

THE TRACT OF LISSAUER AND THE SUBSTANTIA GELATINOSA ROLANDI

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ELEVEN FIGURES

There is located in the apex of the columna posterior between the substantia gelatinosa Rolandi and the periphery of the spinal cord an area of rather widely separated small medullated fibers. These fibers, having for the most part a vertical course, form a tract which is easily distinguished in Pal-Weigert preparations, in which it takes a lighter stain than the remainder of the substantia alba. It has for this reason usually been considered a part of the columna posterior, although it is admitted by all that it properly belongs with the longitudinal fiber tracts of the cord.

In 1885 Lissauer observed that fine medullated fibers grouped themselves on the lateral side of an entering rootlet, and, turning lateralward, separated themselves from the remainder of the radicle to enter the apex of the columna posterior. Here they turned to run vertically in the tract which now bears his name. These observations were confirmed by Bechterew, 1886. The general acceptance of these observations was facilitated by the results obtained shortly afterward by the application of the Golgi stain to the spinal cord. A number of observers, among them Kölliker ('91) working with foetal or newborn mammalian tissue, were able to show that the fibers of the entering dorsal root separate into two bundles, a lateral bundle of very fine axons and a medial bundle of much coarser ones. The lateral bundle of fine axons runs into Lissauer's tract, where the fibers divide into ascending and descending branches. The ascending limbs run upward in the tract for some distance, but the descending limbs are very short (Barker '99). This clear evidence in regard to

the axon content of the entering rootlets apparently established the correctness of the observations of Lissauer and Bechterew, and these have accordingly been generally accepted.

The usual account which is given of this tract is that it is formed of fine, rather sparsely arranged, medullated fibers, which enter the spinal cord from the dorsal roots. There is good reason to believe, however, that this account of the origin of these fine medullated fibers represents but half of the truth, since many of them seem to be of endogenous origin. The evidence in regard to this point has been presented in a previous paper (Ranson '13), and need be only briefly summarized here.

Nageotte ('03) was the first to assert that the medullated fibers of Lissauer's tract were of endogenous origin. He reported a case in which a tumor involved all the nerve roots in the cauda equina up to and including the fourth lumbar without causing any degeneration of the medullated fibers of Lissauer's tract. The presence of an apparently normal number of intact fibers in this case shows conclusively that many, probably a majority, of the medullated fibers of this tract are of endogenous origin. It can not be taken as conclusive proof that none of the medullated fibers in this tract are derived from the dorsal roots. Many human cords, in which extensive degeneration of the dorsal roots had resulted from tumors, syphilis and other causes, as well as the cords of animals in which some of the dorsal roots had been divided, have been studied with the object of tracing the degenerating fibers within the spinal cord. Most of these investigations, although showing extensive degeneration in the posterior funiculus, show no changes in the tract of Lissauer (see the papers of Darkschewitsch '96, Frölich '04, Kopczynski '06, Marguliés '96, Orr '06, Wallenberg '98 and Zappert '98). A small amount of degeneration in Lissauer's tract after lesions of the dorsal roots has been seen by Collier and Buzzard '03), Laignel-Lavastine ('08), Sibelius ('05) and Sottas ('93).

The observations of Lissauer and those of Nageotte are diametrically opposed to each other. But, in view of the finding of a limited amount of degeneration in Lissauer's tract following lesions of the dorsal roots, it may be safely said that both are

in part correct and that the medullated fibers in this tract are in part endogenous and in part exogenous. It is probable that the endogenous fibers predominate.

In fact, the most recent work on this subject tends further to discredit the observations of Lissauer. Leszlényi ('12) made a comparative study of the tract of Lissauer and states that, while in man and many animals horizontal medullated fibers cross the tract to enter the substantia gelatinosa, the dorsal roots contribute practically nothing to the vertical fibers of the tract.

And, as we shall see, the observations of Kölliker and others on Golgi preparations are to be explained on another basis than that furnished by Lissauer's observations. In the cat it has been shown (Ranson '13) that the non-medullated fibers of the dorsal roots separate out from among the medullated fiber just before the rootlet enters the cord, and turning laterally they enter the tract of Lissauer. Most of the fibers of the lateral bundle of the dorsal root seen in Golgi preparations of the cord of newborn animals are fibers which never acquire a myelin sheath. The picture of an entering rootlet which is given by a pyridine-silver preparation of the spinal cord of an adult cat is very similar to that given by the Golgi method in the newborn animal, and very different from that seen in Pal-Weigert preparations of the adult cord.

We wish in this paper to present a study of the entering rootlets and tract of Lissauer in man, the rhesus monkey, the cat, rabbit, squirrel, guinea-pig, and albino rat, and to present at the same time some notes on the character of a closely associated structure—the substantia gelatinosa Rolandi.

TECHNIQUE

For the demonstration of the myelin sheaths sections were stained by the Pal-Weigert method. In differentiating these some sections were not fully decolorized in order to make sure that no fine medullated fibers were lost. The axons were stained by the pyridine-silver technique, the details of which were given in a previous paper (Ranson '11). In some cords, namely, those

of the rat and rabbit, we have succeeded in improving our preparations by a preliminary injection of ammoniated alcohol, as suggested by Huber ('13), but in other cords, especially those of the cat and monkey, excellent results can be secured without preliminary injection.

The pyridine-silver material was imbedded in paraffin and cut into sections 5 to 12 microns thick. The Pal-Weigert cellodin sections were 12 to 24 microns thick.

LISSAUER'S TRACT IN MAN

Parts of four apparently normal cords were obtained for me from autopsies on bodies which had been dead for two, three, six and twelve hours, respectively. The approximate levels of the sections were determined by reference to Marburg's Atlas, comparing the shape of the white and gray columns with that characteristic for each segment. In the third cervical segment (fig. 1) the gray substance proper, capped by the sharply pointed substantia gelatinosa, occupies about two-thirds of the columna posterior. The remaining one-third, the apex, is occupied by Lissauer's tract. In contrast to what is seen in the cat, the tract is not sharply limited either toward the fasciculus cuneatus or the lateral funiculus. It shows, however, no tendency to spread

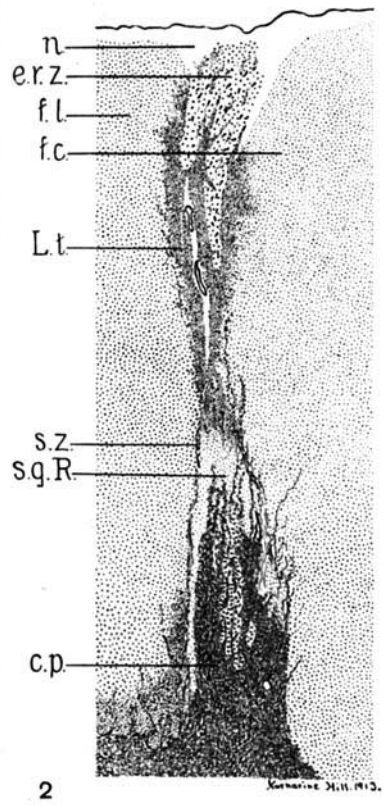
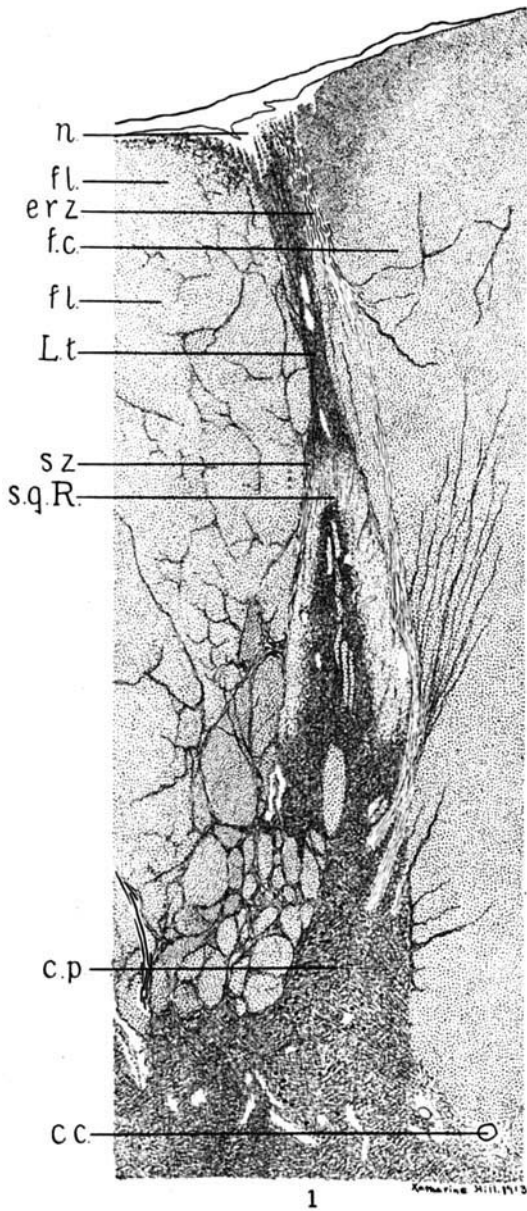
ABBREVIATIONS

The following is a list of abbreviations used on all the drawings:

<i>c.c.</i> , canalis centralis	<i>l.p.p.r.</i> , lateral part of posterior root
<i>c.p.</i> , columna posterior	<i>L.t.</i> , Lissauer's tract
<i>e.r.z.</i> , entering root zone	<i>n.</i> , neuroglia
<i>f.c.</i> , fasciculus cuneatus	<i>p.r.</i> , ring of pia constricting the entering root
<i>f.cs.</i> , fasciculus cerebellospinalis	<i>r.p.</i> , radix posterior
<i>f.l.</i> , funiculus lateralis	<i>s.g.R.</i> , substantia gelatinosa Rolandi
<i>i.l.</i> , intermediate layer	<i>s.z.</i> , stratum zonale
<i>l.e.L.t.</i> , lateral expansion of Lissauer's tract	

Fig. 1 From the third cervical segment of the spinal cord of man; pyridine-silver technique. $\times 32$.

Fig. 2 From the third thoracic segment of the spinal cord of man; pyridine-silver technique. $\times 32$.



downward along the lateral surface of the columna posterior as in the monkey; but near the surface of the cord it becomes diffuse, spreading out into the fasciculus cuneatus on the one hand and the lateral funiculus on the other, and fading off gradually in either direction. The dorsal root fibers on entering the cord pass through the dorso-medial portion of the tract, cutting off the diffuse part of the tract in the fasciculus cuneatus.

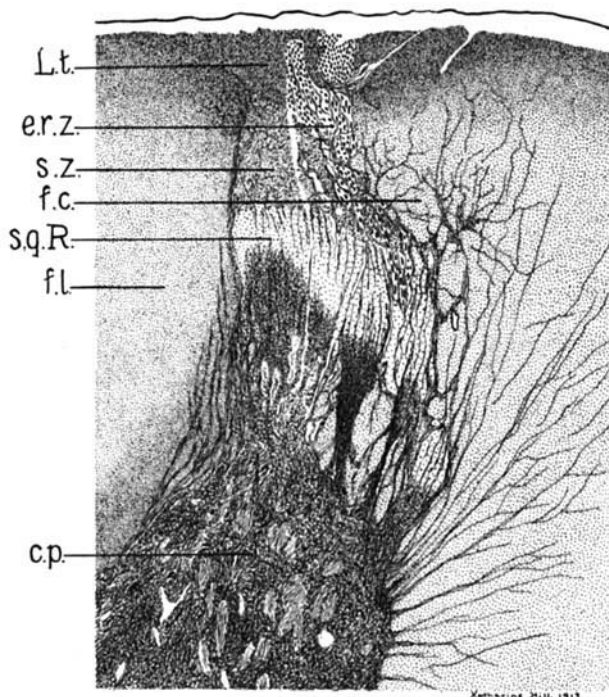


Fig. 3 From the third lumbar segment of the spinal cord of man; pyridine-silver technique. $\times 32$.

In the third thoracic segment (fig. 2) the apex represents about one-half of the length of the columna posterior, and is filled by the tract of Lissauer which reaches from the substantia gelatinosa to the surface of the cord. It is not well-defined on either side, but does not spread out at the periphery of the cord as it does in the third cervical segment, nor does it extend forward

upon the lateral surface of the columna posterior as in the monkey. It is characteristic of the tract in the thoracic portion of the human cord that it is broken up by the entering rootlets, which run through it toward the gray substance.

In the third lumbar segment (fig. 3) the substantia gelatinosa reaches much nearer to the surface than in the two levels just described, and the tract of Lissauer is compressed between it and the surface of the cord. Instead of being long and slender, the tract at this level is short and broad. It is not sharply defined on either side, but spreads out near the surface of the cord into the lateral funiculus and even to a greater degree into the posterior funiculus. It does not extend forward upon the lateral surface of the columna posterior. The fila radicularia pass through it, breaking it up into two or more divisions.

Structure

In Pal-Weigert preparations the tract is clearly outlined from the other fiber columns by its light color. It contains fine and medium-sized medullated fibers rather sparsely arranged. These are for the most part vertical (in line with the long axis of the cord), but there are also horizontal and oblique fibers. In my preparations I was unable to see medullated fibers from the dorsal roots entering and becoming a part of the tract of Lissauer. Large bundles of medullated fibers run through the tract on their way to the fasciculus cuneatus and the columna posterior; but it is difficult to demonstrate individual fibers leaving these bundles to become a part of the tract. A good set of serial Pal-Weigert sections would probably show a few such fibers. Leszlényi believes that such dorsal root fibers as do enter the tract are horizontal and run directly into the substantia gelatinosa.

In pyridine-silver preparations the tract of Lissauer is stained much darker than any other part of the fiber columns of the cord and is seen to be composed of closely packed, fine axons, the majority of which are non-medullated. In the thoracic cord, because of the intimate relation of the entering radicles to the tract of Lissauer, it is more difficult to trace the non-med-

ullated fibers from the radicles into the tract than it is in either the cervical or lumbar regions. In serial sections of the third lumbar segment one can trace these fibers with ease. There is a tendency for these fibers to group themselves near the surface of the fila, they do not, however, form a compact layer on the surface of the fila, as in the cat. In other words, the non-medullated fibers are not entirely separated from among the medullated fibers of the rootlet until after the entrance of the rootlet into the cord. From the accumulation of non-medullated fibers near the surface of the entering radicle bundles of non-medullated fibers can be traced into the tract of Lissauer. The arrangement, while in all essentials the same, is by no means so clear and diagrammatic as in the cat.

LISSAUER'S TRACT IN THE MONKEY: *MACACUS RHEBUS*

The spinal cord of the monkey is very favorable material for the pyridine-silver technique. The preparations are quite as good as those obtained from the cat, and considerably better than those which I have been able to secure of the human cord, or of that of the dog, pig, rabbit, squirrel, guinea-pig or rat. All of these cords give uniformly much poorer pictures than those of the monkey and cat.

In the cervical cord (fig. 4, seg. C. 7) the gray substance including the substantia gelatinosa occupies about four-fifths of the total length of the columna posterior, the apex with the included Lissauer's tract, one-fifth. The tract fills the apex and reaches from the substantia gelatinosa to the surface of the cord. An accumulation of subpial neuroglia is seen at its dorsal extremity (in the drawing the subpial neuroglia and the pia are together represented as a white band). The subpial layer of neuroglia, as well as the accumulation at the apex of the columna posterior and the septa which project into the substance of the cord, is granular not fibrous in appearance. This shows that neuroglia fibers are not differentiated and that there is no danger of confusing neuroglia fibers with fine axons. The limit of the tract is not sharp on the side toward the cuneate fasciculus; and there

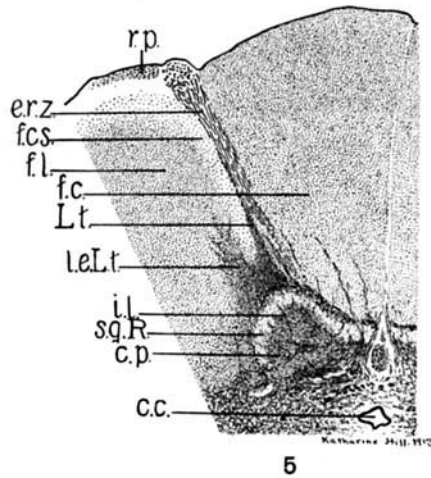
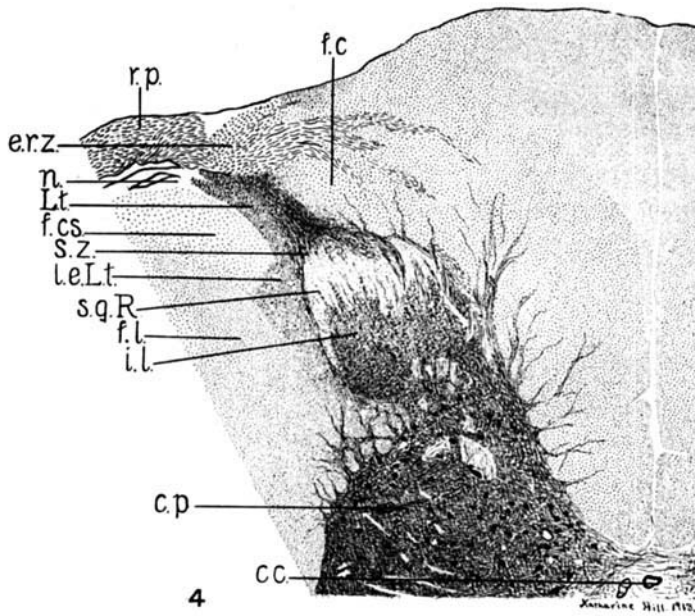


Fig. 4 From the seventh cervical segment of the spinal cord of the monkey (*Macacus rhesus*); pyridine-silver technique. $\times 32$.

Fig. 5 From the eighth thoracic segment of the spinal cord of the monkey (*Macacus rhesus*); pyridine-silver technique. $\times 32$.

is a considerable intermingling of the fibers of the two fascicles. On the side toward the lateral funiculus there is a neuroglia septum which extends into the cord, separating the tract in question from the cerebellospinal fasciculus. The septum does not, however, reach the gray substance, and ventrally to it the tract of Lissauer spreads out into the lateral funiculus upon the lateral surface of the column posterior. It goes over gradually into the fasciculus proprius of the lateral funiculus. The entering

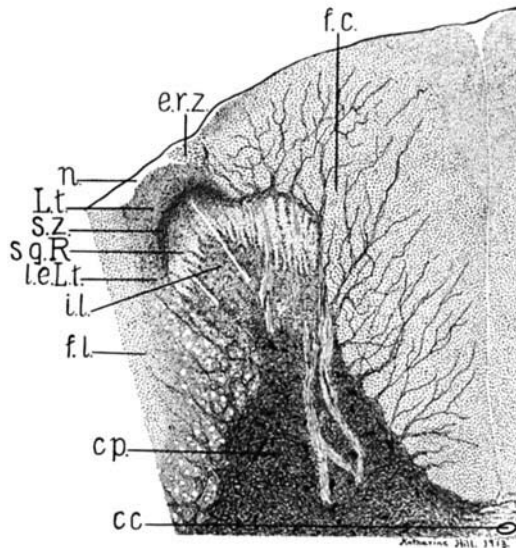


Fig. 6 From the fifth lumbar segment of the spinal cord of the monkey (*Macacus rhesus*); pyridine-silver technique. $\times 32$.

dorsal root bundles pass over the tip of the tract of Lissauer to enter the cord on its medial side. A few fibers are usually cut off from the main part of the tract by the entering radicles and form a small bundle in the dorso-lateral angle of the cuneate fasciculus.

In the thoracic region of the monkey cord (fig. 5, seg. T. 8.) the column posterior is very short, and is almost completely covered by the substantia gelatinosa. The main part of the tract of Lissauer extends dorsalward from the substantia gelatinosa as

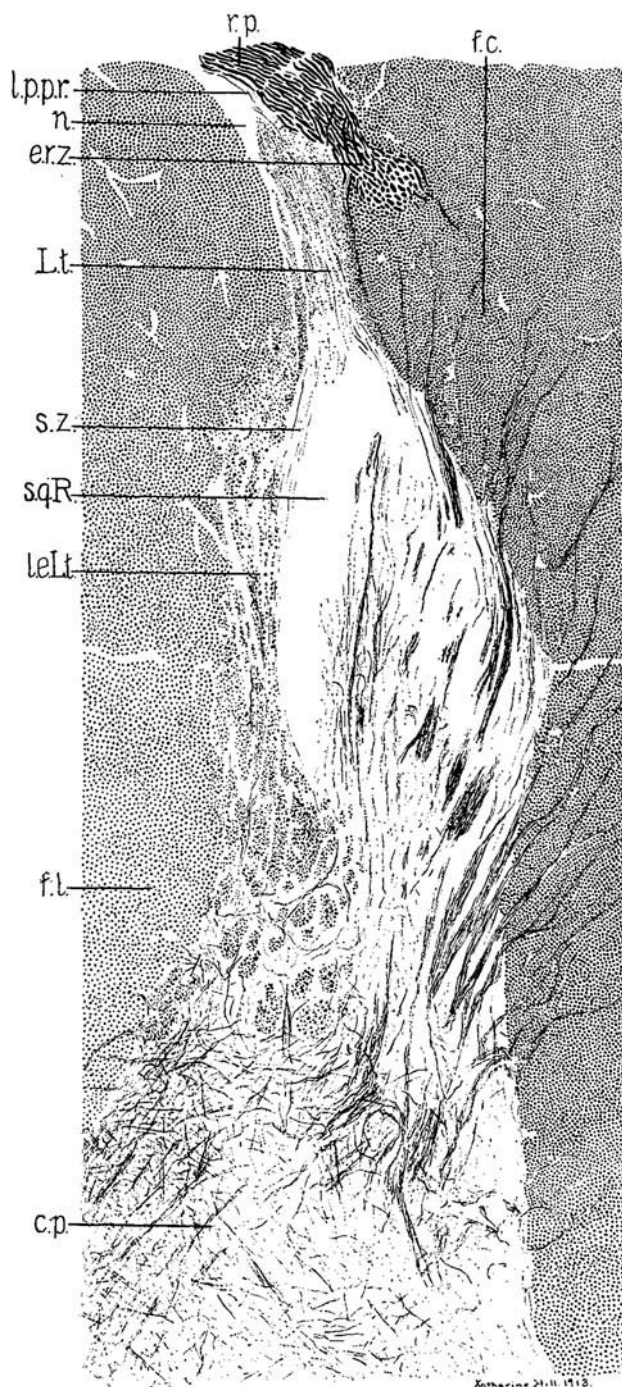


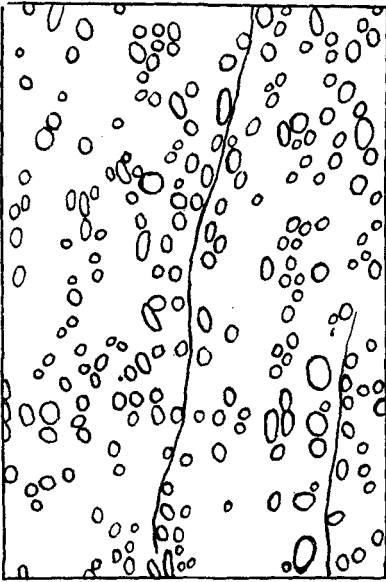
Fig. 7 From the fifth cervical segment of the spinal cord of the monkey (*Macacus rhesus*); Pal-Weigert technique. $\times 63$.

a sharply-pointed triangular area, reaching a little more than halfway to the surface of the cord. It is rather sharply demarcated from the posterior funiculus, but spreads out into the lateral funiculus, as indicated in the drawing. This lateral expansion also presents a somewhat triangular form with the apex pointing dorsally and separated from the apex of the main part of the tract by the cerebellospinal fasciculus. It fades out ventrally into the funiculus proprius on the lateral surface of the columna posterior. The entering dorsal root bundles run toward the posterior horn upon the medial side of the tract.

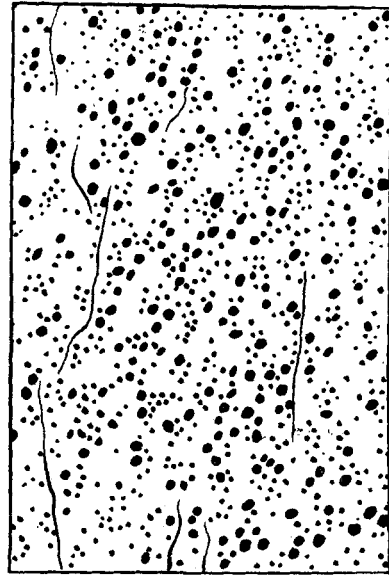
In the lumbar portions of the cord (fig. 6, seg. L. 5.) the columna posterior reaches nearly to the surface of the cord and the tract of Lissauer is compressed between it and the accumulation of subpial neuroglia in the apex. The tract caps only the lateral half of the substantia gelatinosa and is rather sharply delimited toward the medial side. It is less sharply limited on the lateral side and extends ventrally along the lateral surface of the columna posterior as in the cervical and thoracic segments. The entering radicles pass over the dorso-medial surface of the tract, and cut off from the main part of the tract a few fibers which form a small bundle near the surface of the fasciculus cuneatus.

Structure

The tract in the fifth cervical segment (figs. 7 and 8) contains a relatively small number of medullated fibers of varying size. Some are of medium caliber but the majority are very fine. They are more widely separated than in the other fiber tracts of the cord, and the tract as a whole is for this reason very lightly stained in Pal-Weigert preparations. These fibers are for the most part vertical in their course, appearing in the sections as blue rings. There are also scattered oblique and horizontal medullated fibers running through the tract in a dorso-ventral direction. In almost every section through an entering radicle one can trace a few fine medullated fibers (fig. 7, *l.p.p.r.*) out of the radicle and into the tract of Lissauer. Many of these fibers undoubtedly pass directly through the tract as the oblique or



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Fig. 8 From the fifth cervical segment of the spinal cord of the monkey (*Macacus rhesus*); Pal-Weigert technique; a small area of the tract of Lissauer showing medullated fibers. $\times 1160$.

Fig. 9 From the seventh cervical segment of the spinal cord of the monkey (*Macacus rhesus*); pyridine-silver technique; a small area of the tract of Lissauer showing medullated and non-medullated axons. $\times 1160$.

horizontal fibers just mentioned. One fiber was followed from the root more than halfway to the substantia gelatinosa. It is probable that others of these medullated dorsal root fibers go to form vertical fibers in the tract.

In that part of the tract which extends ventrally along the lateral surface of the columna posterior there are a few large medullated fibers; but the small and medium-sized ones are more widely scattered than in the dorsal portion of the tract so that this region takes an even lighter stain than the dorsal portion. There are in this lateral portion a very few oblique fibers, so few that they are practically negligible. On carefully looking through a number of preparations I was unable to see a single

oblique fiber passing from this lateral part into the dorsal part of the tract. Leszlényi has made much of this spreading out of the tract of Lissauer into the lateral funiculus. He saw in a great variety of animals fibers running into Lissauer's tract proper from this extension in the ground bundle of the lateral funiculus, and concluded that many of the fibers of the tract were derived in this way from the ground bundle. Leszlényi was working with Pal-Weigert preparations and was impressed with the similar light staining and open structure of the two regions, and he was led in this way to attempt to show a connection between the two. The similarity in Pal-Weigert preparations is, however, not nearly so striking as in pyridine-silver preparations where both are seen to be crowded with fine axons. Although I can find no evidence in support of Leszlényi's derivation of the dorsal part of the tract out of oblique fibers from the lateral, I do not doubt that the two regions are intimately associated, and are best described together under the head of Lissauer's tract.

In pyridine-silver preparations, the tract of Lissauer is closely packed with many very small and a few medium-sized axons (figs. 4 and 9). The very small axons are non-medullated. If one compares a pyridine-silver preparation (fig. 9) with a Pal-Weigert preparation (fig. 8), one sees that the number of axons is far in excess of the number of myelin sheaths, but that the latter are about as numerous as the medium-sized axons. These closely-packed, darkly-stained axons give the tract its characteristic dark appearance in pyridine-silver preparations. As in Pal-Weigert preparations, most of the fibers are vertical; but there are some that are horizontal and oblique. In the extension of the tract in the lateral funiculus the fine, non-medullated axons are also very numerous. As has been mentioned, a few large medullated fibers are found scattered through this lateral area; and these give this region a lighter appearance than the dorsal part, although between these large fibers the fine axons are as closely packed as in the dorsal portion of the tract.

There are fewer oblique or horizontal fibers in the lateral than in the dorsal part of the tract, and practically none running

ventro-laterally. In case the fibers on the lateral surface of the columna posterior were derived from the dorsal root, one would expect such oblique fibers, since the dorsal root fibers would have to run ventro-laterally in order to reach a position lateral to the columna posterior. The absence of such oblique fibers leads one to suspect that this lateral extension of the tract is of endogenous origin. If this assumption is correct, the non-medullated fibers of the tract of Lissauer are in part of endogenous and in part of exogenous origin. It is, of course, possible that the non-medullated fibers in the lateral part have a long course and are displaced ventro-laterally as they ascend, just as the fibers of the fasciculus gracilis are displaced medially. This, however, is highly improbable.

In the seventh cervical segment the fasciculus cuneatus contains large and small medullated axons, the fasciculus gracilis only medium-sized medullated axons; so that the two tracts are clearly differentiated in the sections (fig. 4). But both fascicles are very poor in non-medullated fibers. This was also found to be true in the cat, and indicates in a negative way that the non-medullated fibers of the dorsal roots become separated from the medullated at their entrance into the spinal cord and pursue a different course within it. The light stain of the cerebellospinal fasciculus is due to the fact that it is composed almost exclusively of large medullated fibers.

It is possible to trace both fine medullated and non-medullated fibers from the cervical dorsal root into Lissauer's tract. But the number of medullated fibers taking this course is relatively small (fig. 7, *l.p.p.r.*). In pyridine-silver preparations bundles containing very large numbers of non-medullated fibers can be seen leaving the peripheral part of an entering radicle and running into the tract of Lissauer. These have been traced in great detail in the paper on "Lissauer's tract in the cat," and numerous illustrations given. Here we will content ourselves with one illustration. The entering rootlet shown in figure 10 is surrounded by a constricting ring of pia, through the upper part of which near the upper surface of the rootlet the section was taken. This constricting band is seen at two points in the drawing

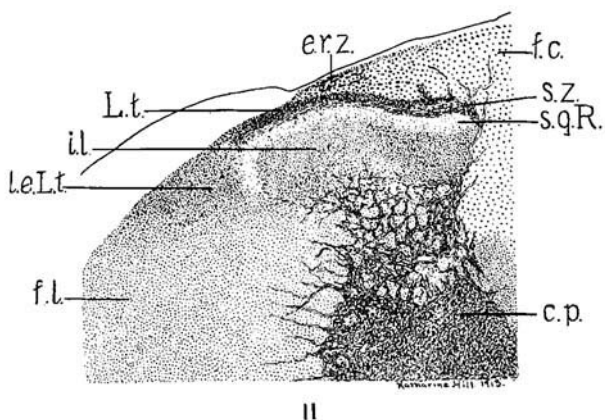
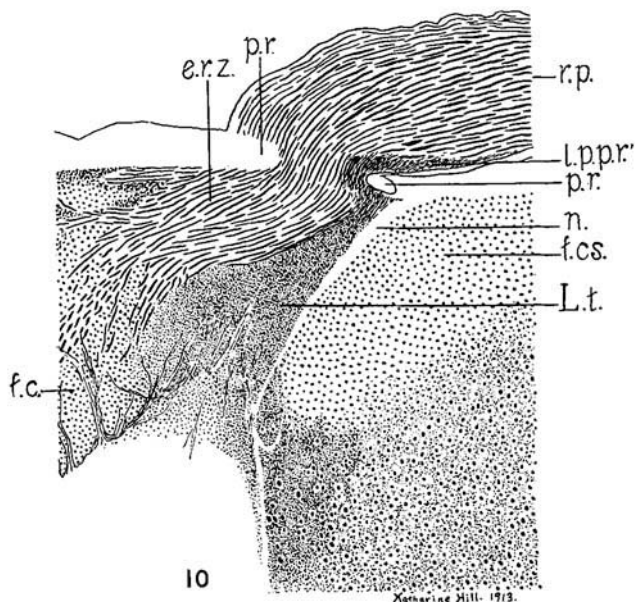


Fig. 10 From the seventh cervical segment of the spinal cord of the monkey (*Macacus rhesus*); pyridine-silver technique. $\times 63$.

Fig. 11 From the twelfth thoracic segment of the spinal cord of the albino rat; pyridine-silver technique. $\times 63$.

(each marked *p.r.*), and these two points are connected in the two preceding sections by the upper limit of the band. A study of the serial sections shows that the non-medullated fibers have

accumulated on the upper, lateral and lower surfaces of the rootlet. At *l.p.p.r.* in the illustration one sees a large bundle of non-medullated fibers from the layer on the lateral surface of the rootlet running over the constricting ring and into the tract of Lissauer. A study of the two sections just above shows that this layer of non-medullated fibers is continuous with that on the upper surface of the rootlet. These non-medullated fibers on the upper surface of the rootlet enter the cord between the constricting ring and the medullated fibers, and turning lateralward enter the tract of Lissauer. Followed downward in the series, a continuous layer of non-medullated fibers is seen passing over the lateral part of the constricting ring and entering the tract of Lissauer, just as in the figure given. On the under surface of the radicle one sees the fibers forming this part of the peripheral layer turning sharply lateralward underneath the entering medullated fibers to reach the tract of Lissauer.

It is very difficult to follow the course of the non-medullated fibers in the thoracic segments because of the close relation of the entering radicles to the tract of Lissauer. In the fifth lumbar segment one sees that as the rootlet passes over the apical accumulation of neuroglia to reach the medial side of the tract of Lissauer numerous small bundles of non-medullated fibers are given off which run ventrally through the apical neuroglia into this tract. It is this arrangement of the non-medullated fibers which was seen in Golgi preparations of newborn animals by Kölliker and others. The lateral part of the root, which they describe as consisting of very fine axons, is shown by pyridine-silver preparations to be still present in the adult and to take the same course into Lissauer's tract. The few fine medullated fibers which take the same course are by no means numerous enough to account for the lateral bundle of the dorsal root as seen in Golgi preparations. With the exception of a few small bundles of non-medullated fibers which are running toward the substantia gelatinosa, the entering root zone is free from non-medullated fibers—few, if any, enter the cuneate fasciculus.

The oblique and horizontal fibers of the tract pass forward into the substantia gelatinosa, and between this and the tract nu-

merous fibers are seen passing back and forth at all angles. The two structures are, in fact, most intimately associated and there is no sharp line of separation between them.

LISSAUER'S TRACT IN THE CAT

The tract of Lissauer in the cat has been described in detail in another paper. In shape and position it is very similar to the dorsal part of the tract in the monkey. It presents the same differences in shape and position in the three principal regions of the cord. In the cat it shows a tendency to spread out ventrolaterally, since the ventral part of the tract fades off gradually into the lateral funiculus. The chief difference in the two animals is, then, the great development of the lateral part of the tract in the monkey, of which there is only a suggestion in the cat.

The tract has the same structure as in the monkey. It is possible to follow a few medullated and a large number of non-medullated fibers into it from the dorsal roots. No oblique fibers either medullated or non-medullated could be followed into the tract from the ground bundle of the lateral funiculus. The substantia gelatinosa and the tract of Lissauer show the same interchange of fibers in the cat as in the monkey.

LISSAUER'S TRACT IN THE RABBIT

In the rodents the substantia gelatinosa Rolandi is highly developed, in some much more so than in others. Associated with the large and varying size of the substantia gelatinosa there are corresponding changes in the tract of Lissauer. There are more differences, so far as this tract is concerned, between the rabbit and the white rat than between the rabbit and man; and the study of the tract in the rodents is therefore of special interest.

Because of the similarity of the tract of Lissauer in the rabbit to that in higher mammals only a brief account need be given. In the seventh cervical segment the substantia gelatinosa is somewhat nearer the surface than in the same part of the monkey cord. The tract is about as long (antero-posteriorly) as

broad. It is more sharply defined medially than laterally, but not very sharply defined on either side. While the transition into the lateral funiculus is somewhat gradual, the tract can not properly be said to extend into that funiculus. The entering bundles from the dorsal root cut through the dorso-medial angle of the tract; and the small part which is thus cut off is spread out somewhat diffusely in the postero-lateral angle of the cuneate fasciculus. Bundles of non-medullated fibers can be traced into the tract of Lissauer from the dorsal roots. None of my preparations show medullated fibers from the dorsal roots entering the tract. But this may be due to the intimate relation of the entering root to the tract. As the bundles of root fibers pass through the tract some of them might separate from the others and become constituent fibers of the tract without being easily detected.

In the eighth thoracic segment the columna posterior is long; and the substantia gelatinosa is about the same distance from the surface as in the seventh cervical segment. But the space between the substantia gelatinosa and the surface of the cord is not fully occupied by the tract of Lissauer which lies close to the surface and is some distance from the substantia gelatinosa. The tract is very diffuse without sharp limits in any direction.

In the fifth lumbar segment the tract is located on the lateral extremity of the substantia gelatinosa and is short and broad. It is better defined medially than laterally; but the lateral extension which is well developed is outward along the surface of the cord rather than along the lateral border of the columna posterior. The entering rootlets pass through the dorso-medial angle of the tract, cutting off a small part, which lies as a thin band along the surface of the cord in the dorso-lateral angle of the cuneate fasciculus. Non-medullated fibers can be traced from the roots into the tract of Lissauer, but not in such a diagrammatic manner as in the cat and the monkey. I have not been able to trace medullated fibers from the dorsal root into the tract.

The structure of the tract is the same in the rabbit as in the monkey and the cat.

The tract of Lissauer in the squirrel is very similar to that in the rabbit and requires no special description.

THE TRACT OF LISSAUER IN THE ALBINO RAT

In the albino rat the substantia gelatinosa Rolandi is very massive, and differs in shape and position from that in the animals already studied. It does not vary much in shape from segment to segment, as in the other animals, but in the cervical, thoracic, and lumbar cord alike it reaches almost to the surface and is only slightly curved. In other words, it is spread out along the dorsal surface of the cord (fig. 11), from which it is separated by a very thin band of fibers representing the tract of Lissauer. The slight curvature brings the two extremities of the substantia gelatinosa somewhat farther from the surface. The superficial band of fibers has the same structure as the tract of Lissauer in other animals, consisting of scattered fine medullated fibers and closely-packed non-medullated ones. This band is very small in proportion to the size of the cord, and especially in proportion to the size of the substantia gelatinosa. At the lateral angle of the substantia gelatinosa the tract becomes continuous with an area which lies just lateral to the substantia gelatinosa and the caput of the columna posterior. This area in the lateral funiculus contains scattered small and medium-sized medullated fibers and is crowded with fine non-medullated axons. It has, in other words, the same structure as the lateral extension of the tract of Lissauer in the monkey. In the rat, due to the excessive development of the substantia gelatinosa, the tract of Lissauer proper has been reduced to a narrow strip between the substantia gelatinosa and the surface of the cord. The main bulk of the tract is located in the lateral funiculus in the region occupied in some other animals by a more or less diffuse lateral expansion of the tract. The tract of Lissauer and its lateral expansion are much the same in each of the three principal regions of the cord.

THE TRACT OF LISSAUER IN THE GUINEA-PIG

In the guinea-pig the tract of Lissauer is much like that in the rat. The substantia gelatinosa is excessively developed and occupies a position near the surface in each of the three principal regions of the cord. The tract is even less developed than in the rat, and is represented by a thin strip between the substantia gelatinosa and the surface of the cord. In the seventh cervical segment there is a lateral expansion of the tract similar to that in the rat, but less well defined. In the thoracic and lumbar regions the lateral expansion is less developed than in the cervical segments.

THE SUBSTANTIA GELATINOSA ROLANDI

The intimate and constant relation of the tract of Lissauer to the substantia gelatinosa and the interchange of fibers between the two suggests the possibility that the latter is the nucleus of reception of the afferent fibers of the former. This raises the question as to whether the structure of the substantia gelatinosa is in keeping with such a conception of its function.

According to all recent observers, nerve cells are very numerous in the substantia gelatinosa Rolandi. Ziehen ('99) has given a good summary of the literature on the nerve cells of this region. Rosenzweig ('05) and Sano ('09) have reworked the subject with the method of Bielschowsky. The larger cells of the zonal layer (the most superficial layer of the substantia gelatinosa) are well known. According to Cajal, their axons run into the lateral funiculus. But the most numerous and most characteristic cells are the small multipolar elements. These are very small, and, according to Rosenzweig, the substantia gelatinosa is 'crammed full' of them. All authors agree that they are demonstrated with difficulty because of the instability of their protoplasm, which is destroyed by the usual fixing and hardening agents. Sometimes the nuclei of these cells alone are visible in such preparations. In good Bielschowsky preparations (Rosenzweig) the substantia gelatinosa contains dendrites in large quantity derived

from these small cells as well as from the cells of the zonal layer and the cells of the nucleus of the columna posterior.

It is a fact of general knowledge that the substantia gelatinosa contains very few medullated fibers, with the exception of the bundles of fibers from the dorsal roots and the posterior funiculus, which run through it on their way to the more ventrally placed portion of the gray substance.

It has been known that non-medullated fibers were present in abundance and Rosenzweig ('05) and Sano ('09) have recently emphasized that fact. Contrary to the opinion of Weigert, Rosenzweig states that neuroglia cells and fibers are present in abundance. According to this author, nerve cells, axons, dendrites, glia cells and glia fibers fill the substantia gelatinosa completely. There is no intermediate gelatinous substance in a good Bielschowsky preparation, but this appears only in proportion as poor fixation has resulted in the destruction of the protoplasmic elements.

In pyridine-silver preparations the cells of the substantia gelatinosa are not very well stained and it is often impossible to distinguish between nerve cells and neuroglia. But the nerve fibers are well differentiated and it seems worth while to give an account of these as they are seen in the monkey cord, and to mention such differences as are seen in other animals.

The substantia gelatinosa presents two well-defined layers, the most superficial of which has received the name of stratum zonale. In the seventh cervical segment of the monkey cord this zonal layer (fig. 4, *S.Z.*) is especially marked in relation to the apex of the substantia gelatinosa, and projects as a triangular area into the tract of Lissauer. And from this apical mass the layer extends forward as a thin covering on either side of the substantia gelatinosa. In pyridine-silver preparations the stratum zonale is deeply stained because of the large number of fine axons which it contains. There is a constant interchange of fibers between it and the tract of Lissauer, and between it and the deeper layer. While the fibers run in every direction, there is a tendency for them to be tangential to the surface of the substantia gelatinosa. From the triangular mass at the apex numerous fibers run for-

ward through the thin part of the layer on either side of the substantia gelatinosa. There are also a very large number of vertical fibers. It would seem from its position and structure as if the stratum zonale served as a means for the passage of the fibers of the tract of Lissauer to and from the substantia gelatinosa. In Pal-Weigert preparations (fig. 7, *S.Z.*) this layer contains but very few fibers, most of which are horizontal and very few vertical in their course. It is easy to see that these are chiefly derived from the vertical and horizontal medullated fibers of Lissauer's tract, and the impression is also gained in Pal-Weigert preparations that this layer serves as a means of interchange of fibers between the tract of Lissauer and the substantia gelatinosa.

The second layer or substantia gelatinosa proper is somewhat lighter in pyridine-silver preparations and contains a considerable amount of light-yellow intermediate substance, which, as has been shown, the most recent authorities regard as an artifact due to the destruction of protoplasmic elements. The picture which this technique gives of this region is therefore not to be regarded as a complete one. This second layer contains, however, a great number of very fine axons running in every direction and forming a loose network. While the number of fibers is large, it is much less than in either the layer just dorsal or the layer just ventral to it, and for this reason it was represented rather light in the drawing to secure the proper contrast. The number of medullated fibers in this region is very small.

We should perhaps distinguish a third layer in the substantia gelatinosa, or better describe a layer of fibers just ventral to it and between it and the nucleus of the columna posterior. Here the fiber plexus is especially dense and there is as an added element a very large number of vertical fibers. In Pal-Weigert preparations only a relatively few medullated fibers are seen, and these are chiefly horizontal, running from the second layer of the substantia gelatinosa toward the nucleus of the columna posterior. Most of the fibers and especially of the vertical fibers in this region are non-medullated. Rosenzweig has called attention to this layer as a longitudinal conduction path com-

posed of non-medullated fibers and named it the 'Grenzschicht.' Kölliker ('91) has described it under the name of the "Plexus der Substantia gelatinosa." Ziehen ('99) regarded it as associated with the caput and not the substantia gelatinosa, and called it the "dorsalen Grenzplexus des Hinterhornkopfs." It seems probable that most of these vertical fibers are directly associated with the substantia gelatinosa.

In the thoracic region the stratum zonale contains more vertical fibers than in the cervical, and there is no sharp line of separation between it and the tract of Lissauer. It is clear that the fibers of the one pass directly over into the other. The vertical fibers of the 'Grenzschicht' or intermediate layer are especially well-developed in the thoracic region, and while the vast majority of them are non-medullated, there are a few medullated vertical fibers to be seen.

In the lumbar region there is an increase in thickness of the stratum zonale immediately underneath the tract of Lissauer: elsewhere it is represented by a thin layer. Here again it is clearly evident that it serves as a means of connection between the substantia gelatinosa and the tract of Lissauer. The vertical fibers of the intermediate layer are slightly more numerous than in the cervical cord, but not so closely packed as in the thoracic cord.

No mention has been made in this account of the bundles of fibers from the dorsal roots and the posterior funiculus, which pass through the substantia gelatinosa on their way to more ventral portions of the gray substance, since these cannot properly be considered as a part of its fiber complex.

The substantia gelatinosa in the cat shows the same close relation between the stratum zonale and Lissauer's tract. The intermediate layer of vertical fibers is the same in the cat as in the monkey and shows the same increase in number of fibers in the thoracic region. The same observations may be made on the rabbit. In the rat the vertical fibers of the intermediate layer tend to accumulate ventrally to the lateral angle of the substantia gelatinosa, especially in the cervical and thoracic segments.

SUMMARY

1. The tract of Lissauer is present in man and in the monkey, cat, rabbit, squirrel, rat and guinea-pig, and possesses the same structure in all.

2. It is composed of small, somewhat widely separated, medullated fibers, and great numbers of fine non-medullated axons.

3. While medullated fibers can be traced from the dorsal root into Lissauer's tract in some animals (cat and monkey), these fibers are not numerous. Some of these run horizontally through the tract to enter the substantia gelatinosa. It is probable that a few of them turn vertically in the tract to lose themselves among the other vertical medullated fibers of the tract.

4. It is clear that the number of medullated fibers entering the tract from the dorsal root is not sufficient to account for all the vertical medullated fibers found there, and that many, probably a majority of these vertical medullated fibers are of endogenous origin. This conclusion is in keeping with the results obtained from the study of the degeneration within the cord produced by lesions of the dorsal roots.

5. Great numbers of non-medullated fibers can be traced into the tract from the dorsal roots in man and in all the animals studied. These root fibers form a large part, perhaps the major part, of the non-medullated fibers of the tract.

6. In all cases there is manifested a tendency for the tract to spread out into the lateral funiculus at some level in the cord. This is particularly evident in the monkey and in the rat. Since there are no oblique fibers running ventro-laterally from the dorsal part of the tract into this lateral expansion of the tract, it seems quite certain that the fibers located here are not derived from the dorsal root. This leads to the conclusion that this lateral part of the tract is of endogenous origin. It would seem probable, therefore, that a part of the non-medullated fibers in the tract of the cat and other animals in which this lateral expansion is not so well developed are also of endogenous origin. Indeed, it would seem that the variations in the shape of the tract in different animals were chiefly due to variations in the position of the endogenous non-medullated fibers.

7. The narrow band-like tract in the rats and guinea-pigs covers a relatively small area. We can best explain the small size of the tract in these animals by assuming that most of the endogenous fibers are located in the lateral expansion of the tract in the lateral funiculus, and that the tract of Lissauer proper is in these animals chiefly composed of exogenous fibers. We need, however, more information on this subject.

8. The tract of Lissauer and the substantia gelatinosa Rolandi are intimately related to each other. But there seems to be no satisfactory explanation at present for the fact that in the rat and guinea-pig, where the substantia gelatinosa is excessively developed, the tract of Lissauer (exclusive of the lateral expansion) is least well developed. Sano's idea, that the enlarged substantia gelatinosa in a purely mechanical way pushes the tract of Lissauer lateralward, does not seem to be satisfactory. If this were the case, we would expect to find oblique fibers marking the course from the dorsal roots to the lateral expansion of Lissauer's tract.

9. Two layers can be distinguished in the substantia gelatinosa Rolandi and a third at the border between it and the ventrally-lying gray substance.

10. The most superficial layer of the substantia gelatinosa is the stratum zonale. It contains many non-medullated axons and fewer medullated fibers. It is most abundant immediately beneath the tract of Lissauer, and between the two there is a free interchange of fibers. From these facts one may assume that this layer serves as a means by which the fibers of Lissauer's tract reach the substantia gelatinosa.

11. The second layer, the substantia gelatinosa proper, contains a plexus somewhat less dense than that in the preceding layer. The fibers are almost all non-medullated.

12. The intermediate layer at the boundary between the substantia gelatinosa and the ventrally-lying gray matter is a dense plexus of fibers mostly non-medullated. A majority of these fibers have a vertical course. Rosenzweig has spoken of them as a special longitudinal conduction path formed of non-medullated fibers.

13. According to the observations of Rosenzweig and others, the substantia gelatinosa contains many nerve cells, mostly of small size, and a fine plexus of dendrites.

14. The tract of Lissauer, the intermediate layer of vertical fibers, and the substantia gelatinosa Rolandi are all intimately related to each other, and, taken together, form a complex system, the function of which is as yet unknown. Rosenzweig thinks that the substantia gelatinosa has a sensory function. Sano thinks that it may have an intimate relation to the sympathetic system, exerting a vasomotor and pilomotor control. He even suggests that it may be the locus of the cells of origin of efferent fibers in the dorsal roots. In view of the non-medullated character of most of the fibers belonging to this system, Sano's theory is especially interesting.

15. I believe we are justified in offering as a tentative interpretation the suggestion that we are dealing here with the apparatus for pain and temperature sensations. The non-medullated fibers of the dorsal roots have been shown to arise from the small cells of the spinal ganglion which are typical unipolar cells with T-shaped processes (Ranson '12). That is to say, from the location and form of the cells of origin of these fibers one may safely assume that they are afferent in function. They can have nothing to do with the afferent impulses which come from the muscles and joints, since these sensations travel upward in the fasciculus cuneatus and fasciculus gracilis, which contain practically none of these fibers. On the other hand, pain and temperature are known to pursue a different course in the cord from that taken by the muscle sense, passing into the gray matter near the level at which they enter the cord. This would correspond to the course of the non-medullated fibers since they are short and run in Lissauer's tract for only a short distance before entering the substantia gelatinosa. It is interesting to note that Ziehen has attributed to this part of the cord the function of conducting pain and temperature sensations. No data is at hand, however, as to how these sensations pass from one side of the cord to the other, although there is an abundance of fine commissural fibers to which this might pos-

sibly be assigned. It should be noted that the assumption that the tract of Lissauer and the substantia gelatinosa form an apparatus for the reception and conduction of pain and temperature sensations, does not exclude the possibility that we are dealing here with a center for vasomotor and pilomotor control, as suggested by Sano. In fact, these autonomic functions are of necessity closely correlated with the afferent impulses, which find their conscious expression in the form of sensations of pain, heat and cold. It is thus possible that the apparatus in question has a double function, serving at the same time as a central autonomic apparatus, and for the reception and conduction of pain and temperature sensations. We offer these suggestions in a most tentative way and without any attempt to support them by arguments, giving them rather as problems for future investigation than as conclusions to be drawn from the present paper.

BIBLIOGRAPHY

- BARKER, L. F. 1899 The nervous system. Appleton and Co., New York.
- VON BECHTEREW, W. 1886 Über einen besonderen Teil der Seitenstränge des Rückenmarks und über den Faserursprung der grossen aufsteigenden Trigeminiwurzel. Arch. f. Anat. u. Physiol., Anat. Abt., p. 1.
- COLLIER, JAMES, AND BUZZARD, E. F. 1903 The degenerations resulting from lesions of posterior nerve roots and from transverse lesions of the spinal cord in man. Brain, vol. 26, p. 559.
- DARKSCHEWITSCH, L. O. 1896 Zur Frage von den secundären Veränderungen der weissen Substanz des Rückenmarks bei Erkrankung der Cauda equina. Neurol. Centralbl., Bd. 15, p. 5.
- FRÖLICH, A. 1904 Beitrag zur Kenntnis des intraspinalen Faserverlaufes einzelner hinterer Rückenmarkswurzeln. Arb. a. d. neur. Inst., Wien, Bd. 11, p. 378.
- GIERKE, H. 1885 Die Stützsubstanz des Centralnervensystems. Arch. f. mikr. Anat., Bd. 25, p. 441.
- 1886 Die Stützsubstanz des Centralnervensystems. Arch. f. mikr. Anat., Bd. 26, S. 129.
- GOLDSTEIN, K. 1903 Die Zusammensetzung der Rückenmarkshinterstränge. Monatsschr. f. Psych. u. Neur., Bd. 14, p. 401.
- GOLGI, C. 1890 Über den feineren Bau des Rückenmarkes. Anat. Anz., Bd. 5, pp. 372, 423.

- HUBER, G. C., AND GUILD, S. R. 1913 Observations on the peripheral distribution of the nervus terminalis in mammalia. *Anat. Rec.*, vol. 7, p. 253.
- JACOBSON, L. 1907 Beiträge zum intramedullären Verlaufe von hinteren Wurzeln des Conus medullaris. *Neurol. Centralbl.*, Bd. 26, p. 383.
- KÖLLIKER, A. 1891 Zur feineren Anatomie des centralen Nervensystems. *Zeit. f. wiss. Zool.*, Bd. 51, p. 1.
- KOPCZYNSKI, S. 1906 Experimentelle Untersuchungen aus dem Gebiete der Anatomie und Physiologie der hinteren Spinalwurzeln. *Neurol. Centralbl.*, Bd. 25, p. 297.
- LAIGNEL-LAVASTINE, M. 1908 Le système des fibres endogènes des cordons postérieurs dans la dégénérescence ascendante des racines de la queue de cheval. *Compt. rend. Soc. de biol.*, T. 64, p. 223.
- LESZLÉNYI, O. 1912 Vergleichend-anatomische Studie über die Lissausche Randzone des Hinterhorns. *Arbeiten a. d. neurol. Inst.*, Wien, Bd. 19, p. 252.
- LISSAUER, H. 1885 Beitrag zur pathologischen Anatomie der Tabes dorsalis und zum Faserverlauf im menschlichen Rückenmark. *Neurol. Centralbl.*, Bd. 4, p. 245.
- MARGULIÉS, A. 1896 Zur Lehre vom Verlaufe der hinteren Wurzeln beim Menschen. *Neurol. Centralbl.*, Bd. 15, p. 347.
- NAGEOTTE, M. J. 1903 Note sur les fibres endogènes grosses et fines des cordons postérieurs et sur la nature endogène des zones de Lissauer. *Compt. rend. Soc. biol.*, T. 55, p. 1651.
- ORR, D. 1906 The descending degenerations of the posterior columns in transverse myelitis and after compression of the dorsal posterior roots by tumors. *Rev. of Neurol. and Psychiat.*, vol. 4, p. 488.
- RANSON, S. W. 1911 Non-medullated nerve fibers in the spinal nerves. *Am. Jour. Anat.*, vol. 12, p. 67.
- 1912 The structure of the spinal ganglia and of the spinal nerves. *Jour. Comp. Neur.*, vol. 22, p. 159.
- 1913 The course within the spinal cord of the non-medullated fibers of the dorsal roots: a study of Lissauer's tract in the cat. *Jour. Comp. Neur.*, vol. 23, p. 259.
- ROSENZWEIG, ELIAS 1905 Beiträge zur Kenntnis des feineren Baues des Substantia Rolandi des Rückenmarks. *J. f. Psy. u. Neur.*, Bd. 5, p. 49.
- SANO, T. 1909 Vergleichend-anatomische und physiologische Untersuchungen über die Substantia gelatinosa des Hinterhorns. *Arb. a. d. neurol. Inst.*, Wien,, Bd. 17, p. 1.
- SIBELIUS, CHR. 1905 Drei Fälle von Caudaaffektionen nebst Beiträgen zur topographischen Analyse der Hinterstrangserkrankungen. *Arbeiten a. d. Path. Inst. Univ. Helsingfors.*, Bd. 1, p. 79.

- SOTTAS, J. 1893 Des dégénérescences de la moelle consécutives aux lésions des racines postérieures. *Rev. de Medicine*, T. 13, p. 290.
- VIRCHOW, H. 1887 Über Zellen in der Substantia gelatinosa Rolando. *Neurol. Centralbl.*, Bd. 6, p. 263.
- WALLENBERG, A. 1898 Beiträge zur Topographie der Hinterstränge des Menschen. *Deut. Zeitschr. f. Nervenheil.*, Bd. 13, p. 441.
- ZAPPERT, J. 1898 Beiträge zur absteigenden Hinterstrangsdegeneration. *Neurol. Centralbl.*, Bd. 17, p. 102.
- ZIEHEN, TH. 1899 Nervensystem. *Handbuch der Anatomie des Menschen von Bardeleben.*, Bd. 4, pp. 179, 292, 294.