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ORIGIN AND DISTRIBUTION OF THE TRACTUS SOLITARIUS IN THE GUINEA PIG

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INTRODUCTORY

Several years ago the writer began a series of experiments and studies on the guinea pig's brain to determine if perchance the central connections of the general visceral and gustatory systems in mammals were comparable to those found by Herrick and Johnston in fishes.

In brief, Herrick's description of the gustatory system of the carp, catfish and Amblystoma may be summarized as follows: Both gustatory and general visceral sensory impulses are conducted by the VII, IX and X nerves to facial and vagal lobes of the medulla. From these primary centers two descending secondary gustatory tracts follow the spinal V tract to the region of the commissural nuclei and two ascending secondary gustatory tracts accompany the spinal V tracts to two superior secondary gustatory nuclei, situated in the isthmus, ventrally to the line of fusion of the valvula cerebelli and the cerebellum. The principal tertiary fibers arising from the superior nuclei pass to the inferior lobes. Herrick notes also the possibility of a relay to lower centers by way of the tractus lobo-bulbaris. Johnston in a number of papers and in his book describes a tractus lobo-epistriaticus or tractus palli connecting the hypothalamus (inferior lobes) with the telencephalon. On p. 174 of his book Johnston figures visceral fibers from the spinal cord entering the secondary visceral tract.

My own studies on this system in mammals, based largely on Marchi preparations, will be reported in three parts. The results of the first phase of the subject will be incorporated in this paper and will include a description of the distribution of the primary gustatory and general visceral fibers in the medulla of the guinea pig. This will be followed by a description of the course of the secondary visceral fibers taking origin from the primary visceral nucleus, namely, the nucleus tractus solitarii, and thirdly by a study of the basal cerebellar nuclei, emboliformis and globosus with a view of determining their relationships.

REVIEW OF LITERATURE

Complete summaries of the early work on the tractus solitarius and its components have been given by Koelliker and Van Gehuchten. As a result of these studies, dating from Stilling to Koelliker the tractus solitarius was found to be a continuous tract extending from the entrance of the VII nerve to the decussation of the pyramids, and to be made up of sensory fibers from the VII, IX and X nerves. Koelliker noted the close proximity of the radix sensibilis nervi facialis to the radix decendens nervi vestibularis. Also he observed the nucleus tractus solitarii extending the entire length of the tractus solitarius from the radix sensibilis nervi facialis to the decussatio pyramidum.

As a result of a study of some Marchi sections of a brain from a patient who had a lesion causing the loss of taste and tactile sensations on the left half of the tongue, Wallenberg traced a degenerated fasciculus, cephalad, from the tractus solitarius at the level of the sensory root of the glossopharyngeal nerve, to the bend of the motor root of the facial nerve. Since only normal fibers were found in the sensory roots of the facial and glossopharyngeal nerves, he concluded that these degenerated fibers came from the trigeminal nerve.

In some surgical cases involving the removal of the ganglion semilunare, Cushing noted that there was no loss of taste in the distal end of the tongue, and concluded therefrom, that the chorda tympani must carry gustatory sensations from the region of the tongue through the ganglion geniculi. Furthermore some experimental work by Hunt, demonstrated that tactile sensations may be present in the tip of the tongue after severing the nervus lingualis, centrally, to the exit of the chorda tympani.

Bruce in 1898, had an opportunity of studying a Marchi series of a human medulla in which a tumor, after having destroyed the trigeminal nerve, completely severed the glossopharyngeal nerve in the jugular foramen, without injuring the vagus. His series demonstrated degenerated glossopharyngeal fibers entering the upper end of the tractus solitarius, which disappeared, caudally, by terminating in the gelatinous substance belonging to the vagus nerve; not a single fiber was traced to the dorsal nucleus or the nucleus ambiguus. Bruce concluded that the upper part of the tractus solitarius belongs to the glossopharyngeal nerve and the lower two-thirds to the vagus nerve. His figure 2, which is from the spinal medullà region, demonstrates a few glossopharyngeal fibers in the tractus solitarius.

Van Gehuchten has given us a most comprehensive work on the nerve components of the tractus solitarius in the rabbit, and my own investigation on this phase of the problem is largely a repetition of this work extended a little further along some lines. A separate review of Van Gehuchten's work will not be included for the reason that frequent reference will be made to it throughout the text.

MATERIAL AND METHODS

The reasons for selecting the guinea pig for these investigations were essentially the same as those set forth in a previous paper (Jour. Comp. Neur., vol. 30, p. 176). For this study it was advisable to have at least three Marchi series of the medulla, showing in one series, on one side, the radix sensibilis nervi facialis in degeneration; a second series, in which the radix sensibilis nervi glossopharyngei of the same side was in degeneration; and a third series having the radix sensibilis nervi vagi also of the same side in degeneration. In fact, I had a number of Marchi series of each of the three components of the left tractus solitarius, one series of a rabbit's medulla where the fibers of the left radix sensibilis nervi glossopharyngei et vagi were degenerated, and a number of series where the tractus solitarius had been cut at different levels. There were also available many Marchi series, which demonstrated the neighboring tracts, such as, the radix descendens nervi vestibularis, radix spinalis nervi trigemini, tractus spino-cerebellaris dorsalis et ventralis, lemniscus medialis, corpus restirforme, brachium conjunctivum, fasciculus longitudinalis medialis, and various motor roots in dengeneration. Then for comparison, the writer had a number of Weigert, Nissl, Golgi, and Cajal series of normal guinea pig's brains.

Operations: The general method of conducting the operations was the same as was described in detail in the paper cited above. For the sake of uniformity, all of the lesions were made on the left side.

In the experiments designed to produce degeneration of the facialis portion of the tractus solitarius (no. 136 and others) an incision was made through the skin, immediately behind and below the left ear. The nervus facialis was carefully dissected to its entrance or exit from the foramen stylomastoideum; from whence it was jerked out with a hemostat, after the technique employed by Van Gehuchten; this carried out about an inch of the nerve from the foramen, including the ganglion geniculi. In other operations, equally good results were obtained, though with more difficulty, by dissecting out the nervus facialis to and including its ganglion, with the aid of a small pair of bone forceps.

The operation intended to bring about the degeneration of the glossopharyngeal component of the tractus solitarius was by far the most difficult of all the operations to perform, due partly to the close proximity of the nervus glossopharyngeus to the vagus and its ganglia and partly to the general inaccessibility of the nervus glossopharyngeus in curving around behind the tympanic bulla. The skin incision was made a little median to the angle of the left mandibula. After reflecting the skin, the salivary and lymph glands were separated from the musculus masseter, bringing into view the posterior belly of the m. digastricus and the nervus hypoglossus traversing its median surface. Carefully separating the nerve from the m. digastricus and expanding the opening exposes the nervus glossopharyngeus crossing the outer surface of the m. stylopharyngeus, which can be followed with some difficulty along the median ventral surface of the tympanic bulla in front of the nervus vagus and ganglion nodosum to the foramen jugulare. After carefully separating the nervus glossopharyngeus from the vagus, the nervus glossopharyngeus and ganglia were jerked from the foramen without injuring the vagus at or above its ganglia.

The general technique employed in destroying the sensory root fibers of the nervus vagus was identical to that used for destroying the glossopharyngeal sensory root fibers. It was, however, much easier to accomplish for the reason that it was not necessary to go in so deep. All that was necessary was to follow the nervus vagus to the ganglion nodosum and to sever the root fibers centrally to the ganglion, without injuring the glossopharyngeal root fibers or its ganglia.

In order to sever the tractus solitarius I made a median incision through the skin of the occipital and neck region. After turning the skin to either side, the median incision was continued through the muscles of the neck to the depth of the median occipital crest and dorsal arch of the atlas. Next the capitus muscles were severed close to the base of the skull and turned to either side, which exposes the membrane covering the foramen occipitale magnum. With a small pair of bone forceps some of the squamus portion of the os occipitale was clipped off in front of the occipital foramen on the right or opposite side from which the lesion is to be made, after which the free cephalic border of the membrane covering the foramen occipitale magnum was seized with a small pair of curved forceps, and turned backward at the same time cutting it free from the skull and atlas with a very small scalpel. This brings into view the entire dorsal surface of the medulla up to the cerebellum. Finally the cerebellum was gently lifted up from the medulla and a shallow lesion was made through the left tractus solitarius, being careful not to injure any of the dorsal tracts or nuclei approximating it. For making this lesion I filed down a piece of $\frac{1}{16}$ in. steel wire in the form of a chisel and bent it at an angle of about 45°, parallel to, and about one inch from the blade.

Microscopical technique. Ordinarily the animal was killed on the 14th day after the operation. According to my experience with the Marchi method, the maximum degeneration appears in mammals about the 11th day, and it is best not to let the animal live more than 14 days after the operation, for the reason that retrograde degeneration will take place from the central motor nuclei, as a result of the chromatolysis of their cells, which will assume considerable proportions by the 18th day. Upon removal the brain was placed in a dish of water, where the cerebral hemispheres were severed and discarded, but leaving the corpus striatum intact with the brain stem. This portion of the brain was then placed in a 3 per cent solution of potassium bichromate for 4 days, from whence it was removed after a superficial hardening, to strip off the dorsal part of the cèrebellar cortex and to cut up into transverse blocks of about 5 or 6 mm. in thickness. (If this procedure, which was necessary for the complete infiltration of osmic acid, was delayed much longer, there was danger of the brain stem becoming brittle and crumbling in making these sections.) These blocks were returned to a 3 per cent solution of potassium bichromate for a period of about 2 weeks to complete the infiltration; from which they were removed to a solution composed of 30 cc. of 3 per cent potassium bichromate plus 10 cc. of 1 per cent osmic acid, for about 3 weeks. Finally these blocks were thoroughly washed in water, dehydrated, thoroughly infiltrated with celloidin, cut 50 microns in thickness, and mounted serially.

TRACTUS SOLITARIUS (PARS NERVI FACIALIS)

A comparison of figure 3 with Van Gehuchten's figure discloses a close resemblance in the guinea pig and the rabbit of the passage of the radix sensibilis nervi facialis or nerve of Wrisberg through the medulla to form the tractus solitarius. About the only difference is that the VII root of the guinea pig separates into four instead of three bundles or rootlets in traversing dorso-ventrally, through the dorsal portion of the radix spinalis nervi trigemini (*Sp.V.*) and its sensory nucleus (*Sp.V.N.*) to reunite medially of the dorso-medial corner of the radix spinalis nervi trigemini in forming the tractus solitarius (*T.S.*). From the dorsal reconstruction, figure, 1A, it is obvious that the four

EXPLANATION OF FIGURES

Figures 1 and 2 are from graphic reconstructions, the remainder are from portions of transverse sections, or in a few instances, from a combination of several adjacent sections.

The graphic reconstructions were made after a method given in an earlier paper (Quart. Journ. Micro. Sci., vol. 59, pp. 352–3). In each case the median sagittal plane of the medulla was chosen for the projection line (*P–L*). The marginal scale is in terms of centimeters, each division equalling 1 cm. In these figures the degenerated components of the tractus solitarius are represented by parallel lines and motor nuclei as irregular coarse dots. The limits of sensory nuclei may be indicated by outlines or their cells may be shown as circles. The boundaries of normal nerve roots entering the tractus solitarius, the radix spinalis nervi trigemini and tract *Z* are drawn in outline; while the borders of the radix descendens nervi vestibuli are shown by very fine dotted lines.

All of the drawings from the transverse sections were made with the aid of a projection drawing apparatus. In these figures degenerated fibers appear as black dots; other structures were drawn in sepia or in case of the sensory nuclei of the IX and X nerves were left in white.

ABBREVIATIONS

B., In fig. 1A, most cephalic nervus facialis fibers and collaterals to the nucleus tractus solitarii. In fig. 1B, most cephalic nervus glossopharyngeus fibers and collaterals to the nucleus tractus solitarii. In fig. 1C, most cephalic nervus vagus fibers and collaterals to the nucleus tractus solitarii

C. C., canalis centralis

C. F., commissural fibers

Com. N., nucleus commissuralis or ganglion commissurale

Cor. Sp. D., tractus cortico-spinalis dorsalis or dorsal pyramidal tract

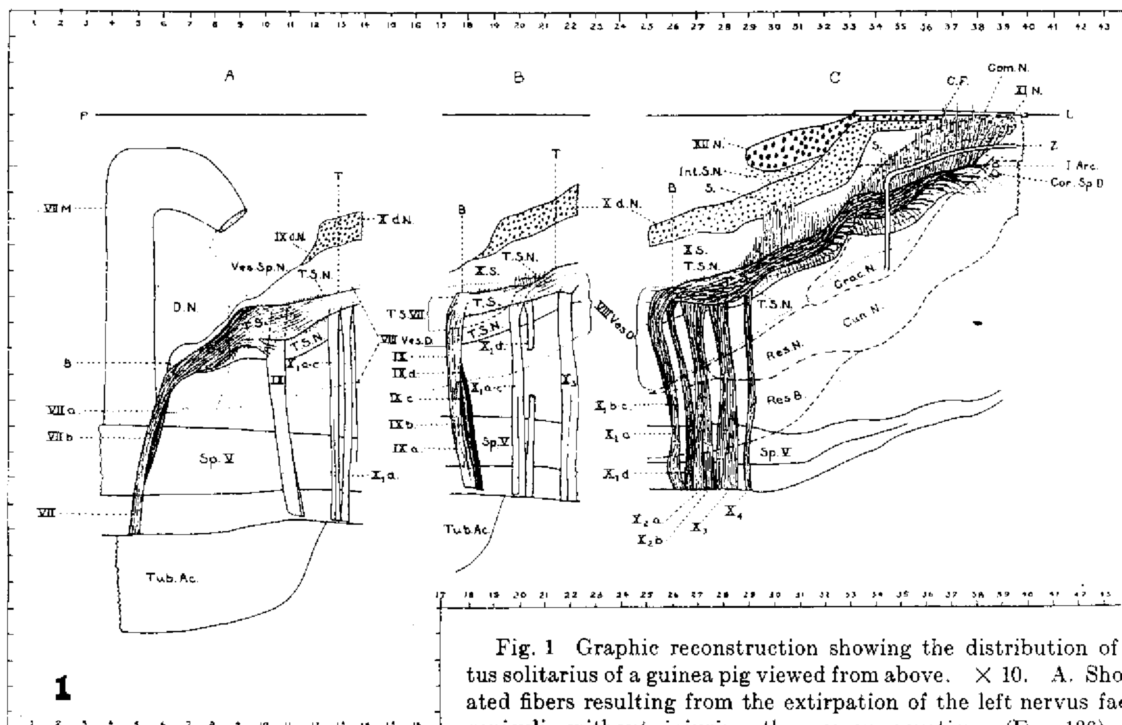
C. Trap., corpus trapezoideum

Cun. N., nucleus fasciculi cuneati or *nucleus of Burdach*

D. Coc. N., nucleus nervi cochlearis dorsalis or dorsal cochlear nucleus

Dec. Pyr., decussatio pyramidum or decussation of the pyramids

D. I. Arc., fibrae arcuate dorsales or dorsal internal arcuate fibers
D. N., nucleus nervi vestibularis lateralis or Deiters nucleus
E. Arc., fibrae arcuatae externae or external arcuate fibers
F. R., formatio reticularis
F. R. L., formatio reticularis lateralis
F. R. M., formatio reticularis medialis
Grac. N., nucleus fasciculi gracilis or nucleus of Goll
I. Arc., fibrae arcuatae internae or internal arcuate fibers
Int. S. N., nucleus intercalatus Staderini
Lem. M., lemniscus medialis or median lemniscus
Mon. N., nucleus Monakow of Winkler's descriptions
Ol. I., nucleus olivaris inferior or inferior olive
P-L., projection line in reconstructions 1 and 2
P. S. N., nucleus parasolitarius
Pyr., tractus cortico-spinalis or pyramis
Res. B., corpus restiforme
Res. N., nucleus proprius corporis restiformis
S., tractus solitarius fibers to nucleus motorius dorsalis nervi vagi
Sp. V., tractus spinalis nervi trigemini or radix spinalis nervi V
Sp. V. N., nucleus tractus spinalis nervi trigemini or substantia gelatinosa trigeminal root
St. Ac., striae acusticae or medullares
T., In fig. 1A, termination of facialis fibers in the tractus solitarius. In fig. 1B, termination of glossopharyngeal fibers in the tractus solitarius
T. S., tractus or fasciculus solitarius
T. S. VII., tractus solitarius (pars nervi facialis)
T. S. IX., tractus solitarius (pars nervi glossopharyngei)
T. S. X., tractus solitarius (pars nervi vagi)
T. S. N., nucleus tractus solitarii
Tub. Ac. tuberculum acusticum
V. Coc. N., nucleus nervi cochlear ventralis or ventral cochlear nucle
Ves. Crb., direct fibrae vestibulae-cer bello
Ves. Sp. N., nucleus nervi vestibulari spinalis
Z., tractus Z
VII, radix sensibilis nervi facialis o nerve of Wrisberg
VIIa-d., rootlets of radix sensibili nervi facialis
VII M., radix motorius nervi faciali (pars secunda)
VII M. N., nucleus motorius nervi facialis
VII T. S., In fig. 1B, tractus solitarius (pars nervi facialis)
VIII Ves., radix nervi vestibularis
VIII Ves. D., radix descendens nervi vestibularis and tractus arcuatus Russell
IX, radix sensibilis nervi glossopharyngei
IXa-d, rootlets of radix sensibilis nervi glossopharyngei
IXd. N., nucleus motorius dorsalis nervi glossopharyngei
IX M., radix motorius nervi glossopharyngei
IX S., nucleus sensibilis nervi glossopharyngei
Xd. N., nucleus motorius dorsalis nervi vagi
X M., radix motorius nervi vagi
Xv. N., nucleus ventralis nervi vagi or nucleus ambiguus
X_1 *a-d*, rootlets of the first radix sensibilis nervi vagi
X_2, second radix sensibilis nervi vagi
X_2 *a-b*, rootlets of the second radix sensibilis nervi vagi
X_3, third radix sensibilis nervi vagi
X_4, fourth radix sensibilis nervi vagi
XI N., nucleus nervi accessorii or caudal continuation of the nucleus motorius dorsalis nervi vagi
XII, radix nervi hypoglossi
XII N., nucleus nervi hypoglossi



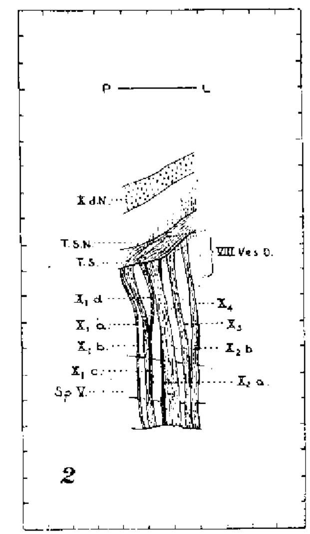


Fig. 1 Graphic reconstruction showing the distribution of the components of the left tractus solitarius of a guinea pig viewed from above. × 10. A. Shows the distribution of degenerated fibers resulting from the extirpation of the left nervus facialis, centrally to the ganglion geniculi, without injuring the nervus acusticus (Ex. 136). B. Illustrates the course of degenerated fibers resulting from pulling out the left nervus glossopharyngeus centrally to its ganglia, without injury to the vagus (Ex. 156). C. Demonstrates the distribution of degenerated fibers caused from severing the left nervus vagus centrally to the ganglion nodosum, without injury to the glossopharyngeal roots or ganglia (Ex. 121).

Fig. 2. Graphic reconstruction showing the arrangement of the sensory roots of the vagus in a different guinea pig (Ex. 132) from the one from which figure 1C was drawn; introduced to show individual variation of the vagus roots. × 6.6.

rootlets (*a-d*) are situated one above the other and that they assume a slightly caudal direction in penetrating the medulla. In agreement with Koelliker and Van Gehuchten these rootlets pursue a parallel but ventral course to a number of radix nervi vestibularis bundles, and might readily be confused with them if the two were not differentiated by the Marchi stain.

Especial note should be made of the close association of the facial and vestibular roots and to the many direct fibrae vestibulae-cerebello (fig. 3, *Ves.Crb.*) entering the cerebellum, and to the fact that no degenerated radix sensibilis nervi facialis fibers are seen going to the cerebellum in this series or in any other series where the facialis fibers were in degeneration. In fact, no degenerated fibers were observed going to the cerebellum when all the components of the tractus solitarius (VII, IX and X sensory roots) were in degeneration. There is no branching of the facialis sensory fibers into superior and inferior branches as is characteristic of the sensory fibers of the trigeminus. All make a sharp caudal bend and continue in a general caudal direction. The degenerated particles of myelin are very minute, which is probably indicative of finely medullated sheaths.

Figures 3 to and including 6 are from sections of the same guinea pig series as reconstruction 1A (Ex. 136) taken at various intervals from higher to lower levels intended to illustrate the distribution and relationships of the left radix sensibilis nervi facialis.

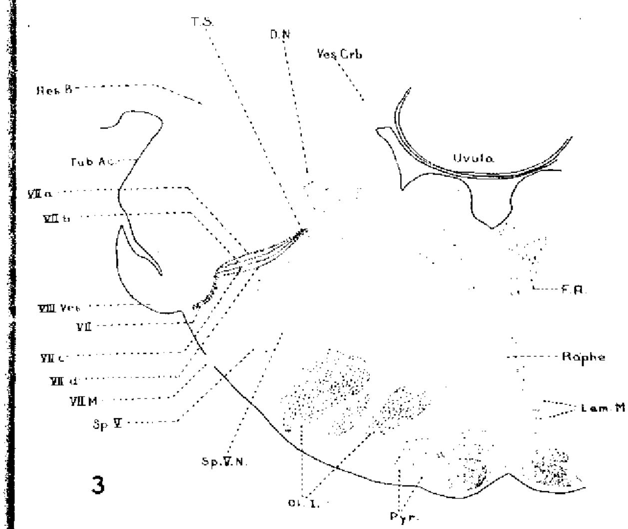
Fig. 3 Left half of a transverse section at the level of the facial and vestibular nerve roots, on which were projected the degenerated fibers of the left radix sensibilis nervi facialis shown in the previous three sections and the following four sections. × 4.

Fig. 4 Rather highly magnified drawing of the left tractus solitarius from a section of the same series as figure 3, taken a short distance from the origin of the tractus solitarius. In reconstruction 1A this section would be situated in the 7th cm. plane. × 45.

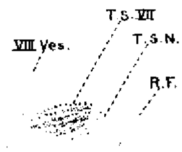
Fig. 5 Left half of a transverse section from the 9th cm. plane in reconstruction 1A. × 4.

Fig. 6 Left tractus solitarius region from the same series as figure 3 at the level of the radix sensibilis nervi glossopharyngei. × 18.

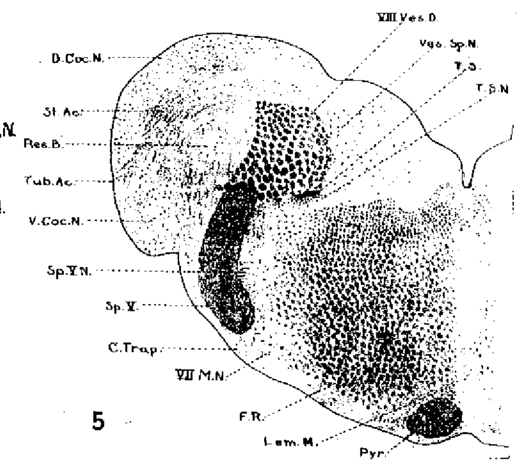
Fig. 7 Reconstruction and projection of the four rootlets of the left radix sensibilis nervi glossopharyngei, taken from five sections of the same series as figure 1B and drawn on the most median section. In this series (no. 156) the left nervus glossopharyngeus was jerked out of its foramen so as to include both of its ganglia. × 4.


T.S.
D.N
Ves.Crb
Res.B.
Uvula
Tub.Ac.
VII a
VII b
VIII Ves.
VII
VII c
VII d
VII M
Sp.V
Sp.V.N.
F.R.
Raphe
Lem.M.
Ol. I.
Pyr.

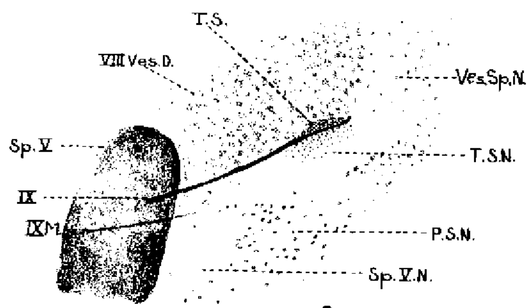
3


T.S.VII
VIII Ves.
T.S.N.
R.F.

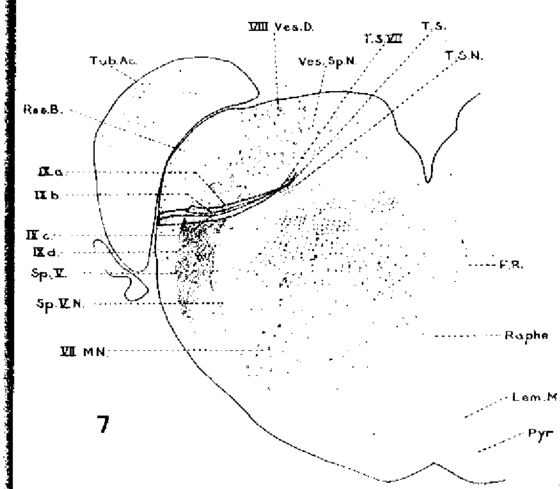
4


VIII Ves.D.
Ves.Sp.N.
T.S.
T.S.N
D.Coc.N.
St.Ac.
Res.B.
Tub.Ac.
V.Coc.N.
Sp.V.N.
Sp.V.
C.Trap.
VII M.N.
F.R.
Lem.M.
Pyr.

5


T.S.
VIII Ves.D.
Ves.Sp.N.
Sp.V
T.S.N.
IX
IX M.
P.S.N.
Sp.V.N.

6


VIII Ves.D.
T.S.VII
T.S.
Tub.Ac.
Ves.Sp.N.
T.S.N.
Res.B.
IX a
IX b
IX c
IX d
Sp.V.
Sp.V.N.
F.R.
Raphe
VII M.N.
Lem.M.
Pyr

7

The general course of the facialis portion of the tractus solitarius of the guinea pig conforms very closely to Van Gehuchten's description of the rabbit, namely, it is in no sense a solitary tract, being at first closely associated with the radix spinalis nervi trigemini and later with the radix descendens nervi vestibularis. Reconstruction 1A demonstrates the tractus solitarius as taking origin at the 6th cm. plane; then for 3 cm. it passes rapidly mesad, and maintains this general position for some distance caudad. A transverse section through the 9th cm. plane (fig. 5) portrays the tractus solitarius (*T.S.*) situated ventrally in the ventromedian corner of the radix descendens nervi vestibularis. To acquire this median position the tractus solitarius gradually crossed the ventral border of the vestibular root. At its origin (fig. 4) the tractus solitarius is oval in section, but in the 9th cm. plane (fig. 5) it has become greatly flattened horizontally.

Differing from Van Gehuchten's description of the rabbit, the tractus solitarius of the guinea pig is accompanied from its very beginning by a terminal sensory nucleus, which in figure 4 is a small light area (*T.S.N.*), situated medially and ventrally to the tractus solitarius. At the level of the 9th cm. plane in figure 1A this nucleus (fig. 5) broadens out laterally under the tractus solitarius, and gradually increases in size caudally until at the level of the entrance of the IX sensory root (fig. 6) it has assumed enormous proportions. Here it is more or less continuous with a larger ventral nucleus, the nucleus parasolitarius (*P.S.N.*).

At its origin (figs. 1A and 4) the nucleus tractus solitarii receives a few degenerated facialis fibers. These are probably collaterals rather than terminal fibers. On a level with the 9th cm. plane in reconstruction 1A (fig. 5) there are many degenerated fibers in the nucleus tractus solitarii. The maximum number of degenerated facialis fibers found in this nucleus occurs in the region of the entrance of the IX sensory root (fig. 6). From this level caudad, the number gradually decreases until very few are present at the level of the entrance of the first root of the X nerve. Before the IX root is received, the tractus solitarius gives off at least two bundles of fibers for the nucleus tractus solitarii. The first of these bundles is a dorsal fasciculus, which leaves the tractus solitarius at the 7.5th cm. plane in figure 1A and extends about 2 cm. in this reconstruction before ending in the nucleus tractus solitarii. This bundle is shown in transverse section in figure 5, where it would be undifferentiated from the bundles of the radix descendens nervi vestibularis, but for the Marchi stain. The second bundle is given off laterally and ventrally from the tractus solitarius at the level of the 9th cm. plane in figure 1A.

Two places on the facialis portion of the tractus solitarius are of especial interest, namely, the entrance of the IX and the first X sensory roots. Inasmuch as their mode of entrance is almost identical, a description of the IX will suffice for the X. Figure 6 demonstrates the normal glossopharyngeal fibers crossing under the degenerated facialis fibers of the tractus solitarius, in part they intermingle with the facialis fibers, but chiefly they add to the width and height of the tractus solitarius, making it crescent-shaped at the ventro-median corner of the radix descendens nervi vestibularis. Contrarily, Van Gehuchten on page 9 of his second paper and in figure 20 of the same paper, represents the IX sensory root as forming a fasciculus, lateral to the nerve of Wrisberg.

No more degenerated facialis fibers appear in the tractus solitarius or its nucleus at the level of the entrance of the second radix sensibilis nervi vagi than are present on the opposite or normal side. The writer would place their ending at the point marked (*T*) in figure 1A; which will be seen to be some distance cephalad of the termination of these fibers in the tractus solitarius of the rabbit as determined by Van Gehuchten. The difference in levels of the ending of the facialis fibers in the tractus solitarius in the guinea pig and the rabbit may be accounted for by the fact that, since the nucleus tractus solitarii began much further cephalad in the guinea pig, it consequently might be expected to terminate further cephalad, thereby bringing about an earlier ending of the tractus solitarius fibers.

TRACTUS SOLITARIUS (PARS NERVI GLOSSOPHARYNGEI)

It is apparent from a superficial examination of the radix sensibilis nervi glossopharyngei in reconstructions 1B and 7 that there is a close resemblance to the radix sensibilis nervi facialis, but many differences from Van Gehuchten's figure 4 of the IX sensory root of the rabbit. Like the facialis root, the degenerated particles of myelin are very small, indicative of minute medullary sheaths.

Transverse reconstruction 7 shows the radix sensibilis nervi glossopharyngei of the guinea pig breaking up into three small bundles upon entering the medulla. Before penetrating the tractus spinalis nervi trigemini, the most dorsal bundle separates into two; so that there are at least four distinct bundles or rootlets of degenerated radix sensibilis nervi glossopharyngei fibers (*IXa-d*) traversing the dorsal portion of the tractus spinalis nervi trigemini (*Sp.V.*) and its sensory nucleus (*Sp.V.N.*). The most dorsal of these bundles, rootlet (*a*), crosses the ventral surface of the radix descendens nervi vestibularis (*VIII Ves. D.*). Rootlets (*b*) and (*c*) unite and their common stem joins dorsally with (*a*), forming a common bundle that soon receives rootlet (*d*) from below. This common fasciculus curves around the ventral and median surfaces of the normal facialis fibers of the tractus solitarius, in part to intermingle with them, but mainly to continue caudad, median and dorsal to them.

Since Van Gehuchten's figure 4 shows such a different arrangement of the rootlets of the IX sensory root within the medulla, it seemed advisable to make a reconstruction of this root from a rabbit's series where the IX and X nerves were in degeneration. This reconstruction (fig. 8) demonstrates an arrangement of four rootlets (*a-d*) more closely resembling the disposition shown in reconstruction (fig. 7) than Van Gehuchten's figure 4. The chief point of difference in the rabbit, as shown in figure 8, consists of an earlier union of rootlets (*a-c*) and the consequent elongation of the combined bundle. It should be recorded that a small portion of the delicate rootlet (*d*) appears in a number of sections, so that it is highly probable that this rootlet would have been overlooked if a reconstruction had not been made.

Throughout the entire course of the glossopharyngeal portion of the tractus solitarius, the tractus solitarius continues to occupy the ventro-median corner of the radix descendens nervi vestibularis. Caudally, it gradually acquires a more dorsal position, to become located medially, in the dorso-ventral corner of the vestibular root. A highly magnified drawing (fig. 9) of the left tractus solitarius from a section immediately behind the entrance of the radix sensibilis nervi glossopharyngei, demonstrates degenerated glossopharyngeal fibers (*IX T.S.*) median to the normal facialis fibers (*VII T.S.*), ventrally, and median to the radix descendens nervi vestibularis fibers, dorsally. It is impossible in this section to discriminate between facialis and descending vestibular bundles, but after examining a similar section from a series where the facialis portion of the tractus solitarius was in degeneration, it is safe to affirm that those bundles designated as (*VII T.S.*) in figure 9 are facialis bundles of the tractus solitarius. At the level of the entrance of the first radix sensibilis nervi vagi (fig. 10) the normal fibers of this root (X_1) are clearly shown below and median to the degenerated glossopharyngeal fibers (*T.S. IX*). Some of the vagus fibers apparently intermingle with the glossopharyngeal fibers but the majority retain their ventral and median positions.

A section taken from the level of the entrance of the third radix sensibilis nervi vagi demonstrates but few degenerated glossopharyngeal fibers in the tractus solitarius or in its nucleus. A section taken immediately caudal of the entrance of the fourth radix sensibilis nervi vagi exhibits no more degenerated glossopharyngeal fibers in the left tractus solitarius or its nucleus than are present on the normal or right side. In the guinea pig the writer would place the caudal ending of the glossopharyngeal fibers, both in the tractus solitarius and its sensory nucleus, opposite the entrance of the third radix sensibilis nervi vagi in the tractus solitarius (fig. 1B, *T.*). This is considerably cephalad of Van Gehuchten's level for the termination of these fibers in the rabbit.

In addition to the previous notes on the termination of the glossopharyngeal fibers in the nucleus tractus solitarii it should be recorded that a few degenerated glossopharyngeal fibers were found in this nucleus opposite the entrance of this root (figs. 1B and 7, *T.S.N.*), and at the level of the entrance of the first vagus root (fig. 10, *T.S.N.*) they were very abundant.

In another Marchi series (No. 161) where a lesion had severed the IX sensory root in its course through the tractus spinalis nervi trigemini, without injuring the tractus solitarius or the X sensory roots, the distribution of the IX sensory fibers in the medulla is identical to those series in which the IX nerve was severed centrally to the ganglia.

It is clear from all sections taken from the region of the entrance of the various sensory roots of the X nerve (fig. 10) that the gray area (white in the figures), situated below and median to the tractus solitarius, and known generally as the dorsal nucleus of the glossopharyngeal and vagus nerves, has assumed such proportions and complications that it merits separate consideration. Van Gehuchten described it on p. 186 as a clear oval spot, traversed by fasciculi belonging to the acoustic nuclei. These

Fig. 8 Similar projection to figure 7, but from a rabbit series (no. 143), where the nervus glossopharyngeus had been severed centrally to its ganglia. To obtain this reconstruction of the radix sensibilis nervi glossopharyngei it was necessary to utilize eleven sections and project them on a drawing of the most median section. × 4.

Fig. 9 From the same guinea pig series as figures 1B and 7 taken through the left tractus solitarius a short distance after the receipt of the left radix sensibilis nervi glossopharyngei. × 45.

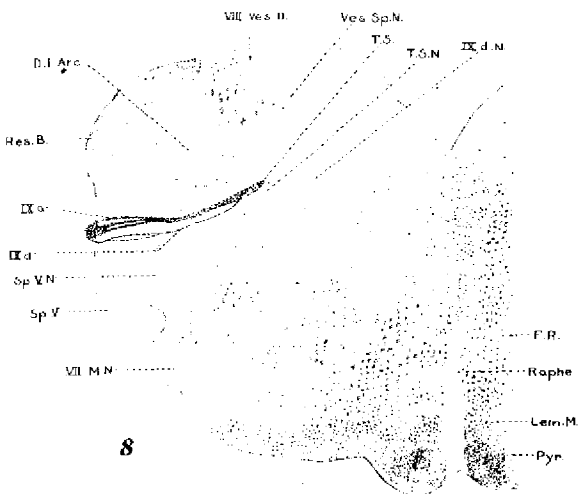
Fig. 10 Portion of a transverse section from the same series as figure 7, including the union of the first radix sensibilis nervi vagi with the tractus solitarius. × 18.

Figs. 11–19 are from transverse sections of a guinea pig's medulla (Ex. 121), where the vagus had been severed centrally to the ganglion nodosum without injuring the glossopharyngeal roots or ganglia.

Fig. 11 A reconstruction of the rootlets of the first left radix sensibilis nervi vagi taken from eleven different sections and projected on a drawing of the most median section. × 4.

Fig. 12 Reconstruction and projection of the second left radix sensibilis nervi vagi taken from seven transverse sections of the same series as figures 1C and 11 and projected on a drawing of the most median section. × 4.

Fig. 12A More highly magnified view of the left tractus solitarius taken from a section of the same series as above, directly below the level of the second left radix sensibilis nervi vagi. × 45.



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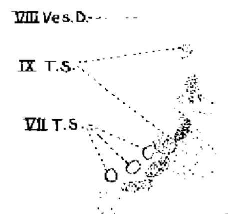

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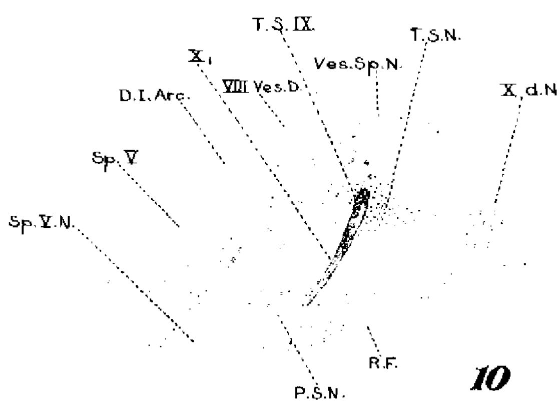

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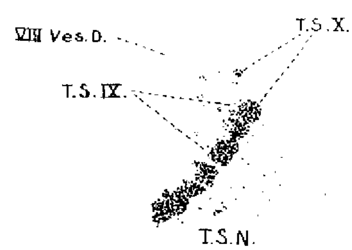
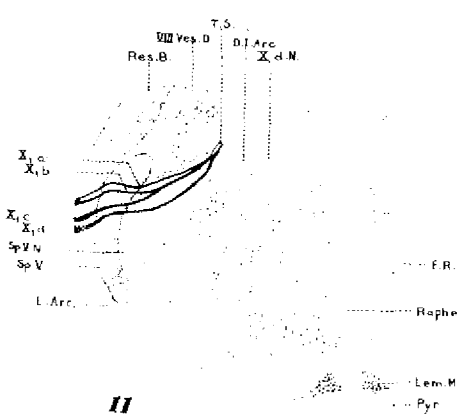
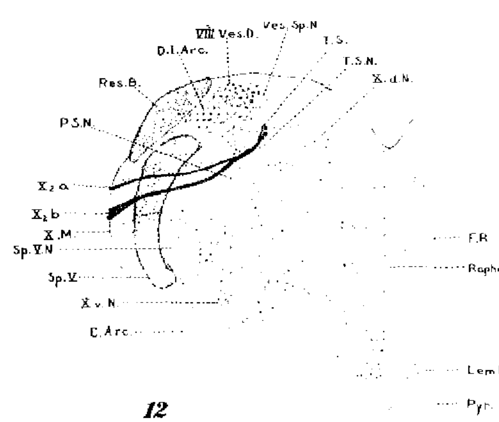


12A



11



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fibers were said to divide the gray mass into two parts: an internal mass of small cells, the motor nucleus; and an external part, the terminal cells of the tractus solitarius. Van Gehuchten's sensory nucleus can readily be subdivided into central and periphereal areas. The former is composed only of small cells possessing little or no Nissl substance and receives few or no degenerated fibers from the tractus solitarius. The latter or more lateral area is situated mainly median and ventral to the tractus solitarius. It includes a few medium-sized cells and numerous degenerated fibers from the tractus solitarius in addition to the small cells described for the more median area. According to von Monakow these larger cells, which contain Nissl substance, are undoubtedly the cells of origin of the secondary visceral tract to the thalamus. It is possible, then, to divide the so-called dorsal glossopharyngeal and vagus nucleus into three parts: A median area, the nucleus motorius dorsalis nervi vagi[1] a lateral area approximating the tractus solitarius, the nucleus tractus solitarii; and an intermediate area composed only of small cells, which may function as a visceral reticular nucleus.

TRACTUS SOLITARIUS (PARS NERVI VAGI)

As was noted by Van Gehuchten, the passage of the vagus sensory fibers through the medulla to the tractus solitarius is very different from either the glossopharyngeal or the facial. Instead of being composed of a single fasciculus or root, separating more or less into several bundles or rootlets, the vagus fibers enter the tractus solitarius through several distinct fasciculi or roots. The relative number of sensory fibers of the X nerve, which contains few, if any, taste fibers is much greater than the combined VII and IX fibers. Also the degenerated particles of myelin are much coarser, indicating thicker medullated sheaths.

According to my interpretation of the vagus sensory complex, there are at least four distinct fasciculi or roots entering the tractus solitarius in the guinea pig. In series 121, the first radix

[1] That this nucleus was in reality a motor nucleus was determined by sectioning the IX and X nerves peripherally to their ganglia and studying this nucleus for chromatolysis and also by tracing retrograde motor fibers to it.

sensibilis nervi vagi (reconstructions 1C and 11) consists of four bundles or rootlets (X_1a-X_1d). The first three rootlets (fig. 1C, X_1a-X_1c) are very closely associated and are situated in about the same vertical plane. In figure 11 rootlets (X_1a-X_1c) pass dorso-ventrally, one above the other, through the fibrae arcuatae externae (*E. Arc.*), to penetrate the dorsal portion of the tractus spinalis nervi trigemini (*Sp.V.*) and its sensory nucleus (*Sp.V.N.*). The most dorsal of these roots (X_1a) continues across the ventral border of the radix descendens nervi vestibularis (*VIII Ves.D.*). Rootlets (X_1b and X_1c) unite in the dorsal part of the nucleus tractus spinalis nervi trigemini and the common stem continues dorso-medially, to unite dorsally with rootlet (X_1a) a short distance from the tractus solitarius. Rootlet (X_1d), which will later be demonstrated to be a somewhat irregular bundle, is situated in figure 1C midway between rootlets (X_1a-c) and rootlet (X_2a), and when about to reach the tractus solitarius, it bends cephalad and dorsad to join the combined trunk of rootlets (X_1a-X_1c). This common fasciculus is shown in figure 11 passing under the normal glossopharyngeal fibers of the tractus solitarius (*T.S.*) to constitute the beginning of the vagus portion of the tractus solitarius, obviously situated median and ventrally to the glossopharyngeal portion of the tractus solitarius.

The second radix sensibilis nervi vagi appears as two medium-sized bundles (X_2a and X_2b) in the dorsal reconstruction, figure 1C, situated one behind the other and pursuing an almost median course. Transverse reconstruction (fig. 12) demonstrates rootlet (X_2b) considerably ventrad as well as caudad of rootlet (X_2a). It occupies almost the same horizontal plane as rootlet (X_1d). Reconstructions 1C and 12 show these two rootlets uniting in a common fasciculus close to the tractus solitarius, which in turn crosses under the tractus solitarius. It is apparent from figure 12a that the tractus solitarius is composed mainly of degenerated vagus fibers from the first two roots (*T.S. X*), immediately behind the entrance of the second vagus root and that the few remaining glossopharyngeal fibers (*T.S. IX*) are situated laterally to the vagus fibers. At the level of figure 12 there are but few degenerated vagus fibers in the nucleus tractus solitarii (*T.S.N.*). A motor root (*X. M.*) will be seen ventrally to rootlet (X_2b).

The third radix sensibilis nervi vagi is a large fasciculus in this series (figs. 1C and 13, X_3) situated caudad to (X_2b). Since its course is directly median, it can be followed in one section (fig. 13) traversing the fibrae arcuatae externae (*E.Arc.*), the dorsal part of the tractus spinalis nervi trigemini (*Sp.V.*) and its sensory nucleus (*Sp.V.N.*); thence across the ventral surface of the radix descendens nervi vestibularis (*VIII Ves.D.*) and the tractus solitarius (*T.S.*), to acquire a position in the tractus solitarius median and ventral to the degenerated fibers of the first two sensory roots of the vagus. It is obvious that there are but few degenerated vagus fibers in the nucleus tractus solitarii (*T.S.N.*) at this level. The fourth and last radix sensibilis nervi vagi (figs. 1C and 14, X_4) is also a single bundle in this series, but differs from the preceding root in being notably smaller and assuming a more caudal direction in its median course to join the tractus solitarius. As a result only a part of it appeared in any one section and it was necessary to utilize three sections to obtain figure 14. It will be seen that (X_4) pursues a more dorsal course than root (X_3), but terminates in the tractus solitarius in like manner.

It is reasonable to suppose that there would be some, if not considerable, variation in the arrangement and number of the roots and rootlets of the sensory part of the vagus. To determine the amount of individual variation, a dorsal reconstruction was made of the sensory roots of the vagus from another guinea pig's

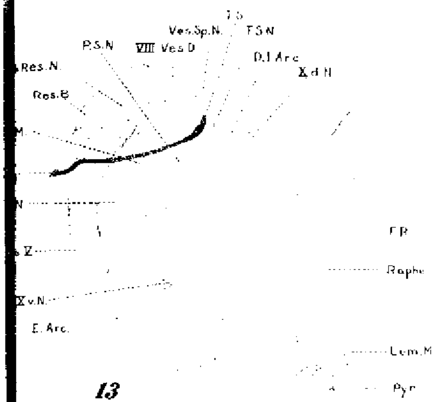
Fig. 13 Left half of a transverse section from the same series as figure 11 at the level of the entrance of the third radix sensibilis nervi vagi. × 4.

Fig. 14 Reconstruction of the fourth left radix sensibilis nervi vagi from three sections of the same series as figures 1C and 11 projected on a drawing of the middle section. × 4.

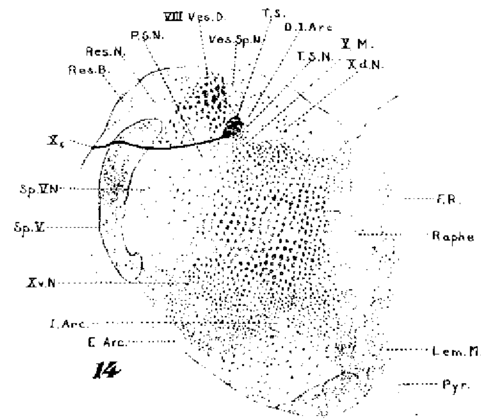
Fig. 15 Portion of the left half of a transverse section from the same series as figure 11, situated in the 30th cm. plane in reconstruction 1C. × 12.

Fig. 16 Left tractus solitarius and adjacent structures from the same series as figure 11, taken from the 32.5 cm. plane in figure 1C or about four sections cephalad of the passage of the ventriculus quartus into the canalis centralis. × 12.

Fig. 17 Left half of a transverse section through the spinal portion of the medulla. In reconstruction 1C this section would lie in the same plane that tractus (*Z*) crosses the tractus solitarius. × 4.


T.S.
Ves.Sp.N.
T.S.N
P.S.N
VIII Ves.D
D.I.Arc
Res.N.
X d N
Res.B
F.R
Raphe
X v.N.
E. Arc.
Lem.M
Pyr

13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Res.N.
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X d.N.
Res.B.
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F.R.
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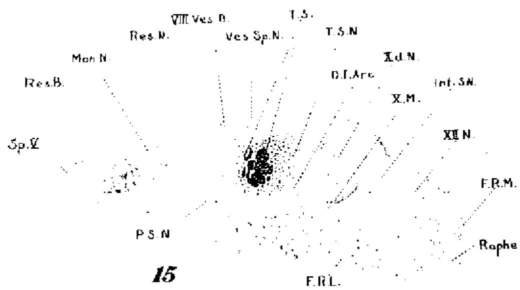
Raphe
X v.N
I. Arc.
E. Arc.
Lem.M.
Pyr.

14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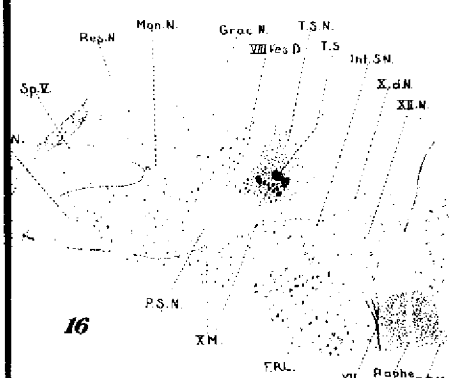
F.R.M.
P.S.N
Raphe
F.R.L.

15


Mon.N.
Res.N
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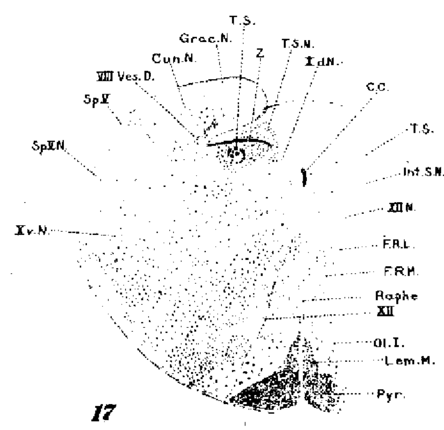
VIII Ves.D
T.S
Int.S.N.
Sp.V.
X d.N.
XII.N.
N.
P.S.N.
X M.
F.R.L.
XII
Raphe
F.R.M.

16


T.S.
Grac.N.
T.S.N.
Cun.N.
Z
X d.N.
VIII Ves.D.
C.C.
Sp.V
T.S.
Sp.V N.
Int.S.N.
XII N.
X v.N.
F.R.L.
F.R.M.
Raphe
XII
Ol.I.
Lem.M.
Pyr.

17

series (no. 132), in which the nervus vagus had likewise been severed centrally to the ganglion nodosum. This reconstruction (fig. 2) when compared with figure 1C discloses surprisingly little variation. The same roots and rootlets are present and a similar arrangement is maintained; some irregularity, however, occurs in connection with rootlet (X_1d). This rootlet will be seen in figure 2 to be closely associated with the other rootlets of this root during the first part of its course through the medulla, but upon approaching the tractus solitarius, it bends caudally to enter the tractus solitarius directly in front of the second radix sensibilis nervi vagi. Future investigation may reveal it best to consider this rootlet as a separate root of the vagus sensory complex. In figure 2 the two rootlets of the second radix sensibilis nervi vagi (X_2a and X_2b) are in about the same vertical plane, in place of (X_2b) being situated at a lower level as in figure 1C. Also in figure 2 the roots (X_3) and (X_4) are about the same size, instead of (X_3) being much the larger.

Throughout the general area of the passage of the sensory vagus roots through the tractus spinalis nervi trigemini there are possibly a few more degenerated fibers in the left tract than in the right, but no degenerated fibers were observed leaving the sensory roots of the vagus to enter the tractus spinalis nervi trigemini. Possibly if the nervus vagus had been severed centrally to the ganglion jugulare, some degenerated general cutaneous fibers would have appeared in the tractus spinalis nervi trigemini. The nucleus parasolitarius is of considerable size in this region, but no degenerated tractus solitarius fibers were distributed to it. There was no bunching of the motor roots in this area, as is characteristic of the sensory roots.

Tractus solitarius proper: Caudally to the entrance of the fourth and last radix sensibilis nervi vagi, the tractus solitarius (pars nervi vagi) as it is from this point caudad, is a true solitary tract. This tract gradually assumes a more median position, is constantly giving off fibers and collaterals until its supply is exhausted in the neighborhood of the decussatio pyramidum, and can conveniently be divided into three parts for descriptive purposes.

The first of these areas is shown in figure 1C to extend from the 29th to the 32d planes. In this region, the tractus solitarius (*T.S.*), its sensory nucleus (*T.S.N.*) and the nucleus motorius dorsalis nervi vagi (*Xd.N.*) are gradually acquiring a more median position in passing caudad. It is a locality where many degenerated fibers are given off to the nucleus tractus solitarii (*T.S.N.*), and at the center of this area, extending between the 29.5th and the 31st cm. planes, some degenerated tractus solitarius fibers or collaterals continue medially into the nucleus motorius dorsalis nervi vagi (*S*). A transverse section taken through the center of this area (fig. 15) discloses the tractus solitarius to be a compact cylindrical bundle, excepting the extreme lateral portion, which is beginning to display a tendency to break up into smaller bundles. It is obviously well separated from the ventro-median corner of the radix descendens nervi vestibularis (*VIII Ves.D.*) by a portion of the nucleus tractus solitarii. The descending vestibular tract has become greatly reduced in size. A number of fibrae arcuatae dorsales (*D.I.Arc.*), cross above, below and even through the tractus solitarius. Many degenerated tractus solitarius fibers and collaterals are present in the nucleus tractus solitarii (*T.S.N.*), which at this level not only surrounds the tractus solitarius, but extends some little distance medially and dorso-medially. Practically all of the area between the tractus solitarius and the nucleus motorius dorsalis nervi vagi contains degenerated fibers, and a string of degenerated fibers extends into the motor nucleus (*Xd.N.*). There are also some degenerated fibers in a radix motorius nervi vagi (*X M.*) and in the ventro-median part of its nucleus, caused from the chromatolysis of the motor cells, resulting from severing the nervus vagus. No degenerated tractus solitarius fibers were seen in the nucleus parasolitarius (*P.S.N.*) or in the nucleus nervi vestibularis spinalis (*Ves.Sp.N.*).

The second or middle area of the true tractus solitarius is short, extending from the 32d to the 33d cm. planes in figure 1C. It is characterized by its abrupt median turn, and by its breaking up laterally into many small bundles. Since the 33d cm. plane in figure 1C marks the level of the termination of the ventriculus quartus into the canalis spinalis, this marked median turn of the tractus solitarius simply conforms to the general contour of the medulla rapidly tapering down into the medulla spinalis. Figure 16, which is from the 32.5 cm. plane in figure 1C, at the level where the medulla is about to enter the medulla spinalis, demonstrates very clearly the migration of all structures medially. The nucleus motorius dorsalis nervi vagi (*Xd.N.*) is near the median sagittal plane, dorsad of the nucleus nervi hypoglossi (*XII N.*). The radix descendens nervi vestibularis (*VIII Ves.D.*) has been reduced to a very small tract, which from a Marchi series after a cerebellar lesion, is shown to be composed almost entirely of tractus arcuatus Russell or fasciculus cerebello-bulbarius fibers at this level. The tractus solitarius has been separated still further from the radix descendens nervi vestibularis by the increase in size of the nucleus tractus solitarii, laterally. It is broken up laterally into many small bundles, which branch and rebranch to terminate, dorsally, ventrally and medially, but especially dorsally in the nucleus tractus solitarii (*T.S.N.*). This nucleus has assumed considerable proportions about the tractus solitarius, dorsally and medially. No degenerated tractus solitarius fibers were found in the nucleus motorius dorsalis nervi vagi (*Xd.N.*), but a few retrograde degenerated motor fibers were present in this nucleus and in a radix motorius nervi vagi (*X.M.*).

The third and last area of the true tractus solitarius is an area of considerable importance that is confined solely to the medulla spinalis. Here the tractus solitarius pursues only a slightly median course; it is rapidly breaking up into small bundles, which soon exhaust themselves in the nucleus tractus solitarii and neighboring nuclei.

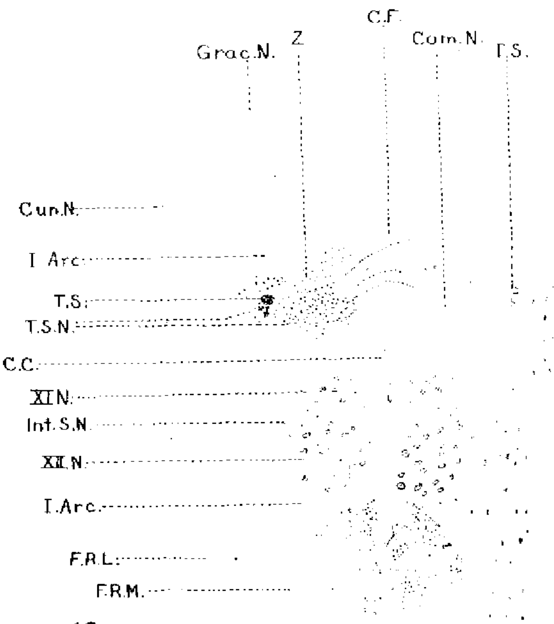
A level of especial interest is shown in figure 17, which is from the 34.5 cm. plane in figure 1C and through the transverse arm of a tract designated as tractus (*Z*). In this region the nucleus motorius dorsalis nervi vagi (*Xd.N.*) is lateral to the canalis centralis, more or less separated from the nucleus nervi hypoglossi (*XII N.*), below, by the nucleus intercalatus Staderini (*Int.S.N.*). Dorsal and lateral will be seen the tractus solitarius (*T.S.*), here completely isolated, circular in outline and composed of a number of small scattered bundles of degenerated fibers. Numerous degenerated tractus solitarius fibers are present in the nucleus tractus solitarii (*T.S.N.*), situated mainly median and dorso-median of the tractus solitarius. This nucleus has maintained its original size, but occupies a more median position, overlying the nucleus motorius dorsalis nervi vagi to some extent, and it is perfectly clear that degenerated tractus solitarius fibers extend into the dorso-lateral corner of this motor nucleus (fig. 17, *Xd.N.* and indicated by *S* in fig. 1C). Also in the rabbit series degenerated fibers appear in the dorso-lateral corner of the nucleus motorius dorsalis nervi vagi at this level. The tractus solitarius and its sensory nucleus is bounded dorsally and laterally in figure 17 by the nucleus fasciculi gracilis (*Grac.N.*), the nucleus fasciculi cuneati (*Cun.N.*) and by the radix descendens nervi vestibularis (*VIII Ves.D.*), here reduced to a small fasciculus composed mainly of tractus arcuatus Russell fibers.

A tract, which might readily be taken for a part of the tractus solitarius in Weigert sections of this region, is a bundle designated previously as tractus (*Z*), for the reason that its relationships have not been fully established. It apparently takes origin from the nucleus cuneatus or nucleus proprius corporis restiformis, the level varying somewhat in different individuals. As shown in figures 1C and 17, it bends abruptly caudad after crossing the tractus solitarius dorsally. Then for some distance it pursues a caudal course, dorso-mesad, of the tractus solitarius, to ultimately bend ventrad, parallel with a bundle of cortico-spinalis dorsalis fibers, with which it decussates, and apparently enters the pyramis rather than the lemniscus medialis. If so, it is probably a descending tract. Sometimes this tract is present on both sides, but often it is confined to one side, and may consist of one or more bundles. To determine accurately the course and relationships of this tract it should be studied from a series showing this tract in degeneration. It is possible that future study may show tractus (*Z*) to be the same as Kosaka and Yagita's fasciculus solitario-spinalis of the dog or Hirose's bulbospinale tract of the rabbit.

The remainder of the tractus solitarius is largely concerned with its termination in the nucleus commissuralis or ganglion commissurale. Figure 18, which is from a level immediately in front of the 37th cm. plane in figure 1C, demonstrates the tractus solitarius (*T.S.*) directly ventrad of a bundle of fibrae arcuate internae (*I.Arc.*) and a little lateral and ventral to tractus (*Z*). It is reduced to a few small bundles of degenerated fibers. The terminal sensory nucleus of the tractus solitarius (*T.S.N.*) not only surrounds the tract at this level, but extends inward to the mid-line to meet the corresponding nucleus of the opposite side. This common nucleus is usually termed the nucleus commissuralis or ganglion commissurale (*T.S.N.* or *Com.N.*). From figure 18 it is apparent that this nucleus receives a very rich supply of degenerated tractus solitarius fibers. It is also obvious that very few of these degenerated fibers cross to the opposite side as commissural fibers (*C.F.*). Most of these fibers are shown in figure 1C. In this series the commissural fibers were mainly normal fibers, taking origin apparently from the nuclei of the general reticular substance; for in another Marchi series, where the reticular substance was destroyed at this level, there were many more degenerated commissural fibers. In the rabbit series not a single degenerated tractus solitarius fiber was seen crossing to the opposite side in the region of the nucleus commissuralis, and no commissural fibers are shown in Van Gehuchten's figure 18, which is a section from this region. In fact, the entire number of commissural fibers is relatively small in mammals, as was demonstrated from a Marchi series where the entire nucleus commissuralis was severed longitudinally on one side. At this level the nucleus commissuralis is situated considerably dorsad of the nucleus nervi accessorii or caudal continuation of the nucleus motorius dorsalis nervi vagi (*XI N.*) and no degenerated tractus solitarius fibers were observed near this nucleus.

Fig. 18 Dorso-central portion of a transverse section through the medulla spinalis from the same series as figure 11. This section passes through the nucleus commissuralis and in figure 1C would lie in the plane (*C.F.*). × 18.

Fig. 19 Left half of a transverse section from the same series as above at a level of the decussatio pyramidum, situated in the 39th cm. plane in figure 1C. × 6.


C.F.
Grac.N.
Z
Com.N.
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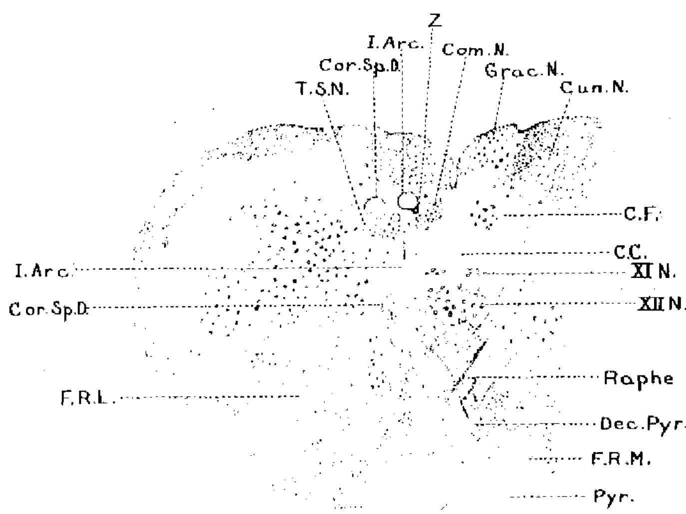
Cun.N.
I. Arc.
T.S.
T.S.N.
C.C.
XI N.
Int.S.N.
XII N.
I.Arc.
F.R.L.
F.R.M.

18


Z
I.Arc.
Com.N.
Cor.Sp.D.
Grac.N.
T.S.N.
Cun.N.
C.F.
I.Arc.
C.C.
XI N.
Cor.Sp.D.
XII N.
Raphe
F.R.L.
Dec.Pyr.
F.R.M.
Pyr.

19

From the region of the 34th cm. plane in figure 1C, caudad, the tractus solitarius (*T.S.*) becomes reduced from very small bundles to individual fibers. In figure 19, which is from the 39th cm. plane in figure 1C, through the decussatio pyramidum, there are a few degenerated tractus solitarius fibers in the caudal end of the nucleus commissuralis (*Com.N.*) and a few in the region occupied by the tractus solitarius in more cephalic sections (*T.S.N.*). The degenerated fibers in the area of the nucleus commissuralis terminate in the third or fourth section caudal to figure 19, while the more lateral area of degenerated tractus solitarius fibers continues a few sections further caudad in the general reticular area. In figure 19, tractus (*Z*), a bundle of fibrae arcuatae internae (*I.Arc.*) and a bundle of tractus cortico-spinalis dorsalis fibers (*Cor.Sp.D.*) will be seen between these two areas of degenerated tractus solitarius fibers and the nucleus fasciculi gracilis and the n. fasciculi cuneati. No degenerated fibers are present in the nucleus nervi accessorii, which is situated lateral to the canalis centralis and dorsal to the nucleus nervi hypoglossi. Both the fibrae arcuatae internae and the tractus cortico-spinalis dorsalis are decussating, and since both are normal fibers it is difficult to discriminate between them. Tractus (*Z*) does not make its ventral bend until a lower level is reached.

SUMMARY AND GENERAL CONSIDERATIONS

As in other mammals, the tractus solitarius in the guinea pig is made up of descending sensory fibers from the VII, IX and X nerves. It begins at the level of the entrance of the radix sensibilis nervi facialis and extends caudally to the level of the decussatio pyramidum. This tract permits of a division into two almost equal parts at about the entrance of the third or fourth radix sensibilis nervi vagi. The cephalic portion is embedded in the ventro-lateral corner of the radix descendens nervi vestibularis, is an area for the reception of sensory root fibers and distributes both gustatory and general visceral sensations to a primary sensory nucleus. On the other hand, the caudal portion is isolated from the radix descendens nervi vestibularis, receives no sensory roots and distributes no gustatory fibers to its sensory nucleus. Caudally the tractus solitarius breaks up into small bundles, which terminate in the nucleus tractus solitarii.

Two of the three components of the tractus solitarius, namely, the radix sensibilis nervi facialis and the radix sensibilis nervi glossopharyngei, are very similar; both separate into at least four bundles or rootlets in traversing the medulla, to reunite in a common fasciculus that gives rise to, or enters the tractus solitarius. No facialis fibers appear in the tractus solitarius caudal to the entrance of the first radix sensibilis nervi vagi, and no glossopharyngeal fibers are present in the tractus solitarius caudal to the entrance of the third radix sensibilis nervi vagi.

In the guinea pig four distinct sensory fasciculi or roots of the X nerve were recognized. The first two are composed of from two to four bundles or rootlets and are readily comparable to the sensory roots of the VII and IX nerves; while the last two consist of one bundle each.

The various roots entering into the formation of the tractus solitarius, cross ventrally the previously formed portion of the tractus solitarius and for the most part continue caudally median to it. This signifies that the VII fibers could be separated laterally from the tractus solitarius with little injury to the IX fibers, and likewise the IX with little injury to the first root of the X. It was recorded, however, that there was some intermingling of these root fibers.

None of the sensory fibers of the VII, IX or X (having cell bodies in the ganglion nodosum) nerves are distributed anywhere but to the tractus solitarius.

If the relative size of degenerated myelin is any indication of the corresponding thickness of medullary sheaths, the VII and IX sensory fibers would be finely medullated and the X would be coarse.

In the guinea pig the nucleus tractus solitarii extends throughout the entire length of the tractus solitarius. At first it is a light area situated ventro-medially to the tractus solitarius, which soon expands, joining other nuclear masses in the formation of the so-called dorsal vagus nucleus. This oval nuclear mass can be divided into three parts: A median mass of cells, the nucleus motorius dorsalis nervi glossopharyngei et vagi; a lateral mass of cells next to the tractus solitarius, the nucleus tractus solitarii; and an intermediate mass of small cells may represent a visceral reticular nucleus for short relays in the medulla. Caudally to the entrance of the last sensory root of the vagus the nucleus tractus solitarii assumes enormous proportions, dorsally and medially, to ultimately unite with its fellow in the spinal portion of the medulla in forming the nucleus commissuralis.

It was noted that the maximum number of facialis tractus solitarius fibers are dispensed to the nucleus tractus solitarii opposite the entrance of the IX sensory root, and that none are found opposite the entrance of the first vagus sensory root. Between the entrance of the IX and first X sensory roots, numerous glossopharyngeal tractus solitarius fibers are distributed to the nucleus tractus solitarii, but none appear caudal to the entrance of the third vagus sensory root. Very few vagus tractus solitarius fibers are present in the nucleus tractus solitarii opposite the entrance of the vagus sensory roots. Caudad, these fibers become very abundant, especially in the nucleus commissuralis.

In at least two places vagus fibers or collaterals are distributed from the tractus solitarius to the nucleus motorius dorsalis nervi vagi (fig. 1, *S.*). One of these areas is in the caudal part of the medulla and the other is in the medulla spinalis. In many other places the neurons of this motor nucleus would not have to possess very long dendrites to come in contact with fibers from the tractus solitarius.

No fibers or collaterals from the tractus solitarius were seen in the nucleus nervi hypoglossi, in the nucleus parasolitarius, or in the nucleus nervi vestibularis spinalis.

A so-called tractus (*Z*), which may be the same as Kosaka and Yagita's fasciculus solitario-spinalis or Hirose's bulbospinale tract, was briefly mentioned on account of its intimate association with the tractus solitarius in the medulla spinalis region.

Since practically all, if not all, of the taste fibers are carried by the VII and IX nerves, and these fibers have ended in the tractus solitarius at the level of the entrance of the third radix sensibilis nervi vagi, it is evident that no part of the tractus solitarius of the guinea pig, caudal of this level, is concerned with conducting taste sensory impulses. It must be associated with general visceral and possibly muscle sense. Visceral or smooth muscle sense will be included under general visceral sensations. Such endings have been described by Ploshko between the smooth muscle bundles of the trachea, by Carpenter in the longitudinal muscle of the stomach and intestine, and by Larsell in the smooth muscle of the bronchial tree. Parts or all of the nucleus tractus solitarii, cephalad of the entrance of the third radix sensibilis nervi vagi into the tractus solitarius, must also relay nervous impulses of general visceral and possibly muscle sense in addition to those of taste.

The description of the entrance, disposition and distribution of the VII, IX and X nerves in the tractus solitarius suggests an original segmental grouping of these roots, corresponding to the existing segmental arrangement of the motor roots throughout the medulla. Apparently certain segmentally arranged sensory roots have been massed in three places and joined with little intermingling, in forming the tractus solitarius, which extends caudad to the level of the first cervical nerve. To reproduce the original primitive segmental condition, all that would be necessary would be to scatter the sensory roots of the VII, IX and X nerves into the intervals between and caudal of these roots, where no sensory root fibers are penetrating the medulla.

If any reduction has occurred in the sensory system of the medulla in mammals, it is in connection with the somatic and not the visceral system.

As a result of this study the writer has been impressed with the possibilities of the caudal part of the medulla and the medulla spinalis as a region for correlating the vital activities of the body.

LITERATURE CITED

Ariëns Kappers, C. U. 1920 Die Vergleichende Anatomie des Nervensystems der Wirbeltiere und des Menschen. 1 Abschnitt. Haarlem.

Autore, P. 1915 Morphologia e svilluppo del nucleo dorsale del vago in Sus scopha. Monit. Zool. Ital. An. 26, p. 134.

Beccari, N. 1922 Studi comparitivi sulla struttura del Rhombencefalo. Arch. Ital. di Anat. e di Emb. Vol. 19, fasc. 1–2, pp. 122–291.

Berkelbach van der Sprenkel, H. 1915 The central relations of the cranial nerves of Silurus glanis and Mormyrus caschive. Jour. Comp. Neur., vol. 25, pp. 5–63.

Bok, S. T. 1915 Die Entwicklung der Hirnnerven und ihrer Zentralen Bahnen. Folia Neuro-biol., Bd. 9, S. 475–565.

Bregmann, L. E. 1892 Ueber experimentelle aufsteigende Degeneration motorischer und sensibiler Hirnnerven. Arb. a. d. Inst. f. Anat. u. Physiol., Wien.

Bruce, A. N. 1898 On the dorsal or so-called sensory nucleus of the glossopharyngeal nerve and nuclei of origin of the trigeminal nerve. Brain, vol. 21, pp. 383–387.

Carpenter, F. W. 1918 Nerve endings of sensory type in the muscular coat of the stomach and small intestine. Jour. Comp. Neur., vol. 29, pp. 553–559.

Cushing, H. 1903 The taste fibers and their independence of the nervus trigeminus. Johns Hopkins Hosp. Bull., vol. 14, pp. 71–78.

Held, H. 1892 Die Endigungsweise der sensibilen Nerven im Gehirn. Arch. f. Anat. u. Entwicklungsgeschichte, S. 33–40.

Herrick, C. J. 1905 The central gustatory paths in the brains of bony fishes. Jour. Comp. Neur., vol. 15, pp. 375–456.

1907 On the commissura infima of the brains of fishes. Anat. Rec., vol. 1, p. 88.

1908 On the commissura infima and its nuclei in the brains of fishes. Jour. Comp. Neur., vol. 18, pp. 409–431.

1914 The medulla oblongata of larval Amblystoma. Jour. Comp. Neur., vol. 24, pp. 343–427.

Hirose, K. 1916 Über eine bulbospinale Bahn. Folia Neuro-biol., Bd. 10, S. 371–382.

His, W. 1887 Die Entwicklung der ersten Nervenbahnen beim menschlichen Embryo. Arch. f. Anat. u. Physiol., S. 367–378.

Holm, H. 1893 Die Anatomie und Pathologie des dorsalen Vaguskerns. Virchow's Arch., S. 78–120.

Hunt, J. R. 1909 The sensory system of the facial nerve, and its symptomatology. Journ. Nerv. and Mental Disease, vol. 36, pp. 321–350.

Johnston, J. B. 1901 The brain of Acipenser. Zool. Jahrb., Bd. 15, pp. 1–204.

1906 Nervous system of vertebrates. Philadelphia.

1902–1912 Various papers on the telencephalon of fishes. Jour. Comp. Neur.

Koelliker, A. 1896 Handbuch der Gewebelehre des Menschen. Leipzig.

KOHNSTAMM UND HINDERLANG 1910 Der Nucleus intermedius sensibilis als Ursprung einer gekreuzt aufsteigenden Bahn (Viszeralbahn?). Monatschr. Psych. Neurol., Bd. 28, S. 82–83. Also, Neurol. Centrabl., Bd. 29, S. 663.

KOSAKA, K. 1909 Ueber die Vaguskerne des Hundes. Neurol. Centralbl.

KOSAKA UND YAGITA 1905 Experimentelle Untersuchungen über den Ursprung des N. vagus und die centralen Endigen der dem Plexus nodosus entstammenden sensibilen Vagusfasern, sowie über den Verlauf ihrer sekundären Bahn. Shinkeiguku Zasshi, Tokyo, Bd. 4, S. 29–49.

LARSELL, O. 1922 The ganglia, plexuses and nerve terminations of the mammalian lung and the pleura pulmonalis. Jour. Comp. Neur., vol. 35, pp. 97–132.

MOLHANT, M. 1910 Le nerf vague, étude anatomique et expérimentale. Le Névraxe, T. 11, pp. 137–249.

MÖLLGAARD, H 1911 Eine morpologische Studie über den Nervenkomplex vago-glossopharyngeo-accessorius. Skand. Arch. f. Physiol., Bd. 25, S. 69–80.

1912 Studien über das respiratorische Nervensystem bei den Wirbeltieren. As above, Bd. 26, S. 315–383. Folia Neuro-biol., Bd. 6, S. 622–623.

MUCHIN, N. 1893 Der Nucleus dorsalis und der sensorische Kern des Nervus glossopharyngeus. Centrabl. f. Nervenh. u. Psych., Bd. 4, S. 212–217.

OBERSTEINER, H. 1912 Anleitung beim Studium des Baues der nervösen Zentralorgane. Leipzig.

PLOSCHKO, A. 1897 Die Nervenendigungen und Ganglien der Respirationsorgane. Anat. Anz., Bd. 13, S. 12–22.

POPE, F. M. 1889 Thrombosis of vertebral artery pressing on glossopharyngeal nerve; unilateral loss of taste at back of tongue. Brit. Med. Journ., vol. 2, pp. 1148–1149.

RAMÓN Y CAJAL, S. 1911 Histologie du système nerveux de l'homme et des vertébrés, Paris, T. 2.

RHINEHART, D. A. 1918 The nervus facialis of the albino rat. Jour. Comp. Neur., vol. 30, pp. 81–126.

ROLLER, C. F. W. 1881 Der centrale Verlauf des Nervus glossopharyngeus. Der Nucleus lateralis medius. Arch. f. Mikr. Anat., Bd. 19, S. 347–383.

SOLOMONSOHN, H. 1888 Ueber den Weg der Geschmacksfasern zum Gehirn. Reviewed, Neurol. Centrabl. Bd. 7, S. 295–296.

STADERINI, R. 1896 Ubicazione e rapporti di alcuni nuclei di sostanza grigia della midolla allungata. Internat. Monatschr. f. Anat. u. Physiol., Bd. 13, S. 326–357.

STILLING 1842 Ueber die Textur der Medulla oblongata. Quoted by Van Gehuchten.

TRICOMI-ALLEGRA, G. 1903 Sulle connessioni bulbari del nervo vago. Riv. d. patol. nerv., Firenze.

TUMBERLAKA, R. 1916 Konsekutive Veränderungen eines kleinen Herdes in dem ventro-lateralen Thalamuskern und das demselben zugrunde liegende klinische Bild. Psychiatrische en Neurologische Bladen. Amsterdam.

Turner, W. A. 1895 The central connections and relations of the trigeminal, vago-glossopharyngeal, vago-accessory, and hypoglossal nerves. Jour. Anat. and Physiol., vol. 29, pp. 1–15.

1897 Note on the course of the fibers of taste. Edin. Med. Journ., vol. 2, pp. 261–262.

Turner and Bullock 1894 Observations upon the central relations of the vago-glossopharyngeal, vago-accessory, and hypoglossal nerves, from a study of a case of bulbar paralysis. Brain, vol. 17, pp. 693–709.

Van Gehuchten, A. 1900 Le nerf intermédiaire de Wrisberg. Le Névraxe, T. 1, pp. 5–12.

1900 Le faisceau solitaire. Le Névraxe, T. 1, pp. 173–195.

1906 Anatomie du système nerveux de l'homme. Louvain.

Von Lenhossék, M. 1894 Das Ganglion geniculi Nervi facialis und seine Verbindungen. Quoted by Van Gehuchten.

Von Monakow, C. 1913 Zur Kenntnis der Grosshirnanteile (Vago-glosso-pharyngeusschleife, Fasc. bulbo-thal. II). Neurol. Centrabl., Bd. 32, S. 331–333.

Wallenberg, A. 1898 Des dorsale Gebiet der spinalen Trigeminuszwurzel und seine Beziehungen zum solitären Bündel beim Menschen. Deuche Zeitschr. f. Nervenheilkunde.

1907 Die kaudale Endigung der bulbo-spinalen Wurzeln des Trigeminus, Vestibularis, und Vagus beim Frosche. Anat. Anz., Bd. 30.

Weed, L. H. 1913 Reconstruction of the nuclear masses in the rhombencephalon. Anat. Rec., vol. 7, pp. 443–448.

Wilson, J. G. 1905 The structure and function of the taste buds of the larynx. Brain, vol. 28, pp. 339–357.

Winkler and Potter 1911 An anatomical guide to experimental researches on the rabbit's brain. A series of 40 frontal sections. Amsterdam.

1914 Same of the cat. Thirty-five frontal sections. Amsterdam.

Yagita, K. 1910 Experimental Untersuchungen über den Ursprung des Nervus facialis. Anat. Anz., Bd. 37, S. 195.

1914 Einige Experimente an dem Nervus petrosus superficialis major zur Bestimmung des Ursprungsgebietes des Nerven. Folia Neurobiol., Bd. 8, S. 361–382.

Ziehen, T. 1913 Anatomie des Centralnervensystems. II Abtheilung, Teil 1, Jena.