Contributions from the Biological Laboratory of the U. S. Fish Commission, Woods Hole, Massachusetts.

THE PERIPHERAL NERVOUS SYSTEM OF THE BONY FISHES.

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For some two years past the writer has been engaged upon a microscopical examination of the cranial and first spinal nerves of the teleostean fishes. To any-one acquainted with the literature of the nervous system of the fishes it is apparent that great confusion prevails regarding the morphology of their peripheral nerves. Not only are the homologies with the higher and lower forms obscure, but even within the groups of fishes the variations in the courses of these nerves are so great as to complicate the problem enormously. Previous workers along these lines have, as a rule, either confined themselves to gross dissections, or, if the microscopical method has been used, such studies have usually been confined to the proximal or root portions of the nerves.

Now, by gross methods the topographical relations of the nerves can be and have been determined for most of the groups of larger fishes with precision. Indeed, the great monograph of Stannius in 1849 has covered this ground with remarkable completeness and accuracy. This method, however, leaves us almost entirely in the dark as to the composition of the several rami; for it is impossible to determine more than approximately what classes of sensory and motor fibers are included within each nerve, and even such an approximation is often out of the question. On the other hand, the microscopical study of the nerve roots and their nuclei within the brain is also unsatisfactory; for unless we know the exact peripheral distribution of each of these roots we may be led into grave errors of interpretation, as several of the most recently published researches in this field forcibly illustrate.

In view of these facts, the present demand, it seems to me, is for a minute and exhaustive study of the exact relations of the several nerve components through the entire courses of the several cranial nerves in a few typical fishes. The common silverside, *Menidia*, so abundant about Woods Hole and other points along the Atlantic coast, was chosen as the first type to be examined. These little fishes stand about midway between the physostomous and the physoclystous types of fishes, and may be regarded as relatively simple, generalized forms. Though the organs of special sense (eye and ear) are very highly developed, and in some other minor features there is considerable specialization, yet the nervous system, as a whole, is very simply and evenly developed, and conforms to the central position given to these fishes by the taxonomists.

Menidia is a favorable type for such study, not only on account of its central position and small size, but the tissues seem to react histologically better than those of some other fishes. Moreover the nervous system of the family *Atherinidæ* has not before been examined even by gross dissection, and several points have been brought out in the topography which are either new for teleosts or shed light on vexed morphological questions, such as the discovery of a pre-trematic branch of the facial nerve, a ramus ophthalmicus profundus of the trigeminus, and a true spinal accessory nerve emerging with the vagus to supply the trapezius muscle.

The research was conducted by means of reconstructions from serial sections cut through the entire head of the adult fish and stained by a modification of the Weigert method,* the aim being to trace each nerve component continuously from its nucleus of origin or termination in the brain through the root and ganglionic complex to its peripheral end. Thus, ultimately, the exact composition of each peripheral nerve and ganglionic complex would be given. This attempt has been crowned with a fair measure of success, and plots have been prepared to exhibit graphically the courses of the several kinds of fibers.

The doctrine of nerve components dates properly from the systematic separation of sensory and motor roots and the formulation of Bell's law. Gaskell's suggestive "four-root theory" of the nerves has been a stimulus to further advance, though probably that theory will not stand in exactly its original form. Our precise knowledge of the sensory components in the cranial nerves of lower vertebrates begins with Strong's paper on "The Cranial Nerves of the Amphibia" in 1895, and the present investigation was carried out upon the basis of that work. The cranial nerves of the fish which I have studied have reduced themselves to a plan which is so simple and so similar to what Strong found in the Amphibia that we are justified, I think, in regarding this arrangement in its main outlines as a type to which the nerves of all the higher fishes may provisionally be referred (see diagram). A careful study of nearly all of the existing literature supports this belief. At any rate this scheme will serve, it is hoped, as a basis for future work in the attempt to unify and correlate our knowledge of the nerves of the lower vertebrates.

The spinal nerves.—Following Gaskell, four components are now generally recognized in the spinal nerves of vertebrates: (1) somatic motor from the ventral horn cells, supplying the striated body musculature; (2) somatic sensory (general cutaneous), terminating in the dorsal horn and supplying the skin of the body; (3) visceral motor; (4) visceral sensory. The last two components are supposed to be related to the "intermediate zone," or lateral horn region of the spinal cord, the sensory fibers coming in by the dorsal roots and the motor fibers going out by both roots.

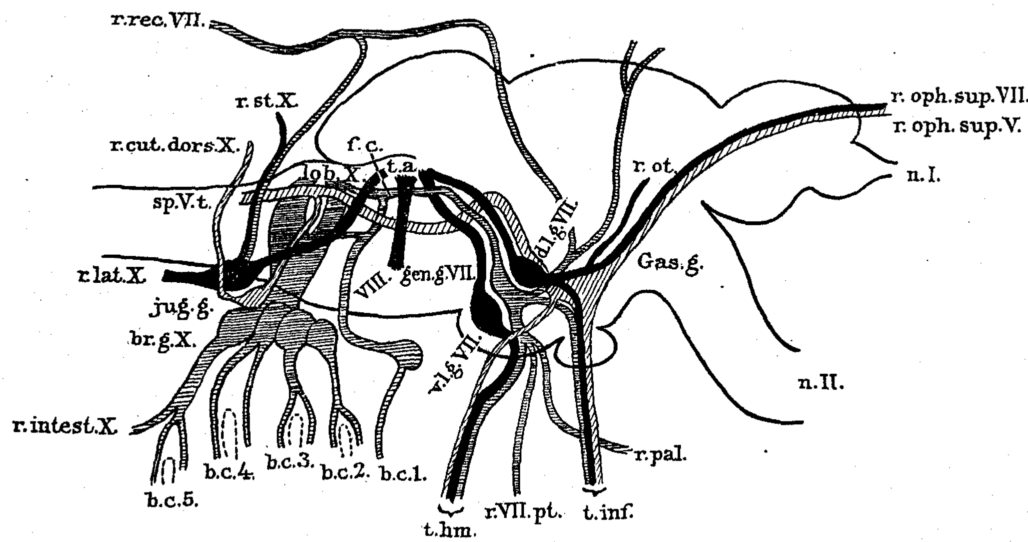
In *Menidia* the r. medius (r. lateralis of authors) of the several spinal nerves usually anastomoses with a twig of the r. lateralis vagi. The two nerves can, however, be distinguished after the anastomosis by the difference in the size of the fibers, and it is seen that the spinal nerve never participates in the innervation of the lateral line organs, but always goes to the skin adjacent. The anastomosis has no

* The technique employed here and in numerous other experiments with the Weigert processes carried on in connection with this work has been fully reported in a previous paper—"Report upon a Series of Experiments with the Weigert Methods," State Hospitals Bulletin, vol. II, Nos. 3 and 4, Utica, N. Y., 1897; also a full abstract of the above in Jour. Comparative Neurology, vol. VIII, Nos. 1 and 2, July, 1898.

morphological significance. The first spinal is obviously a fusion of two segmental nerves, possibly of more than two.

The cranial nerves.—The four components found in the trunk are also found in the head, though in some cases strangely modified; and in addition to these there is a fifth, the acustico-lateral component, which is not represented in any spinal nerve. There is no cranial nerve which contains all of these components, not even of the original four, and there is an obvious tendency toward the concentration of the fibers of each component so as to form a single system with a common center in the medulla oblongata, this being more marked in the case of the most highly specialized components and less so in those which are more feebly developed.

Of the motor systems, the somatic motor is represented only by the eye-muscle nerves and the hypoglossus. Undifferentiated viscero-motor fibers of uncertain connections probably go out with the vagus. The motor roots of the X, IX, VII, and V nerves probably represent highly specialized viscero-motor nerves developed in connection with the elaborate striated visceral musculature of the branchial arches and their derivatives. They appear to correspond to the viscero-motor fibers contained in the dorsal roots of the spinal nerves.



Description of figure.—A diagrammatic view of the sensory components of the cranial nerves of *Menidia*, as seen from the right side. The diagram is based upon a projection of the cranial nerves upon the sagittal plane made by reconstruction from serial sections. The general cutaneous component is indicated by the wide cross-hatching, the communis component by narrow cross-hatching and the acustico-lateral is drawn in black. The following explains the reference letters:

b. c. 1 to b. c. 5. The five branchial clefts.
b. r. g. X. The ganglia of the four branchial rami of the vagus, the last one containing also the ganglion of the r. intestinalis.
d. l. g. VII. The dorsal lateral line ganglion of the VII nerve.
f. c. Fasciculus communis.
Gas. g. Gasserian ganglion.
gen. g. VII. Geniculate ganglion of the VII nerve.
jug. g. The general cutaneous ganglion of the vagus nerve—jugular ganglion of Shore and Strong.
lob. X. The lobus vagi.
n. I. The olfactory nerve.
n. II. The optic nerve.
r. cut. dors. X. Ramus cutaneous dorsalis of the vagus.
r. intest. X. Ramus intestinalis of the vagus.
r. lat. X. Ramus lateralis of the vagus.
r. oph. sup. V. Ramus ophthalmicus superficialis trigemini.
r. oph. sup. VII. Ramus ophthalmicus superficialis facialis.
r. ot. Ramus oticus.
r. pal. Ramus palatinus facialis.
r. rec. VII. Ramus lateralis accessorius, or r. recurrens facialis.
r. st. X. Ramus supratemporalis vagi.
r. VII pt. Ramus pretrematicus facialis.
sp. V. t. Spinal V tract ("ascending root of the trigeminus").
t. a. The tuberculum acusticum.
t. hm. Truncus hyomandibularis of the facial nerve.
t. inf. Infraorbital trunk, containing the r. mandibularis V, the r. maxillaris V, and the r. buccalis VII, together with communis fibers.
VIII. The eighth nerve.
v. l. g. VII. The ventral lateral-line ganglion of the VII nerve.

The relations of the sensory nerves in the head of *Menidia* are exhibited in the preceding diagram. The somatic sensory or *general cutaneous nerves* of the head all terminate in the sp. V tract, which is the continuation into the head of the dorsal horn of the spinal cord and which is represented in human anatomy by the "ascending root" and the chief sensory nucleus of the fifth nerve. This system receives a small root from the vagus nerve and all of its other fibers from the trigeminus, comprising the whole of the sensory portion of the latter nerve. The general cutaneous component appears at first sight to have been reduced in the head as compared with the trunk. Such, however, is not the case; it has merely been compacted. On the other hand, the skin of the face is certainly more richly supplied with general cutaneous (tactile) nerves than areas of corresponding size on the trunk.

The *communis system* of the head corresponds, in my judgment, with the viscero-sensory system of the trunk. Under this term I include all nerves which supply the mucous lining of the mouth and pharynx, sensory fibers of the r. visceralis vagi, and those for taste buds and their allies, the terminal buds of the outer skin. In *Menidia* all of these nerve fibers terminate in a single center, the lobus vagi, which corresponds to the sensory nucleus of the vagus in man. In some other bony fishes there is, in addition, a similar pre-auditory center, the so-called lobus trigemini (which is not, however, homologous with the "lobus trigemini" of ganoids and selachians). These communis fibers enter by way of the X, IX, and VII nerves, and are not represented in any other cranial nerve roots. Like the general cutaneous nerves, they have been unified into a very compact system with a single center. This system has been enormously hypertrophied in the head, and for a double purpose. In the first place, the viscero-sensory nerves of the trunk seem to have been in large measure supplanted by the r. intestinalis vagi. In the second place, the cephalic end of the digestive tract requires a proportionally greater nerve supply for its elaborate branchial and labial apparatus. And, in connection with the latter, more highly specialized sense organs (taste buds) have been developed in response to an obvious functional need. The advantage to be derived from such a centralization of the sensory apparatus of the entire digestive tract is obvious. In *Menidia* the fibers of this system enter the lobus vagi either directly by the vagus or through the mediation of the fasciculus communis from the IX and VII nerves.

The *acustico-lateral system* has no direct representative in any spinal nerve. To it belong all the nerves which supply the lateral line organs and the organs of the internal ear. These nerves all terminate together in the tuberculum acusticum, and the auditory nerve is the only survivor of this system in the higher vertebrates. What may be the relationship between this system and the other, probably phylogenetically older, sensory systems is as yet problematical; it has probably been derived from the general cutaneous.

It is obvious that in making comparisons between cranial and spinal nerves more attention should be paid to the morphological differences between these several types of nerve fibers than has hitherto been done by most morphologists and embryologists. There is to-day as little justification for the direct homologizing of general cutaneous nerves of the trunk with, say, the nerves supplying taste buds in the head as there would be for the comparison of a motor with a sensory root; and yet it is not infrequent to see dorsal spinal roots compared with all dorsal cranial roots indiscriminately.

The following paragraphs give the components of the several cranial nerves as I have found them in *Menidia*, together with a few items concerning their distribution.

XII nerve.—This nerve is represented in the first member of the first spinal complex. It supplies the post-hyal ventral somatic musculature. The pre-hyal somatic musculature is not present in the teleosts, the so-called m. genio-hyoideus not being homologous with the muscle of that name in the other vertebrates.

XI nerve.—The spinal accessory nerve can be positively identified, going out with the vagus and innervating the trapezius muscle. It probably arises from the nucleus ambiguus and is viscero-motor in nature.

X nerve.—This nerve contains viscero-motor, viscero-sensory (communis), general cutaneous and lateral line fibers. The two first types make up most of the nerve. The general cutaneous component is small, but has its own ganglion and enters the rami cutanei dorsales. The large root of the lateral line nerve of the trunk is conventionally assigned to the vagus, though it is really distinct.

IX nerve.—The glossopharyngeus contains only viscero-motor and communis fibers. A small bundle of the latter passes by intra-cranial anastomosis into the root of the n. lateralis vagi. These fibers pass out with the first three or four branches of the n. lateralis (the first of these being the n. supra-temporalis vagi), accompanying the proper lateralis fibers, and ultimately they anastomose with the r. lateralis accessorius. The IX nerve in *Menidia* lacks the r. pre-trematicus and the r. supra-temporalis.

VIII nerve.—This nerve supplies the usual organs of the internal ear and belongs exclusively to the acustico-lateral system.

VII nerve.—The facial nerve contains viscero-motor, communis, and lateralis fibers. The communis fibers form the whole of the pre-auditory fasciculus communis, are provided with a special ganglion, the geniculate g., and are distributed to nearly all of the rami of the V + VII complex, as follows: (1) To the r. palatinus (comprising the whole of that nerve), for the mucosa and taste buds of the roof of the mouth; (2) to the truncus hyomandibularis VII, for the mucosa and taste buds of the inside of the lower jaw and lip; (3) to the r. maxillaris V, to taste buds within the upper lip; (4) fibers passing dorsally into the cranial cavity, forming in the meninges an elaborate plexus, and finally combining to form the facial root of the r. lateralis accessorius (r. recurrens VII), which runs the length of the body superficially near the median line. (5) Other communis fibers supply some terminal buds on the top of the head and run forward with the r. ophthalmicus superficialis. (6) In addition to the preceding, there is a small twig which leaves the geniculate ganglion between the truncus hyomandibularis and the r. palatinus, running directly ventrally to the roof of the mouth, supplying its mucosa in the region between the areas supplied by the IX and palatine nerves. It passes along the cephalic face of the very large pseudobranch and also innervates this organ. This nerve represents, apparently, the pre-trematic branch of the facial, the truncus hyomandibularis being the post-trematic. The pseudobranch of this fish, then, represents a vestigeal spiracular gill on the mandible, such as we find a rudiment of in the adult *Torpedo*.

The acustico-lateralis component of the VII nerve is represented by two lateral line roots. (*a*) The ventral lateralis root has a separate ganglion and supplies organs of the opercular and mandibular canals, via the truncus hyomandibularis. (*b*) The dorsal lateralis root also has a separate ganglion and supplies organs of the infraorbital and supra-orbital lines, via the r. buccalis and r. ophthalmicus superficialis VII, respectively.

VI nerve.—A somatic motor nerve.

V nerve.—The trigeminus contains viscero-motor and general cutaneous components. The sensory fibers enter the spinal V tract, with which is doubtless associated the chief sensory nucleus of the V nerve. The Gasserian ganglion is clearly separable from the other ganglia of the V + VII complex, though most of the earlier writers on fish nerves have treated the whole collection together as the Gasserian. Cutaneous fibers go out from it to the r. ophthalmicus superficialis V (which is fused with the nerve of the same name from the seventh nerve), the r. maxillaris V, the r. mandibularis V, the truncus hyomandibularis VII for the operculum, and, finally, the r. ophthalmicus profundus V. The latter nerve consists of a few fibers which accompany the sympathetic radix longa of the ciliary ganglion to that ganglion, beyond which they can no longer be separately followed. The relations of this nerve, which has not been reported by previous students of the teleosts, indicates that the embryonic profundus ganglion has fused with the Gasserian.

The motor fifth supplies the muscles usually described for teleosts, and in addition the so-called m. genio-hyoideus. The innervation of this muscle has hitherto been usually assumed to come in teleosts from the VII nerve. This muscle is almost certainly not homologous with the muscle in the corresponding position of other vertebrates, which is innervated by the first spinal or hypoglossus nerve.

The IV and III nerves are purely somatic motor, while the II and I nerves can not as yet be placed in any of these categories.

This investigation, which is still incomplete, has been carried out partly at Columbia University, partly at the Pathological Institute of the New York State Hospitals, and during the summer of 1898 at the laboratory of the United States Fish Commission at Woods Hole, Mass. Several morphological points which remain obscure can be finally cleared up only by the embryological method. Accordingly, during the present season I have secured and raised the eggs of *Menidia*, putting up series of the embryos with a view to some studies in the organogeny in the near future.

The eggs of our two common species (which I have elsewhere described) are very similar. Those of the larger species, *Menidia notata*, after artificial fertilization, can be easily reared in ordinary hatching jars, and I obtained stages up to 6 days after hatching (16 days after fertilization) and later stages by towing in the harbor at Woods Hole. But the eggs of the smaller species, *Menidia gracilis*, which inhabits the tide pools and protected bays, I was never able to hatch, though the eggs seemed normal and fertile and the conditions were the same as for the other species. The eggs would grow for from 6 to 12 hours and would then gradually die out. Possibly these fishes normally spawn in brackish water.

I am under very special obligation to the United States Fish Commission, which has freely furnished all things needful for this work, and particularly to the director of its laboratory for many unusual courtesies.

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