

## FUNCTION OF THE CELLS IN THE MOTOR ROOT OF THE NERVUS TRIGEMINUS IN THE CAT

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FOUR FIGURES

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### INTRODUCTORY

The purpose of this investigation is to determine through experimental-histological methods the function of certain large and small nerve cells found in and about the motor root of the nervus trigeminus in close proximity to the ganglion semilunare. These cells were noted in a previous paper and it was suggested that some of them in the connective-tissue sheath of the motor root were probably mandibular or maxillary-ophthalmic ganglion cells that had migrated centrally along the path of the motor root and others inside the motor root might be proprioceptive (muscle) sense cells.

Similar cells have been recorded for the eye muscle, facial, and hypoglossal nerves. Those found in the eye-muscle nerves, especially in the oculomotor nerve, have received considerable attention, and the consensus of opinion is that they are concerned with proprioceptive sense.

One of the first and most important studies on this subject is by Thomsen in 1887. He found normal and altered nerve cells in the oculomotor, abducent, and facial nerves in man, but none in the trochlear nerve. In addition to finding normal cells, both with and without capsules, Thomsen observed clusters 'Heerde' of two or three to ten or twenty altered cells in a section. These cells are said to be for the most part round or oval, to have a vacuolated, faded-out protoplasm, and to possess an indistinct nucleus or none at all. The author thinks that these 'Heerde' are not pathologic for the following reasons: 1) Normal and altered cells are found in close proximity. 2) When there is an abundance of clustered altered cells, normal cells are scarce. 3) Groups were found in which the change from normal cells to altered cells is taking place; cells in which the nucleus and some of the adjacent protoplasm is normal, and a peripheral portion that is vacuolated and opaque. 4) In a child at birth only normal cells were found in the oculomotor nerve, while similar sections from a normal child of four years who was killed accidentally show some altered cells. As a result of these findings, Thomsen is of the opinion that these altered cells are formed early in life.

Gaskell, two years later, finds clumps of fibrillar tissue or degenerated ganglia in the roots of the III, IV, VI(?), and VII nerves, obviously the altered cell clumps 'Heerde' of Thomsen's descriptions, which Gaskell considers as vestigial remnants of once functional nerve cells.

Marchi, in 1882, described muscle-tendon sense organs for all of the eye muscles in cattle, in the pig, cat, rabbit, and man. Huber ('99) did not find the ordinary muscle-tendon type of endings in the extrinsic muscles of the rabbit, but described a simpler type of sensory ending for these muscles in this animal. A year later, Huber confirmed Marchi's observations of the presence of neuro-tendinous organs on the tendons of all the eye muscles in cats. He found them most abundant on the superior rectus muscle, where some twenty-five or thirty end-organs were counted.

In 1894, Sherrington severed the III and IV cranial nerves at their superficial origins and found no sound medullated fibers in the eye muscles supplied by these nerves. He raises the question if these nerves are not therefore both sensory and motor. Tozer and Sherrington ('10) demonstrated the presence of sensory fibers in all the eye-muscle nerves. Severance of III, IV, and VI nerves centrally produced a degeneration of practically all of the receptive nerve fibers and end-organs in the eye muscles of monkeys, cats, and rabbits. The few normal fibers that were present even after the ophthalmic branch of the V was severed in addition, were said to be sparsely medullated and were thought to originate from the ciliary ganglion. More likely, however, as suggested by Miss Nicholson in a recent paper, these normal fibers came from cells situated in the peripheral (orbital) portions of these nerves.

In 1909, Harrison performed some experiments on dogs in which he severed intracranially the oculomotor nerve in some of the animals and the trigeminal in others. In the former, with one exception which he attributes to faulty technique, there is said to be a satisfactory staining of some or many of the nerve fibers and muscle spindles of the muscles innervated. This was also true in the experiments where the trigeminal roots were cut.

Three years later, Miss Tozer added a very important contribution to this subject. In young monkeys she found the altered ganglion cells (fibrillar tissue) described previously by Thomsen and Gaskell, and in the same animals she observed encapsulated normal ganglion cells in the III roots between their exit from the brain and their passage through the dura. In six monkeys in which the eye-muscle nerve cells were counted intracranially Miss Tozer found from none to four up to seventy-four normal ganglion cells in the III nerve. In the individual possessing seventy-four cells, the cells were located in the connective tissue surrounding the roots. In one animal seventy-eight normal cells were counted in the VI nerve intracranially. Miss Tozer also

found normal nerve cells in the eye-muscle nerves of a bird and a fish. In one experiment where the III nerve was cut intracranially, leaving a stump attached to the brain, chromatolytic nerve cells were found in this stump. According to the author, the varied number of intracranial nerve cells observed in the eye-muscle nerves of different individuals did not permit of drawing any conclusions concerning the functions of these cells.

In serial sections of a shark's brain Nicholls found some seventy intracranial ganglion cells in one III nerve and some fifty-odd cells in the opposite root. These ganglion masses Nichols thinks are proprioceptive in function.

The most recent paper on this subject is by Miss Nicholson. She sectioned the entire contents of one orbit of a human foetus at birth, and in addition to finding the normal intracranial ganglion cells in the root of the III nerve she observed normal intraorbital ganglion cells in the III and VI nerves, but none in the IV nerve. In the III nerve some thirty-odd cells were counted in the intracranial portion of the nerve and fourteen in the orbital portion; while approximately thirty cells were observed in the orbital portion of the VI nerve. The writer states that the orbital cells are not scattered along the fibers, as is the case with the intracranial cells, but rather they are grouped along the margin of the nerve in ganglion formation.

These observations of Miss Nicholson's are of prime importance in that they offer a very plausible explanation of how it was possible for Harrison and for Tozer and Sherrington to find some normal fibers and sensory endings in the eye muscles after severing their respective nerves intracranially. Furthermore, Miss Nicholson calls attention to the fact that the normal number of ganglion cells in the orbital portion of the VI nerve corresponds very well to the number of sound fibers and sensory endings that Tozer and Sherrington found in the lateral or external rectus muscle after severing the VI nerve intracranially. In addition, it is of interest to note that the number of neuro-tendinous endings

counted by Huber for the superior rectus muscle of the cat (twenty-five or thirty), in which muscle more sensory nerve endings were counted than in any of the other eye muscles, is about the same or even less than the number of ganglion cells in the VI nerve (approximately thirty orbital cells were counted by Miss Nicholson and seventy-eight intracranial cells were recorded for the monkey by Miss Tozer). This nerve supplies the lateral or external rectus muscle—a muscle that probably has fewer nerve endings than the superior rectus. Therefore, after making allowance for some nerve endings that may not have been stained, there are apparently sufficient cells accounted for in the VI nerve to supply each nerve ending of the lateral rectus muscle with at least one nerve fiber.

MICROSCOPICAL STUDY OF THE SMALL CELLS IN THE MOTOR  
ROOT OF THE NERVUS TRIGEMINUS

There is apparently some variation in the number of these cells, but about the normal number is shown in the reconstruction of the ganglion semilunare (fig. 2 of the previous paper). Some sections through the motor root as it crosses the ganglion exhibit one or two cells, other sections, as figure 6 of the previous paper and figure 4 of this paper, portray ten or a dozen cells. Some of these cells are well within the motor root (fig. 4, *p*), others are in the extreme border (fig. 4, some of the cells in group *m*), still others while within the nerve root are surrounded by connective tissue that has migrated into the root, and, lastly, others are located in the connective-tissue sheath enveloping this root. The last are usually small cells and often in small groups (fig. 4, *r*).

The small cells in the motor root of the trigeminus are usually spherical, elliptical, or oval in shape, finely granular, and frequently with eccentrically placed nuclei. These nuclei, however, are relatively large, round, and sharply differentiated from the rest of the cell. Examples of these cells highly magnified and stained with a Nissl stain are shown in figure 3 (*B* and *D*). To make certain that these cells are

true sensory nerve cells and not plasma cells, such as Mayer described as occurring in the ganglion semilunare of man or the clasmatocytes of McKibben's descriptions for the olfactory nerve and meninges of *Necturus*, the following preliminary study was made.

A large full-grown cat was injected subcutaneously with 60 cc. of 1 per cent trypan blue. Twenty-four hours later, the animal was killed and all the tissues including the ganglion semilunare presented a deep blue appearance. Both semilunar ganglia and the cranial portions of the III and VI nerves were removed, fixed in formalin, and cut serially. The ganglion and nerves from the left side were prepared without further staining, while those from the opposite side were stained with safranin. Of these two sets of series those that were counterstained possessed a decided advantage over those that were only stained by the intra-vitam method for the reason that the ganglion cells were stained red in sharp distinction from the wandering cells, which assumed a general blue color due to the absorption of the dye by their granules. On the other hand, the granules in the cytoplasm of the nerve cells were not stained with the blue in any of the series.

Any section through the ganglion semilunare where the motor root of the trigeminus is crossing or has just crossed the ganglion will demonstrate one or more sensory nerve cells in and about the motor root and in addition many wandering cells or clasmatocytes in the ganglion, in the motor root, and in the connective tissue sheath surrounding both structures. Within the ganglion the wandering cells appear at first to be nearly as numerous as the small capsule cells surrounding the ganglion cells, with which in some instances they might be confused without the aid of a differential stain. The wandering cells, clasmatocytes, as shown in figure 1 (*Clas.*), are grouped irregularly among the nerve fibers between the encapsulated ganglion cells. In my preparations they are coarsely granulated cells spherical, elliptical, or oval in shape, and vary considerably in size. The smallest cells

are about the same size as the ganglion capsule cells and the small nerve fibers, while the largest are about the size of the largest nerve fibers. The largest wandering cells noted were found in the connective-tissue sheath surrounding the ganglion and the nerve roots, but they lack considerably of being as large as the smallest ganglion<sup>1</sup> cells in and about the motor root or the neighboring fat-cells. In figure 1A the following cells were accurately drawn side by side with the same magnification: 1) At the extreme left a very large wandering cell or clasmatocyte (*Clas.*) taken from the connective-tissue sheath of the motor root of the trigeminus nerve from the trypan blue-safranin series; 2) a large fat-cell (*F.C.*) from the motor root of a Marchi series where the fat was stained black with the osmic-acid treatment; 3) to the right, a large and a small ganglion cell (*G.C.*) from the connective-tissue sheath of the motor root from the same section as the above wandering cell. It is obvious from figure 1A that the small ganglion cell, which is an example of one of the smallest motor root cells, is considerably larger than one of the largest wandering cells or fat-cells. Both ganglion cells in figure 1A and in fact all of the ganglion cells in this series were stained red with the safranin and none of the Nissl bodies or granules absorbed any of the trypan blue, while all of the granular substance in the wandering cells was brilliantly stained with the trypan blue. Concerning the fat-cells which are stained black in the Marchi series and are fairly abundant in the motor root of the trigeminus, there is little or no danger of mistaking these cells for nerve cells.

A number of the Cajal series demonstrate the processes of many of the large and small ganglion cells in and about the motor root. In nearly every instance the cells are round or oval and the processes are always unipolar, never multipolar. Consequently, they could not be classified as visceral or sympathetic cells. Figure 2, which is from a Cajal series,

<sup>1</sup> The term ganglion cell as applied to the motor root of the nervus trigeminus means a nerve cell of the sensory type, resembling a spinal ganglion cell. It does not necessarily signify that this cell belongs to the ganglion semilunare or that it took origin from the neural crest.

illustrates a group of ganglion cells in the connective-tissue sheath directly outside of the motor root of the trigeminus and some little distance from the semilunar ganglion. Two of these cells are enclosed in capsules and disclose unipolar processes. An adjoining capsule contains a coiled process which belongs to a ganglion cell appearing in the next section in the series. A fourth process is shown close to the motor root. Figure 2A illustrates a ganglion cell also from a Cajal series, but taken from the center of the motor root of the trigeminus. The proximal portion of its unipolar process is clearly revealed.

Most of the ganglion cells within the motor root or its connective-tissue capsule are typical trigeminal ganglion cells enclosed in capsules composed of neurilemma cells. Few if any of the motor-root cells in the Nissl series could be com-

#### ABBREVIATIONS

- |   |   |
|---|---|
| <i>a</i> and <i>b</i> , normal ganglion cells (in fig. 3)                           | <i>Max. &amp; Opth.C.</i> , n. maxillaris and n. ophthalmicus cells   |
| <i>A</i> and <i>B</i> , same cell as <i>a</i> and <i>b</i> , more highly magnified  | <i>n</i> , normal ganglion cell (in fig. 4)   |
| <i>A.C.</i> , axis cylinder   | <i>N</i> , same cell as <i>n</i> (fig. 4), more highly magnified (in fig. 4A)   |
| <i>c</i> and <i>d</i> , normal ganglion cells (in fig. 3)                           | <i>N.Man.S.</i> , sensory portion of the n. mandibularis  |
| <i>C</i> and <i>D</i> , same cells as <i>c</i> and <i>d</i> , more highly magnified | <i>p</i> , chromatolytic cell (in fig. 4)   |
| <i>Cap.</i> , capsule of the V ganglion   | <i>P</i> , same cell as <i>p</i> (fig. 4), more highly magnified (in fig. 4A)   |
| <i>Clas.</i> , wandering cell or elasmatocyte                                       | <i>r</i> , group of chromatolytic cells (in fig. 4)   |
| <i>e</i> , chromatolytic cell (in fig. 4)   | <i>R</i> , same group of cells as <i>r</i> (fig. 4), more highly magnified (in fig. 4A)   |
| <i>E</i> , same cell as <i>e</i> (fig. 4), more highly magnified (in fig. 4A)       | <i>R.Ant.V.</i> , radix anterior n. trigemini (motor root)  |
| <i>f</i> , chromatolytic cell (in fig. 4)   | <i>R.Post.V.</i> , radix posterior n. trigemini (sensory root)  |
| <i>F</i> , same cell as <i>f</i> (fig. 4), more highly magnified (in fig. 4A)       | <i>X</i> , chromatolytic cell (in fig. 3A) from the motor root of another section than figure 3, its location is shown at <i>x</i> (fig. 3) |
| <i>F.C.</i> , fat-cell  | <i>Z</i> , chromatolytic cell (in fig. 4A) from another section than figure 4, its position is shown to be at <i>z</i> (fig. 4)             |
| <i>G.C.</i> , ganglion cell (in figs. 1 and 1A)                                     |   |
| <i>i</i> , normal or chromatolytic cell(?) (in fig. 4)                              |   |
| <i>Lin. &amp; Alv.I.C.</i> , n. lingualis and n. alveolaris inferior cells          |   |
| <i>m</i> , group of chromatolytic cells (in fig. 4)                                 |   |
| <i>M</i> , same group as <i>m</i> (fig. 4), more highly magnified (in fig. 4A)      |   |



pared to the degenerated or altered cells described for the eye-muscle nerves. Some of the ganglion cells in and about the motor root in the Cajal series which were paler and ir-

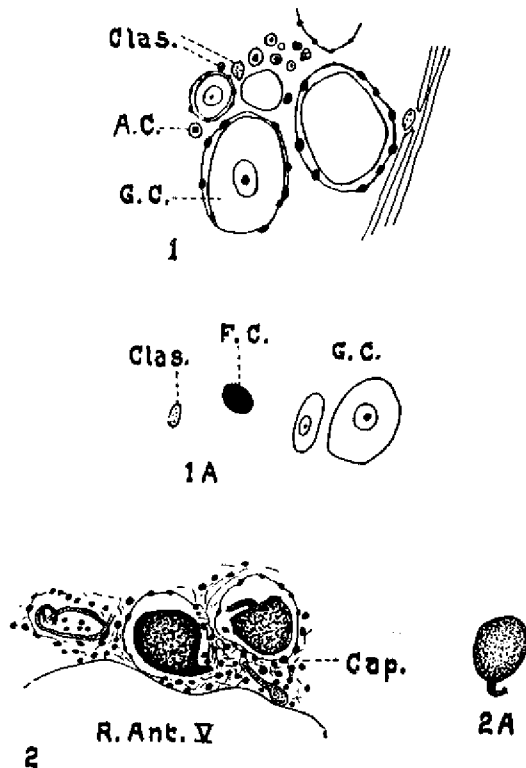


Fig. 1 Small area taken from a section of the ganglion semilunare of a cat stained intra vitam with trypan blue and with safranin after sectioning. The blue granules of the wandering cells sharply differentiate these cells from the red ganglion cells. Camera-lucida drawing, Leitz apo. 4-mm. obj. and per. oc. 6x.  $\times 140$ .

Fig. 1A From left to right: *Clas.*, large wandering cell (clasmatocyte) from the trypan blue-safranin series; *F.C.*, large fat-cell from the motor root of the trigeminus from a Marchi series through the semilunar ganglion of the cat; *G.C.*, a large and small ganglion cell from the motor root of the trigeminus from the same series as the wandering cell. Camera-lucida drawing, Leitz apo. 4-mm. obj. and per. oc. 6x.  $\times 140$ .

Fig. 2 Encapsulated ganglion cells and unipolar processes in the connective-tissue sheath of the motor root of the trigeminus from a Cajal series through a cat's semilunar ganglion. Camera-lucida drawing, Leitz apo. 4-mm. obj. and per. oc. 6x.  $\times 140$ .

Fig. 2A Unipolar ganglion cell from the center of the motor root of the trigeminus from a Cajal series through a cat's semilunar ganglion. Camera-lucida drawing, Leitz. apo. 4-mm. obj. and per. oc. 6x.  $\times 140$ .

regularly shaped might be taken for them, but similar cells also appear in the ganglion proper. The presence of these cells might easily be accounted for through the vigorous treatment that the Cajal technique calls for. It can be stated that nearly all of the experimental animals were full-grown cats and that the so-called altered cells of Thomsen's and Gaskell's descriptions for the eye-muscle nerves are so scarce, if present at all, in the motor root of the trigeminus, that they need no further consideration.

#### EXPERIMENTS

In the previous paper it was demonstrated in series 203 where the nervus maxillaris was severed that an occasional chromatolytic cell appeared in the connective-tissue sheath separating the motor root of the trigeminus from the sensory root at the level where the first motor fibers had crossed the semilunar ganglion. (This region is cephalad of the entrance of the sensory fibers of the n. mandibularis into the ganglion.) These cells were scarce and never extended centrally very far along the path of the motor root. On the other hand, in series 196 and 197, where the n. alveolaris inferior and the n. lingualis were cut, respectively, a number of chromatolytic cells were always present in the connective-tissue sheath separating the motor and sensory roots and also outside, lateral, to the motor root at the level where most of the motor fibers had crossed the ganglion (in this region the presence of chromatolytic cells in the mandibular portion of the ganglion proves that the sensory fibers of the n. mandibularis had entered the semilunar ganglion). It should be stated in connection with these two experiments that it was not known for certain whether or not the n. mylohyoideus was cut. Also, it was shown in the previous paper in connection with series 207, where the n. mylohyoideus was cut in addition to severing both the n. alveolaris inferior and the n. lingualis, that there were numerous chromatolytic cells in the motor root as well as in the connective-tissue sheath surrounding it. This observation when viewed in the light

of some previous work on the mesencephalic root (cited in the previous paper) supports the hypothesis that the chromatolytic cells exhibited in the motor root took origin from the mylohyoid and the diagastric muscles. To establish this point the following additional experiments were performed which constitute the main part of this investigation.

Nissl series were prepared after the same manner as described in the previous paper from the semilunar ganglion of a cat in which the n. alveolaris inferior and the n. lingualis had been severed close to their union; from the semilunar ganglion of a cat in which the n. mylohyoideus had been cut close to its union with the n. alveolaris inferior, and also from the semilunar ganglia of cats in which the n. massetericus had been severed shortly before it reached the masseter muscle.

*Chromatolysis resulting from severing the nervus alveolaris inferior and the nervus lingualis*

To illustrate this experiment the writer possesses one series of an adult cat no. 176 in which the above nerves were severed with absolutely no damage to the n. mylohyoideus or to the central portion of the n. mandibularis.

Almost any section of this series passing through the semilunar ganglion where the motor root of the trigeminus is crossing or has crossed the ganglion will show one or more chromatolytic cells in the connective-tissue sheath of the motor root approximating the ganglion, either outside, lateral to the motor root, or medially, between the motor and sensory roots. In a few instances a chromatolytic cell may have migrated some little distance centrally along the margin of the motor root. In one section a chromatolytic cell is located in a narrow strip of connective tissue separating the motor from the sensory root at the point marked (*x*) in figure 3. This chromatolytic cell is shown more highly magnified to the right in figure 3 (*X*). In the section from which figure 3 was drawn there are five normal ganglion cells (represented in solid black in distinction from chromatolytic cells

in the ganglion that were drawn in outline) situated within or in close proximity to the motor root. Normal cells (*c* and *d*) are inside the motor root, while normal cells (*a*, *b*, and another cell not lettered) are outside in the connective-tissue sheath. It is obvious that these five cells are some little distance from the semilunar ganglion proper. Also a more

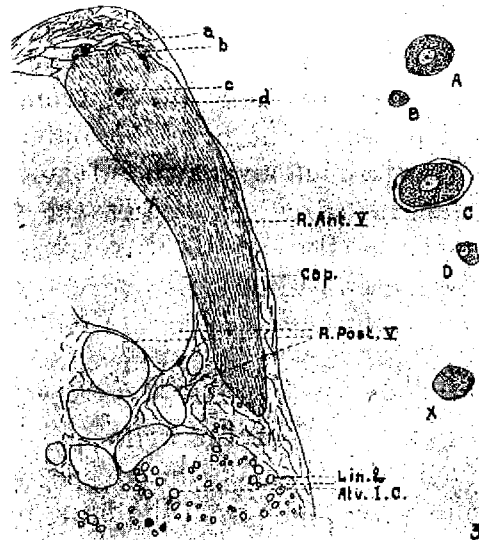


Fig. 3 Transverse section through a portion of the ganglion semilunare of a cat from series 176 at the level where the motor root had crossed the ganglion. In this animal the n. alveolaris inferior and the n. lingualis were severed. A chromatolytic cell is represented in outline and a normal cell in solid black. The normal ganglion cells in the motor root (*a-d*) are reproduced more highly magnified to the right (*A-D*). *X* is a chromatolytic cell from the connective-tissue sheath of the motor root of the trigeminus from another section of this series. Its position is shown by *x* in this figure. Camera-lucida drawing, Leitz obj. 2 and oc. III.  $\times 23$ . Isolated cells (*A-D*) apo. 4 mm. obj. and per. oc. 6x.  $\times 93\frac{1}{2}$ .

highly magnified camera-lucida drawing of these cells, to the right, in figure 3 reveals them (*A*, *B*, *C*, and *D*) perfectly normal. Previously it was noted that the small cells (*B* and *D*) and similar small cells from a normal series possess a finely granular cytoplasm and may contain eccentrically placed nuclei. If not compared with similar cells that have undergone chromatolysis, these cells might be taken for

degenerated cells, but they can generally be distinguished from similar small chromatolytic cells (fig. 4A) by the fact that they possess relatively large round nuclei which are sharply marked out from the cell cytoplasm. Also the cytoplasm is more granular.

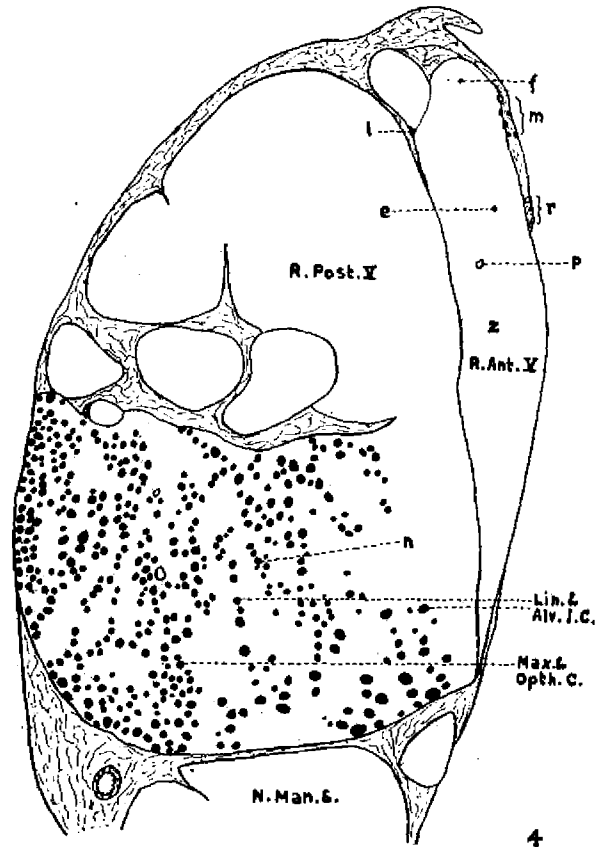


Fig. 4 Transverse section through the ganglion semilunare of a cat at the level where most of the motor fibers of the trigeminus had crossed the ganglion, from series 176 in which the n. mylohyoideus was cut. As in figure 3, the chromatolytic cells are drawn in outline and the normal cells in solid black. Leitz obj. 2 and oc. III.  $\times 23$ .

It is evident, then, from a study of this series that not many of the ganglion cells inside the motor root and not all of the cells in the connective tissue outside the motor root undergo chromatolysis on severing the two main components of the sensory part of the mandibular nerve.

As additional proof to the autopsy findings that both the inferior alveolar and lingual nerves were severed in this experiment, it is obvious that nearly all of the cells in the mandibular portion of the semilunar ganglion are chromatolytic. Only two normal cells (shown in black) are visible in the small portion of the ganglion exhibited in figure 3. They doubtless represent axones that entered the mandibular nerve centrally to the lesion.

*Experiment in which the nervus mylohyoideus was severed*

In this experiment, series 173, an old and very large cat was used. A short skin incision was made along the inner border of the mandible, the digastric muscle was gently retracted away from the jaw and the nervus mylohyoideus was severed close to its junction with the n. alveolaris inferior. After killing the animal and removing the semilunar ganglion, an autopsy showed no apparent damage to the inferior alveolar, lingual, or mandibular nerves. Also the entire series reveals very few chromatolytic cells in the semilunar ganglion, no more than can be explained from cutting some subcutaneous nerves in the technique of the operation. In the section from which figure 4 was drawn two chromatolytic cells were observed in the ganglion. They are drawn as circles in distinction from the normal cells represented in solid black.

The ganglion cells in the motor root and many of the ganglion cells in the enveloping connective-tissue sheath, especially those that are some distance from the ganglion, are chromatolytic. They present a very different picture than the corresponding cells did in the previous experiment, where most of these cells remained normal after severing the main sensory branches of the mandibular nerve. In the section from which figure 4 was drawn (selected because it contained a large number of ganglion cells in the motor root) all of the cells are chromatolytic with the possible exception of *i*, a cell located in the connective tissue between the motor and sensory roots some little distance from the ganglion,

which may be normal—at any rate, I have given it the benefit of the doubt. Of the dozen chromatolytic ganglion cells shown in the motor root in figure 4, a large one (*p*) and two small ones (*e* and *f*) are isolated cells situated well within the limits of the nerve root; the remaining cells for the most part are

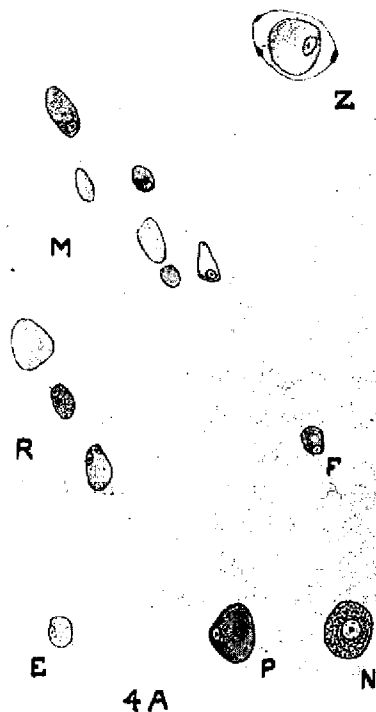


Fig. 4A (*E*, *F*, *M*, *P*, and *R*) are chromatolytic ganglion cells from the motor root of the same section as figure 4. *Z* is a chromatolytic cell from the motor root from another section of the same series as figure 4; its position is indicated by *z* in figure 4. *N* is a normal cell located in the ganglion proper from the same section as figure 4. Camera-lucida drawing, Leitz apo. 4-mm. obj. and per. oc. 6x. × 93½.

small and are located in two groups (*m* and *r*) in the connective-tissue sheath to the right, lateral to the motor root. It should be noted that both of these clusters of ganglion cells are some little distance from the ganglion proper and that one or two of the cells in group *m* are in the outer border of the nerve root rather than in the connective-tissue sheath.

All of the chromatolytic cells shown in the motor root in figure 4 are accurately drawn with a much higher magnification in figure 4A. Group *M* consists of six small elliptical or oval-shaped cells, three of which are sectioned through the center of the nuclei and the remainder peripherally to the nuclei. Group *R*, appearing below group *M*, is composed of three chromatolytic cells, two small nucleated cells, and one medium-sized cell sectioned peripherally to the nucleus. All of the cells in both groups are typical chromatolytic cells. Cells *E* and *F* are small chromatolytic cells, which, when compared to two similar normal cells (*B* and *D*) from figure 3, show a marked difference. The normal cells *B* and *D* exhibit relatively large, round, but eccentrically placed nuclei, sharply differentiated from the finely granular cytoplasm; while the chromatolytic cells *E* and *F* portray more peripherally placed nuclei and relatively much smaller nuclei, which are little differentiated from the homogeneous cytoplasm. The large chromatolytic cell *P* is drawn by the side of a normal cell (*N*) of about the same size taken from the ganglion area of the same section; the marked difference is so obvious that no further explanation is required. Other sections disclose fully as characteristic cells in the motor root as those shown in figures 4 and 4A. Cell *Z* in figure 4A is a large chromatolytic cell taken from the motor root of another section than figure 4 from the above series. Its position is indicated by *z* in figure 4.

It can be stated for this series, where the n. mylohyoideus was severed, that practically all of the cells situated in the motor root show chromatolytic changes. Also that many of the cells located in the connective-tissue sheath of this root, especially those that are some distance from the ganglion, disclose degenerative changes. Then, in addition to these chromatolytic cells in the connective-tissue sheath of the motor root, there are a number of small cells that appear quite normal; some of these normal cells are unquestionably n. mandibularis cells that have migrated centrally along the path of the motor root, but it is impossible to state whether



all of these normal cells can be accounted for by this explanation.

*Experiment in which the nervus massetericus was severed*

In this experiment, as in the previous one, every attempt was made to destroy as few subcutaneous nerves as possible. A short skin incision was made opposite the ventral border of the zygomatic arch, a portion of the masseter muscle was severed crosswise at the level of the ventral border of the zygomatic arch, and upon pulling the distal portion of the cut muscle outward and downward the n. massetericus was exposed and cut. This experiment was performed on a kitten and one a full-grown cat, series 186 and 168.

A careful examination was made of all the ganglion cells in and about the motor trigeminal root, with the result that they all appeared normal. As in the case of the previous experiment, a few chromatolytic cells were scattered through the mandibular portion of the semilunar ganglion. They are but little more numerous than in a normal series, so that they could readily be accounted for through the technique of the operation.

SUMMARY AND DISCUSSION

None of the cells that were described in the previous paper as being situated in and about the motor root of the nervus trigeminus in close proximity to the ganglion semilunare are wandering cells (clasmatocytes) or fat-cells. They are all true ganglion cells, in most instances possessing neurolemma capsules.

Practically all, if not all, of the above-mentioned ganglion cells are normal and not comparable to the altered cells and fibrillar masses that have been described for some of the cells of the eye-muscle nerves.

Many of the small normal ganglion cells in and about the motor root of the cat are finely granular and frequently have eccentrically placed nuclei. They can ordinarily be distinguished from corresponding chromatolytic cells by the

fact that the latter have a relatively much smaller nucleus, which is usually situated more peripherally and is but little differentiated from the surrounding homogeneous cytoplasm.

Series in which the maxillary and ophthalmic nerves were severed demonstrate an occasional chromatolytic cell in the connective-tissue sheath separating the motor from the sensory roots at the level where the first few fibers of the motor root had crossed the ganglion. The number, however, is insufficient to be of any significance.

A series in which the n. alveolaris inferior and the n. lingualis were severed with no damage to the n. mylohyoideus discloses some chromatolytic cells near the ganglion semilunare in the connective-tissue sheath enveloping the motor root of the n. trigeminus, both lateral to the motor root, and medially between the motor and sensory roots. Also, in rare instances these chromatolytic cells have invaded the motor root along with some connective tissue. On the other hand, all of the ganglion cells within the motor root are normal.

A series in which the n. mylohyoideus was cut with no damage to the n. alveolaris inferior, n. lingualis, or the central portion of the n. mandibularis reveals that practically all of the ganglion cells within the motor root of the trigeminus are chromatolytic. Also a number of the ganglion cells in the connective-tissue sheath of the motor root are chromatolytic; especially is this true of cells some little distance from the ganglion. It was doubtless the destruction of these cells in the experiments of the writer in 1919, which, when the ganglion semilunare was extirpated, produced the ascending degeneration noted in the mesencephalic root.

None of the cells in and about the motor root of the trigeminus show any changes as a result of severing the n. massetericus. It was demonstrated in 1919 that proprioceptive sense for the masseter and temporal muscles is amply taken care of by neurons situated in the midbrain nucleus of the mesencephalic root.

It is clear from these experiments that substantially all of the ganglion cells in the motor root proper of the trigeminus

originate from the digastric and mylohyoid muscles. Also a large number of the ganglion cells in the connective-tissue sheath surrounding the motor root have the same origin; while others are the cell bodies of fibers located in the inferior alveolar and the lingual nerves, but in series 207, where all three of these nerves were cut, there are a few normal cells left in the connective tissue outside the motor root. The exact source of these cells is unknown, they may represent fibers that entered the sensory portion of the mandibular nerve centrally to the lingual and inferior alveolar nerves.

From this and the previous studies of others it is apparent that all of the cranial nerves possessing motor roots contain proprioceptive sensory cells within these roots. There is, then, a tendency for the proprioceptive sensory cells of the cranial nerves to retain the primitive condition exhibited by the sensory nerve cells of the spinal nerves of *Amphioxus* and to a lesser extent in *Bdellostoma* and other vertebrates, where these cells are scattered irregularly in the spinal cord and in the spinal nerves. In the trigeminal nerve of the cat and guinea-pig the proprioceptive cells are present both in the brain stem and in the motor root. In many other mammals, including man, proprioceptive sensory cells appear in the motor roots of the other cranial nerves, extending well out into the orbit in connection with two of the eye-muscle nerves. It would be of interest to know how these cells migrated out into the motor root. Their adult relationship suggests a course following the motor root rather than from the neural crest.

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