

THE NERVE TERMINATIONS IN THE LATERAL- LINE ORGANS OF AMBLYSTOMA

O. LARSELL

*The Effingham B. Morris Biological Farm of The Wistar Institute of Anatomy
and Biology and the Anatomical Laboratory, University of Oregon
Medical School, Portland*

FOUR FIGURES

The lateral-line organs of various Amphibia have been described, both as to distribution and general histology, by a number of investigators. The contribution of Kingsbury ('95) gives an excellent account of the distribution and general structure of these organs in many American Amphibia, including larval and adult Amblystoma. The method of termination of the lateral-line nerves is, however, left uncertain. Retzius ('92 a), using the Golgi method, found free terminal brushes about epithelial cells in the neuromasts of larval Salamandra, and states that there is no continuity between the neuromast cells and the nerve fibers. He gives a figure in which the relations of terminal fibers to the cells are shown, but details are lacking because of the limitations of the Golgi method.

Not only in Amphibia, but in fishes also, the nature of the lateral-line terminations was not altogether clear until the beautiful work of S. E. Johnson ('17, '18) demonstrated clearly and convincingly in sharks the fact that the neuromast cells have the same type of terminal baskets about their bases as Morrill ('97), Retzius ('92), and others have shown in the ampullae of the inner ear and semicircular canals. Johnson found in pyridine-silver preparations that the lateral-line nerves terminate about the hair cells of the lateral-line canals in *Mustelus* and *Squalus* as delicate fila-

ments. The branches of a single nerve fiber spread out to such an extent that they may approximately cover the base of a group of hair cells. They divide into fine terminal twigs which pass between the hair cells, extending for varying distances toward the free ends of the cells and showing variabilities in their course. They terminate as end knobs on the surface of the hair cells at various levels, from one-fourth to three-fourths of the distance between the base and the free end of the cell. Johnson found no cup-like expansions or anastomosing networks around the bases of the cells.

The lateral-line organs of Amphibia differ from those of selachians in that they do not lie in the floor of a lateral-line canal, but rather are more or less exposed on the skin surface as individual neuromasts. These individual organs are supplied by the branches of the lateralis VII and lateralis X nerves, as in fishes. In larval *Amblystoma* the fibers of these nerves acquire myelin sheaths very early, and the nerves are conspicuous in sections stained to show myelinated fibers. Groups of fibers branch from the main nerve trunk to pass to the bases of the neuromasts. Here the myelin sheath is lost and the fibers ramify into terminal twigs (fig. 1) which end as small knobs on the sensory epithelial cells. Two or three fibers, sometimes more, enter each neuromast. The terminal twigs of each fiber come into relation with a number of hair cells, as shown in figures 1 and 2. Figure 1 shows a section cut vertically through a neuromast, with a portion of the nerve trunk beneath and three fibers entering the sensory organ. Figure 2 shows a neuromast cut obliquely so that the basal ends of the hair cells are visible. The relation of the terminal twigs from a single nerve fiber to several hair cells is clearly shown. Charipper ('28) describes nerve fibers as ending within the sense cells of the neuromasts of *Necturus* in a cup-like arrangement which encases the proximal portion of the nucleus. Neither the silver material examined by me nor that stained by the neutral-red and Janus-green method shows any indication of intracellular nerve fibers in *Amblystoma*. On the contrary, the terminal knobs of the nerve fibers

appear to lie in contact with the cell membrane of the sensory cells.

It will be noted that there is no such spread of branches from a single nerve fiber as Johnson found in the shark, and the fibers consequently engage a smaller number of hair cells. The amphibian neuromast is smaller and less differentiated

ABBREVIATIONS

| | |
|--------------------------|--|
| <i>ca.</i> , canals | <i>n.ter.</i> , nerve termination |
| <i>epi.</i> , epidermis | <i>n.tr.</i> , nerve trunk |
| <i>h.c.</i> , hair cells | <i>po.</i> , external opening of neuromast |
| <i>nm.</i> , neuromast | |

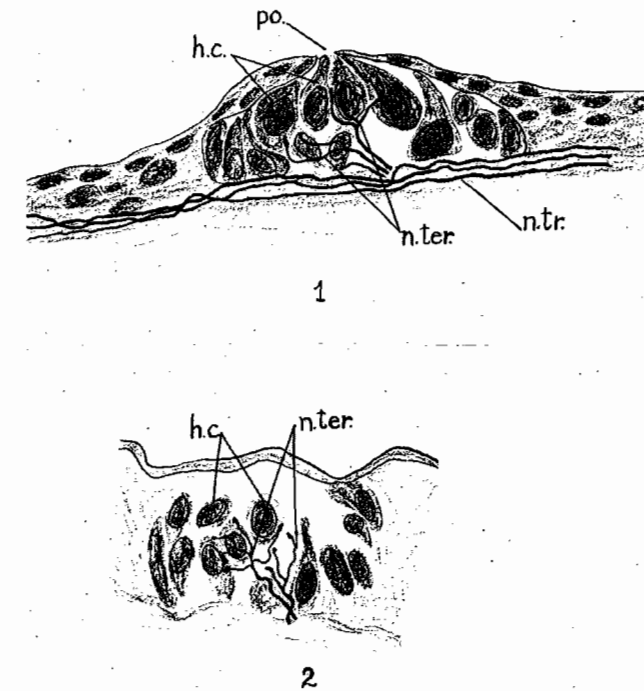


Fig. 1 Nerve terminations in a neuromast 1.2 mm. from the tip of the tail in larval *Amblystoma punctatum*. W. I. series 16644, 5-1-4. Harrison stage 46. Paton-Bielschowsky stain; camera lucida. $\times 600$.

Fig. 2 Oblique section through a neuromast in the head, innervated by the lateralis VII nerve, showing the relation of the terminal baskets to the bases of the hair cells. Same series as figure 1. Camera lucida. $\times 600$.

than are the corresponding masses of sensory epithelium in the elaborate lateral-line organs of the shark. The method of innervation, however, as well as the fundamental plan of structure, is the same in the two classes.

Nerve terminations of the type described were observed in larval *Amblystoma* of various stages in material impregnated by the Paton-Bielschowsky procedure and also occasionally in material stained by Coghill's neutral-red and Janus-green method. Fairly well-differentiated neuromasts are present in larvae as young as the early swimming stage, as shown by Coghill ('14). At this stage, which approximates stage 36

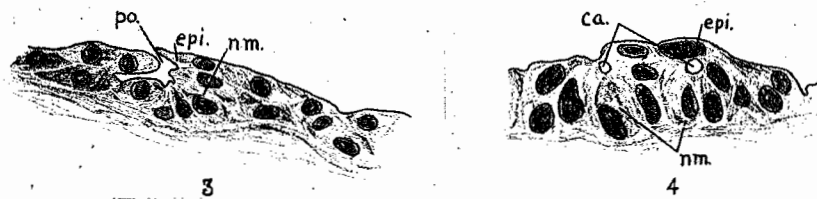


Fig. 3 Section through a neuromast of larval *Amblystoma*, showing a portion of a canal and its external pore. W. I. series 16793, 1-2-13. Physiological stage two days three hours after early swimming, Harrison stage 39. Modified Pal-Weigert stain; camera lucida. $\times 270$.

Fig. 4 Section through two adjacent neuromasts of larval *Amblystoma*, showing canals covered by a layer of epidermal cells. W. I. series 16674, 1-8-5. Early swimming stage, Harrison stage 36. Neutral-red and Janus-green stain; camera lucida. $\times 270$.

of Harrison, the neuromasts which I have examined are generally covered with a single layer of epithelium in the head region. Some open directly to the surface through this layer by a short canal. Others have canals which course parallel to the surface beneath the outer layer of epithelium. Such canals may be followed for nine or ten sections and then are seen to open to the surface by vertical canals (fig. 3). Occasionally, two neuromasts lie close together (fig. 4) and two more or less parallel canals are observed. These frequently open to the surface. Kingsbury ('95, fig. 45) illustrates a similar condition in larval *Amblystoma*, with the interpretation that the two neuromasts represent the result of binary

fission of a submerged developing pit organ. In the trunk and tail region of the various series I have examined, the neuromasts appear to open directly to the surface of the skin by a pore. Kingsbury states (p. 130) that in the terrestrial adult stage of *Amblystoma* the neuromasts again become covered by a layer of epithelium, to reappear on the surface when aquatic life is resumed.

Nerve endings were observed in some of the neuromasts of the early swimming stage and in subsequent stages. Their presence in the early swimming stage, at least partially developed, indicates that the neural mechanism of the lateral-line system appears to be present. Central branches of the lateral-line nerves were observed to pass into the medulla oblongata at this and earlier stages. No experiments were made to determine if the lateral-line system is functional at the early swimming stage or if the mechanism is merely present in the partially developed but prefunctional stage described by Coghill ('14, '24) for other elements in the nervous system of *Amblystoma*.

SUMMARY

The nerve endings in the lateral-line organs of *Amblystoma* larvae take the form of terminal twigs which end about the hair cells of the neuromasts in a manner similar to the nerve endings of the inner ear in the vertebrates and in the lateral-line organs as described in sharks.

The neuromasts are present in a fairly well-developed condition at the early swimming stage, but whether or not they are functional at this stage was not determined.

LITERATURE CITED

- CHARIPPER, HARRY A. 1928 Studies on the lateral-line system of Amphibia. I. Cytology and innervation of the lateral-line organs of *Necturus maculosus*. *Jour. Comp. Neur.*, vol. 44.
- COGHILL, G. E. 1914 Correlated anatomical and physiological studies of the growth of the nervous system of Amphibia. I. The afferent system of the trunk of *Amblystoma*. *Jour. Comp. Neur.*, vol. 24.
- 1924 Correlated anatomical and physiological studies of the growth of the nervous system of Amphibia. III. The floor plate of *Amblystoma*. *Jour. Comp. Neur.*, vol. 37.
- JOHNSON, S. E. 1917 Structure and development of the sense organs of the lateral canal system of Selachians (*Mustelus canis* and *Squalus acanthias*). *Jour. Comp. Neur.*, vol. 28.
- 1918 The peripheral terminations of the nervus lateralis in *Squalus sucklii*. *Jour. Comp. Neur.*, vol. 29.
- KINGSBURY, B. F. 1895 The lateral line system of sense organs in some American Amphibia, and comparison with the Dipnoans. *Trans. Amer. Micros. Soc.*, vol. 17.
- MORRILL, A. D. 1897 Innervation of the auditory epithelium of *Mustelus canis*. *Jour. Morph.*, vol. 14.
- RETZIUS, GUSTAF 1892 Die Endigungsweise des Gehörnerven. *Biol. Untersuch.*, N. F., Bd. 3.
- 1892 a Die Nervenendigungen in den Endknospen, resp. Nerven-
hügeln der Fische und Amphibien. *Biol. Untersuch.*, N. F., Bd. 4.