Anat. Embryol. 149, 29—46 (1976)

The Vestibular Nuclei in the Domestic Hen (*Gallus domesticus*)

I. Normal Anatomy

Jan Egil Wold

Anatomical Institute, University of Oslo, Oslo, Norway

Received November 14, 1975

Summary. The topography and the cyto- and fiber architecture of the vestibular nuclear complex in the domestic hen are described as seen in transverse and horizontal thionine and myelin impregnated sections. The subdivision of the nuclear complex arrived at from these studies is discussed in the light of some experimental studies of the fiber connections of the vestibular nuclei in birds and compared with the well known organization of the vestibular nuclei in mammals.

Six main vestibular nuclei are identified, the superior nucleus, the nucleus Deiters ventralis, the nucleus Deiters dorsalis, the tangential nucleus, the medial nucleus and the descending nucleus. In addition two cell groups (the cell group A and B) lying in close relation to the other nuclei are described and considered as parts of the vestibular complex. The map of the vestibular complex arrived at is largely in agreement with the maps presented by most earlier authors on other species. Furthermore, it appears that the organization of the vestibular complex in birds is more similar to the organization of the complex in mammals than hitherto recognized.

Key words: Vestibular nuclei — Birds.

Introduction

On the basis of studies of cell and myelin impregnated sections, the vestibular nuclear complex in birds has in the past been divided into different nuclear masses in a variety of species (for references, see Discussion). There has been considerable disagreement among authors concerning the delimitations and the nomenclature of the nuclei.

The present study was undertaken simultaneously with experimental studies of the fiber connections of the nuclei (Wold, 1975), since a study of fiber connections requires a detailed knowledge of the normal anatomy of the region under study. On the other hand, knowledge of the fiber connections of the vestibular nuclear complex permits a more rational subdivision of the nuclear complex than can be made on the basis of cell and myelin impregnated sections only.

The vestibular nuclear complex in birds is closely associated with the cerebellar nuclei and is differentiated in several nuclei. According to most authors, however, the complex shows considerable differences in the degree of differentiation among the various species of birds. Brandis (1894) and Craigie (1928, 1930) were inclined to relate the differences among species to their different abilities to fly. Bartels (1925) divided the avian species into song-birds and non-song-birds, and was of the opinion that the former show a higher degree of differentiation into particular nuclei than do the latter. Renggli (1967) classified the va-

rious species of birds into three groups according to the varying development of the cerebellar and vestibular nuclear complexes as studied in cell and myelin impregnated sections. The bird described in the present study (the domestic hen) is represented in Renggli's group two, having a moderately well differentiated vestibular complex. The findings made in the present study should, therefore, be representative for a large number of avian species. It should be noted that the nomenclature used in the present study follows the nomenclature most commonly used in mammals (Brodal and Pompeiano, 1957; Sadjadpour and Brodal, 1968) and used by Karten and Hodos (1967) in the pigeon (except for the Deiters' nuclear complex). This however, does not necessarily imply that nuclei given the same name in the two classes of vertebrates are homologous and have the same function or corresponding efferent and afferent fiber connections. A more detailed review of the relevant literature will be given in the discussion.

Material and Methods

Brains from chickens and hens have been used in the present study. The animals were killed by an overdose of sodium pentobarbital (Nembutal) intraperitoneally, perfused through the heart with physiological saline, followed by 10% formalin solution. The brain were then dissected free and immersed into 70% or directly into 96% alcohol. The brains were fixed in 96% alcohol for one week or more.

The brain were then embedded in paraffin, either in toto or only the part containing the vestibular complex. Each block was cut serially at 15 or 20 μ, either in the transverse, sagittal or horizontal plane. All sections were mounted and stained with either thionine for staining of the cells or with the Woelcke modification of the Weigert method (Woelcke, 1942) for staining of myelin sheaths. The Woelcke sections were counterstained with cresyl-violet. With this method, developed by E. Pettersen, chief technician in the Anatomical Institute, both cells (red-violet) and fibers (dark-blue) can be demonstrated.

The sections were drawn under a projecting apparatus, and the findings made under the microscope were entered in the drawings. The drawings reproduced in Figs. 1, 2 and 3 contain information from both Nissl and Woelcke-Pettersen sections.

Results

In the following the vestibular nuclear complex in the domestic hen will be described with reference to the drawings in Fig. 1, 2 and 3, showing the outlines of the nuclei in transverse and horizontal sections.

The main vestibular nuclei described in the following are the nucleus superior, the nucleus Deiters ventralis, the nucleus Deiters dorsalis, the nucleus medialis, the nucleus descendens and the nucleus tangentialis. In addition to these main vestibular nuclei, two small cell groups (cell groups A and B) are distinguished, found in close topographical relationship to the main nuclei. The longitudinal extent of some of the vestibular nuclei in the brain stem is given with reference to the more easily outlined cochlear nuclei, the nucleus angularis, the nucleus magnocellularis and the nucleus laminaris (see Wold and Hall, 1975).

The Nucleus Vestibularis Superior

The superior nucleus (Fig. 1, drawings 1 to 6; Fig. 3, drawings 1 to 3; Fig. 4 A, B, C) is the vestibular nucleus which is situated most rostrodorsally. When followed from rostral to caudal, it appears at the level of the middle of the principal trigeminal nucleus and extends a little caudal to the rostral pole of the nucleus Deiters dorsalis.

The superior nucleus borders laterally on the fiber bundles running to and from the cerebellum. Dorsally, the rostral half of the nucleus is capped by cerebellar afferent and efferent fibers while the caudal half of the nucleus is found in close contact with the lateral cerebellar nucleus (see Fig. 1, drawings 4 to 6). However, the lateral cerebellar nucleus and the superior vestibular nucleus do not fuse, but are separated by fiber bundles. The medial border of the superior nucleus is found close to the lateral wall of the IVth ventricle. Between the nucleus and the ventricle are interposed, from rostral to caudal, the caudal end of the locus ceruleus (see Fig. 1, drawings 1 to 3), the cell group A (Fig. 1, drawing 4) and the medial vestibular nucleus (Fig. 1, drawings 5 and 6). Fiber bundles separate the superior nucleus from the locus coeruleus and the medial vestibular nucleus, while in some sections it fuses medially with the cell group A. Ventrally, the rostral part of the superior nucleus caps the principal sensory trigeminal nucleus. The caudal third of the superior nucleus borders ventrally on the nucleus Deiters ventralis. There appears to be some intermingling of elements between the latter two nuclei, and the borders are therefore difficult to identify with certainty.

The superior nucleus changes in form from rostral to caudal. The size of the cells and the cellular density of the nucleus vary in different areas of the nucleus. Only some of the characteristics will be mentioned.

The rostral pole of the superior nucleus is of triangular shape in transverse sections, consisting mainly of small cells of varying forms. Some medium-sized and a few larger cells are found intermingled among the smaller ones, mainly medially. The nucleus has its typical structure at the middle of its rostrocaudal extension (see Fig. 1, drawings 3 and 4 and Fig. 4A). Here, the cell structure of the nucleus is rather loose. The cells appear to be larger centrally than peripherally. Most of the centrally placed cells are round to oval, some are triangular, and have rather coarse, intensively stained Nissl bodies. The peripherally situated cells are small, pale and of varying shapes. The ventrolateral extension of the nucleus consists of smal cells (Fig. 4B).

The superior nucleus is traversed by fibers running from dorsomedial to ventrolateral. Fibers are seen to enter the nucleus along its ventral border, these are probably ascending primary afferents to the nucleus.

The superior nucleus expands in size from dorsal to ventral, and the ventralmost part of the nucleus close to the nucleus Deiters ventralis consists of larger and more multipolar cells than is the case in other areas of the nucleus.

The Cell Group A

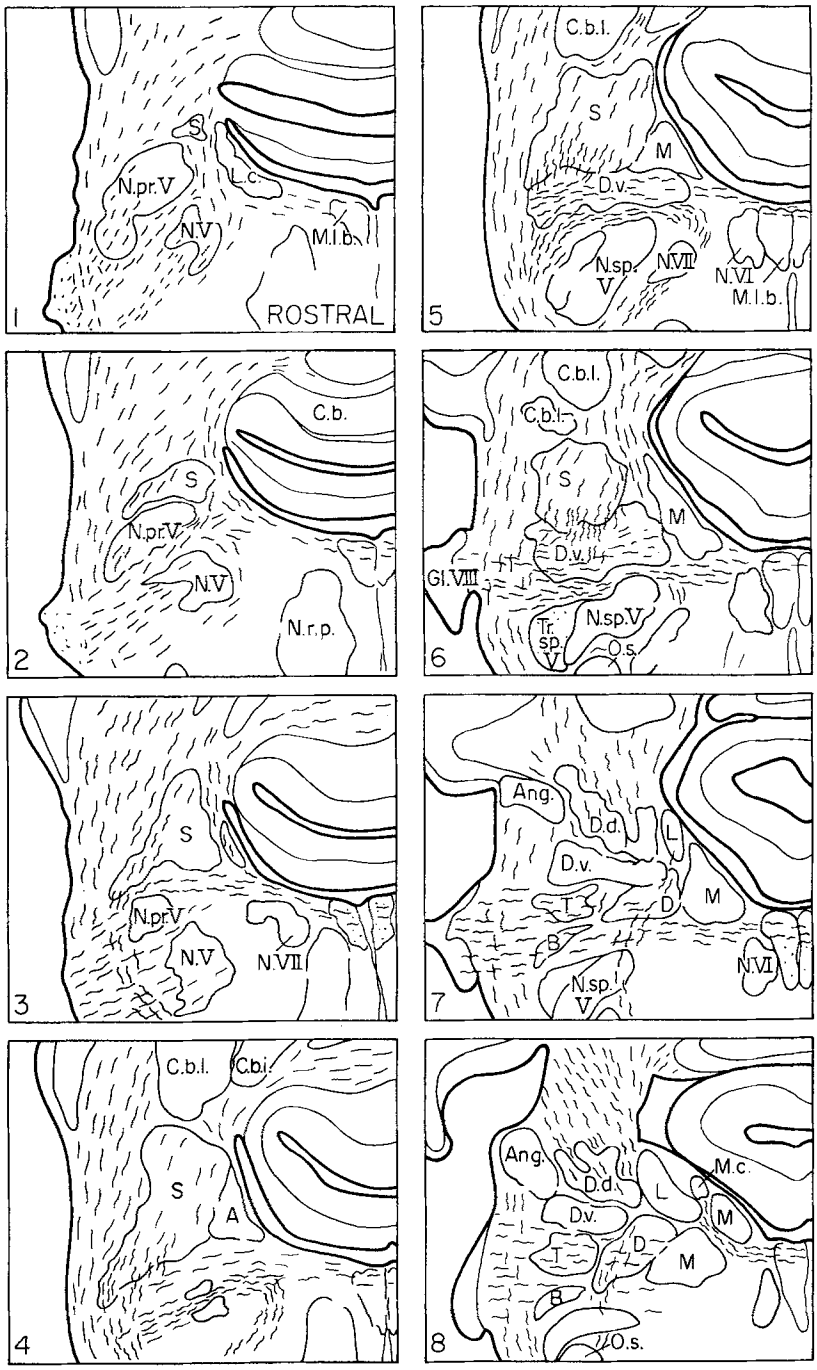
The superior nucleus fuses with a group of cells, here called group A, whose cells differ in form and size from those in the superior nucleus. It is difficult to be sure whether this is a particular nucleus or only a part of the superior nucleus. The cell group A (see Fig. 1, drawing 4, Fig. 3, drawing 2, and Fig. 4B) is found between the superior nucleus and the lateral wall of the IV ventricle, caudal to the locus ceruleus and rostral to the appearance of the medial vestibular nucleus, separated from the latter two by fiber bundles. The cells in the cell group A have a very uniform size and are rather densely packed. The medium sized cells have oval somata and stain more intensely than most cells in the superior nucleus. From 5 to 20 cells can usually be found in each section.

The Nucleus Deiters Ventralis

The nucleus Deiters ventralis (Fig. 1, drawings 5 to 8; Fig. 3, drawings 4 and 5; Fig. 4C) is found in the rostrolateral part of the vestibular complex and consists of giant, medium-sized and small cells.

The rostral pole of the nucleus is found at about the level of the rostral pole of the medial vestibular nucleus. Caudally, it extends to the rostral pole of the magnocellular (cochlear) nucleus. The rostral part of the nucleus has an almost rectangular shape with its longest axis oriented mediolaterally in transverse sections (Fig. 1, drawings 5, 6 and 7). The caudal part of the nucleus is found dorsal to the nucleus tangentialis (Fig. 4C).

The rostral part of the nucleus borders dorsally on the superior vestibular and the medial vestibular nucleus, while the caudal part borders on the nucleus angularis and the nucleus



Figs. 1—3. Drawings (×20) showing the form and position of the vestibular nuclear complex described in the text. The drawings numbered from rostral to caudal (Fig. 1 and 2) and from dorsal to ventral (Fig. 3) are made from equally spaced transverse (Fig. 1 and 2) and horizontal (Fig. 3) thionine and myelin sheath stained sections. Wavy lines represent normal fibers, the dots represent fibers cut transversally

Deiters dorsalis. Laterally, the nucleus borders on the restiform body. Medially, it borders (from rostral to caudal) on the medial vestibular nucleus, the nucleus Deiters dorsalis and the descending vestibular nucleus. The ventral borders of the nucleus Deiters ventralis are clear-cut rostrally where it is separated from the spinal trigeminal nucleus by the efferent fibers in the facial nerve and fibers in the spinal tract of the trigeminal nerve. At caudal levels the nucleus fuses ventrally in some sections with the cell group B. At rostral levels of the descending nucleus the ventral border towards this is difficult to draw with certainty because of similarities in cytoarchitecture of the nuclei, while the borders towards the tangential nucleus are rather clearcut because of the homogeneity of the latter. The borders of the nucleus Deiters ventralis are more easily defined in myelin-stained sections than in Nissl sections because of the heavy amount of myelinated fibers (probably vestibular nerve fibers) running from lateral to medial through the nucleus. The cells in the nucleus are often found in small clusters surrounded by these fibers. In addition, some dorsoventrally running fibers are found (cerebellar afferents ?).

The nucleus Deiters ventralis consists of cells of varying forms and sizes. However, the giant cells with triangular or multipolar shape are prominent. Their perikaryon is packed with coarse Nissl bodies which stain intensely. The dendrites can usually be followed a short segment after leaving the perikaryon and some Nissl bodies are observed within the dendrites. More large cells are found laterally than medially within the nucleus. In addition to the giant cells the nucleus contains many medium-sized and small cells of varying forms. Generally, the small cells tend to be stained lighter than the giant and medium-sized cells.

The Nucleus Deiters Dorsalis

The nucleus Deiters dorsalis (Fig. 1, drawings 7 and 8, Fig. 2, drawing 9; Fig. 3, drawing 1 to 3; Fig. 4C) is one of the most homogeneous of the vestibular nuclei. The nucleus is relatively easily outlined because of its composition of giant cells.

When passing from rostral to caudal, the nucleus appears together with the nucleus laminaris (cochlear), and its caudal pole is found at about the level where the lateral part of the nucleus laminaris expands in size from a line of single cells to a dense aggregation of cells.

The nucleus Deiters dorsalis is dorsally enveloped by fibers running to and from the cerebellum. Medially, the nucleus borders at all levels on the nucleus laminaris. Laterally, most of the nucleus borders on the nucleus angularis. The nucleus Deiters dorsalis borders ventrally on the nucleus Deiters ventralis in the rostral part, while more caudally it borders on the nucleus tangentialis and the descending vestibular nucleus.

The nucleus is traversed by numerous myelinated fibers running dorsoventrally (cerebellar afferents ?), which separate the cells into groups. The most constant and largest of these cellular groups is found medially, close to the nucleus laminaris, and consists of 5 to 15 cells

Abbreviations used in all figures: *A* cell group A, Ang, ANG nucleus angularis, *B* cell group B, *C* cuneate nucleus, *C. b.* cerebellum, *C. b. i.* internal cerebellar nucleus, *C. b. l.* lateral cerebellar nucleus, *C. c. d.* dorsal cochlear commissure, *C. e.* external cuneate nucleus, *C. s.* crossing primary afferents of the solitary tract, *D* descending vestibular nucleus, *D. d.* dorsal nucleus of Deiters, *D. v.* ventral nucleus of Deiters, *Gl. VIII* vestibular ganglion, *L* nucleus laminaris, *L. c.* locus ceruleus, *L. o.* lamino-olivary tract, *M* medial vestibular nucleus, *M. c.*, *Mc*, *MC* nucleus magnocellularis, *M. l. b.* medial longitudinal bundle, *N. V* motor trigeminal nucleus, *N. VI* abducens nucleus, *N. VII* motor nucleus of the facial nerve, *N. IX* glossopharyngeal nucleus, *N. X* vagus nucleus, *N. p. g. l.* nucleus paragigantocellularis lateralis, *N. pr. V* principal trigeminal nucleus, *N. r. g.* nucleus reticularis gigantocellularis, *N. r. p.* pontine gigantocellular reticular nucleus, *N. s.* nucleus of the solitary tract, *N. sp. V* spinal trigeminal nucleus, *n. VIII* cochlear nerve, *O. s.* superior olive, *S.* superior vestibular nucleus, *S. t.* solitary tract, *T* tangential vestibular nucleus, *Tr. sp. V* spinal trigeminal tract, *IX* glossopharyngeal nucleus.

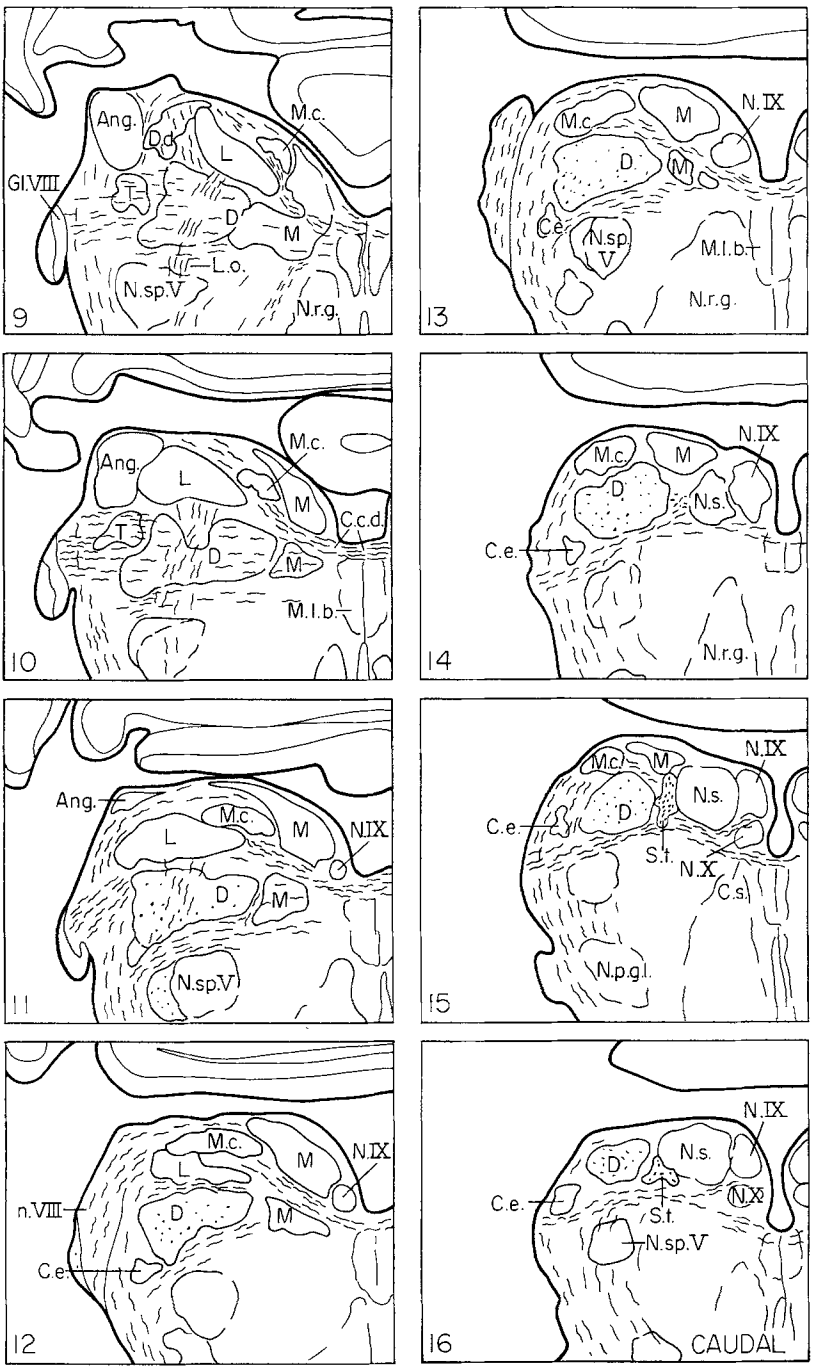

Ang.
M.c.
Dd
L
Gl.VIII
T
D
M
L.o.
N.sp.V
N.r.g.
9
M.c.
M
N.IX
D
M
C.e.
N.sp.V
M.l.b.
N.r.g.
13
M.c.
Ang.
L
M
C.c.d.
T
D
M
M.l.b.
10
N.IX
M.c.
M
D
N.s.
C.e.
N.r.g.
14
Ang.
M.c.
L
M
N.IX
D
M
N.sp.V
11
N.IX
M.c.
M
N.s.
C.e.
D
S.t.
N.X
C.s.
N.p.g.l.
15
M.c.
L
M
N.IX
n.VIII
D
M
C.e.
12
N.IX
N.s.
D
C.e.
N.X
S.t.
N.sp.V
16
CAUDAL

Fig. 2

in each section. The dorsoventral course of the fibers crossing the nucleus Deiters dorsalis facilitates the determination of the border between the nucleus and the rostral part of the descending nucleus and the nucleus Deiters ventralis where most fibers run in a lateromedial direction.

Most of the cells in the nucleus Deiters dorsalis are very large, somewhat larger than the giant cells in the nucleus Deiters ventralis. While in the latter the cells are triangular to multipolar in form, most of the cells in the nucleus Deiters dorsalis have oval to round shapes. Most of the cells have coarse and densely packed Nissl bodies. In thionine-stained sections a short segment of the thick dendrites can usually be followed. The cells tend to be somewhat larger medially than laterally. Whereas the giant cells are in great majority, there are also some medium-sized cells which differ from the giant cells only in size. A few small cells with relatively little cytoplasm are found mainly laterally, and on the borders towards the descending nucleus.

The Nucleus Tangentialis

The nucleus tangentialis (see Fig. 1, drawings 7 and 8; Fig. 2, drawings 9 and 10; Fig. 3, drawings 4 and 5; Fig. 4C) is found among the entering vestibular nerve fibers in the medulla oblongata. The nucleus is distinguished from the surrounding nuclei by the homogeneous form and size of its cells.

The nucleus appears where many vestibular fibers enter the medulla. Its caudal pole is found a few sections caudal to the nucleus Deiters dorsalis.

The nucleus borders laterally on the fibers running to the cerebellum in the restiform body, medially the nucleus Deiters ventralis (in a few sections rostrally) and the nucleus descendens. Dorsally it borders on the lateral part of the nucleus Deiters ventralis and the nucleus angularis. Ventrally, it borders on the cell group B and the lateral part of the descending vestibular nucleus (Fig. 2, drawing 10). The border towards the descending nucleus is difficult to draw with certainty, both in cell and myelin-stained sections. There is probably some intermingling of cellular elements between the nuclei.

In the fiber and cell-stained sections it is clearly seen how the cells in the nucleus lie tangential to the nerve fibers. Most of the cells are medium-sized, oval, with their longest axis oriented parallel to the incoming nerve fibers. Vestibular nerve fibers even separate individual cells from their neighbours. Only rounded to oval cells have been included in the nucleus. Some differences in size are noted between the cells. From 3 to 15 cells are found in each section.

The Cell Group B

The cell group B forms a narrow column of cells extending rostrocaudally lateral to the descending nucleus and ventral to the nucleus tangentialis (Fig. 1, drawings 7 and 8; Fig. 3, drawings 6 and 7; Fig. 4C). Its rostral pole appears at the same level as the rostral pole of the tangential nucleus, and it disappears caudally some sections caudal to the rostral pole of the descending vestibular nucleus.

The cell group is dorsally separated from the tangential nucleus by the incoming vestibular nerve fibers. Ventrally, the cell group B borders on fibers in the spinal trigeminal tract.

The cell group appears to be continuous rostrally with the caudal pole of the nucleus Deiters ventralis and has many cytoarchitectonic features in common with the latter. The cell group consists of cells of different forms and sizes. Most of the cells are, however, large multipolar or triangular with a cytoplasm densely packed with coarse Nissl bodies. Small and medium-sized cells are also found. From 2 to 15 cells are found in each transverse section.

The Nucleus Vestibularis Medialis

The medial vestibular nucleus is the longest (Fig. 1, drawings 5 to 8; Fig. 2, drawings 9 to 15; Fig. 3, drawings 3 to 6; Fig. 4C; Fig. 5A, B) and the most cell dense of the major vestibular nuclei. It is situated close beneath the floor of the fourth ventricle. The oral pole of the nucleus fuses with the caudal pole of group A and appears at the same level as the oral pole

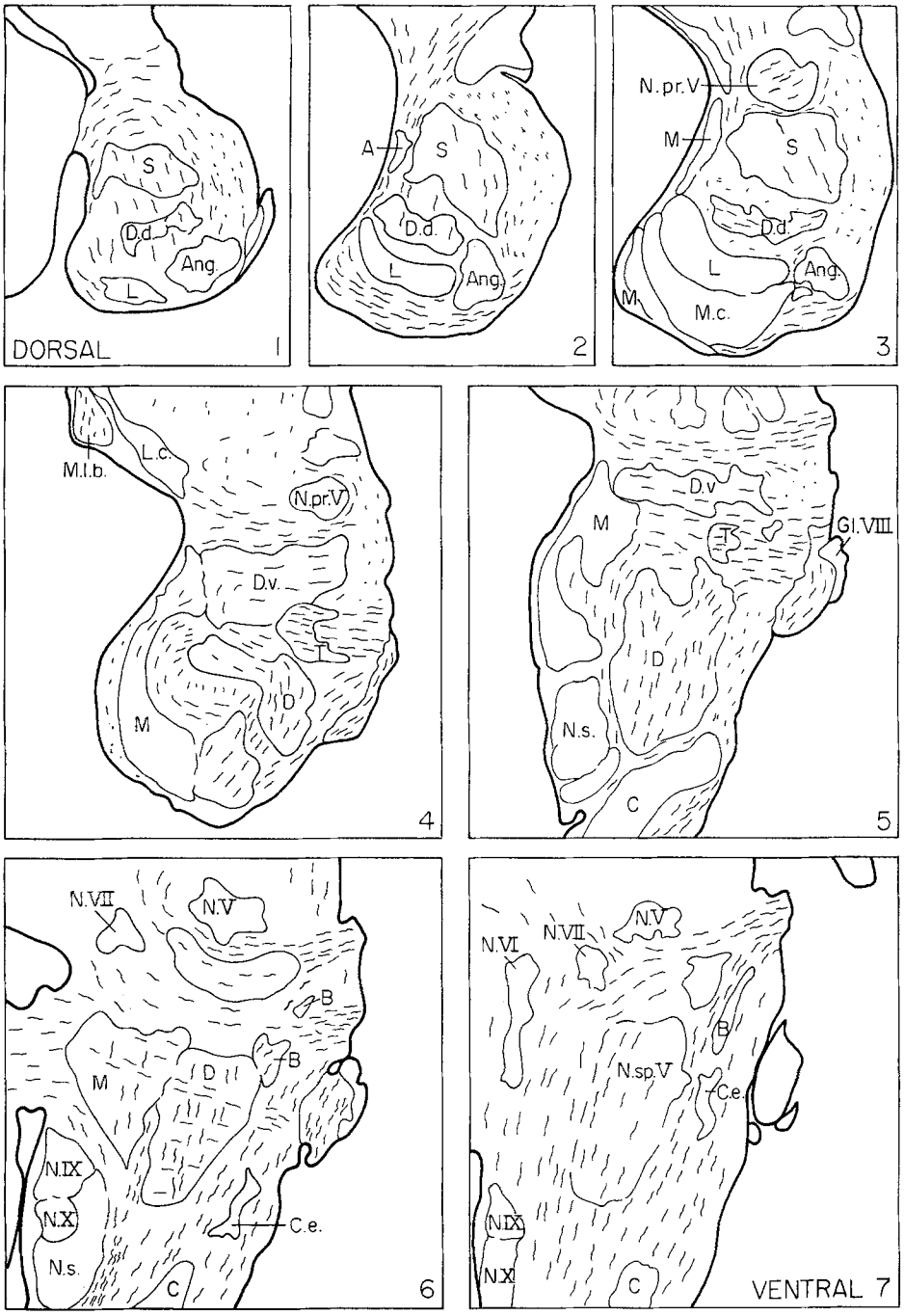

DORSAL
1
S
D.d.
Ang.
L
2
A
S
D.d.
L
Ang.
3
N.pr.V
M
S
D.d.
L
Ang.
M
M.c.
4
M.l.b.
L.c.
N.pr.V
D.v.
L
D
M
5
D.v
M
Gl.VIII
L
D
N.s.
C
6
N.VII
N.V
B
B
M
D
N.IX
N.X
N.s.
C.e.
C
VENTRAL 7
N.VI
N.VII
N.V
B
N.sp.V
C.e.
N.IX
N.X
C

Fig. 3

of the nucleus Deiters ventralis. Its caudal pole extends only a little less caudally than the descending nucleus.

Laterally, the nucleus borders on many of the vestibular and cochlear nuclei. From rostral to caudal these are the superior nucleus, the nucleus Deiters ventralis, the laminar nucleus, the magnocellular nucleus and finally its close companion in the brain stem, the descending nucleus. The cochlear nuclei laminaris and magnocellularis are found dorsal to the descending nucleus.

Medially, the nucleus borders in its rostral $^3/_4$ on the floor of the IV ventricle. Caudally, however, the medial nucleus moves laterally and borders on the glossopharyngeal nucleus and in the caudalmost part on the nucleus of the solitary tract. Ventrally, the nucleus is separated from the reticular formation by a cell-free region with fiber bundles running in a mediolateral direction.

It should be noted that on the basis of differences in cytoarchitectonics as seen in thionine sections the borderline between the medial nucleus and the nucleus Deiters ventralis and the descending nucleus, respectively, is difficult to draw in some sections rostrally, purely fiber stained sections are better suited. For example, large numbers of myelinated fiber bundles run longitudinally within the descending nucleus, while very few such fibers are found in the adjoining areas of the more cell dense medial nucleus (Fig. 5B). The primary afferent cochlear fibers which cross the midline on their way to the contralateral nucleus laminaris divide the medial nucleus into a larger ventrolateral part and a smaller dorsomedial part (see Fig. 1, drawing 8; Fig. 2, drawing 9 to 13). Caudally, the dorsomedial part increases in size, while the ventrolateral part becomes smaller.

Cytoarchitectonically the medial nucleus is a dense condensation of mainly small cells, the cell density is greater caudally than rostrally. It should be noted, however, that the nucleus has a relatively cell free zone closely beneath the floor of the IVth ventricle. The nucleus is most voluminous at the appearance of the glossopharyngeal nucleus (Fig. 2, drawing 11) where it has its typical triangular shape. The cell shape varies greatly, in transverse sections cells which apparently are round to oval, fusiform, triangular and even multipolar are found. Differences between the dorsomedial and the ventrolateral parts are clearcut rostrally. The ventrolateral part contains the largest cells; some cells resemble medium-sized cells in the nucleus Deiters ventralis. In addition, there are more transversely running myelinated fibers in the ventrolateral than in the dorsomedial part. Such differences are less marked caudally.

The Nucleus Vestibularis Descendens

The descending vestibular nucleus (Fig. 1, drawings 7 and 8; Fig. 2, drawings 9 to 16; Fig. 3, drawings 4 to 5; Fig. 4C; Fig. 5A,B) is found lateral to the medial nucleus. The nucleus is large, but has a low cellular density. Its cells vary greatly in form and size.

The rostral pole of the descending nucleus fuses with the caudal pole of the nucleus Deiters ventralis. There appears to be some intermingling of cellular elements between these nuclei; no clearcut borderline between the two can therefore be ascertained in the rostralmost sections. The caudal pole of the descending nucleus is found at the level where the dorsal column nuclei appear.

The descending nucleus borders medially on the medial vestibular nucleus at most levels. The border between the two nuclei is rather diffuse rostrally (see above), while caudally fiber bundles separate the two (Fig. 5B). The caudal $^1/_4$ of the descending nucleus, dorsolateral in the brain stem, borders medially on the solitary tract and its nucleus. Laterally the nucleus borders from rostral to caudal on the nucleus Deiters ventralis, the nucleus tangentialis and finally, on the restiform body. The external cuneate nucleus is found ventrolaterally to the caudal half of the descending nucleus.

At rostral levels the descending nucleus borders dorsally on the nucleus Deiters dorsalis, more caudally on the nucleus laminaris and the nucleus magnocellularis. Ventrally, it borders on the spinal trigeminal tract, while in the caudalmost part fiber bundles (belonging to the IXth and Xth nerves) separate the descending nucleus from the spinal trigeminal complex.

The descending vestibular nucleus is densely traversed by myelinated fiber bundles. Rostrally, vestibular nerve fibers run lateromedially. More caudally fibers run longitudinally.

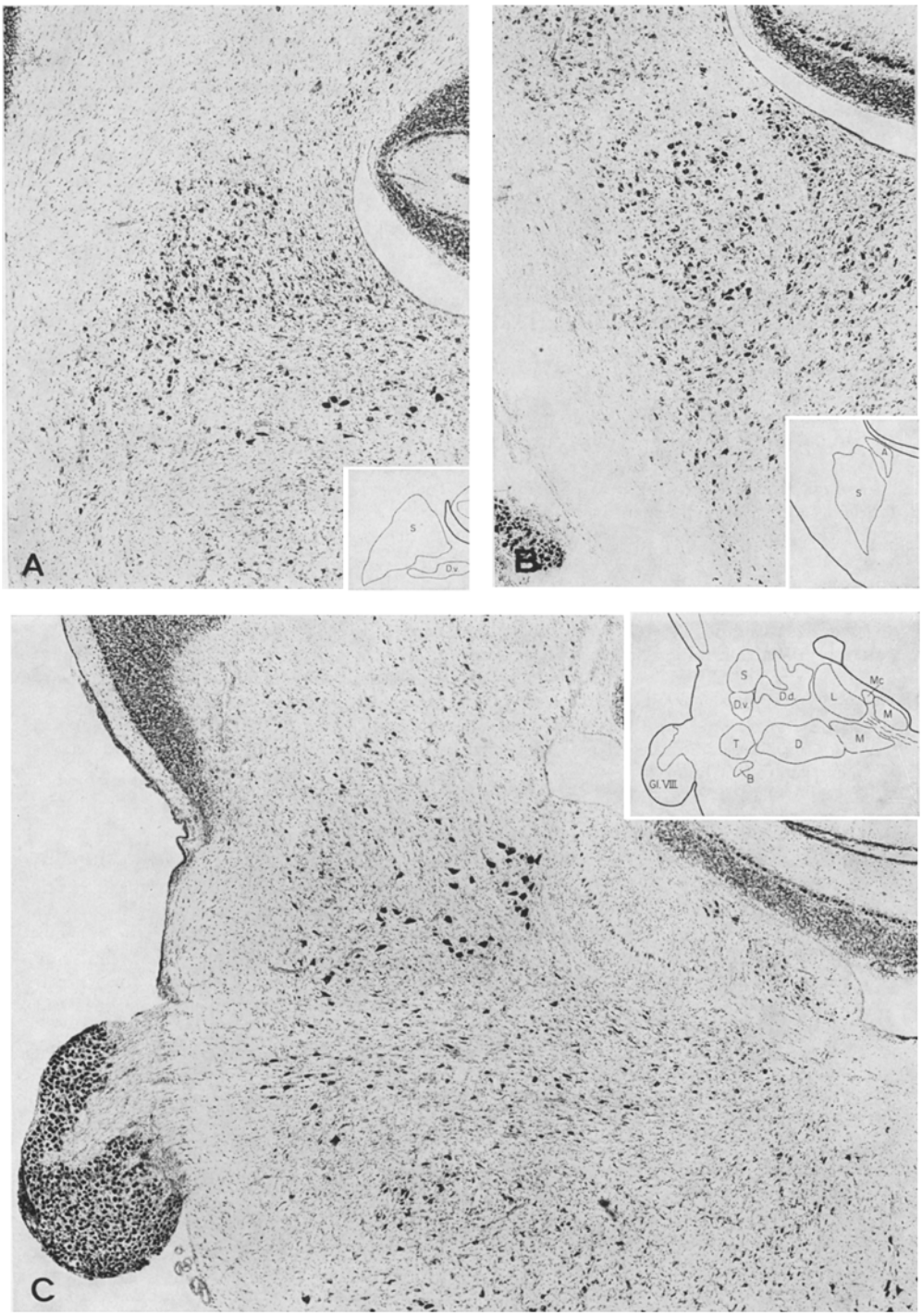


Fig. 4

These latter fiber bundles are found with the highest density ventrally in the nucleus. Some of the fibers are primary afferents to the nucleus (Wold, 1975), while others probably are efferent and afferent fibers to and from the cerebellum. Caudally the distance between the fiber bundles increases, resulting in an increasing cellular density. In addition to the above mentioned fibers, the nucleus is crossed by the dorsoventrally running fiber bundles from the nucleus laminaris to the superior olive.

The cytoarchitecture of the nucleus is not uniform. Only certain features will be mentioned. Generally, the cells in the nucleus are found in clusters separated by fiber bundles.

At rostral levels the medially situated cells are more multipolar and larger than those found laterally, where they generally are oval or round. The medium-sized, multipolar cells, packed with Nissl bodies, closely resemble the cells in the nucleus Deiters ventralis, although very few large cells are present.

In the middle of the nucleus' rostrocaudal extent (see Fig. 2, drawings 10 and 11), the the nucleus has its most typical cytoarchitecture. The cell density is greater laterally than medially, and the cells in the former area are larger, more multipolar and stain more intensely with thionine than the cells medially. In some of the sections in this region (see Fig. 2, drawing 11) the nucleus is continuous with a group of small, intensely stained cells found at the nucleus' ventrolateral margin.

The differences between medial and lateral parts of the nucleus become less prominent as the cellular density increases caudally. Here, the cells are smaller and paler than rostrally. Only a few medium-sized cells are found (mainly ventrolaterally) in these sections.

Discussion

The present paper presents a map of the vestibular nuclear complex in the domestic hen which for most of the nuclei is in agreement with the map presented by Karten and Hodos (1967) in their stereotaxic atlas of the brain of the pigeon. However, the map differs somewhat from most of the earlier studies on the subject in birds. In the following the different nuclei and their organization are discussed in the light of earlier findings and data obtained in an experimental study of the primary afferents to the vestibular complex in the hen (Wold, 1975). The experimental findings have been of great value in avoiding a subdivision of the nuclear complex into too many subnuclei solely on the basis of minor differences in cytoarchitecture and fiber pattern. It appears from the findings that some of the vestibular nuclei described are remarkably similar to nuclei given the same name in mammals. The nuclei are discussed as they appear from rostral to caudal in the brain stem.

Fig. 4 A—C. Photomicrographs (×40) showing the vestibular nuclei in the domestic hen in transverse thionine sections. For abbreviations, see legend to Fig. 1. A corresponds approximately to the level of drawing 3, Fig. 1, B to drawing 4, Fig. 1 and C to a level between drawing 6 and 7, Fig. 1. Note in A the triangular shape of the superior nucleus, and that its cells are larger centrally than peripherally. The most rostral pole of the nucleus Deiters ventralis is seen below. Note that the nucleus consists of cells of different sizes with prominent giant cells. Note in B the difference between the cytoarchitecture of the superior nucleus and the cell group A. In the latter group the cells have a rather uniform size and are densely packed. Note in C the vestibular ganglion situated close to the brain stem, the cells in the nucleus tangentialis found among the incoming vestibular nerve fibers, the cell group B with larger cells situated ventral to the tangential nucleus, the nucleus Deiters dorsalis consisting mainly of giant cells crossed by dorsoventrally running fibers, the rostral pole of the descending nucleus and finally, the medial vestibular nucleus divided by the dorsal cochlear commissure

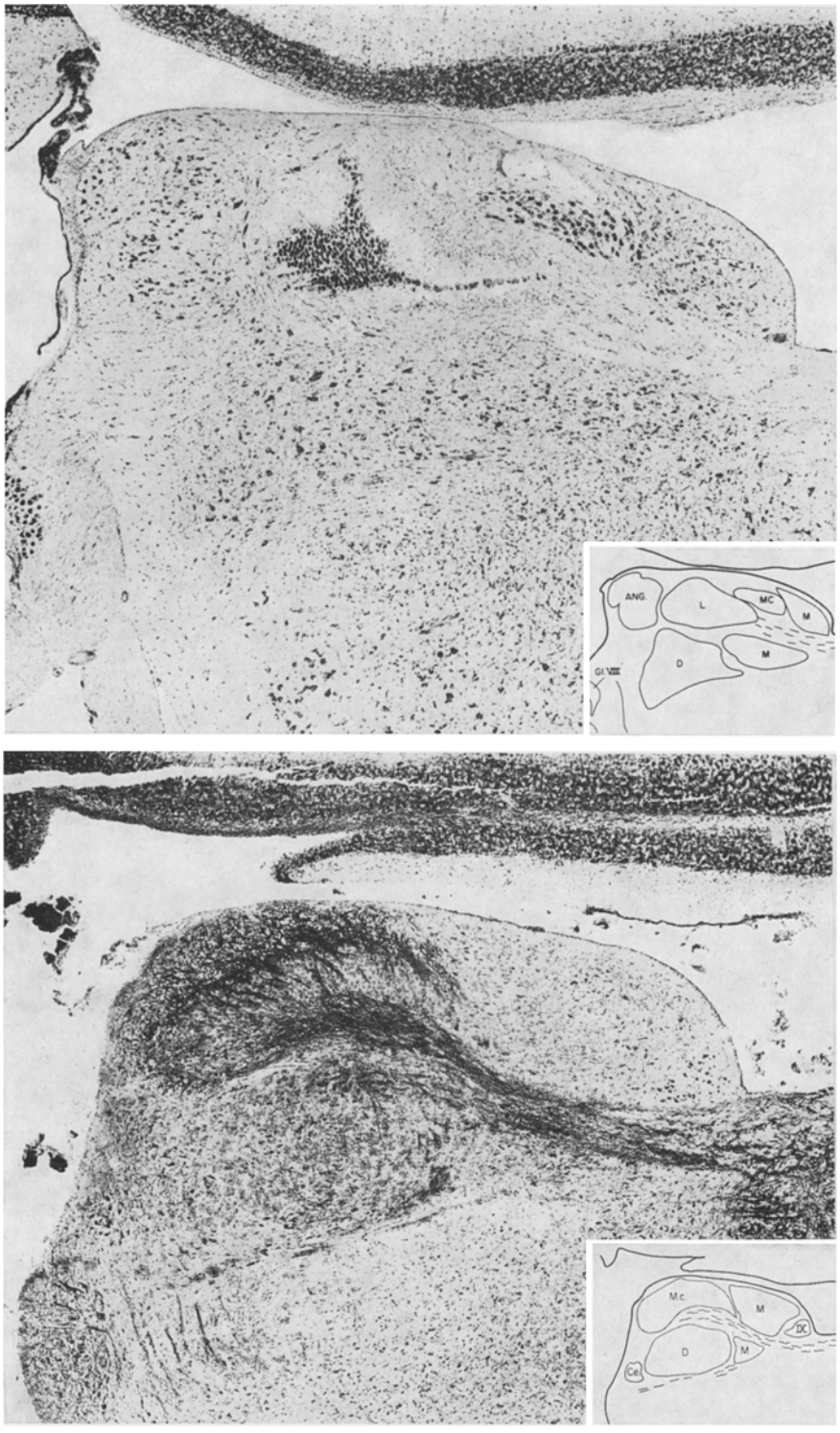


Fig. 5

The superior vestibular nucleus described above appears to be homologous to the nucleus Bechterew of Sinn (1913), the nucleus oralis of Bartels (1925) and Craigie (1928, 1930) and the superior nucleus of Sanders (1929) and Stingelin (1965) in birds. According to the position in the brain stem and the cytoarchitecture described, the superior nucleus defined above appears to include part of the nucleus (or formatio) quadrangularis and the nucleus vestibulo-cerebellaris of Ramón y Cajal (1908b), Craigie (1928) and Renggli (1967), and a part of the dorsoventral nucleus of Sanders (1929). For example, the formatio quadrangularis of Renggli (1967) in the domestic hen appears to include the superior nucleus (as defined in the present study) together with parts of the cerebellar nuclei, and of the nucleus Deiters ventralis of the present study. It would seem to be of little value to use a common designation for these cell groups.

In the superior nucleus, the cells centrally placed and the cells on the borderline to the nucleus Deiters ventralis are larger than those in peripheral parts of the nucleus. This is strikingly similar to what is found in the cat (Brodal and Pompeiano, 1957) and in man (Sadjadpour and Brodal, 1968). Another similarity between the superior nucleus in birds and in mammals concerns the termination of primary afferents within the nucleus. In both classes of vertebrates (Walberg, Bowsher and Brodal, 1958; Gacek, 1969, in the cat; Wold, 1975, in the hen) the primary afferents terminate mainly centrally within the nucleus. These similarities when considered in conjunction with the similar position of the superior nucleus within the vestibular nuclear complex in the two classes of vertebrates make it justifiable to consider the nucleus in the hen (as defined here) as an entity which is homologous to the superior vestibular nucleus in mammals.

The cell group A found medially to the superior nucleus differs from this and the more caudally situated nucleus medialis in cytoarchitecture, and is separated from the latter by fiber bundles. The suggestion that cell group A is a cell group different from the superior nucleus receives support from the distribution of primary afferents to the vestibular complex, since a particular branch of vestibular nerve fibers courses to and terminates in the cell group A.

The cell group A probably corresponds to the nucleus piriformis of Ramón y Cajal (1908c), Craigie (1928) and Renggli (1967) and what is indicated by Sanders (1929) as the rostral part of the medial division of the dorsolateral vestibular nucleus. In mammals, a particular cell group does not appear to have been described in the area of the vestibular complex where cell group A is found in the hen. Further studies of the fiber connections of the vestibular nuclei in birds are needed to decide whether the cell group A should be considered to represent a particular vestibular nucleus.

Fig. 5. (A) Photomicrograph (×40) showing the nucleus Deiters ventralis in a transverse myelin and cell stained section. The vestibular nerve fibers enter from the right. Note that the nucleus is crossed by the incoming vestibular nerve fibers running lateromedially within the nucleus. (B) Photomicrograph (×40) showing the medial and descending vestibular nucleus in a transverse Woelcke-Pettersen stained section. Note the large number of transversally cut longitudinally running fibers within the descending nucleus in contrast to the cell dense, but almost fiber free medial nucleus. Note that fibers separate the two nuclei

The nucleus Deiters ventralis is named according to the nomenclature proposed by Bartels (1925). The nucleus appears to correspond to the Deiters nucleus of Ramón y Cajal (1908c), Sinn (1913), Craigie (1928, 1930) and Renggli (1967) and the ventrolateral nucleus of Sanders (1929) and Stingelin (1965). The nucleus consists of a mixture of giant, medium-sized and smaller cells. However, the giant cells are prominent and serve as the main criterion for differentiating this nucleus from others. The nucleus is crossed by entering vestibular nerve fibers. Following lesions of the nerve (Wold, 1975) degenerating coarser fibers continuing to the medial vestibular nucleus as well a terminal field of degenerating fibres were found within the nucleus. This is taken as evidence that the nucleus receives vestibular nerve fibers.

In newly hatched chickens, retrogarde cellular changes have been observed in the nucleus Deiters ventralis following lesions of the cervical part of the spinal cord, showing that the nucleus sends axons to the spinal cord (Wold, unpublished observations). Lesions of lower segments of the spinal cord, however, did not produce retrogarde cellular changes in any of the vestibular nuclei. It cannot be decided by this method how far caudally the Deiterospinal tract reaches.

It is difficult to find a homologue to the nucleus Deiters ventralis in mammals, since in birds there are two nuclei with giant cells projecting to the spinal cord (the nucleus Deiters ventralis and the nucleus Deiters dorsalis) while only one such nucleus with giant cells (the lateral nucleus) is present in mammals (Pompeiano and Brodal, 1957). It should, however, be noted that in mammals the rostroventral part of the lateral nucleus receives vestibular nerve fibers (Walberg, Bowsher and Brodal, 1958; Carpenter, 1960; Mugnaini, Walberg and Brodal, 1967; Gaeck, 1969) while its dorsocaudal part does not receive primary afferents. It can therefore be suggested that the nucleus Deiters ventralis in birds is homologous to the rostroventral part of the lateral nucleus in mammals. In addition, the nucleus Deiters ventralis and the rostroventral part of the lateral nucleus appear to be cytoarchitectonically similar and situated in the same area of the vestibular nuclear complex in both vertebrate classes. However, the rostroventral part of the lateral nucleus in the cat projects only to cervical segments of the spinal cord (Pompeiano and Brodal, 1957; Nyberg-Hansen and Mascitti, 1964) while the area of termination for the axons from the nucleus Deiters ventralis in the spinal cord of the hen remains unknown.

It should be noted that before the proposed homology of the nucleus Deiters ventralis in the domestic hen with the rostroventral part of the nucleus lateralis in mammals can be accepted, more experimental studies are necessary to elucidate the organization of the vestibular nuclear complex in the domestic hen.

The nucleus Deiters dorsalis is rather easily outlined in cell impregnated sections because of its giant-sized cells. By most previous authors the nucleus is subdivided into a number of smaller nuclei because of the large number of dorsoventrally running fibers (to and from the cerebellum ?) which separate the cells into particular minor cell groups. Judging from its cell size, form and situation in the brain stem, the nucleus Deiters dorsalis as outlined in the present study corresponds to the nucleus Deiters dorsalis of Bartels (1925), the nuclei gemelli of Ramón y Cajal (1908c), Craigie (1928), Renggli (1967) and the intermediate part of Sander's (1929) dorsolateral nucleus. In the Deiters nucleus of Sinn (1913) the cells in the nucleus Deiters dorsalis appear to be included.

It should be noted that different avian species may have a differently developed vestibular complex in the area occupied by the nucleus Deiters dorsalis in the domestic hen. This may explain the discrepancies between earlier authors and the present author in defining the various nuclei in this region.

The nucleus Deiters dorsalis is the only vestibular nucleus in the hen which does not receive primary afferents (Wold, 1975). It does, however, project to the spinal cord (Wold, unpublished observations) as does the nucleus Deiters ventralis. Because of its position in the brain stem, it is deemed practical to consider the nucleus as part of the vestibular nuclear complex, even if it does not receive primary afferents.

The nucleus Deiters dorsalis may be homologous to the dorsocaudal part of the lateral nucleus in mammals. In the cat (Brodal and Pompeiano, 1957) as well as in man (Sadjadpour and Brodal, 1968) the dorsocaudal part of the lateral nucleus consists predominantly of giant cells as does the nucleus Deiters dorsalis in the present study. In addition, the dorsocaudal part of the lateral nucleus in the cat does not receive primary afferents (Walberg, Bowsher and Brodal, 1958). In mammals, the dorsocaudal part of the lateral nucleus projects to the lumbosacral region of the spinal cord (Brodal and Pompeiano, 1957; Nyberg-Hansen and Mascitti, 1964) while the area of termination in the spinal cord for the axons from the cells in the nucleus Deiters dorsalis in the hen remains unknown. More information is needed before the nucleus Deiters dorsalis in birds can be considered as homologous to the dorsocaudal part of the lateral nucleus in mammals.

Since the first description of *the nucleus tangentialis* by Ramón y Cajal (1908a) it has been recognized by most workers. The nucleus is situated among the incoming vestibular nerve fibers and consists predominantly of oval, medium-sized cells with their longest axis oriented parallel to the incoming vestibular nerve fibers. There is general agreement concerning its position in the vestibular complex (Bartels, 1925; Craigie, 1928; Sanders, 1929; Renggli, 1967). However, it appears to be situated more lateral in some avian species than in others.

In fiber impregnated material Ramón y Cajal (1908a) and later Sanders (1929) noted that the cells were contacted by calyx formed endings of the vestibular nerve fibers. Recent ultrastructural evidence for the presence of spoon type endings on the cells (Hinojosa and Robertson, 1967) appears to confirm the classical notion.

The situation of the nucleus tangentialis within the vestibular nuclear complex of the hen corresponds to that of the nucleus interstitialis in the cat (Brodal and Pompeiano, 1957) as well as in man where it is more developed (Sadjadpour and Brodal, 1968). In the cat, the nucleus interstitialis sends axons to the spinal cord (Pompeiano and Brodal, 1957) as well as ascending fibers to the medial longitudinal fasciculus (Brodal and Pompeiano, 1958). In the hen, retrogarde cellular changes have so far not been observed in the nucleus tangentialis following spinal cord lesions (Wold, unpublished observations). Because of lack of experimental evidence of the connections for the nucleus tangentialis in birds, it is at the moment difficult to say whether it is homologous to the nucleus interstitialis in mammals.

The cell group B consists of small, medium-sized and large cells as does the nucleus Deiters ventralis with which it fuses rostrally. The cell group is situated

ventrally to the nucleus tangentialis. The cell group B not appear to have been described by earlier authors. The cells are, however, seen in Renggli's (1967) illustrations of the brain stem, but have apparently not been regarded as a component of the vestibular nuclear complex. The cell group B receives vestibular fibers (Wold, 1975) and sends axons to the spinal cord (Wold, unpublished observations). In the present study the cell group is regarded as a particular cell group, but because of the cytoarchitectonical similarities with the nucleus Deiters ventralis as well as the similarities concerning primary afferents and efferent projections, it may also be considered as a caudally running tail of the latter. Further studies of the anatomical and functional organization of the vestibular nuclear complex are needed to decide whether the cell group B should be regarded as a separate unit of the nuclear complex.

The medial vestibular nucleus has been recognized by most authors under the name of nucleus triangularis or nucleus dorsomedialis (Wallenberg, 1900; Holmes, 1903; Sinn, 1913; Bartels, 1925; Craigie, 1928, 1930; Sanders, 1929; Stingelin, 1965). The nucleus was not regarded as belonging to the vestibular nuclear complex by Ramón y Cajal (1908c) since he was not able to trace vestibular fibers to it. However, Wallenberg (1900) Sinn (1913), Bartels (1925), Craigie (1928, 1930) and Sanders (1929) on the basis of normal material reached the conclusion that such fibers exist. This has been confirmed experimentally by the present author (Wold, 1975). It should be noted that the relatively cell free band on the borderline towards the IVth ventricle should be regarded as belonging to the nucleus, since this is part of the main area of termination of primary afferents within the nucleus. At most levels the dorsal cochlear commissure divides the nucleus into two, a mediodorsal and a ventrolateral part. Most authors do not include the ventrolateral part in their medial vestibular nucleus. As far as its position in the brain stem and its cytoarchitecture is concerned, the medial nucleus in the domestic hen is remarkably similar to the medial nucleus of mammals (Brodal and Pompeiano, 1957; Sadjadpour and Brodal. 1968). In mammals, however, the primary afferents terminate in the ventrolateral part (Walberg, Bowsher and Brodal, 1958), while in the domestic hen they terminate in the most dorsomedial part. Thus the medial vestibular nucleus is differently organized in the two vertebrate classes.

The descending vestibular nucleus in birds has been recognized by various authors. Brandis (1894) described it, but did not name it. Ramón y Cajal (1908c) called it noyau descendent, Sinn (1913) formatio fasciculata, Bartels (1925), Craigie (1928) and Sanders (1929) the nucleus descendens and finally, Renggli (1967) formatio vestibularis descendens. There is no agreement concerning the rostro caudal extension of the nucleus and the borderline towards the medial nucleus. It appears that most authors have found it to extend less far caudalward than described in the present study. In addition, the rostral delimitation of the nucleus is debated by Renggli (1967). Thus, the region occupied by the rostral part of the descending nucleus according to the present study is described as two separate nuclei (named the nucleus vestibularis medialis and the nucleus vestibularis lateralis). The rostral border of the nucleus is difficult to draw because it fuses with the nucleus Deiters ventralis. In most areas. however, the longitudinally running myelinated fiber bundles furnish a criterion for distinguish-

ing this nucleus from its neighbours. Many of these fibers are primary vestibular nerve fibers (Wold, 1975). The cell size, form and cellular density vary in different regions of the nucleus and can hardly be used as criteria for differentiating the nucleus from others.

In mammals, the descending nucleus is described as occupying a corresponding region of the brain stem and is likewise characterized by the numerous longitudinally running fibers. Whether the descending nucleus in birds is organized in the same manner with regard to efferent and afferent fibers to and from the cerebellum as found for mammals [for a review, see Brodal (1972) and Walberg (1972) respectively] remains to be seen.

References

Bartels, M.: Über die Gegend des Deiters- und Bechterewskernes bei Vögeln. Z. Anat. Entwickl.-Gesch. **77**, 726—784 (1925)

Brandis, F.: Untersuchungen über das Gehirn der Vögel. II Theil: Ursprung der Nerven der Medulla oblongata **43**, 96–116 (1894)

Brodal, A.: Vestibulocerebellar input in the cat: Anatomy. In: Basic aspects of central vestibular mechanisms. (A. Brodal and O. Pompeiano, eds.). Progress in Brain Research **37**, 315–327. Amsterdam: Elsevier Publishing Company 1972

Brodal, A., Pompeiano, O.: The vestibular nuclei in the cat. J. Anat. (Lond.) **91**, 438–454

Brodal, A., Pompeiano, O.: The origin of ascending fibers of the medial longitudinal fasciculus from the vestibular nuclei. Acta morph. neerl.-scand. **1**, 306–328 (1958)

Carpenter, M. B.: Experimental anatomical-physiological studies of the vestibular nerve and cerebellar connections. In: Neural mechanisms of the auditory and vestibular systems (G. L. Rasmussen and W. Windle, eds.), p. 297–323. Springfield, Ill.: Thomas 1960

Craigie, E. H.: Observations of the brain of the humming bird. J. comp. Neurol. **45**, 377–481 (1928)

Craigie, E. H.: Studies of the brain of the kiwi (apteryx australis). J. comp. Neurol. **49**, 223–357 (1930)

Gacek, R.: The course and central termination of first order neurons supplying vestibular end organs in the cat. Acta oto-laryng. (Stockh.) Suppl. **254**, 1–66 (1969)

Hinojosa, R., Robertson, J. D.: Ultrastructure of the spoon type synaptic endings in the nucleus vestibularis tangentialis of the chick. J. Cell Biol. **34**, 421–430 (1967)

Holmes, G.: On the comparative anatomy of the nervus acusticus. Trans. roy. Irish Acad. **32**, 101–144 (1903)

Karten, H. J., Hodos, W.: A stereotaxic atlas of the brain of the pigeon (Columba livia). Baltimore, Maryland: The John Hopkins Press 1967

Mugnaini, E., Walberg, F., Brodal, A.: Mode of termination of primary vestibular fibres in the lateral vestibular nucleus. An experimental electron microscopical study in the cat. Exp. Brain Res. **4**, 187–211 (1967)

Nyberg-Hansen, R., Mascitti, T.: Sites and mode of termination of the vestibulospinal tract in the cat. An experimental study with silver impregnation methods. J. comp. Neurol. **122**, 355–367 (1964)

Pompeiano, O., Brodal, A.: The origin of vestibulospinal fibres in the cat. An experimental-anatomical study with comments on the descending medial longitudinal fasculus. Arch. ital. Biol. **95**, 166–195 (1957)

Ramón y Cajal: Sur un noyau special du nerf vestibulaire des poissons et des oiseaux. Trab. Lab. biol. Madrid **6**, 1–20 (1908a)

Ramón y Cajal: Los ganglios centrales del cerebelo de las aves. Trab. Lab. biol. Madrid **6**, 176–194 (1908b)

Ramón y Cajal: Les ganglions terminaux du nerf acoustique des oiseaux. Trab. Lab. biol. Madrid **6**, 195–224 (1908c)

Renggli, F.: Comparative anatomical studies of the cerebellar and vestibular nuclei in birds. Rev. Suisse. Zool. **74**, 701–778 (1967)

Sadjadpour, K., Brodal, A.: The vestibular nuclei in man. A morphological study in the light of experimental findings in the cat. J. Hirnforsch. **10**, 299–323 (1968)

Sanders, E. B.: A consideration of certain bulbar, midbrain and cerebellar centers and fiber tracts in birds. J. comp. Neurol. **49**, 155–222 (1929)

Sinn, R.: Beitrag zur Kenntnis der Medulla Oblongata der Vögel. Mschr. Psychiat. Neurol. **33**, 1–39 (1913)

Stingelin, W.: Qualitative und quantitative Untersuchungen an Kerngebieten der Medulla oblongata bei Vögeln. Bibl. Anat. **6**, New York: S. Karger, 1965

Walberg, F.: Cerebellovestibular relation: Anatomy. In: Basic aspects of central vestibular mechanisms (A. Brodal and O. Pompeiano, eds.), Progr. Brain Res. **37**, 361–376 (1972)

Walberg, F., Bowsher, D., Brodal, A.: The termination of primary vestibular fibers in the vestibular nuclei in the cat. An experimental study with silver impregnation methods. J. comp. Neurol. **110**, 391–419 (1958)

Wallenberg, A.: Über centrale Endstätten des Nervus octavus der Taube. Anat. Anz. **17**, 102–108 (1900)

Woelcke, M.: Eine neue Methode der Markscheidenfärbung. J. Psychol. Neurol. (Lpz.) **51**, 199–202 (1942)

Wold, J. E.: The distribution of primary afferents to the vestibular nuclei in the domestic hen (Gallus domesticus), Brain Res. **95**, 531–543 (1975)

Wold, J. E., Hall, J. G.: The distribution of primary afferents to the cochlear nuclei in the domestic hen (Gallus domesticus), Anat. Embryol. **147**, 75–89 (1975)

Jan Egil Wold
Anatomical Institute
Karl Johansgt. 47
University of Oslo,
Oslo
Norway