introduction, the following account of the anatomy of the vestibular nuclei will be devoted to a large extent to the presentation of findings made by the authors and their collaborators. Most of our personal investigations have been experimental studies of afferent and efferent fibre connections of the vestibular nuclei. In order to facilitate the presentation of our experimental findings and in order to avoid repetition it is appropriate to start with a brief consideration of the experimental methods employed, and to discuss the criteria used in the evaluation of degenerative changes in nerve cells and fibres. Some comments on the methods used in the study of the normal anatomy are also appropriate.

1. Methods employed in Anatomical Studies of the Vestibular Nuclei

Several methods may be used for the study of the anatomy of the vestibular nuclei. It will suffice here to draw attention to some points of relevance for the following presentation.

In order to achieve a complete picture of the fine anatomy of the vestibular nuclei three principal methods may be used. In the first place the classical procedure of *mapping the cytoarchitecture in Nissl-stained serial sections* gives information of the types and distribution of the cells. The method usually permits the drawing of boundaries between aggregations of nerve cells and the sub-division of a nuclear complex into minor territories if such exist. However, there is little doubt that subdivision on this basis may easily be overdone, and it is probably safer, when in doubt, to be conservative, especially since individual variations are common. The proof that a subdivision of a nuclear complex is justified is that the minor territories distinguished on a cytoarchitectonic basis are shown to differ also in other respects, such as the pattern and arrangement of their intrinsic fibres, their afferent or efferent connections, the patterns of dendrites, or their cytochemistry.

As a supplement to the cytoarchitectonic analysis investigations with the *Golgi method* are valuable, since these may demonstrate differences with regard to the patterns of dendrites, axons and collaterals of the cells in various groups, as well as differing patterns in the termination of afferent fibres. As a relevant example of what can be achieved in this way, the studies on the inferior olive by M. and A. Scheibel (1955) and Scheibel, Scheibel, Walberg and Brodal

(1956) may be mentioned. The Golgi method may also give information on synaptic patterns.

To some extent the latter aspect can be studied in sections treated with one of the many *silver impregnation methods*, since most of these bring out the terminal boutons, although usually only a small proportion of those actually present will be impregnated. An analysis of their sizes and types (on the soma and/or processes of nerve cells) may be of value for functional interpretations and, furthermore, is essential for the correct evaluation of the picture of degenerating boutons in a nucleus when its afferent fibres are interrupted. Finally silver impregnation methods are useful for determining the general pattern of the nerve fibres within a nucleus. In some instances such preparations give more convincing evidence of dissimilarity between subdivisions than Nissl-stained sections. A relevant example is the difference between the medial and the descending vestibular nuclei (Pl. V, Fig. 24).

Most *studies of the efferent fibre connections* of the vestibular nuclei have in the past been made by placing lesions in them and following in Marchi preparations the fibres degenerating as a consequence of the lesions. However, by this approach fibres passing or traversing the nucleus in question are almost always interrupted, thus making definite conclusions concerning the true origin of the fibres impossible. This difficulty is a major one in the vestibular nuclei, and consequently many of the observations on their efferent connections made in this way must be evaluated with caution. The only safe procedure for determining the exact origin of fibres from a nuclear complex such as the vestibular nuclei, is to study the *occurrence of retrograde changes* in its nerve cells following lesions which transect the efferent fibres. However, it is essential to record as positive only cells showing unequivocal changes, namely (1) tigrolysis of an intensity which produces a milky, almost homogenous appearance of the cytoplasm, and (2) a displacement of the nucleus to the periphery of the cell (see Figs. 16-23 on Pls. IV and V). If cells of this type occur in a nucleus or cell group following transection of its efferent fibres, there will usually also be cells which show lesser changes, only slight degrees of tigrolysis and moderate displacement of the nucleus. Although it is likely that such cells have suffered transection of their axon, changes of this type are difficult to evaluate since there are considerable variations between normal cells in their content of Nissl-granules and the position of the nucleus. It is safest, therefore, not to consider such cells as pathological, even if in this way the number of cells recorded as pathological will necessarily represent only a proportion of those which have actually suffered transection of their axon.

Some authors have interpreted dark and shrunken cells as showing retrograde changes, when they occur in a nucleus after transection of its efferent fibres. Although it cannot be denied that under certain circumstances and in

certain nuclei a cell whose axon has been cut may react by shrinkage (see Brodal, 1939), this is not a typical feature. Cells of this type are not infrequently met with in normal material, and there is reason to believe that they usually represent artefacts (as most recently discussed and documented by Cammermeyer, 1960). Conclusions concerning the origin of efferent fibres based on the presence of such cells are, therefore, to say the least, not convincing and should be avoided. If longer survival periods are used, in order to show the loss of cells in a nucleus consequent on transection of its efferent fibres, it is necessary that the cell loss be very marked if interpretations based on this method are to be reliable.

In our experience it has proved useful to employ young animals (kittens aged 6-15, occasionally up to 21, days) for the study of retrograde changes. The animals are killed 4-10 days after the lesion. This modified Gudden method (Brodal, 1940*b*) has been used in the studies on the efferent connections of the vestibular nuclei to be dealt with here. In such young animals the retrograde changes appear earlier and are more marked than in adult animals (see Brodal, 1939). Furthermore, it appears that all cells affected disintegrate acutely and disappear completely within a few days in very young animals, while in adults many cells affected by retrograde changes fall victim to a slow atrophy after the initial acute stage.[1]

The presence of cells with typical retrograde changes in a nucleus may be considered proof that the axons of the affected cells have been transected. However, it is important to realize that the absence of such changes in a nucleus following lesions does not permit the conclusion that cells of the nucleus do not give rise to fibres passing through or into the damaged part. The reason for this negative reaction is not always clear, but in some instances there is evidence that preserved collaterals may protect the cells against the consequences of axonal damage. Examples of this have been noted in our studies on the efferent fibres of the vestibular nuclei to be described below (p. 27ff). In other instances, however, a cell giving off a bifurcating axon appears to react equally well to transection of either of the two axonal branches. This seems to be the case with cells in the lateral vestibular nucleus (p. 46) and is especially marked in some cells of the reticular formation (see Brodal, 1957).

In studies of the *afferent connections to the vestibular nuclei* to be reported here, silver impregnation methods have been used almost exclusively. In all cases sections have been prepared according to the Glees (1946) modification of the Bielschowsky method. In studies on the primary vestibular fibres and

[1] When the modified Gudden method is used it is, however, essential to employ very young animals, since the "newborn" type of reaction changes to the "adult" type shortly after birth. This transition appears to take place rather rapidly and although the age at which it occurs is not the same for all nuclei in the central nervous system, the critical phase is seldom later than the end of the second week.

the fibres from the cerebellum to the vestibular nuclei, alternate sections have been impregnated according to the modification of the original method of Nauta and Gygax (1954) described by Nauta (1957). Since a discussion of the relative merits of the two methods has recently been published elsewhere (Bowsher, Brodal and Walberg, 1960) it will suffice to mention a few points. The two methods give concordant results, but on some points they supplement each other since the Nauta method gives the best demonstration of the course of degenerating fibres and their overall distribution, while the Glees method is superior in showing details of synaptic contacts. As will be shown, it has been possible by the combined use of the two methods to obtain valuable information on the minute organization of the vestibular nuclei.

In our descriptions of silver impregnated material the expression *"terminal degeneration"* will be used for degenerative changes occurring in terminal boutons and in the finest terminal fibres leading to them. On account of the difficulties in identifying a silver impregnated particle as a degenerating bouton, no structure has been interpreted as such unless it is seen to be connected to an unequivocally degenerating fibre of the finest type. (For a more complete discussion, see Rossi and Brodal, 1956; Bowsher, Brodal and Walberg, 1960.) The term *"preterminal degeneration"* will be used for the finest degenerating particles visible in Nauta sections. It is, however, likely that in some instances such products of degeneration may actually represent true terminal structures as discussed by Bowsher, Brodal and Walberg (1960).

All our studies have been made on the cat, which has also been used by most other workers on the anatomy and physiology of the vestibular nuclei. Accordingly, the following account will deal chiefly with findings in the cat, occasional reference only being made to observations in other species. It appears that in general the principles of organization of these nuclei are the same in most mammalian species including man.

2. Normal Topography and Cytoarchitecture of the Vestibular Nuclei

When we started our experimental studies on the fibre connections of the vestibular nuclei, it soon became obvious that it would be essential to undertake, as a first step, a close analysis of the normal anatomy of this nuclear complex. Although several authors have described the vestibular nuclei, there are many discrepancies both in nomenclature and in the topographical descriptions of the various nuclei.

The divergent views on the subdivision of the vestibular nuclear complex seem to be due largely to the fact that only normal material has served as a basis for the analysis. Our experimental investigations were undertaken simultaneously with our studies of the normal anatomy and this made it possible

to correlate the two sets of data. Thus on many points, differences with regard to fibre connections provide evidence that boundaries drawn between particular cell groups on the basis of their cytoarchitecture are significant. Accordingly, the subdivision employed in our maps of the vestibular nuclei represents a synthesis of information obtained by various methods of study.

It would take too long to trace the historical development of our knowledge of the vestibular nuclei and to consider the various modes of subdivision employed (See Fuse, 1912). Most authors have subdivided the vestibular complex into four major nuclei, the superior, lateral, medial and descending (inferior) vestibular nuclei. Some have either described subdivisions of one or more of these, or distinguished additional small cell groups closely related to the four major nuclei. For a consideration of these questions and references to the literature the reader is referred to our original paper (Brodal and Pompeiano, 1957*a*).

As will be shown below (p. 17ff), there are within each of the four major vestibular nuclei regions which do not receive primary vestibular fibres. In spite of this, however, it seems for practical reasons to be advantageous to retain the current nomenclature, the more so since "vestibular" and "non-vestibular" parts of the various nuclei show common features with regard to other fibre connections, and also with regard to their architecture. In keeping with this view, some smaller cell groups, topographically closely related to the four principal vestibular nuclei, will be included in the vestibular complex, even if they do not receive primary vestibular fibres.

Text-figs. 1 and 2 show the vestibular complex as seen in a series of transverse Nissl-stained sections through the brain stem of young cats (Brodal and Pompeiano, 1957*a*). The drawings were made by means of a projection apparatus and subsequently carefully controlled under the microscope. Additional information of the normal anatomy of the vestibular nuclei was obtained from a series of fibre-stained preparations (methods of Weil, Bodian and Glees). Text-fig. 3 shows the appearance of the vestibular nuclei in horizontal silver impregnated sections.

Since the maps of Text-figs. 1-3 show the major points concerning the topography of the various nuclei and cell groups of the vestibular complex it will suffice here to mention some features only, and to direct attention to some details which appear to be important. Each nucleus will be considered separately.

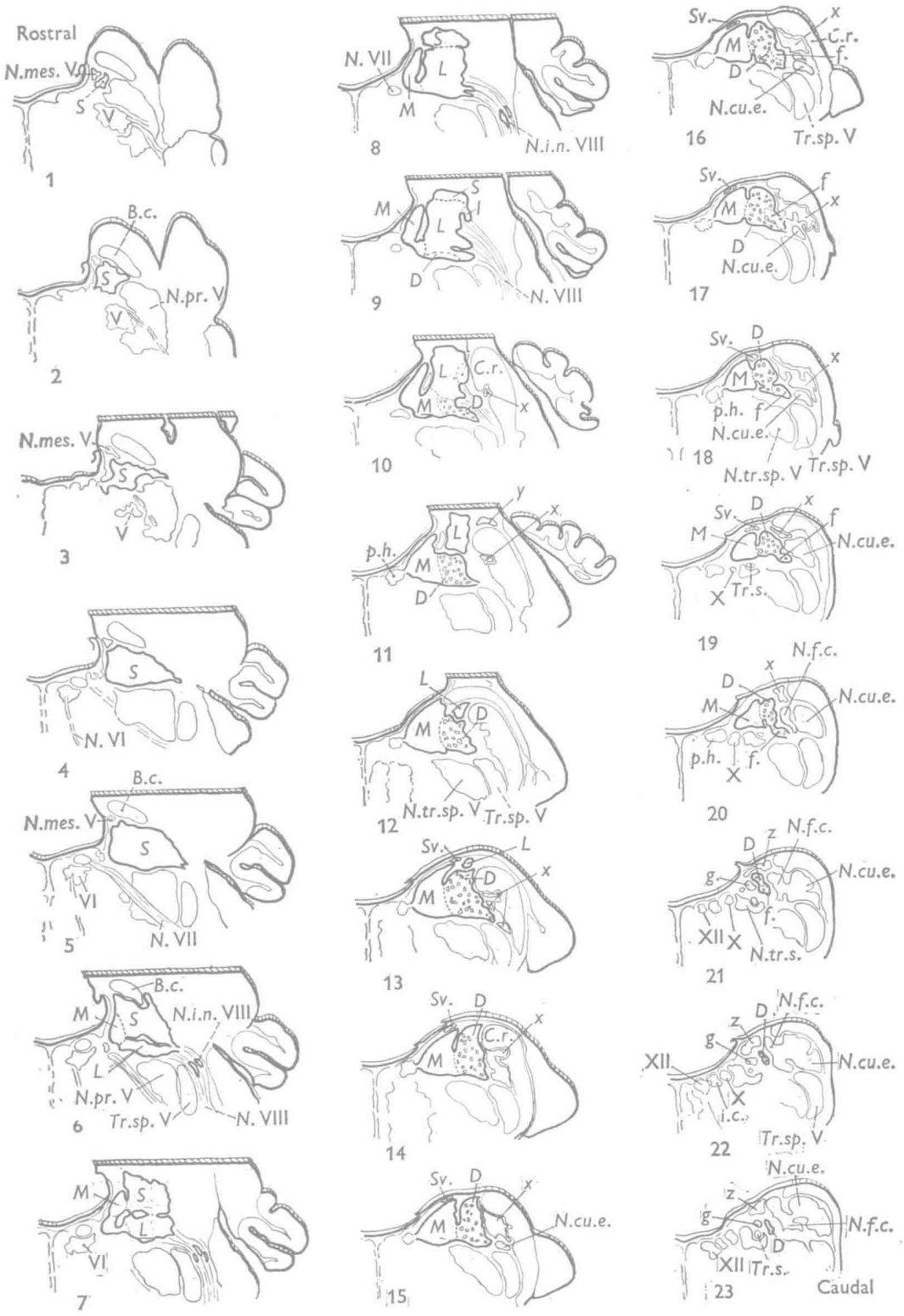
The *superior vestibular nucleus* is fairly easily outlined as a separate nucleus (except most rostrally), and our delimitation as shown in Text-figs. 1-3 corresponds to those made by most previous authors (Cajal, 1909, in the mouse; Meessen and Olszewski, 1949, in the rabbit; Winkler and Potter, 1914, in the cat; Sabin, 1897, Jacobsohn, 1909, Marburg, 1910, and Olszewski and Baxter, 1954, in man). Other names employed for it are the *angular nucleus* or the

Abbreviations employed in Text-figs.

B.c.: Superior cerebellar peduncle (Brachium conjunctivum).
Br.p.: Middle cerebellar peduncle. (Brachium pontis).
C.m.: Mammillary body.
C.r.: Inferior cerebellar peduncle (Corpus restiforme).
D.: Descending (inferior) vestibular nucleus.
Dt: Dentate nucleus.
f.: Cell group *f* in descending vestibular nucleus.
F.: Fastigial nucleus.
F.l.m.: Medial longitudinal fasciculus.
Flocc.: Flocculus.
g: Group rich in glia cells, caudal to the medial vestibular nucleus.
I: Nucleus interpositus.
i.c.: Nucleus intercalatus (Staderini).
I.c.p.: Inferior cerebellar peduncle.
L: Lateral vestibular nucleus (Deiters).
l: Small-celled lateral group of lateral vestibular nucleus.
L.: Left.
Lt: Left.
Lob. ant.: Anterior lobe.
L.p.m.: Paramedian lobule.
M: Medial (triangular or dorsal) vestibular nucleus.
MLF: Medial longitudinal fasciculus.
N.c.: Cochlear nuclei.
N.c.p.: Nucleus of the posterior commissure.
N.cu.e.: Accessory cuneate nucleus.
N.D.: Nucleus of Darkschewitsch.
N.dent.: Dentate nucleus.
N.E.-W.: Edinger-Westphal nucleus.
N.f.: Fastigial nucleus.
N.fast.: Fastigial nucleus.
N.f.c.: Cuneate nucleus.
N.f.g.: Gracile nucleus.
N.i.: Nucleus interpositus.
N.int.: Interstitial nucleus (Cajal).
N.i.n.VIII: Interstitial nucleus of vestibular nerve.
N.m.X: Dorsal motor (parasympathetic) nucleus of vagus.
N.m.d.X: Dorsal motor (parasympathetic) nucleus of vagus.
N.mes.V: Mesencephalic nucleus of N.V.
N.n.III: Nucleus of third nerve.
N.pr.V: Principal sensory nucleus of N.V.
N.pr.n.V: Principal sensory nucleus of N.V.
N.p.s.: Parasolitary nucleus.
N.r.: Red nucleus.
N.tr.s.: Nucleus of solitary tract.
N.tr.sp.V: Nucleus of spinal tract of N.V.
N.tr.sp.n.V: Nucleus of spinal tract of N.V.
N.III, V, VI, VII, VIII: Cranial nerves III, V, VI, VII and VIII.
Ol.i.: Inferior olive.
Ol.s.: Superior olive.
P.fl.: Paraflocculus.
p.h.: Nucleus praepositus hypoglossi.
R.: Right.
Rt.: Right.
S: Superior vestibular nucleus (Bechterew).
S.n.: Substantia nigra.
Sv.: Cell group probably representing the nucleus supravestibularis.
Tr.s.: Solitary tract.
Tr.sp.V: Spinal tract of N.V.
Tr.sp.n.V: Spinal tract of N.V.
Tr.sp.c.d.: Posterior (dorsal) spinocerebellar tract.
III, IV, V, VI, VII, XII: Cranial motor nerve nuclei.
X: Dorsal motor (parasympathetic) nucleus of vagus.
x: Small-celled group *x*, lateral to the descending vestibular nucleus.
y: Small-celled group, lateral to the lateral vestibular nucleus (Deiters).
z: Cell group dorsal to the caudal part of the descending vestibular nucleus.

TEXT-FIGURE 1

A series of drawings of equally spaced transverse sections through the vestibular complex of the cat, stained with thionine. The outlines of the vestibular nuclei are shown as heavy lines. From Brodal and Pompeiano, 1957*a*. *J. Anat. Lond.*, **91**, 438.


Rostral
N.mes. V
S
V
1
B.c.
S
N.pr. V
V
2
N.mes. V
S
V
3
S
N. VI
4
B.c.
N.mes. V
S
VI
N. VII
5
B.c.
M
S
N.i.n. VIII
L
N.pr. V
Tr.sp. V
N. VIII
6
M
S
L
VI
7
N. VII
L
M
N.i.n. VIII
8
S
M
L
D
N. VIII
9
L
C.r.
M
D
x
10
y
x
p.h.
L
M
D
11
L
M
D
N.tr.sp. V
Tr.sp. V
12
Sv.
L
D
x
M
13
Sv.
D
x
C.r.
M
14
Sv.
D
x
M
N.cu.e.
15
Sv.
x
C.r.
M
D
f.
N.cu.e.
Tr.sp. V
16
Sv.
f
x
M
D
N.cu.e.
17
Sv.
D
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M
p.h.
f
N.cu.e.
N.tr.sp. V
Tr.sp. V
18
Sv.
D
x
f
M
N.cu.e.
X
Tr.s.
19
N.f.c.
x
D
N.cu.e.
M
p.h.
X
f.
20
N.f.c.
D
z
g
N.cu.e.
f.
XII
X
N.tr.s.
21
N.f.c.
D
z
g
XII
N.cu.e.
X
i.c.
Tr.sp. V
22
N.cu.e.
z
g
N.f.c.
D
XII
Tr.s.
Caudal
23

nucleus of Bechterew. Along its rostrocaudal extent the superior nucleus is capped dorsally by the superior cerebellar peduncle (drawings 1-6 in Text-fig. 1), and the mesencephalic trigeminal nucleus is situated dorsomedial to its rostral two-thirds. Ventrally the border adjacent to the principal sensory trigeminal nucleus is indistinct, while the border against the lateral vestibular nucleus, ventral to the caudal half of the superior nucleus, is fairly distinct on account of cytoarchitectonic differences.

In Nissl-stained sections the superior vestibular nucleus is distinguished by being composed of rather loosely scattered cells, chiefly medium and small in size (Pl. I, Fig. 4). The former are either multipolar, round or spindle- to pear-shaped with rather fine Nissl-granules. The smallest cells appear rounded, stellate or spindle-shaped and in the centre of the nucleus there are some clusters of somewhat larger multipolar cells (Text-fig. 2, drawing 5). Fibre bundles course from dorsomedial to ventrolateral through the superior nucleus and the cells tend to be arranged in clusters oriented in the same direction.

TEXT-FIGURE 2

A map showing the topography and cytoarchitecture of the vestibular nuclei in the cat as seen in transverse sections. The numbers of the sections correspond to those in Text-fig. 1. The small circles in the descending nucleus represent the fibre bundles of the spinal (descending) root of the vestibular nerve. For details see text. From Brodal and Pompeiano, 1957*a*. *J. Anat. Lond.*, **91**, 438.

See page 8 for key to abbreviations

These fibre bundles are easily seen in suitably stained preparations of normal material and contain some primary vestibular afferents (see section 29 in Text-fig. 4).

We have found no reason to subdivide the superior vestibular nucleus and do not distinguish special parts of it, as some previous authors have done (see Brodal and Pompeiano, 1957*a*, p. 448, for references). Cells in all parts of the nucleus give off fibres ascending in the brain stem (see p. 43). The concentration of larger cells in the central regions of the nucleus is of some interest in view of our demonstration that primary vestibular fibres terminate largely in this part of the nucleus (see p. 17) while the afferents from the nucleus fastigii are distributed chiefly to the peripheral parts of the superior vestibular nucleus (see p. 76).

The *lateral vestibular nucleus or the nucleus of Deiters* was defined by von Monakow (1883, and later) as the part of the vestibular nuclear complex in