

## ORIGIN AND DESTINATION OF THE SECONDARY VISCERAL FIBERS IN THE GUINEA-PIG

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FIFTEEN FIGURES

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### INTRODUCTORY

The following paper, which is the second report on the general subject of comparing the visceral tracts of mammals with those of fishes and amphibians, will consist of a study of the distribution of fibers taking origin from the nucleus tractus solitarii. This problem has been approached from two angles: first, from a study of degenerated fibers resulting from a destruction of various portions of the terminal sensory nucleus of the tractus solitarius; and, secondly, from searching the nucleus tractus solitarii and its caudal expansion, the nucleus commissuralis, for chromatolytic cells, after severing certain tracts that contained these degenerated fibers or after destroying several suspected tertiary visceral nuclei.

## LITERATURE

Considerable evidence has accumulated suggesting the presence of visceral fibers, other than taste, in the forebrain and midbrain. There is general agreement in attributing respiratory functions to the nucleus commissuralis, but there is considerable difference of opinion as to the existence and location of definite heat and respiratory centers in higher areas.

As early as 1884, Ott claimed the existence of certain heat centers about the human corpus striatum. A year later he found that injuries to the anterior part of the thalamus resulted in a rise in temperature, and in 1889, these heat centers were extended to include an area about the Rolandic fissure. Richet, White, Tangl and Sinelnikow have also described rises in temperature in various animals, resulting from lesions in the region of the thalamus and corpus striatum. Howell and Austin found that stimulating the sigmoid gyrus in dogs gave a constant vaso-motor effect, and stimulating the caudate nucleus produced a marked rise in blood pressure with inhibition of respiratory movements. Prince and Hahn found a heat center in cats and rabbits, 5 mm. lateral of the sagittal suture and 5 mm. cephalad of the coronal suture, by stimulating this area with heat, while stimulating a similar region 5 mm. caudad of the coronal suture did not produce a corresponding thermal change. A number of other papers quoted by Sachs ('11) ascribe heat and respiratory centers to the thalamus. Mosso on the other hand attributed this rise in temperature to hemorrhages, excitement, and muscular contractions. Miss Moore also claims that the corpora striata of birds and rabbits are not essential for the maintenance of constant body temperature and doubts the existence of heat centers in the brain.

Sachs ('11) after electrical stimulation of many different parts of the thalamus and corpus striatum in some 60 cats, arrived at the conclusion, that "the optic thalamus contains no centers, which upon direct stimulation, produced changes in temperature." He maintains that the portion of the thalamus which causes changes of blood pressure and respiration are in the regions of the large afferent pathways, and since the results are very similar to those obtained from severing an afferent nerve, he assumes

that there are no circulatory and respiratory centers in the thalamus. Sachs found, however, that stimulating the nucleus lentiformis inhibits respiration.

Rogers observed that pigeons could maintain a normal temperature when placed in a cage at a temperature of from 4° to 38°C., and that decerebrated pigeons could also maintain a normal temperature when placed in a temperature of from 5° to 38°C. In contrast, when the optic thalamus of decerebrated birds was almost completely cauterized, the temperature regulating mechanism was so affected that the temperature of the bird was largely determined by its surroundings. In these pigeons the temperature was lowered to 19° or raised to 46°C., by varying the temperature from 10° to 38°C.

Apparently the reactions of the thalamus of pigeons are very different from those of mammals, and it is possible that there is as much difference in the functions of the thalamus of birds and mammals as there is between the functions of the colliculus superior of the lower vertebrates and mammals.

Lewandowsky, Brown, Treven, Miss Coombs, and others have indicated the possibility of a respiratory center or at least a respiratory relay station in the midbrain. Brown upon stimulating the colliculus superior in the region of the tractus tectospinalis obtained a rapid panting movement of the abdominal respiratory muscles of the monkey, which stopped when the stimulation stopped. Miss Coombs found that sectioning the colliculus inferior in the cat resulted in a deeper and slower respiration. Also severing the dorsal roots of the thoracic and cervical nerves produced a similar diminution of the costal respiration. A section of the colliculus inferior subsequent to sectioning the dorsal roots of the cervical and thoracic spinal nerves produced a greater effect on the costal respiration than severing the spinal roots alone; while the reverse order showed no more change than severing the colliculus inferior alone.

Van Gehuchten states in his textbook (pp. 853-5) that the Marchi method does not reveal any bulbo-thalamic or bulbo-cortical fibers arising from lesions in the region of the tractus solitarius. He is of the opinion that there must be a gustatory

tract to the cerebral cortex, but doubts the existence of ascending visceral fibers from the heart and larynx. Van Gehuchten, however, calls attention to the possible significance of certain direct and indirect reticular cerebellar fibers, described in a previous paper.

Kohnstamm and Hinderlang after severing the spinal cord and medulla in the region of the spino-cerebellar tracts, obtained chromatolysis of the cells of the nucleus intermedius and some of the cells lateral to the tractus solitarius. As a result of this experiment they regard the nucleus intermedius as the origin of a crossed ascending visceral tract.

Von Monakow after studying a series from a pathological brain, where an old blood clot had destroyed the optic thalamus and the central parietal region, was not only able to confirm the work of Spitzka and Dejerine that degeneration occurred in the cells of the dorsal medulla and spinal V nucleus, but in addition, found chromatolytic cells in the substantia gelatinosa of the tractus solitarius and in the formatio reticularis, and degenerated fibrae arcuatae internae. Von Monakow calls this new part of the lemniscus, the 'Vagoglossopharyngeusschleife.' It is said to carry sensory impulses from the jaws, bronchi, and possibly taste.

A number of papers having a general bearing on this subject have been listed in the bibliography, some of which will be quoted in the text.

#### 1. DEGENERATIONS RESULTING FROM THE DESTRUCTION OF DIFFERENT PARTS OF THE NUCLEUS TRACTUS SOLITARI

##### *Methods and technique*

The operation intended to bring about the destruction of the nucleus tractus solitarii was fully described in the first paper of this series. In some of the later experiments where it was not intended to trace degenerated fibers to the cerebellum, the caudal and some of the dorsal wall of the skull was removed and a chisel or needle was forced through the left side of the cerebellum, sufficiently deep, to sever the nucleus tractus solitarii. It is of course imperative to use a chisel having the same width as the nucleus and to confine the lesion to this nucleus; otherwise the series will

have to be discarded later. The animal was killed on the fourteenth day after the operation, and the brain prepared and sectioned serially, 50  $\mu$  thick, after the method described in the above mentioned paper. These lesions were made at different levels in the nucleus tractus solitarii; some of which were mere sections of this nucleus, while others represent extensive destructions of the nucleus.

*Descriptions of the lesions and resultant degenerations*

Series 99 is selected from a number of Marchi series to illustrate the distribution of degenerated fibers resulting from a destruction of the caudal end of the terminal sensory nuclei of the tracts solitarius. The lesion extends, cephalo-caudad, about the length of the nucleus commissuralis. Figure 1 is through the center of

EXPLANATION OF FIGURES

All transverse sections were drawn with the aid of a projection drawing apparatus, using a Leitz 42 mm. lens. The drawings of isolated cells were made with the aid of a camera lucida, using a Leitz 4 mm. apochromatic objective and a no. 6 compensating eyepiece.

ABBREVIATIONS

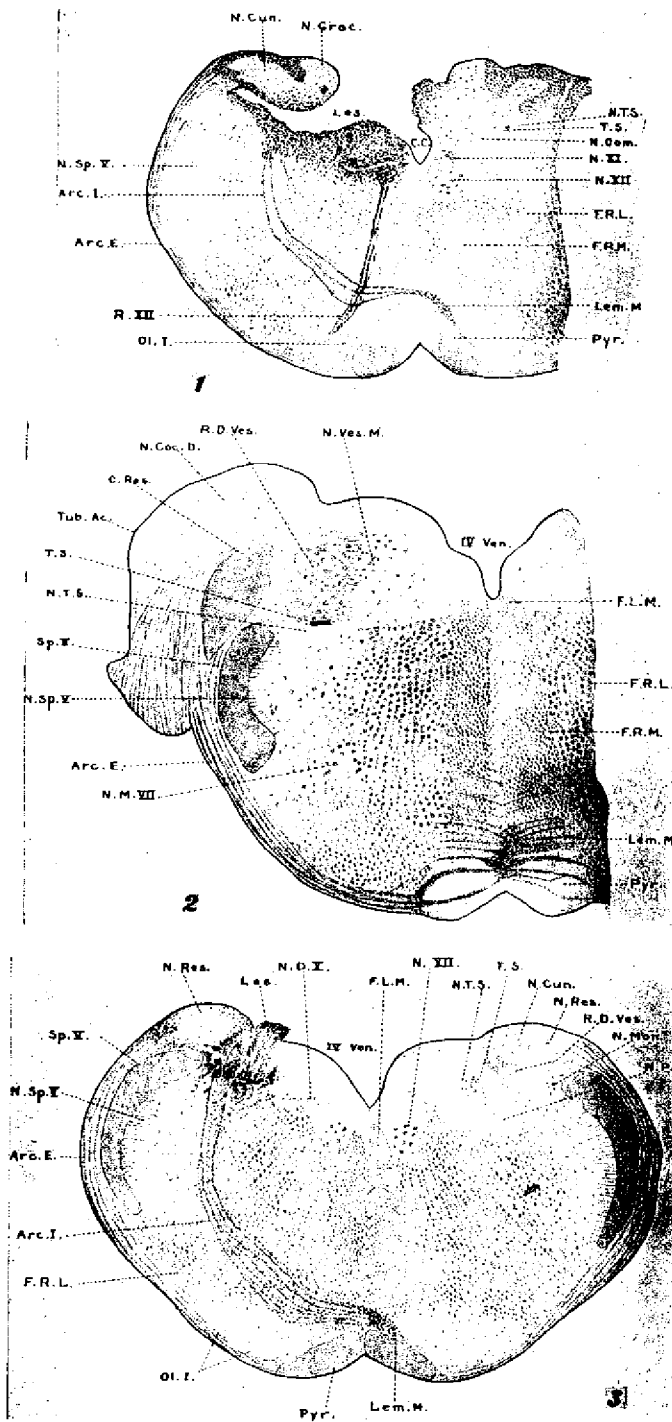
<i>Aq.</i> , aquaeductus cerebri (Sylvii)	<i>F.R.</i> , formatio reticularis
<i>Arc.D.</i> , fibrae arcuatae dorsales	<i>F.R.L.</i> , formatio reticularis lateralis
<i>Arc.E.</i> , fibrae arcuatae externae	<i>F.R.M.</i> , formatio reticularis medialis
<i>Arc.I.</i> , fibrae arcuatae internae	<i>G.Intp.</i> , ganglion interpedunculare
<i>Br.C.</i> , brachium conjunctivum	<i>Lam.V.</i> , lamina medullaris ventralis
<i>Br.P.</i> , brachium pontis	<i>L.Ans.</i> , lobulus ansiformis
<i>C.Ant.</i> , commissura anterior (cerebelli)	<i>Lem.M.</i> , lemniscus medialis
<i>C.C.</i> , canalis centralis	<i>Les.</i> , lesion
<i>C.Gen.L.</i> , corpus geniculatum laterale or dorsale	<i>Lin.</i> , lingula
<i>C.M.</i> , corpus mamillare	<i>M.S.F.</i> , degenerated fibers from dorsal nuclei of medulla intermingled with normal spino-cerebellaris dorsalis fibers in cerebellum
<i>Col.I.</i> , colliculus inferior	<i>n.</i> , normal cells
<i>C.Res.</i> , corpus restiforme	<i>N.Coc.D.</i> , nucleus nervi cochlearis dorsalis
<i>d.</i> , degenerated cells showing chromatolysis	<i>N.Com.</i> , nucleus commissuralis
<i>D.Br.C.</i> , decussation of the brachium conjunctivum	<i>N.Cun.</i> , nucleus fasciculi cuneati
<i>F.L.M.</i> , fasciculus longitudinalis medialis or posterior	<i>N.D.</i> , nucleus nervi vestibularis lateralis (Deiter's)
<i>F.M.T.</i> , fasciculus or tractus mamillo-thalamicus (Vicq d'Azyr)	<i>N.D.Br.C.</i> , nucleus dorsalis brachii conjunctivi
<i>For.</i> , columna descendens fornicis	

<i>N.Den.</i> , nucleus dentatus	<i>N.XI</i> , nucleus nervi accessorii or caudal continuation of the nucleus motorius dorsalis nervi vagi
<i>N.D.X.</i> , nucleus motorius dorsalis nervi vagi	<i>N.XII</i> , nucleus nervi hypoglossi
<i>N.Emb.</i> , nucleus emboliformis	<i>Ol.I.</i> , nucleus olivaris inferior
<i>N.F.</i> , nucleus fastigii or tecti	<i>Parafl.</i> , paraflocculus
<i>N.Glob.</i> , nucleus globosus	<i>Ped.Cer.</i> , pedunculus cerebri
<i>N.Grac.</i> , nucleus fasciculi gracilis	<i>Ped.C.M.</i> , pedunculus corporis mamillaris
<i>N.Lat.T.</i> , nucleus lateralis thalami	<i>Pyr.</i> , pyramis or tractus cortico-spinalis
<i>N.L.F.R.</i> , nucleus lateralis formatio reticularis	<i>R.D.Ves.</i> , radix descendens nervi vestibularis and tractus arcuatus (Russell)
<i>N.L.Lem.</i> , nucleus lemnisci lateralis	<i>R.M.VII</i> , radix motorius nervi facialis (pars secunda)
<i>N.Mon.</i> , nucleus Monakow of Winkler's descriptions	<i>R.M.X</i> , radix motorius nervi vagi
<i>N.M.VII</i> , nucleus motorius nervi facialis	<i>R.Subt.</i> , regio subthalamica or nucleus hypothalamicus
<i>Nod.</i> , nodulus	<i>R.Ves.</i> , radix nervi vestibularis
<i>N.P.D.</i> , nucleus pontis dorsalis	<i>R.III</i> , radix nervi oculomotorii
<i>N.P.S.</i> , nucleus parasolitaris	<i>R.V</i> , radix nervi trigemini
<i>N.P.V.</i> , nucleus pontis ventralis	<i>R.IX</i> , radix nervi glossopharyngei
<i>N.Res.</i> , nucleus proprius corporis restiformis	<i>R.XII</i> , radix nervi hypoglossi
<i>N.R.Mes.V</i> , nucleus of the radix mesencephalicus nervi trigemini	<i>Sp.C.D.</i> , tractus spino-cerebellaris dorsalis
<i>N.Rub.</i> , nucleus ruber	<i>Sp.C.D.</i> , tractus spino-cerebellaris dorsalis
<i>N.Sp.V</i> , nucleus tractus spinalis nervi trigemini	<i>Sp.C.V.</i> , tractus spino-cerebellaris ventralis
<i>N.T.S.</i> , nucleus tractus solitarii	<i>Sp.V.</i> , tractus or radix spinalis nervi trigemini
<i>N.V.Br.C.</i> , nucleus ventralis brachii conjunctivi	<i>St.Ac.</i> , striae acusticae or medullares
<i>N.Ven.T.</i> , nucleus ventralis thalami	<i>T.Hab.Ped.</i> , tractus habenulo-peduncularis
<i>N.Ves.M.</i> , nucleus nervi vestibularis medialis (Schwalbe)	<i>T.S.</i> , tractus or fasciculus solitarius
<i>N.Ves.Sp.</i> , nucleus nervi vestibularis spinalis	<i>Tub.Ac.</i> , tuberculum acusticum
<i>N.V.F.R.</i> , nucleus ventralis formatio reticularis	<i>Ves.Crb.</i> , fibrae vestibulae cerebelli
<i>N.III</i> , nucleus nervi oculomotorii	<i>IV.Ven.</i> , ventriculus quartus

Fig. 1 Transverse section from Marchi series No. 99, showing extent of the lesion through the left nucleus tractus solitarii and nucleus commissuralis, together with resultant degeneration. This figure is from approximately the same level as figure 18 of the previous paper.  $\times 8.3$ .

Fig. 2 Left half of a more cephalic section from the same series as figure 1, at the level of the tuberculum acusticum.  $\times 8.3$ .

Fig. 3 Transverse section from Marchi series 140, showing lesion through center of the general visceral division of the nucleus tractus solitarii, and resultant degeneration. This section is the sixth section above the union of the ventriculus quartus with the canalis centralis and at approximately the same level as figure 16 of the previous paper.  $\times 8.3$ .



the lesion and from about the same level as figure 18 of the previous paper. It shows a rather extensive area of destruction which includes the tractus solitarius (*T.S.*), its neighboring gray mass (*N.T.S.*), and the nucleus commissuralis (*N.Com.*), representing then the general area ventral to the nucleus fasciculi gracilis et cuneati (*N.Grac.* and *N.Cun.*). From the ventral border of this lesion degenerated *fibrae arcuatae internae* (*Arc.I.*) pass to the opposite lemniscus medialis (*Lem.M.*). Any section above this lesion, as figure 2, demonstrates many degenerated fibers in the opposite lemniscus medialis, but none elsewhere. It is obvious from this figure that no more than the normal number of degenerated fibers are present in either fasciculus longitudinalis medialis (*F.L.M.*) or in either corpus restiforme (*C.Res.*).

In series 162 the nucleus commissuralis was completely destroyed on one side and the inner margin of the nucleus fasciculi gracilis scraped slightly, but leaving the tractus solitarius and adjacent gray uninjured. In consequence of this lesion a few degenerated *fibrae arcuatae internae* pass from the nucleus fasciculi gracilis to the lemniscus medialis of the opposite side, but no degenerated fibers appear in either fasciculus longitudinalis medialis or in either corpus restiforme; and apparently there are no degenerated fibers going from the nucleus commissuralis to the lemnisci or to higher centers.

As a result of another superficial lesion (series 141), which involved the gray directly above the tractus solitarius, clipped the inner margin of the nucleus fasciculi gracilis, but missed the nucleus commissuralis; a few degenerated *fibrae arcuatae internae* go from the nucleus fasciculus gracilis to the opposite lemniscus medialis, but there are no degenerated fibers in the corpora restiformia or in the fasciculi longitudinales mediales.

It is probable, then, that nearly all, if not all, of the degenerated fibers found in the lemniscus medialis in the above mentioned series are secondary muscle sense fibers, taking origin from either the nucleus fasciculi gracilis or the nucleus fasciculi cuneati. If there are any ascending medullated visceral fibers arising from the caudal part of the nucleus tractus solitarii or the nucleus commissuralis, they appear in the opposite lemniscus medialis and



not in the corpora restiformia or in the fasciculi longitudinales mediales. No degenerated fibers were seen going to higher levels in one series where the lesion was confined to the nucleus commissuralis.

Series 140 has been selected as a representative lesion through the median portion of the general visceral division<sup>1</sup> of the nucleus tractus solitarii. This lesion destroyed the nucleus tractus solitarii from the level of the junction of the ventriculus quartus with the canalis centralis, cephalad, for fourteen sections of 50  $\mu$  each; then for seven sections it continues, ventrally to this nucleus, to the level of the entrance of the last sensory root of the vagus. The description of this lesion is from the sixth section from the caudal end of the lesion (fig. 3), which is from the same level as figure 16 of the previous paper, and through the center of the general visceral division of the nucleus tractus solitarii. It shows the area of destruction (*Les.*) to include all of the tractus solitarius, its nucleus, and some of the nucleus fasciculi cuneati; and demonstrates degenerated fibers in the nucleus proprius corporis restiformis (*N.Res.*), in the neighboring formatio reticularis, and as fibrae arcuatae internae (*Arc.I.*) contributing to the opposite lemniscus medialis (*Lem.M.*).

Any section through the medulla cephalad of the lesion, as figure 4, discloses degenerated fibers in two places, namely, in the corpus restiforme of the same side (*C.Res.*) and in the opposite lemniscus medialis (*Lem.M.*). There are apparently more degenerated fibers in the lemniscus than in the corpus restiforme. It is obvious from this experiment that, if there are any medullated general visceral fibers taking origin from the nucleus tractus solitarii in the region of the lesion, they are present either in the

<sup>1</sup> In the previous paper the nucleus tractus solitarii was separated into a cephalic or gustatory division (which may also receive general visceral fibers) and a caudal or general visceral division. A section at the level of the entrance of the third sensory root of the nervus vagus into the tractus solitarius marked the line of separation between these two divisions. The distribution of degenerated tractus solitarius fibers demonstrated the gustatory division of this nucleus to be situated mainly ventrad of the tractus solitarius, while the general visceral division was located, for the most part, median and dorso-median, of this tract. Frequent reference will be made to these two divisions of the nucleus tractus solitarius in this paper.

corpus restiforme of the same side or in the lemniscus medialis of the opposite side.

Figure 5 is inserted as illustrative of a lesion through the cephalic end of the general visceral division of the nucleus tractus solitarii. This section is directly behind the level of the entrance of the last sensory root of the vagus and from the same level as figure 15 of the previous paper, which is from the 30th cm. plane in reconstruction 1 of the same paper. The total length of this lesion (series 117) is from the seventh section above the level of the junction of the ventriculus quartus with the canalis centralis to the level of the entrance of the last sensory root of the vagus, and for a few sections cephalad, it is continued ventrally to the nucleus tractus solitarii. Throughout this entire region, the area of destruction, as shown by figure 5, involves the tractus solitarius (*T.S.*), its gray mass (*N.T.S.*), the inner margin of the radix descendens nervi vestibularis (*R.D.Ves.*), its nucleus, and possibly the nucleus proprius corporis restiformis (*N.Res.*). Furthermore, figure 5 discloses degenerated fibers in the left nucleus proprius corporis restiformis, in the left corpus restiforme, and in the adjacent formatio reticularis. From the ventral side of the lesion, degenerated fibers pass as *fibrae arcuatae internae* (*Arc.I.*) to the opposite lemniscus medialis (*Lem.M.*), and as *fibrae arcuatae dorsales* (*Arc.D.*) to the opposite corpus restiforme and nucleus proprius corporis restiformis. The latter are undoubtedly the fibres reticulo-cérébelleuses dorsales and fibres nucléo-cérébelleuses of Van Gehuchten's ('04) and Molhant's descriptions.

It is apparent from figure 5, but more obvious in another series (122) where the lesion was superficial and median to the nucleus tractus solitarii, that these *fibrae arcuatae dorsales* cross dorsally to the opposite side through the formatio reticularis. They lose their identity to some extent in the middle line, and upon reaching the opposite tractus solitarius, a few fibers may pierce this tract, but the majority traverse it, dorsally or ventrally; from whence they pass through the radix descendens nervi vestibularis (*R.D.Ves.*) to enter the inner margin of the corpus restiforme. It is possible, however, that a few of these arcuate fibers terminate in the region of the opposite radix descendens nervi vestibularis, but

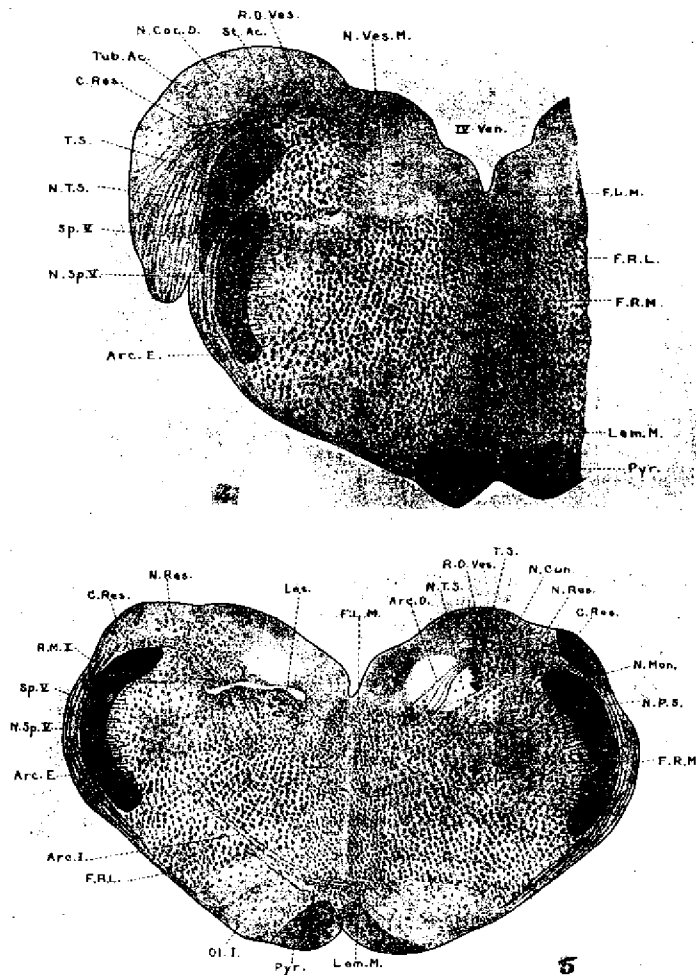


Fig. 4 Left half of a more cephalic section through the tuberculum acusticum of the same series as figure 3.  $\times 8.3$ .

Fig. 5 Section from Marchi series 117, showing the lesion through the cephalic end of the general visceral division of the left nucleus tractus solitarii, directly behind the entrance of the last sensory root of the vagus or at approximately the same level as figure 15 of the previous paper.  $\times 8.3$ .

there is no evidence that any of these fibers originate in or end in the nucleus tractus solitarii.

A section from above the lesion in series 117 demonstrates many degenerated fibers in the left corpus restiforme (fig. 6, *C.Res.*) and in the opposite lemniscus medialis (*Lem.M.*). There are also a few degenerated fibers in the opposite or right corpus restiforme, but none in either fasciculus longitudinalis medialis (*F.L.M.*), and furthermore figure 6A shows the absence of degenerated fibers in the fasciculi longitudinales mediales at the level of the III nuclei. The degenerated fibers in the cerebellum will be considered later.

Unfortunately many of the lesions that were intended to destroy the cephalic or gustatory division of the nucleus tractus solitarii were too median or too superficial. In one cephalic lesion (series 85) extending from the entrance of the sensory root of the glossopharyngeus to the entrance of the sensory root of the facialis, the area involved is wide and includes a part of the corpus restiforme and tuberculum acusticum, destroying the nucleus tractus solitarii for about 300  $\mu$ . cephalad of the entrance of the sensory root of the nervus glossopharyngeus. A distinct bundle of fibrae arcuatae internae appears at the lower border of this lesion, passes ventrally, median to the radix spinalis nervi trigemini, bends inward and spreads out in the formatio reticularis to end apparently in the lemniscus medialis of the opposite side. In series 89 where the lesion was confined to the extreme cephalic end of the gustatory division of the nucleus tractus solitarii, there are no degenerated fibrae arcuatae internae going to the opposite lemniscus, and the fibrae arcuatae dorsales, present in this series, are evidently striae acusticae.

In experiment 116, an attempt was made to sever all of the fibers that might go from the nucleus tractus solitarii to the lemniscus medialis of the opposite side. This was accomplished by making two separate lesions: first, the caudal or visceral division of the nucleus tractus solitarii was destroyed by drawing a chisel dorsally and superficially through the entire caudal portion of the left half of the medulla; then after lifting up the cerebellum, a more cephalic lesion was made by inserting a needle

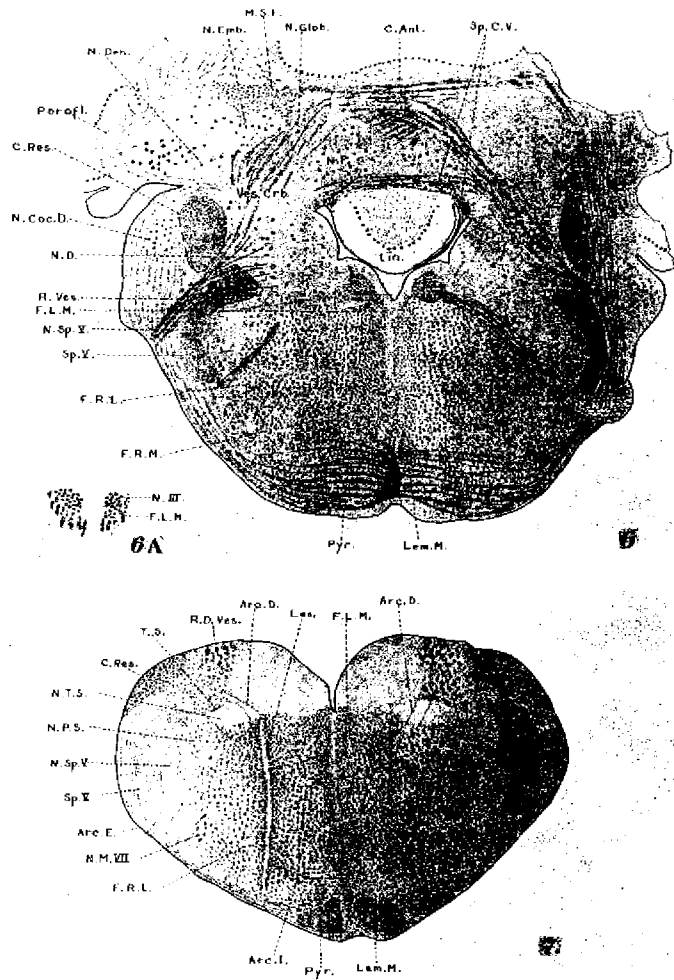


Fig. 6 Transverse section through the center of the basal cerebellar nuclei from the same series as figure 5.  $\times 6.6$ .

Fig. 6A Section through the median longitudinal bundles and III nuclei from the same series as figure 5.  $\times 8.3$ .

Fig. 7 Section from Marchi series 116, showing that part of the lesion which would sever the fibrae arcuatae internae and dorsales coming from the central portion of the gustatory division of the left nucleus tractus solitarii. This section is a little above the level of the entrance of the sensory root of the glossopharyngeus, which places it immediately cephalad of figures 6 and 7 of the previous paper.  $\times 6.6$ .

clear through the medulla, a little to the left of the median line, at the level of the entrance of the nervous facialis, and finally drawing the needle caudad to the level of the entrance of the last sensory root of the vagus. A study of these two lesions in series 116 reveals that all of the fibers going from the nucleus tractus solitarii to the opposite lemniscus would be severed. Consequently if the secondary visceral fibers enter the opposite lemniscus medialis as von Monakow maintains, and they are medullated, their distribution can be followed in this series.

An examination of a section (fig. 7) of series 116 at the level of the center of the gustatory division of the nucleus tractus solitarii, clearly shows the narrow cephalic lesion (*Les.*) severing the left formatio reticularis. As a direct result of this lesion, degenerated fibrae arcuatae dorsales (*Arc.D.*) appear on both sides of the incision. Since these fibers cannot be traced beyond the descending vestibular root fibers, since they pass through the nuclei of the solitary tracts, and since this area is cephalad of the dorsal muscle sense nuclei and caudal of the tuberculum acusticum; it is probable that the fibrae arcuatae dorsales are vestibular fibers at this level. Furthermore this lesion severs some fibers designated as fibrae arcuatae internae (*Arc.I.*), which apparently go to the lemniscus medialis (*Lem.M.*) of the opposite side. These fibers may be gustatory fibers from the nucleus tractus solitarii or they may be general cutaneous fibers from the nucleus tractus spinalis nervi trigemini or both. Fibrae arcuatae internae were also observed in several neighboring sections, but in other neighboring sections they were either absent or mixed with the formatio reticularis. The more extensive caudal lesion undoubtedly accounts for most of the degenerated fibers found in the corpora restiformia, in the fasciculi longitudinales mediales, and in the left lemniscus medialis.

*Distribution of the degenerated lemniscus medialis fibers*

Before describing the distribution of the lemniscus medialis in series 116 it seems advisable to record briefly some of the earlier work on this tract. It can be stated at the outset that considerable disagreement exists concerning the distribution of the lem-

niscus medialis fibers. For example, direct fibers have been described going to the cerebellum and cerebral cortex. Bruce ('93), Rothmann, and Wallenberg think that lemniscus medialis fibers supply the colliculus inferior; while Ferrier and Turner traced a few fibers to the colliculus superior, and Wallenberg followed a few fibers to the corpus mamillare and to the hypothalamus. Mott ('98) clearly states that all fillet fibers end in the optic thalamus and none continue to the cerebral cortex. Van Gehuchten followed lemniscus medialis fibers to the nucleus lateralis of the thalamus, and claims that no direct fibers go to the cerebellum, corpora quadrigemina, or to the cerebral cortex. Probst traced the lemniscus chiefly to the ventral thalamic nucleus.

The lemniscus medialis (fig. 8B, *Lem.M.*) is situated immediately dorsal of the pedunculus cerebri (*Ped.Cer.*) and lateral to the ganglion interpedunculare (*G.Intp.*) at the level of the colliculus inferior in series 116. There is no evidence of degenerated fibers supplying this ganglion or the colliculus inferior. Degenerated lemniscus fibers, however, extend out laterally, nearly to the outer margin of the section. This section also shows degenerated fibers in the fasciculi longitudinales mediales, but they were accounted for through the direct caudal destruction of these tracts.

A section through the lemniscus medialis (fig. 8A, *Lem.M.*) at the level of the colliculus superior and the caudal end of the corpora mamillaria demonstrates this tract as being spread out, ventro-laterally, directly beneath the nucleus ruber and brachium conjunctivum (*N.Rub.* and *Br.C.*). It lacks considerably the width it possessed in figure 8B and its fibers are much more condensed. In this and adjacent sections there are apparently a few more degenerated fibers in the ventral part of the nucleus ruber, in the ventral formatio reticularis, and in the regio subthalamica or nucleus hypothalamicus (*R.Subt.*) than are present in areas not supplied by lemniscus fibers. There are apparently more degenerated fibers in the nucleus ruber than in the hypothalamic region and more in the cephalic end of the nucleus than in the caudal end. The number of these degenerated fibers is not striking in any place, and nothing resembling a tract can be traced to these areas. In all of my series where the nucleus

tractus solitarii was destroyed and in several series where only the nucleus fasciculi cuneati et gracilis were injured, there are some degenerated fibers in the nucleus ruber and in the hypothalamic region. It would not be surprising if the nucleus ruber receives muscle sense fibers from the dorsal nuclei of the medulla and it is possible that some lemniscus medialis fibers pass through the cephalic end of the nucleus ruber to end further cephalad in the thalamus. There are a number of very minute black granules in the pedunculus corporis mammillaris (*Ped.C.M.*) and also in the tractus opticus. These granules are much finer than the ordinary particles of degenerated myelin, and since they appear in all my Marchi series, irrespective of where the lesion was made, they probably have no especial significance to this problem.

A few sections cephalad of figure 8A, many of the degenerated lemniscus fibers assume a more dorsal and lateral course and acquire a position between the nucleus ruber, medially, and the corpus geniculatum mediale, laterally; so that the fibers in the median portion of the lemniscus appear in transverse section, and those more dorsal and lateral are cut obliquely or longitudinally. It is obvious that Probst is correct in stating that the general position of the lemniscus medialis fibers is ventral and lateral to those of the brachium conjunctivum. There may be some intermingling, medially, between these two tracts, a point which will be determined in connection with the next report on the distribution of fibers originating from the basal cerebellar nuclei. Within the formatio reticularis, cephalad of the nucleus ruber, both parts of the lemniscus medialis radiate dorsally to enter and terminate in the nucleus ventralis thalami and in the nucleus lateralis thalami (fig. 8, *N.Ven.T.* and *N.Lat.T.*). At the level of figure 8 a few of the most median fibers of the lemniscus medialis have continued cephalad into what is known as the lamina medullaris ventralis (*Lam.V.*), and a few others may be present in the ventral formatio reticularis (*F.R.*) and in the regio subthalamica (*R.Subt.*).

Attention should be directed to the fact that in series 140, where the lesion involved the general visceral division of the nucleus tractus solitarii and in series 153 and 159, where the



lesions were limited to a destruction of the nucleus fasciculi cuneati et gracilis, there is a distribution of degenerated lemniscus medialis fibers identical with those of series 116 described above, where all of the visceral and muscle sense secondary nuclei were destroyed by the lesion.

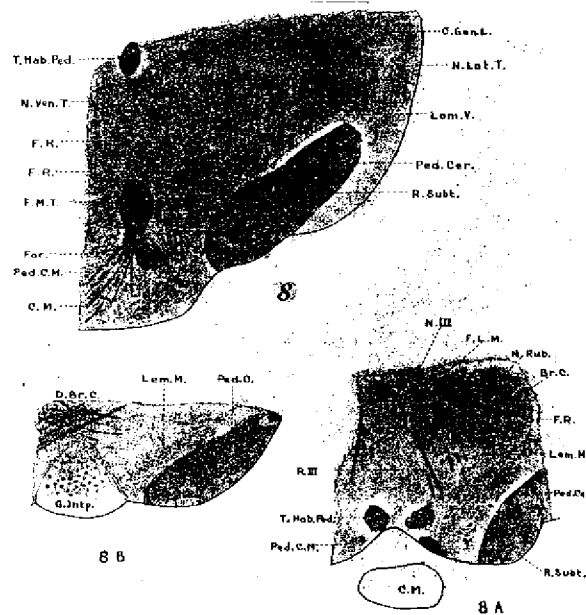


Fig. 8 Section of the right thalamus and hypothalamus regions from the same series as figure 7.  $\times 6.6$ .

Fig. 8A Section through the right nucleus ruber and hypothalamus from the same series as figure 7.  $\times 6.6$ .

Fig. 8B Section through the right lemniscus medialis and ganglion interpedunculare from the same series as figure 7.  $\times 6.6$ .

#### *Distribution of the degenerated corpus restiforme fibers*

Figure 6 is consulted again to illustrate the relationship of the corpus restiforme fibers to the basal cerebellar nuclei. This figure is from series 117, where the lesion involved a large part of the general visceral division of the nucleus tractus solitarii. In this figure a mass of degenerated fibers (*M.S.F.*) are passing caudad, dorsally to the nucleus emboliformis et globosus (*N.Emb.*

and *N.Glob.*); a second or smaller mass of degenerated fibers is likewise passing caudally, above and between the left and right nucleus fastigii (*N.F.*); while other degenerated fibers are crossing to the opposite side in the commissura cerebelli anterior (*C.Ant.*). These degenerated fibers pursue a course parallel to many normal fibers, which will be shown to be, in part, tractus spino-cerebellaris dorsalis fibers. A section taken from below the last cerebellar peduncle and lingula, demonstrates that many of the degenerated fibers in the lateral tract (*M.S.F.*) have acquired a more ventral position between the nucleus globosus (or the combined intermediate nuclei) and the left nucleus fastigii. The median group of degenerated fibers has increased in number and has likewise attained a more ventral position, some degenerated fibers appearing even ventrally to the nucleus fastigii. Also at this level there are more than the normal number of degenerated fibers in the left nucleus fastigii, but the other more lateral cerebellar nuclei contain no more than the normal number of degenerated fibers. The degenerated fibers in the right or opposite corpus restiforme, although much fewer in number, have apparently a similar relationship to the right cerebellar nuclei.

Most of the series, where the lesion involved the cephalic or gustatory portion of the nucleus tractus solitarii, could not be used for this phase of the problem, on account of direct injury to one or more of the basal cerebellar nuclei. In series 138, where the lesion destroyed the caudal part of the gustatory division of the nucleus tractus solitarii in addition to a large part of the general visceral division of this nucleus, there is identically the same relationship of degenerated corpus restiforme fibers to the basal cerebellar nuclei as was shown in series 117 described above. Also in series 116, where the lesion destroyed all of the general visceral division of the nucleus tractus solitarii and all of the fibrae arcuatae dorsales going to the right or opposite corpus restiforme, there is the same relationship of degenerated corpus restiforme fibers to the basal cerebellar nuclei as was described above for series 117. Likewise in series 164 and other series, where the lesion involves only the dorsal muscle sense nuclei of the medulla, the degenerated fibers in the corpus restiforme have

a distribution identical with those described above for series 117. Finally, the distribution and relationship of the degenerated corpus restiforme fibers in the cerebellum of series 117 and the above mentioned series, are identical with the left tractus spino-cerebellaris dorsalis fibers, as shown by series 113 where this tract was severed in the upper cervical region, and by series 93 where this tract was severed in the lumbar region.

The literature discloses some differences concerning the distribution of the tractus spino-cerebellaris dorsalis. Mott does not mention the relation of this tract to the cerebellar nuclei. Collier and Buzzard found tractus spino-cerebellaris dorsalis fibers supplying the nucleus dentatus in man. Bruce ('98), and MacNalty and Horsley did not describe any tractus spino-cerebellaris dorsalis going to the nucleus dentatus, but the latter found collaterals from the tractus spino-cerebellaris ventralis supplying the nucleus fastigii. Ingvar states that a small part of the tractus spino-cerebellaris dorsalis fibers appear to end in the cephalic cerebellar nuclei, especially in the nucleus tecti (fastigii).

In the way of a summary for this section it can be stated that series 117 and the following series described above, show degenerated corpus restiforme fibers curving over the cephalic surface of the nucleus dentatus. These fibers pass caudally, in lateral and median bundles, situated above and between the three medial cerebellar nuclei, and they end caudally in the adjacent cortex. There is always more than the normal number of degenerated fibers in the nucleus fastigii, but whether these fibers terminate in this nucleus or continue through it to end in the adjoining cortex was not determined. No more than the normal number of degenerated fibers is found in the nucleus dentatus, emboliformis, et globosus, but on the other hand it must be admitted that the cells of these nuclei would not have to possess very long dendrites to form a synapse with these corpus restiforme fibers. The general indication is, however, that the degenerated fibers in the corpus restiforme of these series are for the most part, if not entirely, muscle sense fibers passing to the cerebellar cortex.

*Secondary visceral tracts from the spinal cord*

It is clear from the studies of Head, Scaffidi, Ranson and Billingsley, and others that a number of afferent visceral fibers enter the white rami communicantes of the thoracic nerves, and recently Rossi traced peripheral processes of spinal ganglion cells into the rami communicantes. If any secondary visceral fibers from the spinal cord enter the brain they probably run in the tractus spino-cerebellaris dorsalis, and this tract takes origin from the cells of the column of Clark, according to Mott and others. The writer has little or nothing to add to this subject, unless it be to express doubt if many visceral fibers from the spinal cord reach a higher level than the nucleus commissuralis.

Hoche, Thiele and Horsley, and Collier and Buzzard describe a dorsal plexus of collaterals in man, which originates from the tractus spino-cerebellaris dorsalis and passes through the radix spinalis nervi trigemini to be collected in the gray mass directly lateral of the tractus solitarius. The last authors state that this plexus consists of very fine collaterals, which are only preserved if the sections are cut with a freezing microtome or after gum embedding and examined in glycerine. These fibers, which are suggestive of secondary visceral fibers, were not observed in any of my series, possibly for the reason that they were all embedded in celloidin. My series, however, demonstrate degenerated tractus spino-cerebellaris dorsalis fibers scattered through the nucleus proprius corporis restiformis, which brings them over into the region of the radix descendens nervi vestibularis and the nucleus of Monakow of Winkler's descriptions. Moreover these series, which represent lesions of the tractus spino-cerebellaris in both cervical and lumbar regions, did not exhibit any degenerated fibers going to the lemniscus medialis, to the fasciculus longitudinalis medialis, to the nucleus commissuralis or to the tractus solitarius or its nucleus. One series (113), in which the two most cephalic dorsal spinal nerve roots were severed, discloses some direct degenerated spinal nerve fibers passing to the caudal part of the nucleus commissuralis and to other neighboring effective nuclei, but it would be useless to guess the impulse that these fibers carry.

## 2. CHROMATOLYSIS EXPERIMENTS

It is apparent from the previous section that, while the evidence favored the secondary visceral fibers going to the thalamus by way of the opposite lemniscus medialis rather than to the intermediate basal nuclei of the cerebellum, it was not conclusive, for the reason that one could not always exclude the possibility of mistaking secondary muscle sense, secondary cutaneous and secondary vestibular fibers for secondary visceral fibers. It therefore seemed advisable to supplement this work with a search for chromatolytic cells in the terminal sensory nuclei of the tractus solitarius in certain Nissl series, where the lemniscus medialis was severed in some of the brains and where the nucleus emboliformis et globosus was destroyed in others.

*Microscopical Technique:* Essentially the same microscopical technique was employed in all of these experiments. It consisted in fixing the brains in either Carnoy's alcohol acetic mixture (alcohol 60 cc., glacial acetic acid 10 cc., chloroform 30 cc.), or in the following formalin alcohol acetic mixture—10 per cent formalin 50 cc., alcohol 50 cc., glacial acetic acid 5 cc. Either fluid gave excellent fixation and the sections stained readily with toluidin blue or neutral red. After paraffin embedding the sections were cut, serially, 20  $\mu$  thick. They were stained over night, on the slide, in a 1/5 per cent solution of toluidin blue at a temperature of 38°C.; destained in the process of dehydration and cleared in Johnston's xylol-castor oil mixture.

*Lesions of the lemniscus medialis*

In this experiment it was attempted to sever the lemniscus medialis at the level of the colliculus inferior, without injuring the fasciculi longitudinales mediales, the opposite lemniscus medialis, or any part of the cerebellum. The mode of procedure was to make a median incision of the scalp, sever the left musculus temporalis from the skull and turn it to the left. After this the caudal portion of the left cerebral hemisphere was exposed by clipping a hole through the skull with a small pair of bone forceps, being careful not to cut the adjacent blood sinuses. If any hemor-

rhage occurred it was stopped with bone wax, prepared after a formula given in a previous paper. The instrument used in making this lesion consisted of a small chisel, having a blade about one third of the width of the brain stem. The incision was made through the left cerebral hemisphere, directly in front of the sinus transversus, and extending from the median line laterally. The chisel was at first pointed caudo-ventrad; then after bending outward to avoid cutting the fasciculus longitudinalis medialis, it was brought back to the median line and finally carried deep enough to completely sever the left lemniscus medialis and pedunculus cerebri, without crossing to the opposite side and without severing the main ventral arteries. The two temporal muscles were sewed together with fine sterile thread so as to cover the hole in the skull, and finally the skin incision was closed with coarse sterile thread and coated with iodine.

Since the cells of the nucleus tractus solitarii are relatively small, the animals were killed 6 to 8 days after the operation. If they were permitted to live much longer, many of these cells would undergo complete degeneration and become obliterated.

After many failures, some of which resulted in the severance of the fasciculus longitudinalis medialis, the destruction of parts of both lemnisci, or the failure to completely sever the left lemniscus medialis, series 177 was obtained, which demonstrated a very satisfactory lesion. This lesion (fig. 9, *Les.*) passed to the side of the left fasciculus longitudinalis medialis (*F.L.M.*), completely severed the left lemniscus medialis and pedunculus cerebri, but apparently did not injure the opposite lemniscus or pedunculus cerebri (*Lem.M.* and *Ped.Cer.*). Unfortunately the sections of this series were inverted so that the lesion appears on the right side instead of the left.

Figure 10 illustrates a section through the extreme caudal end of the general visceral division<sup>2</sup> of the right or opposite nucleus tractus solitarii and nucleus commissuralis from series 177. This section is approximately at the same level as figure 18 of the previous paper, which shows many degenerated fibers ending, medially, in the nucleus commissuralis, and a few, laterally, in

<sup>2</sup> See footnote 1, p. 283.

the nucleus tractus solitarii. It is obvious from figure 10 that the large cells in the nucleus tractus solitarii (*N.T.S.*) are perfectly normal in every respect. Likewise the larger cells of the nucleus

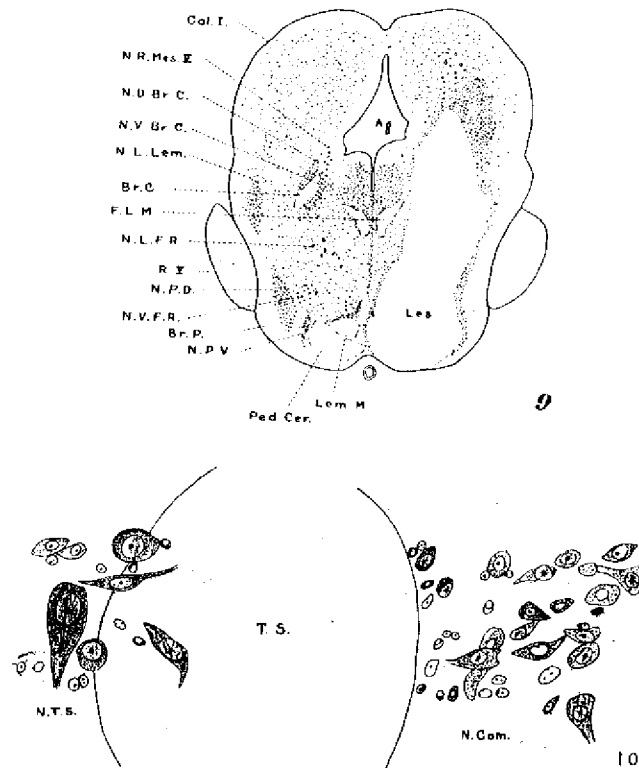


Fig. 9 Taken through the center of the lesion from Nissl series 177. The lesion has severed the left lemniscus medialis, without injuring the opposite lemniscus, or either fasciculus longitudinalis medialis, or the cerebellum. In this series the sections were inverted so that the lesion appears on the right side instead of the left.  $\times 6.6$ .

Fig. 10 Section showing normal cells in the right nucleus tractus solitarii and nucleus commissuralis (caudal portion of the general visceral division of this nucleus), from the same series as figure 9 and at approximately the same level as figure 18 of the previous paper  $\times 127$ .

commissuralis (*N.Com.*) have sharply defined and centrally placed nuclei with perfectly normal and sharply differentiated Nissl substance. The opposite nucleus tractus solitarii and

nucleus commissuralis, which are on the same side as the severed lemniscus medialis, also possess perfectly normal cells. Furthermore the adjacent sections demonstrate normal cells in the nucleus tractus solitarii and in the nucleus commissuralis of both sides. The area of perfectly normal cells of the nucleus of the right tractus solitarius is, however, limited to the spinal part of the medulla, which area is shown in figure 1 of the previous paper to represent the caudal half of the general visceral division of the nucleus tractus solitarii. It is safe to state that this portion of the general visceral nucleus receives three times as many degenerated tractus solitarius fibers as the cephalic half received. Also the caudal half of the general visceral division of the nucleus tractus solitarii (composed largely of the nucleus commissuralis) contains fully three times as many cells as the cephalic half. Moreover, the cells of the caudal half are mainly median to the tractus solitarius; while in the cephalic half they are chiefly dorso-median. In the light of what is to follow, the fact that the cells in the commissural or caudal half of the general visceral division of the nucleus tractus solitarii have not undergone chromatolysis in experiment 117 probably signifies that their axones go to lower levels or to the nuclei of the medulla. They may be distributed to the respiratory effective nuclei of the spinal cord.

A section through the caudal end of the cephalic half of the right nucleus tractus solitarii is shown in figure 11.<sup>3</sup> This section is from the same series as figure 10 (series 177) and the third section above the junction of the ventriculus quartus with the canalis centralis, or approximately at the same level as figure 16 of the previous paper. It is obvious from figure 11 that all of the larger cells of the right nucleus tractus solitarii (*N.T.S.*) dorsal to the tract, exhibit a diffuse or homogeneous appearance of the protoplasm. There is little differentiation between the nuclei and the cytoplasm. Cell (a) discloses decided vacuolation of the outer cytoplasm, and cell (b) shows a disintegration of the outer cytoplasm; while only an outer ring or shadow is all that

<sup>3</sup> As previously stated the sections of series 177 were inverted, so that the right tractus solitarius and nucleus is on the left side in figures 10 to 14.



persists of some of the smaller cells. Furthermore there is considerable chromatolysis throughout the entire length of the cephalic half of the general visceral division of the right nucleus tractus solitarii, but the corresponding cells of the opposite side, namely, the side where the lemniscus medialis was cut, show few, if any, chromatolytic changes.

According to the previous paper the gustatory division of the nucleus tractus solitarii extends from the entrance of the sensory root of the nervus facialis to the third sensory root of the vagus.

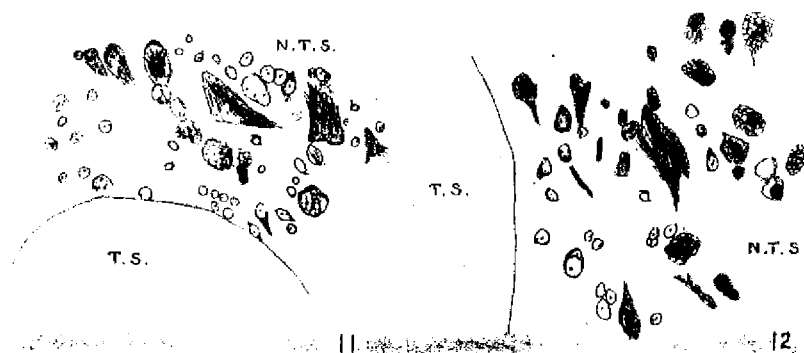


Fig. 11 Chromatolytic cells from the center of the general visceral division of the right nucleus tractus solitarii from the same series as figure 9. This section is three sections above the union of the ventriculus quartus with the canalis centralis and approximately at the same level as figure 16 of the previous paper.  $\times 191$ .

Fig. 12 Shows chromatolytic cells at the end of the gustatory division of right nucleus tractus solitarii from the same series as figure 9; taken slightly cephalad of the entrance of the third sensory root of the vagus and close to the level of figure 13 of the previous paper.  $\times 191$ .

It is situated ventrally to the tractus solitarius, cephalad, and ventro-laterally, caudad. In series 117 practically all of the gustatory division of the right nucleus tractus solitarii (opposite side from the severed lemniscus) is composed largely of degenerated cells or cells undergoing chromatolysis. Figure 12, which is through the extreme caudal end of the gustatory division of the right nucleus tractus solitarii, demonstrates a diffuse staining and vacuolation of the cytoplasm of the larger cells (a); together with little differentiation between nucleus and cytoplasm. Many of

the smaller cells show more advanced stages of atrophy. Adjacent sections through this nucleus present a similar picture; while sections through the opposite nucleus tractus solitarii exhibit, for the most part, perfectly normal cells. A section through the middle portion of the gustatory division of the right nucleus tractus solitarii (fig. 13) also discloses cells in all stages of chromatolysis. An early stage is illustrated by (a), a medium stage by (b) and an advanced stage by (c). Many of these cells are representatives of an early stage of chromatolysis, portraying a diffuse staining of the protoplasm and an eccentric position of the nucleus. One cell (n) is apparently normal. Adjacent sections also show a similar chromatolysis of the cells of this nucleus. The cells in the opposite or left nucleus tractus solitarii of this section (fig. 14A) are perfectly normal, with the possible exception of (d), which gives evidence of some disintegration. In the next section of the left nucleus (fig. 14B) the cells are all normal. In Nissl series it is impossible to locate with certainty the extreme cephalic end of the nucleus tractus solitarii; so that nothing definite can be stated for the extreme cephalic end of the gustatory division of this nucleus. No chromatolytic cells, however, were found in this general region in series 177.

It is apparent from this experiment (177), that severing the left lemniscus medialis in the midbrain region, without injuring the fasciculi longitudinales mediales, opposite lemniscus, or cerebellum, causes chromatolysis of most of the cells throughout the entire gustatory division of the opposite nucleus tractus solitarii, excepting possibly a small area in the extreme cephalic end of this nucleus. It also produces chromatolysis of many of the cells of the cephalic half of the general visceral division of the opposite or right nucleus tractus solitarii; but does not bring about any chromatolysis of the cells of the caudal or commissural half of the general visceral division of the right nucleus tractus solitarii. The caudal half of the general visceral division of this nucleus, which is composed largely of the nucleus commissuralis, comprises three fourths of the bulk of the general visceral division of the nucleus tractus solitarii. It might be mentioned in this connection that the 33d cm. plane, or the junction of the ventric-

ulus quartus with the canalis centralis in figure 1 of the previous paper, indicates a more or less clear dividing point of the tractus solitarius fibers supplying the sensory nuclei, which corresponds very well to the line of separation between the two halves of the general visceral division of the nucleus tractus solitarii described above.

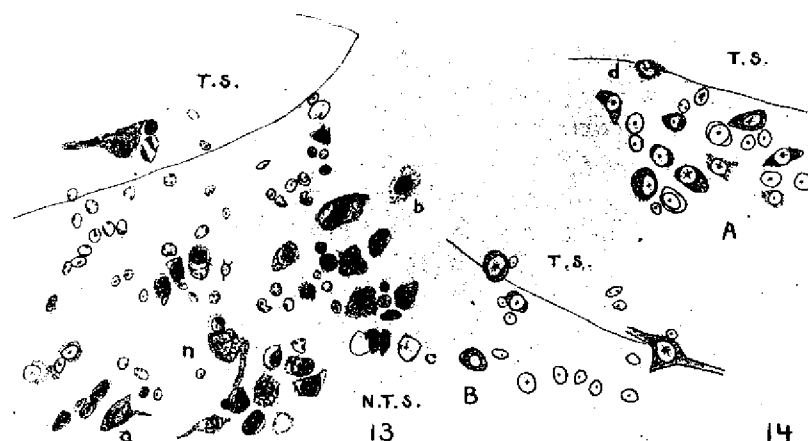


Fig. 13 Chromatolytic cells from the center of the gustatory division of the right nucleus tractus solitarii from the same series as figure 9 and from approximately the same level as figures 6 and 7 of the previous paper.  $\times 191$ .

Fig. 14A Normal cells in the opposite nucleus tractus solitarii of the same section as figure 13 and on the same side as the lesion of the lemniscus.  $\times 191$ .

Fig. 14B Normal cell from the same nucleus as 14A, but from the next section.  $\times 191$ .

The previous Marchi and Nissl experiments, together with the fact that it is very doubtful if any ascending fasciculus longitudinalis medialis fibers reach the diencephalon, are sufficient to exclude this tract from the possibility of conveying secondary visceral fibers to the thalamus. As further evidence that this tract does not contain secondary visceral fibers, series 168 is introduced. In this series the lesion severed both fasciculi longitudinales mediales without injuring the lemnisci, with the result that there are no more than the normal number of chromatolytic cells in either nucleus tractus solitarii or in the nucleus commissuralis.

*Lesions of the basal cerebellar nuclei*

The first part of the operation designed to destroy the left nucleus globosus et emboliformis is very similar to the operation for severing the lemniscus medialis, previously described. A large part of the dorsal surface of the left side of the cerebellum and sinus transversus was exposed, after which an electric cautery, composed of a 2.5 mm. platinum ball placed between two platinum wires, was inserted to the depth of the ventriculus quartus, directly behind the second cerebellar gyrus and about 3 mm. to the left of the median line. The electric current was then turned on for about 3 seconds and the cautery removed. In other experiments this lesion was accomplished by inserting a 3 or 4 mm. blade chisel at the same place to a similar depth, and rotating it around several times. The chief difficulty in this operation was to stop the cautery or chisel at the correct depth; to go too far resulted in injuring the tractus solitarius and its nucleus. As an aid for securing the correct depth of this lesion, the writer measured off the exact distance on the cautery and chisel from a section through a fresh brain of a specimen, the same size as the one to be operated upon. Inasmuch as these nuclei are some distance from the surface of the cerebellum, there was also some danger of directing the instruments too far lateral or median.

For various reasons it was necessary to discard a number of these series; two of them (172 and 174) were all that could be desired. The lesion in the former was made with a chisel and in the latter with a cautery. For descriptive purposes number 174 was selected because the area of destruction was a little more extensive. Figure 15, which is a section through the center of the lesion (*Les.*), shows also the extent of scar tissue on all sides. It is apparent from this figure that the lesion destroyed all of the left basal nuclei of the cerebellum but the nucleus dentatus (*N.Den.*), and that the tractus solitarius and its nucleus (*N.T.S.*) have escaped injury. In addition, a microscopical study of the lesion reveals that practically all of the left corpus restiforme fibers have been destroyed.

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As a result of this lesion there is no more than the normal number of chromatolytic cells in any part of the nucleus tractus solitarii of either side or in the nucleus commissuralis. Chromatolytic cells, however, are present in large numbers in the vestibular nuclei and in the reticular formation of both sides, especially on the side of the lesion.

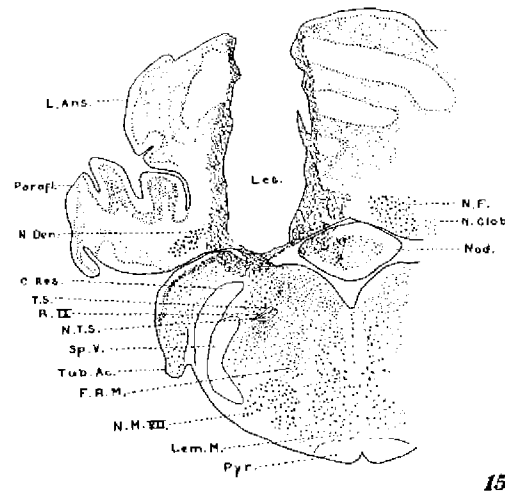


Fig. 15 Section from Nissl series 172, showing lesion through the left nucleus emboliformis, globosus, and fastigii, without injury below to the nucleus tractus solitarii.  $\times 6.6$ .

Incidentally it might be mentioned that a number of experiments were performed on young guinea-pigs and rabbits with a view of determining if any secondary chromatolysis takes place in the cells of the basal nuclei of the cerebellum. These animals were killed several months after the operation and the cerebellum region sectioned and stained with a Nissl stain. In one series of a young rabbit the taste buds of the left side of the tongue were completely destroyed by cauterization. This was readily accomplished in the rabbit on account of the taste buds being bunched in one place on the side of the tongue. In another series of experiments, the VII, IX and X nerve roots were jerked out of their respective foramina in such a manner as to carry their ganglia

with them; and in a third series of experiments the spinal cerebellar tracts were severed in the upper cervical region. The results were identical in all series, namely, the cells of the basal cerebellar nuclei of both sides are perfectly normal.

#### SUMMARY AND GENERAL CONSIDERATIONS

*Marchi experiments.*—On account of the close relationship of the nucleus tractus solitarii to the fibrae arcuatae internae from the dorsal muscle sense nuclei of the medulla and to the vestibular, secondary trigeminal, and auditory fibers it is impossible in the Marchi experiments to exclude the possibility of severing some of the above fibers in destroying the nucleus tractus solitarii, no matter how restricted the lesion may be.

Lesions of the caudal part of the nucleus tractus solitarii and nucleus commissuralis always produce degenerated fibrae arcuatae internae going to the opposite lemniscus medialis. These are largely, if not entirely, muscle sense fibers from the nucleus fasciculi gracilis. Apparently, lesions that are confined to the nucleus commissuralis do not result in the degeneration of any ascending fibers. Lesions through the cephalic half of the general visceral division of the nucleus tractus solitarii and all but the extreme cephalic portion of the gustatory division of the nucleus tractus solitarii bring about degeneration of fibers in the opposite lemniscus medialis and in the corpus restiforme of the same and opposite sides, especially in the former.

As a result of tracing these degenerated corpus restiforme fibers into the cerebellum, none are visible in the nucleus dentatus, emboliformis, and globosus; some are present in the nucleus fastigii, but they may only penetrate this nucleus to reach the cortex. For the most part these fibers pass, caudally, above and between the cerebellar nuclei to the more caudal cortex. They have a course identical with the degenerated tractus-spino-cerebellaris dorsalis fibers, resulting from lesions of this tract in the lumbar and in the upper cervical regions of the spinal cord. Probably these degenerated fibers are muscle sense fibers destined to go to the cortex of the cerebellum.

The Marchi series in which all of the *fibrae arcuatae internae* going to the opposite lemniscus were cut, and, in fact, all of the more restricted lesions of the nucleus tractus solitarii that produced degenerated fibers in the opposite lemniscus prove that, if there are any medullated general visceral and gustatory fibers of the second order in the lemniscus medialis, they are distributed mainly to the nucleus ventralis et lateralis thalami. It was noted that there are apparently a few degenerated lemniscus fibers in the *formatio reticularis* surrounding the thalamus, in the *regio subthalamica* and in the nucleus ruber; but none are present in the ganglion interpedunculare, corpora mamillaria or tuber cinereum. An identical distribution of lemniscus medialis fibers was also recorded for several series where the lesion was confined to the nucleus fasciculi cuneati et gracilis.

It is apparent that these Marchi series would not account for any non-medullated fibers that might go to the diencephalon or to the basal nuclei of the cerebellum.

*Chromatolysis experiments.*—A Nissl series in which the left lemniscus medialis was severed in the midbrain region without injuring the corresponding fasciculus longitudinalis medialis, opposite lemniscus, or cerebellum demonstrates chromatolytic cells throughout the gustatory division and cephalic half of the general visceral division of the nucleus tractus solitarii of the opposite side from the lesion; but no more than the normal number of chromatolytic cells are visible in the commissural or caudal half of the general visceral division of this nucleus. The caudal or commissural half of the general visceral division of the nucleus tractus solitarii, which apparently does not send axones to higher levels, represents at least three fourths of the bulk of this general visceral nucleus. It may send fibers to the respiratory nuclei of the spinal cord and to the motor nuclei of the medulla.

Two Nissl series in which the nucleus emboliformis, nucleus globosus, nucleus fastigii, and practically all of the corpus restiforme fibers from one side were destroyed, show no chromatolysis of the cells of any part of either nucleus tractus solitarii or the nucleus commissuralis.

A lesion through the fasciculi longitudinales mediales in the midbrain region results in finding the sensory nuclei of the tractus solitarius of both sides of the brain composed of normal cells.

These experiments on the guinea-pig's brain not only confirm the work of von Monakow that a tumor in the optic thalamus of a human brain caused the chromatolysis of cells of the substantia gelatinosa of the tractus solitarius and a retrograde degeneration of the fibrae arcuatae internae, but they eliminate the fasciculus longitudinalis medialis and the corpus restiforme plus the brachium conjunctivum as tracts which might conduct gustatory and general visceral impulses to the diencephalon and to higher centers. They demonstrate that both gustatory and general visceral impulses are probably conducted to higher centers by way of the opposite lemniscus medialis or adjacent fibers. Furthermore they indicate that no ascending general visceral fibers for higher centers take origin from the caudal or commissural end of the nucleus tractus solitarii.

It is obvious, then, that the visceral fibers of the second order in mammals do not follow the general scheme described for fishes and amphibians, unless, perchance, the secondary gustatory nucleus of fishes and amphibians, which approximates the ganglion isthmi, has been carried cephalad in its phylogenetic development.



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