IDENTIFICATION OF THE CELLS AND FIBERS CONCERNED IN THE INNERVATION OF THE TEETH

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FIVE FIGURES

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INTRODUCTORY

It is generally conceded that the nervus alveolaris inferior, which supplies the teeth, gums, and alveolar processes of the mandible, is in the main a general cutaneous nerve. So far as known, it contains no proprioceptive (muscle sense) fibers and few, if any, visceral fibers. The terminal nerve endings of the teeth, like those of the conjunctiva, are very sensitive to pain. In so far as the writer's experience goes, any mild thermal or tactile stimulation in the neighborhood of the nerve endings in a tooth has always resulted in a painful sensation and in no other. Therefore, a study of the chromatolytic cells of the ganglion semilunare after the removal of the teeth and a study of cross-sections of the n. alveolaris inferior and the cephalic portion of the n. maxillaris should supply us not only with some information concerning the

type or types of cells and fibers concerned with the general cutaneous sense, but also with the sense of pain.

In two dogs the writer extracted all of the teeth, except the most median incisors, from the upper and lower jaws of the left side. In this operation the gum was carefully and deeply lanced from each tooth before extraction, so that laceration to the mucous membrane and injury to the alveolar process would be reduced to a minimum. The animals were killed on the fourteenth day after the operation and Nissl series were prepared of both the left and the right semilunar ganglia, the right serving for controls. One of the ganglia on the lesion side was cut for a transverse series and the other as a sagittal series, the former proved more useful on account of the greater ease of orientation.

RELATIVE NUMBER OF SMALL CHROMATOLYTIC CELLS TO LARGE AND MEDIUM-SIZED CHROMATOLYTIC CELLS IN THE GANGLION SEMILUNARE AFTER REMOVAL OF THE TEETH

Both series disclose numerous chromatolytic cells of various stages scattered through the mandibular and maxilloophthalmic divisions of this ganglion. Figure 1, which includes a large part of a section through both portions of the semilunar ganglion from series 80 or any other section from this series, reveals a large number of altered cells sprinkled uniformly throughout the section. It is apparent from this figure that the total number of small cells slightly outnumber the large and medium-sized cells, although, as a matter of fact, there seems to be a gradation of cells from the smallest to the largest. A count of the number of cells covered by this figure shows 292 normal cells and thirty-seven chromatolytic cells. Of the total number of chromatolytic cells, thirty are large and medium-sized cells and seven are small cells. This means that about one-eighth of the total number of cells covered by this figure are chromatolytic, and of these altered cells, one-fourth are small cells and the remainder are large and medium-sized cells. About the same ratio would probably hold for the entire ganglion.

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id it if is e A group of three cells from the mandibular portion of the ganglion, taken from the same section as figure 1, a, is reproduced in figure 2, A, with considerably higher magnification to show cell structure. A comparison of the two upper cells in this group, examples of small and large cells, with

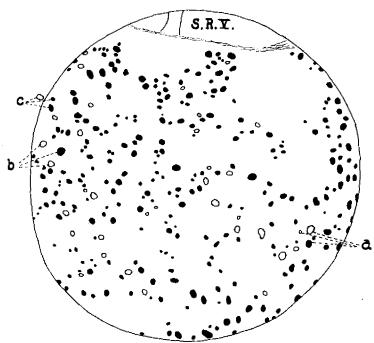


Fig. 1 Camera-lucida drawing from Nissl series 80, a transverse series through the left ganglion semilunare of a dog, in which all of the teeth on the left side, excepting the most median incisors, had been extracted from both jaws. The drawing covers over one-half of the cells of this section and includes the mandibular portion of the ganglion to the right and the maxillary-ophthalmic division of the ganglion to the left. Chromatolytic cells are represented in outline and normal cells appear as solid black. Index letters: S.R.V. stands for the sensory root of the n. trigeminus; a, a group of cells from the mandibular division of the ganglion; b and c, similar groups of cells from the maxillary-ophthalmic portion of the ganglion. Leitz 16-mm. apo. obj. and per. oc. $6x. \times 35.$

the large cell below, demonstrates that the two upper cells are in an advanced stage of chromatolysis, while the lower cell is perfectly normal. Both upper cells exhibit a homogeneous opaque cytoplasm that is destitute of granules, surrounding small undifferentiated and peripherally placed

nuclei. These cells are in sharp contrast to the normal cell below, which possesses a granular cytoplasm, enveloping a sharply differentiated, large, and centrally placed nucleus. Group B illustrates three highly magnified cells from the maxillary-ophthalmic portion of the ganglion, the same cells as b (fig. 1). In this group we have a large normal cell to the left and two large chromatolytic cells to the right. Of the two chromatolytic cells, the lower cell is an example of an advanced or pronounced chromatolysis, identical to the two altered cells in group A, while the upper cell is in a much less advanced state of chromatolysis. In this cell the cytoplasm is an opaque non-granular homogeneous mass. nucleus is but little reduced in size, spherical, centrally placed, but on the other hand is little differentiated from the surrounding cytoplasm. It represents a type of a large number of the chromatolytic cells that are scattered throughout this ganglion, which may be accounted for by the fact that the injury to the nerve took place close to its peripheral endings. Group C in figure 2 represents group c of figure 1, more highly magnified. This group is comprised of two normal cells and one large chromatolytic cell, the latter, when considered as to its degree of Nissl degeneration, can apparently be placed midway between the two altered cells reproduced in group B.

Other sections in this series reveal about the same number of large and small cells, about the same proportion of altered cells, and about the same ratio of large and medium-sized chromatolytic cells to small chromatolytic cells as are shown in figure 1.

It is also possible to utilize the figures from the papers of Spitzer and Perna to furnish additional data for this problem. These authors also studied sections of the ganglion semilunare after extraction of the teeth, but paid no attention to the relative number of small and large chromatolytic cells.

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Spitzer's work was in the nature of an experimental-pathological-neurological study, in which he compared the ganglion semilunare cells of a dog after severing the n. alveolaris in-

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ferior in the mandible with altered human semilunar ganglion cells, which were brought about through tooth removal, tooth decay, and the effects of long infection, as in tuberculosis. Spitzer's figures 1 and 2, which show true axonal

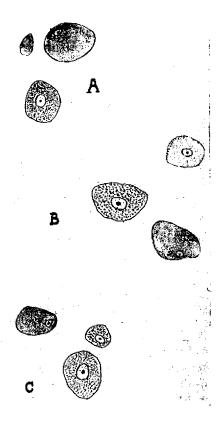


Fig. 2 Same group of cells a, b, and c as in figure 1, more highly magnified, to show cell structure. A, a large and small chromatolytic cell and a large normal cell; B, two large chromatolytic cells and one large normal cell; C, one large chromatolytic cell and a large and small normal cell. Camera-lucida drawing, Leitz 4-mm. apo. obj. and per. oc. 6x. \times 140.

degeneration in the semilunar ganglion of the dog and man, are especially useful for this investigation. They very conclusively demonstrate that the chromatolytic cells are nearly all large or medium sized.

Perna, on the other hand, was concerned mainly in mapping out the area in the ganglion semilunare that supplied the

teeth and the alveolar processes. He removed all of the teeth, or various teeth, from one side of both jaws of a monkey and observed the region in the ganglion in which altered Perna's paper contains nine beautifully cells appeared. colored figures in which the normal and chromatolytic cells are apparently accurately drawn. Figure 3 of plate IX shows twenty-three chromatolytic cells, out of which only six or seven are small cells, and figure 5 of plate X portrays fortynine chromatolytic cells, of which only eight or nine are small cells. It is possible in making these computations that some of the peripheral portions of large cells may have been counted for small cells; if so, the number of small cells should be further reduced. A general comparison of these figures with my sections and with my figure 1, indicates more chromatolytic cells, but about the same ratio of small chromatolytic cells to large and medium-sized chromatolytic cells in either case, which is obviously a large predominance of large and medium-sized chromatolytic cells over small chromatolytic cells.

RATIO OF SMALL TO LARGE AND MEDIUM-SIZED FIBERS IN THE DIFFERENT BRANCHES OF THE NERVUS TRIGEMINUS

In order to determine the above relationship, a number of branches of the trigeminus, including the inferior alveolar, lingual, mandibular, lacrimal, maxillary, frontal, and ophthalmic nerves were sectioned transversely after treating the material with various modifications of Ramón y Cajal's silver method of staining. Ranson's pyridine modification, using pyrogallic acid as the reducing agent, which has given the writer most excellent differentiation of fibers in the spinal nerves, failed, for some reason or other, to give the required contrast to the axones of the trigeminal nerve. Usually the entire field was stained a uniform yellow or brown color and the smallest fibers were invisible. Afterward, the writer ran a second lot of tissue through Ranson's pyridine-silver solutions, but substituted a more contrasty reducer, namely, hydroquinone for the pyrogallic acid. A third lot was put

through another modification of Ranson's pyridine-silver method, but using an alcoholic-formalin-ammonia fixing solution (100 cc. alcohol plus 1 cc. ammonia, one part, and 100 cc. of 10 per cent formalin plus 3 cc. of ammonia, one part). Lastly, a fourth lot was treated according to the chloral hydrate-silver method of Ramón y Cajal—chloral hydrate, alcohol-ammonia, silver nitrate, and hydroquinone used in the order mentioned.

The chloral hydrate-silver method gave most excellent preparations of all the fibers in and near the semilunar ganglion, but peripherally the results were not uniformly satis-The best material was obtained from Ranson's pyridine-silver method, using hydroquinone for the reducing agent, or from my modification of the above, using an alcoholformalin-ammonia fixing agent. Both of the above methods gave all of the axones a very sharp and contrasty staining, but there is no especial differential staining of the medullated and non-medullated (if there are such) fibers. former method, all of the axones were stained from a light brown to a dark brown color, and after the latter treatment, the axones were stained from a dark brown to a black. In either method the smallest fibers were usually stained the darkest, and if the myelin sheaths were present, they were colored yellow, but if completely dissolved, that area appears as a clear space about the axone.

All of the drawings of nerve fibers in figures 3, 4, and 5 were accurately made with the aid of a camera lucida, using a Leitz $\frac{1}{12}$ objective and a 6x periplan ocular. It should be recorded that the region covered in each drawing represents an area showing the greatest number of small fibers. Other portions of these sections could have been chosen in which not nearly as many small fibers would have been exhibited. Nevertheless, if such areas were selected, the different drawings would have demonstrated about the same relative proportion of fibers, the only difference being in the presence of a lesser number of small fibers in each illustration.

In my material it is impossible to distinguish whether the smallest fibers (figs. 3 and 4, N.M.F.) are sparsely medulated or non-medulated. When examined with a 4-mm.

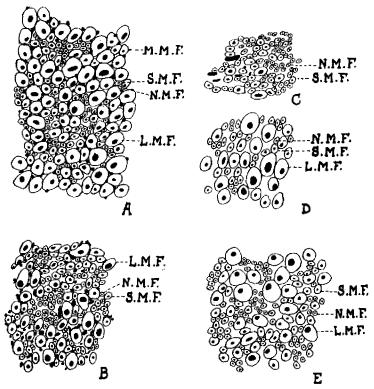


Fig. 3 Selected areas from modified Ramón y Cajal stained sections of the various branches of the n. trigeminus, from regions where the small fibers were most abundant. A, nervus alveolaris inferior at level of its exit from the mandibular foramen; B, n. lingualis; C, n. ophthalmicus from the median side of a section, taken close to the ganglion; D, n. frontalis from the orbital region; E, n. maxillaris, peripheral end. Index letters: L.M.F., large-sized medullated fibers; M.M.F., medium-sized medullated fibers; N.M.F., non-medullated or sparsely medullated fibers; S.M.F., small medullated fibers. Camera-lucida drawing, Leitz $\frac{1}{12}$ oil obj. and per. oc. $6x. \times 270$.

objective, they present almost identical pictures to the non-medullated fibers shown in plate 1, figure 1, of Ranson's ('11) paper. It is, however, immaterial, in so far as this problem is concerned, whether we are dealing with small imperfectly medullated fibers or small non-medullated fibers. It is highly

probable that the small fibers are the peripheral processes of the small cells of the ganglion semilunare.

Figure 3, drawing A, is from a section of the nervus alveolaris inferior and drawing B is from a similar section through the n. lingualis. It is obvious that these two sections, which were taken from regions of the section where the small fibers

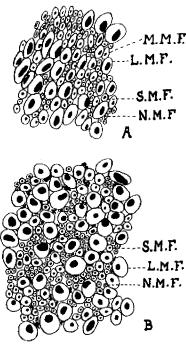


Fig. 4 Selected areas of fibers similar to those in figure 3, but from other branches of the trigeminus. A, motor root of the n. trigeminus; B, sensory division of the n. mandibularis after the motor fibers have left. For index letters see figure 3. Camera-lucida drawing. \times 270.

were most abundant, disclose more small fibers (N.M.F.) than large and medium-sized fibers (L.M.F.) and M.M.F.). Also it is apparent that there are no more, if as many, small fibers in the n. alveolaris inferior, a nerve supplying the teeth, gums, and alveolar processes, than there are in the n. lingualis. To the right, in figure 3, are shown similar drawings through the n. ophthalmicus, C, n. frontalis, D, and n. maxillaris, E. The illustration for the n. ophthalmicus is taken from the

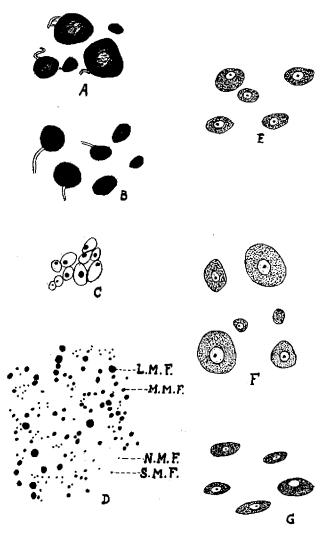


Fig. 5 Miscellaneous camera-lucida drawings of normal cells and fibers. A, selected cells from a modified Ramón y Cajal stained section through a spinal ganglion of a guinea-pig. \times 140. B, selected radix mesencephalica n. trigemini cells from the same series as A. \times 140. C, radix mesencephalica n. trigemini fibers from the same series as A. \times 270. D, radix spinalis n. trigemini fibers from the same series as A at the level of the IX root. \times 270. E, selected radix mesencephalica n. trigemini cells from a Nissl series of a rabbit's brain. \times 140. F, selected ganglion semilunare cells from a Nissl series of a cat. \times 140. G, selected radix mesencephalica n. trigemini cells from a Nissl series of a cat. \times 140. Index letters: L.M.F. represents a large-sized medullated fiber; M.M.F., a medium-sized medullated fiber; N.M.F., non-medullated or sparsely medullated fiber; S.M.F., small medullated fiber.

median surface of the nerve, immediately before the fibers enter the ganglion. This small area of the nerve is composed very largely of small fibers (N.M.F.), which probably originate from the innermost cells of the semilunar ganglion, noted and figured in a previous paper ('24). It should be recorded that the remaining or much larger portion of the nerve exhibits no such proportion of small fibers; in fact, no more than are present in the other branches of the trigeminal nerve. The section of the n. frontalis is taken from the orbital region and portrays only about the ordinary number of small fibers. Drawing E is from a piece of the n. maxillaris cut out from the cephalic end of the orbit. It is clear from this section that the n. maxillaris, which supplies the maxilla and the maxillary teeth, resembles the n. alveolaris inferior in not possessing an extraordinary proportion of small fibers. Also sections of the n. maxillaris, taken directly in front of the ganglion semilunare, show proportionately as many small fibers as the sections from the orbit.

The upper section in figure 4, A, is from the motor root of the n. trigeminus, while the lower drawing, B, is from a section through the sensory division of the n. mandibularis after the motor fibers have left the nerve and directly before the sensory fibers enter the ganglion. It is obvious, from the regions of these drawings, that the small fibers are more abundant than the large and medium-sized fibers, but it is doubtful if this majority would hold if the entire sections are considered. In the section of the motor root the large and medium-sized fibers would predominate, and in the n. mandibularis the number of small fibers would about equal or possibly slightly exceed the total number of large and medium-sized fibers. The writer is unable to detect much difference in the proportion of small to large and mediumsized fibers in sections through the sensory portion of the n. mandibularis and sections of the n. alveolaris inferior.

There can be no question but that there are more small non-medullated or sparsely medullated fibers than there are large and medium-sized medullated fibers in certain areas of all the branches of the n. trigeminus, but it is a question if this majority would hold throughout the entire section. In no case would there be any excessive number of small fibers. Also there is no sharp demarcation into small and large fibers. There are all gradations of medium-sized fibers, which very completely fill the gap between the largest and the smallest fibers. This is also in harmony with the observations on the size of the cells in ganglion semilunare previously recorded.

RELATIVE SIZE OF THE CENTRAL FIBERS FROM THE GANGLION SEMILUNARE

In 1916, Koch recorded large and small medullated fibers and a few unmyelinated fibers in the intracranial portion of the trigeminal nerve of the dog. More recently, Mrs. Gerard has shown experimental and clinical evidence which indicates that tactile impulses are relayed in the main sensory V nucleus and that pain is relayed in the spinal V nucleus. A special relay center for the pain fibers from the cornea was located directly below the first 7 mm. of the spinal V tract. In addition, Mrs. Gerard made some computations on the various kinds of fibers at different levels of the spinal V tract, and noted a disappearance of the larger fibers and an increase of the smaller non-medullated fibers in passing caudally. She offered two explanations to account for the nonmedullated fibers: first, that the medullated fibers may lose their sheaths in passing to lower level and, second, the caudal end of the spinal V tract may have received non-medullated fibers from Lissauer's tract. There is possibly a third explanation, namely, that many of the pain fibers may be medullated, and that they terminate cephalically in the so-called pain portion of the nucleus of the spinal V tract.

It is apparent that the central sensory trigeminal fibers do not separate into a medullated tract and a practically nonmedullated tract corresponding to Ranson's description of Lissauer's tract in the spinal cord. An examination of the radix spinalis n. trigemini in a modified Ramón y Cajal series if In s. ;e s, d

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of a guinea-pig's brain (fig. 5, D) demonstrates that this tract, which ultimately terminates in a sensory nucleus that is continuous with the substantia gelatinosa of the spinal cord and is probably comparable to Lissauer's tract (practically a non-medullated tract), consists of large medullated fibers (L.M.F.), medium-sized medullated fibers (M.M.F.), small medullated fibers (S.M.F.), and very small non-medullated or sparsely medulated fibers (N.M.F.). It should be noted that this section was taken from the level of the IX root and that the fibers in the drawing were selected from the outer portion of the tract, to avoid drawing numerous collaterals that are constantly being given off to the median sensory nucleus. A comparison of figure 5, D, with similar sections of the various branches of the n. trigeminus (figs. 3 and 4) reveals about the same proportion of small to large and medium-sized fibers. Furthermore, it is clear from Marchi preparations in which the ganglion semilunare was destroyed that the large and medium-sized medullated fibers figured in drawing D took origin from the ganglion semilunare.

A similar section through the radix mesencephalica n. trigemini, a little cephalad of the trigeminal motor nucleus and from the same series as drawing D, discloses a very different picture. Here the mesencephalic tract (fig. 5, C) is composed of fairly small to medium-sized or moderately large medulated fibers. No extremely large medulated fibers were observed in this root, and the few very small fibers that are sometimes present are probably of other origin.

To check up further on the differences in the fibers of the radix mesencephalica n. trigemini and the radix spinalis n. trigemini, a comparative study was made of their cells of origin. In every instance selected examples of the largest,

¹Previous work has shown that the proprioceptive fibers of the n. trigeminus, which are probably comparable to the ascending tracts of the dorsal column of the spinal cord, are situated in the radix mesencephalica and in the motor root and nerves of the trigeminal nerve. Likewise, their ganglion cells are found along the mesencephalic root and in the motor root approximating the ganglion semilunare.

smallest, and medium-sized cells were compared. Wherever possible, Nissl stained series were used and only such cells were chosen as were cut through the center of a nucleus that was situated at the center of a cell. All of the drawings were accurately made with the aid of a camera lucida, using the same magnification in each case.

In G, figure 5, we have selected a group of cells taken from a Nissl series through the radix mesencephalica n. trigemini of a cat, which can be compared with a similar group F from the ganglion semilunare of a cat. In group F it is obvious that we are dealing with very large cells, very small cells. and medium-sized cells. On the other hand, the mesencephalic root cells in group G range from medium-sized cells to fairly small cells, but none of them are as small as the smallest semilunar ganglion cells that possess non-medullated or sparsely medullated sheaths. The cytoplasm of these cells is usually dense, being filled with Nissl substance. They are often more or less elliptical, rather than spherical in shape. Frequently the nucleus is placed peripherally, but always sharply marked off from the surrounding cytoplasm. other words, they strongly resemble the proprioceptive cells that were described ('25) in the motor root of the n. trigeminus. A similar selected group of radix mesencephalica n. trigemini cells from a Nissl series of a rabbit's brain is shown in figure 5, E. As to size, they closely resemble the mesencephalic root cells of the cat, but exhibit a general tendency to be slightly more spherical. The writer has no sections of the ganglion semilunare of a rabbit for comparing these cells, but since the spinal ganglion cells of the rabbit and cat are very similar, there is every reason to believe that their semilunar ganglion cells are also very similar. In B and A are selected cells from the mesencephalic root and spinal ganglion of a guinea-pig, stained after a modified Ramón y Cajal method. The former discloses large, small, and medium-sized cells, and the latter only fairly large to moderately small cells.

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It is apparent from the above discussion that the radix spinalis n. trigemini, which contains the general cutaneous fibers of the n. trigeminus, including pain, and is doubtless homologous to the non-medullated Lissauer's tract of the spinal cord, resembles the various branches of the trigeminal nerve in being composed of large medullated, medium-sized medullated, and small-sized non-medullated or sparsely medullated fibers. On the other hand, the proprioceptive fibers, which run in the motor and mesencephalic roots, are mainly, if not entirely, medullated. They are composed of medium-sized or fairly large to moderately small fibers.

SUMMARY AND CONCLUSIONS

In two Nissl series through the semilunar ganglia from dogs, in which all of the teeth but the most median incisors had been extracted from both left jaws, with very little laceration to the gums or alveolar processes, it was shown that about one-eighth of the total number of cells exhibited chromatolysis or Nissl degeneration. Of the total number of altered cells, about three-fourths are large and medium-sized cells and only one-fourth are small cells.

In my preparations these altered cells appear to be scattered uniformly throughout the entire ganglion and not confined to a triangular mass at the base of the maxillary and mandibular trunks, as described by Perna for the monkey.

Some of these cells portray a very complete alteration of the cell, involving both a diminution or disappearance of the Nissl substance and a peripheral displacement of the nucleus, while many others show only a reduction in the Nissl substance. Ordinarily, the cell changes are not as pronounced as was noted in a previous study, where the n. alveolaris inferior was injured more centrally, namely, at its exit from the mandibular foramen.

The figures of both Spitzer and Perna, who studied the altered ganglion semilunare cells after removal of the teeth or severing the n. alveolaris inferior, with other purposes in view than to determine the relative proportion of large

and small chromatolytic cells, also, very conclusively demonstrate the presence of a decidedly larger proportion of large and medium-sized chromatolytic cells than small chromatolytic cells.

A study of modified Ramón y Cajal silver preparations of the main branches of the n. trigeminus discloses that certain areas of the section where the small fibers are most abundant, contain a small proportion more of small non-medullated or sparsely medullated fibers than they do of large and medium-sized medullated fibers. In other parts of the same section the reverse would be true.

Both the n. alveolaris inferior and the cephalic end of the n. maxillaris are not characterized by any great predominance of small fibers over large and medium-sized fibers. They contain no more small fibers than the other branches of the n. trigeminus that were studied.

In accord with the previous remarks on the semilunar ganglion cells, it can be stated that, in all branches of the n. trigeminus, there are numerous intergrading fibers coming in between the largest and smallest fibers.

There can be no question but that the radix spinalis n. trigemini is comparable to the practically non-medullated tract of Lissauer. It is the main trigeminal cutaneous pathway and terminates in a sensory nucleus that is continuous with the substantia gelatinosa of the spinal cord. This tract, however, differs from the tract of Lissauer in that it contains a great many large and medium-sized medullated fibers in addition to its small non-medullated or sparsely medullated fibers.

It was previously shown that the proprioceptive trigeminal fibers are confined peripherally to the motor root and centrally to the radix mesencephalica n. trigemini. Modified Ramón y Cajal preparations have demonstrated that the mesencephalic root is composed of medium-sized or moderately large to fairly small medullated fibers, corresponding to the medium-sized and moderately small ganglion cells that are situated in and along these roots. No extremely large

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or very small fibers or cells were found in connection with this tract.

Admitting the possibility of a general cutaneous nerve fiber being capable of carrying more than one type of stimulus and assuming that the cutaneous nerves supplying the teeth function mainly in conducting pain impulses, it appears highly probable, from the experiments reported in this paper, that pain impulses from the teeth are conducted over the large and medium-sized medullated fibers belonging to the large and medium-sized ganglion cells as well as over the small non-medullated or partially medullated fibers.

DISCUSSION

Herrick has shown that while there is a general tendency for each system of peripheral fibers to have definite fiber characteristics, almost any system may show considerable individual variation in caliber and medullation of its fibers. Also, that there is an inclination for most highly developed muscle fibers and sense organs to be innervated by the largest fibers and for small muscle fibers and sensory structures undergoing functional degeneration to be supplied with the smallest nerve fibers. In a more recent paper, Johnston has brought out a number of fundamental points concerning the caliber of the different parts of a neuron and the nature of a nerve impulse. The above work and some unpublished observations of the writer have suggested the following purely tentative hypothesis: The size of the cell body (trophic center), the size of the axone, and possibly the size of the myelin sheath (if a nutrient center), are dependent primarily on the load that the neuron is, normally and under special conditions, required to propagate. This may take into account the size and importance of the terminal ending, the length of the axone, and the amount of terminal branching of the neurite or dendrites. There may be some difference in the structure of a neuron that is continually being called upon to deliver a weak impulse and one that is occasionally required to propagate a very strong impulse. Such a cone-shaped motor neurite as Johnston describes in the lamprey should be capable of delivering a powerful impulse. It is characteristic of small, but very active non-medullated sympathetic fibers, that they have very large cell bodies. Granting that the nerve impulse is a physical-chemical action and that the cell body is the main trophic center of the cell, the relative size of any such storehouse of energy should be of considerable importance to the effective action of any cell, and especially to those cells which are continually propagating impulses. Many examples have been cited, both pro and con, to prove that there is or that there is no relation between the length of a nerve fiber and the size of its cell body. To the writer it seems reasonable to suppose, other things being equal, that a long fiber would require a larger trophic center (cell body) than a shorter fiber.

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