

THE CRANIAL NERVES OF THE BONY FISHES.

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The cranial and first spinal nerves of *Menidia* have been plotted by reconstruction from serial sections in order to exhibit the relations of the nerve components both proximally and distally. In most cases the several components have been traced from their nuclei of origin or termination in the brain through the ganglia to their peripheral termination.

Throughout the gnathostome vertebrates we now commonly recognize four components in the typical spinal nerve—(1) somatic motor, from the ventral horn cells; (2) somatic sensory (general cutaneous), terminating in the dorsal horn; (3) visceral motor; and visceral sensory. The central relations of the last two components are still obscure. They are probably both related to the "intermediate" or lateral horn zone, the sensory fibers coming in by the dorsal root and the motor fibers (in infra-mammalian groups, at least) going out by both dorsal and ventral roots.

Now in the bony fish the cranial nerves exhibit these four components and in addition a fifth, the acustico-lateral. The somatic motor is represented by the eye-muscle nerves; the somatic sensory by the general cutaneous component of the V and X nerves, terminating in the spinal V tract, which is the continuation of the dorsal horn of the spinal cord; the visceromotor by the motor fibers of the other cranial nerves, going out near the sensory fibers by dorsal roots to the branchial musculature. The viscerosensory system, like the visceromotor, has been hypertrophied and is represented by the communis system of the X, IX and VII nerves, terminating, either directly or through the mediation of the fasciculus communis in the vagal lobe (chief sensory vagus nucleus of higher forms). The communis system of the head, unlike the corresponding visceral sensory system of the trunk, receives fibers from taste buds and other sense-organs not belonging to the lateral line

system. The acustico-lateral system receives fibers from the ear and lateral line organs and no others. These fibers all terminate together in the tuberculum acusticum.

In the cranial nerves the motor fibers for the unstriated visceral musculature (with sympathetic connections?) are, as in the trunk, very small, while those for the striated visceral musculature of the branchial arches and for the somatic eye-muscles are large. The general cutaneous fibers are small or medium, the *communis* fibers are all very small, and of the acustico-lateral fibers those from the lateral line organs are for the most part very large, while the auditory fibers are of medium size.

The accompanying diagram exhibits the relations of the sensory components in the cranial nerves of *Menidia* and some of the more important points are reviewed in the following summary.

1. The *ramus medius* (r. *lateralis* of authors) of the spinal nerves usually anastomoses with a twig of the n. *lateralis vagi*; but in all cases the spinal fibers go to the skin around the lateral line, and never to a lateral line organ.

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

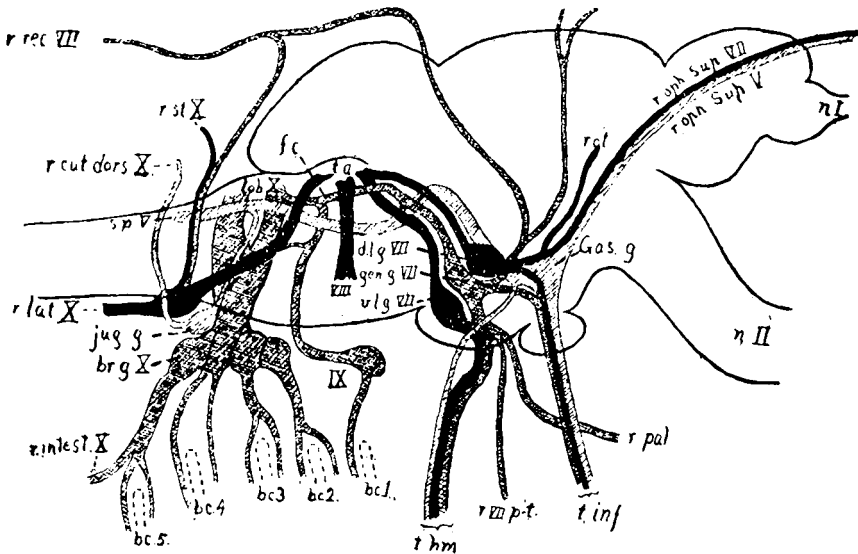
3. The *vagus nerve* contains *general cutaneous* fibers (*rami cutanei dorsales*), which have a special ganglion (jugular g. of Shore and Strong) and which terminate in the spinal V tract.

4. The *vagal lobe* is mainly, at least, the terminal nucleus for visceral sensory fibers and hence is to be regarded as the continuation into the head of the "intermediate zone" of the spinal cord, rather than of the dorsal horn, as some have maintained. These fibers, which will be termed *communis* fibers, are in part general visceral sensory fibers from mucous surfaces and in part fibers from more highly specialized organs—taste buds etc.

5. The nucleus ambiguus, giving rise to the *motor root of the vagus*, has been specialized away from the general visceromotor center in correlation with the development of the striated visceral musculature of the branchial arches. The central ner-

vous connections of fibers for the unstriated visceral musculature of the vagus region are obscure.

6. The *XI* nerve may be identified in teleosts. It arises probably from the caudal part of the nucleus ambiguus and



DESCRIPTION OF THE 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 single cross-hatching, the communis component by double cross-hatching and the acustico-lateral is drawn in black.

REFERENCE LETTERS.

- b. c. 1* to *b. c. 5*.—The five branchial clefts.
br. 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.
IX.—The glossopharyngeal nerve and its ganglion.
jug. g.—The general cutaneous ganglion of the vagus nerve—jugular g. of Shore and Strong.

supplies the trapezius muscle. It is apparently a visceromotor nerve.

7. The *n. lateralis vagi* terminates in the tuberculum acusticum, crossing all of the other vagus roots without, however, being connected with them in any way. It, however, receives a small bundle of communis fibers from the IX root. The latter, apparently go out with the first three or four branches of the *n. lateralis* (the first of these being the *r. supra-temporalis vagi*), accompanying the proper *lateralis* fibers, and ultimately anastomose with the *r. recurrens VII*.

8. The *sensory IX* is composed exclusively of communis fibers. They enter the lobus vagi by way of the fasciculus communis. Neither *lateralis* nor general cutaneous fibers are received during any part of its course, nor is there any connection with any other nerve save the sympathetic chain and the intra-cranial anastomosis with the root of the *n. lateralis vagi* already mentioned. The IX nerve lacks the *r. pre-trematicus* and the *r. supra-temporalis*.

9. The *motor IX* arises from the cephalic part of the nucleus ambiguus, runs for a considerable distance along the lateral

lob. X.—The lobus vagi.

n. I.—The olfactory nerve.

n. II.—The optic nerve.

r. cut. dors. X.—Ramus cutaneus 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 recurrens facialis.

r. st. X.—Ramus supratemporalis vagi.

r. VII p-t.—Ramus pre-trematicus 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.—Infra-orbital 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.

surface of the fasciculus longitudinalis dorsalis and before leaving the latter contributes a considerable bundle of fibers to it.

10. The *auditory nerve* terminates in the tuberculum acusticum, and its fibers are internally so mingled with the lateralis fibers from the X and VII nerves that analysis is impossible in Weigert preparations.

11. The sensory VII roots contain two components. The *communis portion*, enters the fasciculus communis, comprising the whole of that tract except the fibers received from IX. It terminates in the lobus vagi, a lobus trigemini not being developed. This communis root enters the geniculate ganglion and distributes to (1) the r. palatinus (comprising the whole of that nerve) for the mucosa and taste buds of the roof of the mouth; (2) the truncus hyo-mandibularis VII for the mucosa and taste buds of the inside of the lower jaw and lip; (3) the r. maxillaris V to taste buds within the upper lip; (4) the r. recurrens VII. The latter fibers pass dorsally into the cranial cavity, forming in the meninges an elaborate plexus, finally to combine into the r. recurrens which runs the length of the body superficially near the dorso-median line. These communis fibers supply some terminal buds on the top of the head and some others probably run forward with the ophthalmicus superficialis. In addition to the above there is (5) a small twig which leaves the geniculate ganglion between the truncus hyo-mandibularis 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. In its course it passes along the cephalic face of and innervates the very large pseudobranch. This is the only nerve supply which that organ possesses, and this nerve is accordingly, I think, to be regarded as the pre-trematic VII nerve, the pseudobranch representing a spiracular gill and the truncus hyo-mandibularis the post-trematic VII.

12. The second sensory 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 hyo-mandibularis. (b)

The dorsal lateralis root also has a separate ganglion and supplies organs of the infra-orbital and supra-orbital lines, via the r. buccalis and r. ophthalmicus superficialis VII respectively.

13. The nucleus of the *motor VII* corresponds in position and structure to the n. ambiguus and the root is related to the dorso-median fasciculus exactly like the motor IX root. It is, at its origin, distinct from the sensory roots of VII and supplies the mm. levator operculi, adductor operculi, adductor hyo-mandibularis, adductor arcus palatini and the branchio-stegal muscles, as usual among the teleosts. It does not, however, supply the m. genio-hyoideus, as usually stated.

14. The *sensory V* is composed exclusively of general cutaneous fibers. It receives the whole of the pre-vagal spinal V tract. The Gasserian is its proper ganglion and this term should not be applied to any other cells of the V + VII ganglionic complex. From the Gasserian g. are given off general cutaneous fibers into (a) r. maxillaris V, (b) r. mandibularis V, (c) r. ophthalmicus superficialis V, (d) fibers running back into the truncus hyo-mandibularis VII for the operculum, also (e) a very small r. profundus V. The latter accompanies the sympathetic fibers of the radix ciliaris longa of the ciliary ganglion to that ganglion after which they can no longer be separately followed. The relations of this nerve, which has not before been described for teleosts, indicate that the embryonic profundus ganglion has fused with the Gasserian.

15. The *motor V* nucleus resembles that of the motor VII, but lies farther laterad and dorsad. The fibers enter the r. mandibularis V and supply the mm. dilator operculi, levator arcus palatini, adductor mandibularis, inter-mandibularis and genio-hyoideus. The innervation of the latter muscle has hitherto been usually assumed to come in teleosts from the VII. This muscle is almost certainly not homologous with the muscle in the corresponding position of other vertebrates which is supplied by the I spinal or XII nerve.

16. The sympathetic chain has ganglia on nearly all of the cranial ganglia and probably sends fibers into all of the rami from

the latter. In passing from IX to VII ganglia the sympathetic runs external to the ear capsule.

The various components can be followed with great precision proximally in the root portions and through the ganglia of the cranial nerves. Throughout the peripheral courses of the nerves the analysis is somewhat more difficult, but has been satisfactorily accomplished in all but a very few cases. The naked organs of the lateral line series (pit lines) and the terminal buds of the skin (communis system) are sometimes hard to differentiate because their nerve fibers are intermediate in size between the exceedingly large fibers typical for the lateralis system and the very small communis fibers. The general cutaneous system of nerves is, however, as clearly separable from the others peripherally as it is centrally. And this is important in many ways. For example, it will materially assist in the attempt to homologize cranial and spinal nerves to know that not all sensory cranial roots are comparable with spinal dorsal roots. It is, e. g., no longer legitimate to homologize lateral line roots with dorsal spinal roots. The latter are represented in the brain mainly by the spinal V or general cutaneous system, and the special cutaneous systems (terminal bud and lateralis) are probably neomorphs in the head, as Strong has maintained.

If cranial and spinal nerves were derived from a common type, the common ancestral nerve probably contained two kinds of sensory fibers, viz. general cutaneous and general visceral. Both of these kinds of fibers appear to be present in the dorsal roots of *Amphioxus* and of the spinal nerves of *Craniota*. Two of the cranial nerves retain the general cutaneous fibers (viz. X and V); the others seem to have lost them. The viscerosensory fibers have either been lost or rendered unrecognizable on account of their extreme specialization in all but the X, IX and VII nerves. In these nerves they have been centralized to form the communis system and hypertrophied to serve a double purpose: (1) The viscerosensory nerves of the trunk seem to have been in large measure supplanted by the *r. intestinalis vagi*. (2) In the cephalic end of the digestive tract more highly specialized sense-organs (taste buds) have been de-

veloped 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.

The acustico-lateral system is apparently phylogenetically the youngest of the cranial systems. Its relations to the other sensory systems are still problematical.

ADDENDUM. Since this paper was read there has appeared the very suggestive paper on the cranial nerves of the sturgeon (*Anat. Anzeiger*, XIV, 22-23) by J. B. Johnston. His conclusions, which differ somewhat from my own, I shall examine critically at another time, merely mentioning a few of the salient points here. Johnston identifies the general cutaneous and acustico-lateral systems, regarding them both as representing the dorsal horns of the spinal cord. The acustico-lateral is the more highly specialized part and it possesses a spinal portion running parallel with the spinal V, which he calls the spinal VIII. The close internal connections between these two systems and their close parallelism in many other respects certainly favor the belief that the acustico-lateral has been differentiated from the general cutaneous, in spite of the complete discreteness of the two systems peripherally. And it should be noted that this does not imply that the lateralis rami from the head can ever be directly homologized with any rami of spinal nerves; for the former are none the less neomorphs in the head, even though their precursors were in the spinal nerves, as Cole has so ably argued. It is interesting to note that the latter author also regards the acustico-lateralis system as the derivative of the general cutaneous, the evidence in this case being embryological.

Now, Johnston regards the communis system as peculiar to the head, having no spinal representatives. He even goes so far as to state that "no sensory fibers of the spinal nerves supply visceral structures." This, I think, is erroneous, even in the higher forms, though the great reduction and profound modification of the viscero-sensory system of the trunk under the influence of the *r. visceralis vagi* are freely granted. Further-

more, Johnson regards this communis system as exclusively visceral, i. e. entodermal, and opposes to it the other sensory system, viz. the general cutaneous and acustico-lateral, as related to strictly ectodermal sense-organs. This, however, seems to lead us into serious difficulties, for, in the first-place, the terminal buds of the outer skin, which are very numerous in some fishes and which can hardly be other than ectodermal, are apparently all innervated from communis system. Again, the taste buds of the mouth of fishes all or nearly all lie in the region of the stomodæum and are therefore probably of ectodermal origin. These among other facts seem to forbid the employment, in the present state of our knowledge, of any such morphological criteria of the components as Johnston adduces. Indeed, the basis for the segregation of the components may be fundamentally physiological, as Cole and Kingsbury seem inclined to believe.

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REVIEW OF JOHNSTON ON THE CRANIAL NERVES OF THE
STURGEON.¹

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This communication contains a résumé of the results of the author's investigation on the hind brain of *Acipenser rubicundus*, Le Seur. The investigations were made by means of the method of Golgi on the brains of fishes 25 to 40 cm. in length. Only a few of the most striking results will be noted here, leaving a more detailed review till the appearance of the final paper. The work is of a character much needed in this field at present and though surprising in some respects, the results will doubtless be very valuable.

¹ Hind Brain and Cranial Nerves of *Acipenser*, by J. B. Johnston (University of Michigan). *Anatomischer Anzeiger*, XIV Band, Nr. 22 and 23, 1898.