

# Proceedings of the Iowa Academy of Science

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Volume 14 | Annual Issue

Article 25

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1907

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### Recommended Citation

Norris, H. W. (1907) "The Innervation of the Lateral Line System of Amphiuma," *Proceedings of the Iowa Academy of Science*, 14(1), 273-278.

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## THE INNERVATION OF THE LATERAL LINE SYSTEM OF AMPHIUMA.

BY H. W. NORRIS.

Kingsbury<sup>1</sup> has given us an account of the general distribution of the sense-organs of the lateral line system in *Amphiuma*. According to him the arrangement in this form is almost typical of *Amphibia*. On the head: the supra-orbital group dorsal to the eye extends anteriorly to the tip of the snout; the infra-orbital group runs from the angle of the mouth ventral to the eye to the snout region; the oral line on the lower jaw passes along the lower lip; an angular series connects the oral with the infra-orbital; the gular series is found on the ventral surface of the head extending from the branchial region to the tip of the lower jaw; a post-orbital series passes posteriorly from the infra-orbital to meet the gular in the posterior branchial region; a jugular connects the angular with the meeting point of the gular and post-orbital. On the trunk are three longitudinal series: a dorsal, a lateral or median, and a ventral line.

This grouping of the sense-organs of the lateral line system in *Amphiuma* I find to correspond very closely to their innervation. As in *Amphibia* in general so in *Amphiuma* the lateral line organs are innervated by the so-called lateral line divisions of the seventh and tenth cranial nerves. The lateral line division of the seventh cranial nerve, the so-called "dorsal seventh," arises from the medulla oblongata by three rootlets. Of these the dorsal rootlet enters that portion of the medulla which in *Necturus* is designated by Kingsbury as the "dorsal island," a mass of alba occupying the extreme dorsal part of the medulla. This dorsal island suggests an homology to the lateral line lobe (*lobus lineae lateralis*) of *Cyclostomes*, *Selachians* and *Ganoids*, although Johnston<sup>2</sup> asserts that the lateral line lobe and the dorsal root of the dorsal VII are absent in aquatic *Amphibia*. In the fishes mentioned the lateral line fibers of the seventh nerve distributed to the neuromasts of the

1. Kingsbury, B. F. The Lateral Line System of Sense Organs in some American *Amphibia*, and Comparisons with *Dipnoans*. Proc. Amer. Micr. Soc., Vol. XVII, 1895.

2. Johnston, J. B. The Nervous System of Vertebrates, Philadelphia, 1906.

head arise from the medulla by two roots, a dorsal root from the lateral line lobe and a more ventral one from the acusticum. The dorsal island in the medulla of *Necturus* and *Amphiuma* seems to be the representative of the lateral line lobe of fishes, for into it passes the dorsal rootlet of the dorsal VII nerve, while the more ventral rootlets enter the underlying sensory column. In *Amphiuma* the dorsal island extends from a level a little posterior to the point of entrance of the lateralis root of the vagus nerve into the medulla to a level a little anterior to the entrance of the dorsal rootlet of the dorsal VII. Of the three rootlets of the dorsal VII the dorsal enters the brain a little posterior to the level of the others. In *Amblystoma*, according to Coghill,<sup>3</sup> the dorsal rootlet corresponds to the ophthalmicus superficialis VII. In *Acanthias*, according to Strong,<sup>4</sup> it is the mandibularis externus VII (mentalis VII) and buccalis VII branches that are related to the dorsal root, while the ophthalmicus superficialis VII enters chiefly the ventral root. Kingsbury<sup>5</sup> says that in *Necturus* the two roots of the dorsal VII do not correspond to divisions between the portions that join the V and VII nerves. In *Amphiuma* because of the intertwining of the fibers of the various rootlets it is difficult to distinguish between the portions that correspond to the different branches. Apparently the dorsal rootlet is derived largely from the mentalis VII (mandibularis externus VII), but the preparations do not permit exact statements in this regard.

From the points of entrance of the rootlets into the brain the root of the dorsal VII passes anteriorly as a flattened band closely compressed between the brain and the skull. From its ventral border many fibers pass antero-ventrally into the acustico-facial ganglion, a complex of ganglion cells from the auditory nerve, from the communis component of the VII nerve, and from the descending lateralis fibers just mentioned. The lateralis ganglion cells occupy the anterior ventral part of the mass, some of the cells crowding out a short distance with the exit of the VII nerve. As the VII nerve leaves the skull the lateralis component occupies the dorsal anterior part of the nerve trunk, and as the latter passes posteriorly comes to lie on the dorsal lateral border.

3. Coghill, G. E. The Cranial Nerves of *Amblystoma tigrinum*. Jour. Compar. Neurol., Vol. 12, No. 3, 1902.

4. Strong, O. S. The Cranial Nerves of *Squalus acanthias*. Abstract. Science, N. S., Vol. 17, No. 424, 1903.

5. Kingsbury, B. F. On the Brain of *Necturus maculatus*. Jour. Compar. Neurol., Vol. 5, 1895.

The first lateral line branch given off from the trunk of the seventh nerve is the ramus mentalis externus VII. At the point where this branch leaves the main trunk there arises either from the main trunk or from the lateral line ramus a small branch that divides into two or three divisions that supply the post-orbital and jugular series of neuromasts. It will be seen that this small branch with its divisions extends over a considerable territory. Dorsally it encroaches upon the occipital region so that a number of neuromasts included by Kingsbury in the dorsal series of the trunk are supplied by it. The R. mentalis externus VII supplies the oral and angular groups of neuromasts. Some distance posterior to the emergence of the R. mentalis externus VII another large lateral line ramus leaves the trunk of the seventh nerve to supply the gular series of neuromasts. This ramus is termed by Kingsley<sup>6</sup> as the R. hyomandibularis accessorius, and by Druner<sup>7</sup> as the R. cutaneus mandibulae medialis. This is evidently, as Druner recognizes, the ramus that in most Urodela arises with the R. mentalis externus in a common trunk from the seventh nerve. It is designated here as the R. mentalis internus VII, following the example of Coghill. Like the R. mentalis externus it consists solely of lateralis fibers.

Three or four neuromasts of the extreme posterior portion of the jugular series have a somewhat peculiar innervation. From the R. jugularis VII as it enters the kerato-mandibularis division of the depressor mandibulae muscle there are given off two small twigs that pass laterally and posteriorly out through the muscle and emerging subcutaneously, go one to the most dorsal of the neuromasts mentioned, while the second twig divides into three parts, one of these divisions supplying a second of these neuromasts, another division the third neuromast in part, and the third division joining a nerve that connects with that peculiar branch of the seventh nerve, designated by Druner as the N. lateralis VII. This latter nerve deserves a more extended mention. It was first described by Fischer<sup>8</sup> as a structure peculiar to Amphiuma and said to be traced to the hyotrachealis (interbranchialis IV) muscle. Kingsley believed that

6. Kingsley, J. S. The Cranial Nerves of Amphiuma. Tufts College Studies, No. 7, 1902.

7. Druner, L. Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopf-musculatur der Urodelen, II Theil. Zool. Jahrb., Abt., f. Anat. u. Ontog. d. Thiere, Bd. XIX, Hft. 3 u. 4, 1902.

8. Fischer, J. G. Anatomische Abhandlungen uber die Perennibranchiaten und Derotremen. Hamburg, 1864.

it supplied the dorsotrachealis muscle. In 1904 I read a paper<sup>9</sup> before the Iowa Academy of Sciences describing this nerve, showing that it did not end in the dorsotrachealis muscle, even if it supplied that muscle, but passed posteriorly into the trunk region as far posteriorly as the pelvis. I suggested a possible relation to the neuromasts of the trunk, and provisionally designated the nerve as the R. lateralis VII. In the same year appeared the paper of Druner in which he gave a brief description of the nerve, designating it as N. lateralis VII, asserting that it supplied in part the median series of neuromasts of the trunk, that is, he considered it as a lateral line nerve. The following year I published a second paper<sup>10</sup> in which I withheld the name, N. lateralis VII, believing that the evidence of the presence in it of lateralis fibers was not convincing. I can now assert with considerable confidence that the nerve contains lateralis fibers.

After the fibers destined to form the mentalis VII leave the trunk of the dorsal VII the latter passes anteriorly into its ganglion lying just dorsal to and confluent with the gasserian ganglion. Anteriorly to the ganglion the lateralis fibers are joined by general cutaneous fibers from the gasserian ganglion. The latter fibers are in two distinct bands, of which one is applied to the ventral and the other to the median surface of the lateralis trunk. As the combined nerves pass anteriorly the general cutaneous components shift their positions, the median band becoming dorsal and the ventral ones shifting to a lateral position. The main trunk soon divides into a dorsal and a ventral division, each consisting of lateralis and general cutaneous fibers. The ventral, or infra-orbital division, evidently represents the maxillaris V and the buccalis VII, while the dorsal supra-orbital portion is made up of an ophthalmicus superficialis VII and of what we may term the ophthalmicus superficialis V. Each division now divides into two rami. The infra-orbital trunk forms the maxillaris V, of general cutaneous fibers, and the buccalis VII, of lateral line fibers. The latter after giving off twigs to the posterior portion of the infra-orbital series of neuromasts divides into two branches. One of these, the dorsal and larger, unites with a branch of the ophthalmicus profundus nerve, and the combined trunk of general cutaneous and lateralis fibers, supplies the skin and the neuromasts of the infra-orbital series along the side of the snout. The smaller ventral branch of the

9. Norris, H. W. The So-called Dorsotrachealis Branch of the Seventh Cranial Nerve in Amphiuma. Proc. Iowa Acad. Sci., Vol. X, 1904.

10. Norris, H. W. The so-called Dorsotrachealis Branch of the Seventh Cranial Nerve in Amphiuma. Anat. Anz., Bd. 27, 1905.

buccalis passes anteriorly and comes into close relation with another branch of the ophthalmicus profundus. I find no evidence that any anastomosing, such as Wilder<sup>11</sup> described, occurs between these two nerves except between some of their minute twigs. The buccalis branch supplies the infra-orbital neuromasts at the end of the snout. The supra-orbital division of the main trunk of the dorsal VII divides into a ventral branch, consisting entirely of lateralis fibers, and a dorsal branch containing both lateralis and general cutaneous fibers. The latter branch divides into a number of smaller divisions supplying the skin and the neuromasts of the supra-orbital series posterior to the eye. It should be noted that the transverse line of four or five neuromasts just at the posterior edge of the eye belongs to the infra-orbital series. The ventral branch passes anteriorly and dorsally and supplies the neuromasts of the orbital region, and then anastomoses with the median nasal branch of the ophthalmicus profundus. The mixed nerve thus formed supplies the skin and the supra-orbital series of neuromasts of the anterior dorsal region of the head.

The lateral line fibres of the tenth cranial nerve in *Amphiuma* enter the brain by the anterior root of the vagus ganglion. With them are associated the motor and communis components of the glossopharyngeal nerve. The lateralis fibers enter the medulla by two rootlets. At this level the lateral line lobe has nearly disappeared and the two rootlets correspond to the middle and the ventral rootlets of the dorsal VII. Four nerves containing lateralis fibers leave the vagus ganglion. The anterior of these is the R. supra-temporalis, composed exclusively of lateralis fibers. Before reaching the occipital series of neuromasts it anastomoses with the R. auricularis and thus comes to possess general cutaneous fibers. The auricularis branch leaves the vagus ganglion just posterior to the supra-temporalis. It contains both lateralis and general cutaneous fibres. After the anastomosing the combined nerves supply ten or twelve neuromasts in the occipital region. The R. lateralis medius leaves the posterior end of the vagus ganglion and passes posteriorly in a nearly straight line. It supplies the neuromasts of the median series of the trunk. Shortly after leaving the ganglion it gives off the R. lateralis superior that supplies the dorsal series of neuromasts of the trunk, not including those of the occipital region. The R. intestino-accessorius, com-

11. Wilder, H. H. Die Nasengegend von *Menopoma alleghaniense* und *Amphiuma tri-dactylum*. Zool. Jahrb., Abtheil. Anat., Bd. V. 1892.

posed of lateralis, communis and motor fibers, leaves the ganglion close to the R. lateralis medius and runs parallel with it as far as the level of the posterior border of the dorso-laryngeus muscle. Here it divides into its branches. One of these, the R. lateralis inferior, passes laterally, at first anteriorly and then posteriorly, and supplies the ventral series of neuromasts of the trunk. In the region of the shoulder girdle the R. lateralis inferior becomes closely associated with portions of the brachial plexus, but in no respect does it contribute fibers to muscles or other structures of the limb girdle, as Bowers<sup>12</sup> inferred in *Spelerpes*.

The distribution of the lateral line nerves may be summarized as follows: The "dorsal VII" through its branches supplies (a) through the superficial ophthalmic VII the supra-orbital series including the infra-orbital transverse line just posterior to the eye; (b) through the buccalis VII the infra-orbital series exclusive of those neuromasts posterior to the level of the eye; (c) through the mentalis externus VII the post-orbital, the jugular, the angular and the oral series; and (d) through the mentalis internus VII the gular series. The IX-X complex supplies (a) through the supra-temporal and auricular branches the occipital group; (b) through the R. lateralis superior the dorsal series of the trunk; (c) through the R. lateralis medius the middle series; and (d) through the R. lateralis inferior the ventral series.

It will be seen from the foregoing that the classification of the lateral line organs of *Amphiuma* as given by Kingsbury needs some revision from the standpoint of nerve supply. The infra-orbital series, supplied by the buccalis branch, ends posteriorly at the level of the posterior border of the eye. The post-orbital series includes those neuromasts posterior to the eye classed by Kingsbury with the infra-orbital series. It also includes those occipital neuromasts that Kingsbury describes as a part of the trunk series curving ventrally toward the post-orbital group. It is evident that a group of neuromasts in the occipital region, innervated by the supra-temporal and auricular branches forms a distinct series.

The association of lateral line fibers with general cutaneous fibers is not uncommon in the Urodela, but the anastomosing of lateralis branches with those of the ophthalmicus profundus seems to be unusual.

12. Bowers, Mary A. The Peripheral Distribution of the Cranial Nerves of *Spelerpes bilineatus*. Proc. Amer. Acad. Arts and Sci., XXXVI, 1900.