

The Lateral Line System of the Axolotl

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The lateral line system of axolotls, like that of most other salamanders, anuran larvae, and fishes, consists of numerous epidermal sensory organs arranged in well-defined lines that extend over the whole body surface. The distribution (Kingsbury, 1895; Platt, 1896; Escher, 1925; Chezar, 1930; Hilton, 1947; Harris and Milne, 1966; Flock and Jørgensen, 1974; Münz et al., 1984; Lannoo, 1985, 1987; Northcutt, 1989) and development (Platt, 1896; Harrison, 1904; Stone, 1922; Fritsch and Bolz, 1986; Northcutt, 1986; Smith et al., 1988) of these sensory organs in salamanders have been studied extensively and have contributed much to our understanding of the structure and function of lateral line systems in anamniotes. In spite of these studies many details of the distribution of the lateral lines in salamanders are not known, their homologous lines in other amphibians and fishes have not been recognized, and the pattern of their innervation is only now being established.

Within the last ten years, two additional classes of lateral line organs, electroreceptors and pit organs, have been discovered in salamanders (Fritsch, 1981; Fritsch and Wahnschaffe, 1983; Northcutt, 1989), and experimental neuroanatomical studies have radically altered our understanding of the cranial nerves that innervate the lateral line organs of amphibians and fishes (Fritsch, 1981; Münz et al., 1984; Northcutt, 1989; Puzdrowski, 1989; Song and Northcutt, 1990). Many of these studies have utilized axolotls or other ambystomatid salamanders because of the ease with which their lateral line organs can be visualized. In this group, the lateral line organs are located on the surface of the epidermis, unlike in most fishes where they occur in bony canals within the dermis. The superficial location of these organs and the thin epidermis in axolotls facilitate removal and preparation of flat mounts of essentially the entire epidermis so that the histology, distribution, and in-

nervation of these organs can be easily visualized. Axolotls offer a particular advantage, as the development of mucous and granular organs, which obscure the details of the lateral line organs in many salamanders, is delayed. Furthermore experiments on the nerves that innervate these sensory organs in ambystomatid salamanders are facilitated by an extensive description of the peripheral distribution of the cranial nerves of *Ambystoma* (Coghill, 1902).

Details of the histology, distribution, and innervation of the lateral line organs of axolotls will be summarized in the following sections. Unfortunately similar detailed information does not exist for other salamanders and anamniotes, so it is presently impossible to compare many aspects of the organization of this system.

Classes of Lateral Line Organs

The lateral line system of axolotls consists of three morphologically distinct classes of sensory organs: neuromasts, pit organs, and ampullary organs. Although all three types of sensory organs consist of hair cells surrounded by support cells, neuromasts and pit organs function as mechanoreceptors, sensitive to low frequency water displacement, whereas ampullary organs are electroreceptors and sensitive to weak electric fields (Münz et al., 1984; Northcutt and Bleckmann, unpublished observations).

Neuromasts are elliptically shaped organs with a major axis of approximately 150 to 200 μm ; their central zone comprises approximately 20 hair cells that are surrounded by a peripheral zone of support cells. The apical surface of a neuromast hair cell possesses a ciliary bundle composed of several stereocilia whose length increases toward a single much longer kinocilium. This anatomical polarization of the ciliary bundle underlies the directional response of individual hair cells (Flock, 1965), such that a given hair cell is sensitive to water displacement only across its stereocilia toward the kinocilium. The neuromasts of axolotls, like those of all other anamniotes examined, are characterized by hair cells whose ciliary bundles are oriented in two opposing directions parallel to the major axis of the neuromast. Thus it is possible to determine the directional sensitivity of a given neuromast by noting the orientation of its major axis (Flock and Jørgensen, 1974; Lannoo, 1987). The

kinocilia of the hair cells of neuromasts are embedded in a gelatinous cupula that is believed to be secreted by the support cells (Münz, 1979).

The pit organs of axolotls are a second class of more circular mechanoreceptors, smaller (120-140 μm in diameter) than neuromasts and with fewer hair cells (7 to 10). Pit organs, like neuromasts, possess an elongated central sensory strip of hair cells, whose ciliary bundles in this case are oriented along the major axis of the hair cell strip. In addition, compared to the hair cell kinocilia of neuromasts, those of pit organs are much longer and are embedded in much longer cupulae. Similar size differences in the surface area of neuromasts and the length of their kinocilia have been noted in bony fishes, which suggests that the neuromasts of axolotls are homologous to the canal neuromasts of fishes and that the pit organs of axolotls are homologous to superficial lines of neuromasts in fishes, lines sometimes referred to as pit or accessory lines.

In order to establish that pit organs in axolotls are mechanoreceptors, similar to neuromasts, Dr. Horst Bleckmann of the University of Bielefeld and I have been recording unit activity from hair cells of neuromasts and pit organs. Both types of organs are extremely sensitive to low amplitude and low frequency water displacements, with the pit organs exhibiting a displacement sensitivity significantly lower than that of the neuromasts. These results clearly indicate that the pit organs of axolotls are mechanoreceptors and suggest that they are more sensitive than neuromasts to lower frequencies. Similar results have been reported in comparing the superficial (pit) organs and canal neuromasts in teleost fishes (Münz and Claas, 1983), which supports the suggested homology between the pit organs of axolotls and the superficial neuromasts of fishes.

The ampullary organs of axolotls are recessed below the surface of the epidermis in shallow tubes whose floors consist of support cells and 8 to 10 hair cells. In anamniotes other than teleost fishes, the apical surface of the hair cells of ampullary organs frequently consist of stereocilia and kinocilia like those of neuromasts. However the hair cells of ampullary organs possess only stereocilia in many species of salamanders (Fritsch and Wahnschaffe, 1983). Data on the electron microscopy of axolotl ampullary organs do not exist, and we therefore do not know whether their hair cells possess kinocilia.

Physiological studies indicate that the ampullary organs of axolotls are sensitive to sinusoidal stimuli in the range of 5 to 250 μVcm^{-1} , with an optimal response frequency at approximately 10 Hz (Münz et al., 1984). This suggests that the ampullary organs of axolotls are approximately as sensitive as those of catfishes and somewhat less sensitive than the tonic electroreceptors of other electroreceptive teleost fishes.

Distribution of Lateral Line Organs

Neuromasts in axolotls, as in most other salamanders and anamniotes, occur in distinct lines on the head and trunk (Figs. 1 and 2). In most salamanders and other anamniotes, neuromasts form a single row, with their major axes parallel to the long axis of the line. This is also true of axolotls at hatching, but each of these single neuromasts, termed primary neuromasts, subsequently gives rise to additional neuromasts such that primary and secondary neuromasts form an aggregate termed a stitch (Harris and Milne, 1966; Lannoo, 1987). Thus each lateral line in axolotls consists of a series of stitches composed of from three to five neuromasts (Fig. 1). Stitch formation occurs not only in axolotls but also in other ambystomatids, and in cryptobranchids, proteids, and salamandrids; it has been claimed to represent the primitive condition for salamanders and, possibly, for anurans (Lannoo, 1987).

There are numerous nomenclatures for the lateral lines of the head of salamanders (Kingsbury, 1895; Platt, 1896; Escher, 1925; Chezar, 1930; Allis, 1934; Hilton, 1947; Stensiö, 1947; Holmgren and Pehrson, 1949; Lannoo, 1985, 1987) based, in some cases, on purely descriptive considerations or suspected homology with the lateral lines of fishes. It is clearly important to establish a nomenclature based on homology, as this is the only way to reconstruct the phylogeny of individual lateral lines and generate hypotheses concerning their genesis and variation. Three lines of evidence are relevant for recognizing homologous lateral lines among anamniotes: topographic position, embryonic origin from placodal material, and innervation of the receptors. The nomenclature used to describe the lateral lines of axolotls illustrated in Figures 1 and 2 is based on an extensive review of the literature (Northcutt, 1989) and on unpublished observations of the innervation of these lines (Fig. 3).

As in most other jawed anamniotes, there

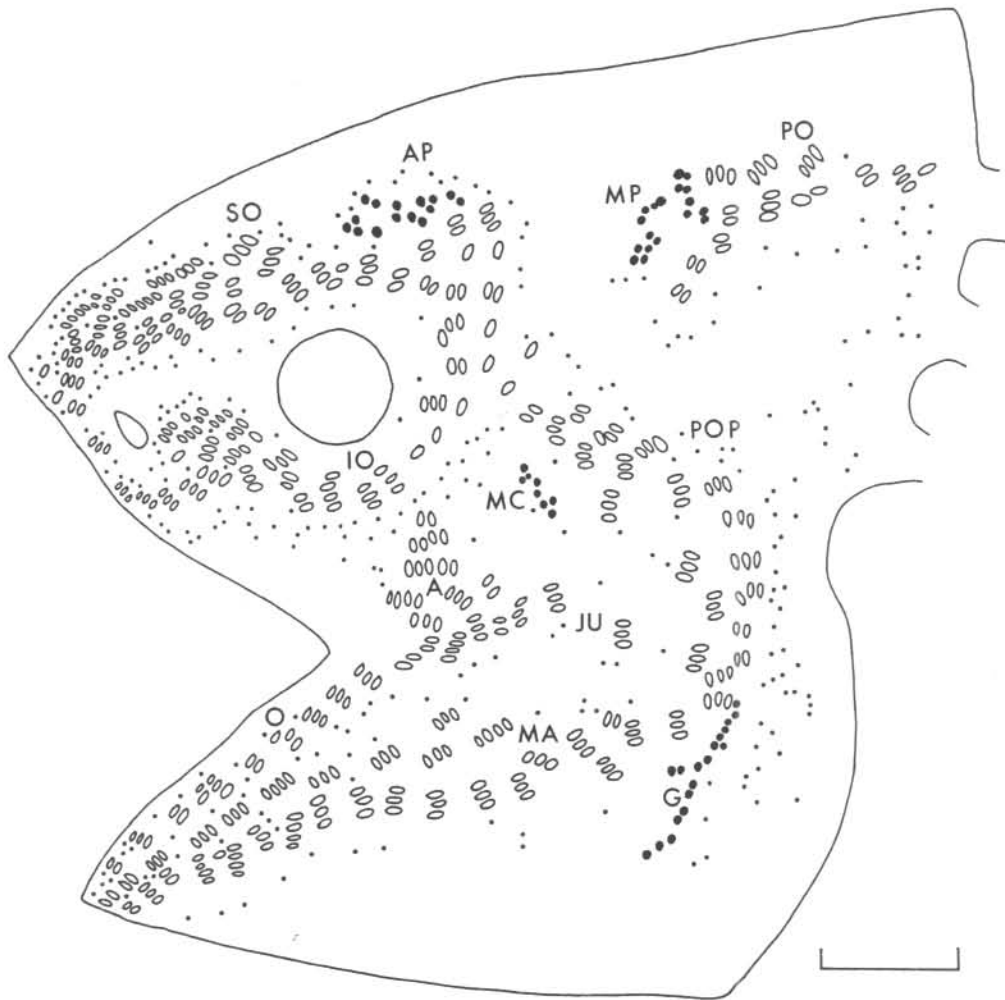


Figure 1. Distribution of ampullary organs (black dots), neuromasts (open ovals), and pit organs (solid circles) on the head of a juvenile axolotl. A, angular line; AP, anterior pit line; G, gular line; IO, infraorbital line; JU, jugal line, MA, mandibular line; MC, middle cheek pit line; MP, middle pit line; O, oral line; PO, postotic line, POP, preopercular line; SO, supraorbital line. Bar scale equals 2 mm.

Axolotl Newsletter Number 19

are supraorbital and infraorbital lines surrounding the eye in axolotls. A short angular line interconnects the infraorbital and oral lines. The oral line of the lower jaw consists of a single line of neuromast stitches, whose major axes are oriented parallel to the long axis of the jaw. The continuation of the oral line caudal to the perpendicularly oriented angular line is termed the jugal line, based on the existence of a topographically comparable line in other gnathostomes and on similarities in the innervation of the neuromasts of the angular and jugal lines (Fig. 3). Traditionally, the angular and jugal lines have been considered homologous to the rostral and caudal segments, respectively, of a horizontal cheek line that is particularly prominent in elasmobranch fishes and in several groups of fossil fishes (Allis, 1934; Holmgren, 1942).

A preoperculo-mandibular line runs across much of the cheek region in axolotls (Fig. 1). This line connects dorsally with the infraorbital line and continues ventrally and rostrally to end at the very tip of the lower jaw. Throughout its rostro-caudal extent the preoperculo-mandibular line consists of a dorsal (mandibular segment) or rostral (preopercular segment) row of neuromast stitches, whose major axes are oriented perpendicular to the long axis of the line, and a ventral or caudal row of neuromast stitches, whose major axes are oriented parallel to the long axis of the

line. The double row of stitches comprising the preopercular segment of the line in axolotls and *Necturus* has been interpreted as evidence that the preopercular line of salamanders was ancestrally two separate lines that are compressed in modern forms (Stensiö, 1947; Holmgren and Pehrson, 1949). These claims have resulted in a proliferation of different names for the neuromasts located in the cheek region of salamanders and other anamniotes. Re-examination of the development of the neuromasts of the cheek region of axolotls, (Northcutt, 1989 and unpublished observations), however has revealed no indications of a folded line of neuromasts in the cheek region and supports the earlier claims (Allis, 1934; Holmgren, 1942) that a single homologous preoperculo-mandibular line occurs in most jawed anamniotes.

Axolotls do not possess a line of neuromasts lateral to the inner ear (Fig. 1), as do most anamniotes, where the caudal continuation of the supra-infraorbital lines is termed the otic line. A double line of neuromast stitches does occur caudal to the inner ear, however, and is identified as a postotic line (Fig. 1). In most fishes, this region of the head is characterized by rostral (temporal) and caudal (post-temporal) longitudinal lines that are intersected dorsally by a perpendicularly coursing supratemporal commissural line (Song and Northcutt, 1990). Although similar

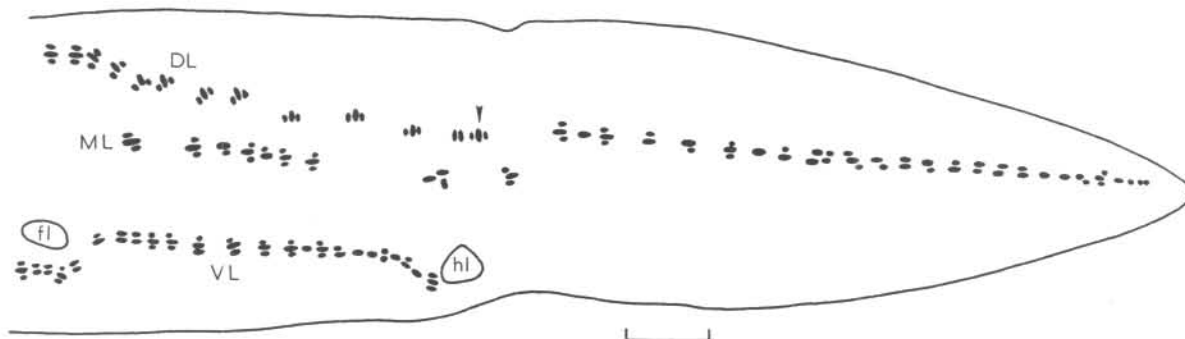


Figure 2. Distribution of neuromasts (black ovals) on the trunk and tail of a juvenile axolotl. DL, dorsal trunk line; ML, main trunk line; VL, ventral trunk line; fl, position of forelimb; hl, position of hindlimb. Bar scale equals 3 mm.

distinct lines cannot be recognized in this region of the head of axolotls, the innervation of the neuromasts in this post-otic region (Fig. 3) indicates that these neuromasts are homologous to those of all three postotic head lines of fishes.

Axolotls, like most other salamanders, possess three lines of neuromasts on the trunk: dorsal, main and ventral trunk lines (Fig. 2). Each of these trunk lines consists of stitches, but only the main trunk line extends onto the tail. The dorsal trunk line comprises neuromasts whose major axes are oriented initially obliquely and subsequently perpendicularly to the long axis of the body; major axes of the neuromasts of the main and ventral trunk lines are oriented parallel to the long axis of the body. As the main trunk line passes onto the tail, it could easily be confused with the dorsal trunk line. The neuromasts of the two lines are oriented differently, however, and each line is innervated by separate rami of the posterior lateral line nerve (Fig. 3).

Among living anamniotes, only amphibians and lungfishes possess ventral as well as dorsal and main trunk lines. A survey of fossil forms, however, indicates that the presence of three trunk lines constitutes the primitive pattern for jawed anamniotes (Northcutt, 1989). An examination of the number and distribution of the lateral lines of the head of salamanders and lungfishes also indicates that these taxa exhibit the most primitive pattern among living jawed anamniotes (Northcutt, 1989). The superficial location of the neuromasts in salamanders is a derived trait, however, as is the absence of an otic line and the absence of distinctly recognizable temporal, supratemporal and post-temporal lines.

In axolotls pit organs are restricted to the head and form four distinct groups: an anterior group, located dorsal to the caudal end of the supraorbital line; a middle group, immediately rostral to the postotic line; a middle cheek group, rostrally adjacent to the dorsal end of the preopercular line; and a gular group, a ventral extension of the preopercular line (Fig. 1). Only some of these groups of pit organs were noted in a single earlier study (Stensiö, 1947), possibly because they are smaller than the other class of lateral line mechanoreceptors, the neuromasts, and they may have been interpreted as immature neuromasts or, after the discovery of electroreceptors, as large ampullary organs, particularly in juveniles. They are, however, easily recognizable in epidermal flat mounts.

I have interpreted the different groups of pit organs of axolotls as homologues of the comparably named lines of pit organs in bony fishes, based on similarities in topography and innervation. Primitively, bony fishes possess a similarly positioned anterior pit line, adjacent to the supraorbital line or as a dorsomedially directed continuation of it and always innervated by the first ramule arising from the superficial ophthalmic ramus of the anterodorsal lateral line nerve. The anterior group of pit organs in axolotls is innervated in the same manner (Fig. 3).

Primitively in bony fishes, two additional pit lines occur dorsally on the head: a middle pit line and a posterior pit line. The group of pit organs located immediately rostral to the postotic neuromast line is topographically compatible with being either a middle or a posterior pit line. There is indication in some individual axolotls that two groups of pit organs in fact occur in this region as seen in Figure 1, whereas in other axolotls there appears to be a single group. In fishes, however, the middle pit line is innervated by a middle lateral line nerve, whereas the posterior pit line is innervated by the supratemporal ramus of the posterior lateral line nerve, a distinctly separate cranial nerve (Song and Northcutt, 1990). The innervation of the more dorsocaudally located group of pit organs in axolotls indicates that this group is homologous to the middle pit line of fishes, as it is innervated by the middle rather than the supratemporal ramus of the posterior lateral line nerve (Fig. 3). Thus, it appears that axolotls have lost the posterior pit line.

Two pit lines occur dorsally on the cheek of fossil gnathostomes and some living sharks (Holmgren, 1942; Northcutt, 1989): a vertically oriented middle cheek line and a more ventrally located horizontal line. Either or both of these lines may occur as neuromasts, located in canals or grooves, or they may be located superficially in the epidermis as pit lines. Unfortunately, the sensory receptors of both lines, as well as those of all remaining cheek and lower jaw lines, are innervated by the external mandibular ramus of the anteroventral lateral line nerve (Fig. 3), so that innervation offers no clue as to their identity.

The group of pit organs located immediately rostral to the dorsal end of the preopercular line in axolotls is considered to be homologous to the middle cheek line of other anamniotes, based primarily on the topography of this group and because a well-

developed horizontal line, formed by angular and jugal segments, occurs more ventrally, as in sharks (Northcutt, 1989).

The group of pit organs that continues ventromedially from the ventrocaudal edge of the preopercular line in axolotls is interpreted to be a gular pit line, as a topographically similar pit line occurs in most other groups of living anamniotes. The only pit lines other than the gular line that occur on the lower jaw of gnathostomes are located more rostrally and dorsal to the mandibular neuromast line and thus could not be homologous to this pit line in axolotls.

The electroreceptive ampullary organs of axolotls and other salamanders were not discovered until recently (Fritzschn, 1981). This is particularly surprising, considering the number of earlier descriptions of the lateral line system in these organisms. Several earlier workers appear to have noticed these receptors, but they interpreted them as immature neuromasts or compound mucous glands, which is understandable when we consider that electroreceptors were not described in other vertebrates until the early 1950's.

Ampullary organs in axolotls, as in other salamanders, are restricted to the epidermis of the head and primarily occur immediately adjacent to the lines of neuromasts (Fig. 1). Some ampullary organs do occur, however, among the neuromasts of a given line, particularly in the rostral supraorbital, infraorbital, oral, and mandibular lines (Fig. 1). The ampullary organs located at the base of the external gills are the only exception to the rule that ampullary organs occur immediately adjacent to neuromasts. As we shall see in the next section, these ampullary organs are also innervated in a very unique way.

Innervation of Lateral Line Organs

Historically, the lateral line receptors of amphibians and fishes were thought to be innervated by rami of the facial, glossopharyngeal, and vagal nerves (Herrick, 1899; Coghill, 1902; Norris, 1925) and were thus considered as a special somatic sensory component of the branchiomic cranial nerves. With the advent of experimental neuroanatomical methods in the 1960s and '70s, however, neurobiologists quickly discovered that the nerves that supply lateral line organs are closely associated with the branchiomic cranial nerves but are, in fact, separate from these nerves, and that the

cranial nerves that innervate lateral line organs end in brainstem centers (Boord and Campbell, 1977; Münz, 1979; Fritzschn, 1981; McCormick, 1981; New and Northcutt, 1984) separate from those of the branchiomic cranial nerves. These experiments, in conjunction with the rediscovery of earlier embryological studies (Landacre, 1912, 1916; Stone, 1922) indicating that the ganglionic cells innervating lateral line receptors arise from sources distinctly different from those of branchiomic nerves, lead comparative neurobiologists to conclude that the lateral line receptors of the head were innervated by an anterior lateral line nerve and those on the trunk by a posterior lateral line nerve.

The earlier experimental neuroanatomical studies of the late '70s relied on modifications of the Fink-Heimer method, a silver stain that allows visualization of anterogradely degenerating axons, after transection of, in this case, cranial nerves proximal to their ganglionic cell bodies. Little attention was paid to the ganglia or the peripheral course of these nerves, as there were no experimental methods available to test earlier descriptive claims regarding patterns of innervation. With the advent of the horseradish peroxidase method, which does allow the experimental determination of peripheral patterns of innervation, and a renewed interest in morphogenesis, a new series of studies (Northcutt, 1989; Puzdrowski, 1989; Song and Northcutt, 1990) have corroborated the claim of earlier experimental studies that separate cranial lateral line nerves do exist, but these newer studies also indicate that not just two, but as many as five or six, separate cranial nerves innervate lateral line organs (Fig. 3).

In axolotls a distinct anterodorsal lateral line nerve innervates the pit organs of the anterior pit line and the neuromasts of the supraorbital and infraorbital lines as well as all ampullary organs located adjacent to these lines (Fig. 3). The ganglion of the anterodorsal lateral line nerve lies dorsolateral to the combined ganglion of the profundus and trigeminal nerves but is clearly a separate ganglion. The profundus and trigeminal roots enter the medulla far rostral to the roots of the anterodorsal lateral line nerve, which enters the medulla at approximately the level of entry of the eighth cranial nerve.

A distinct anteroventral lateral line nerve innervates all lateral line receptors on the lower jaw and the cheek region in axolotls (Fig. 3). The ganglion of this cranial nerve is fused

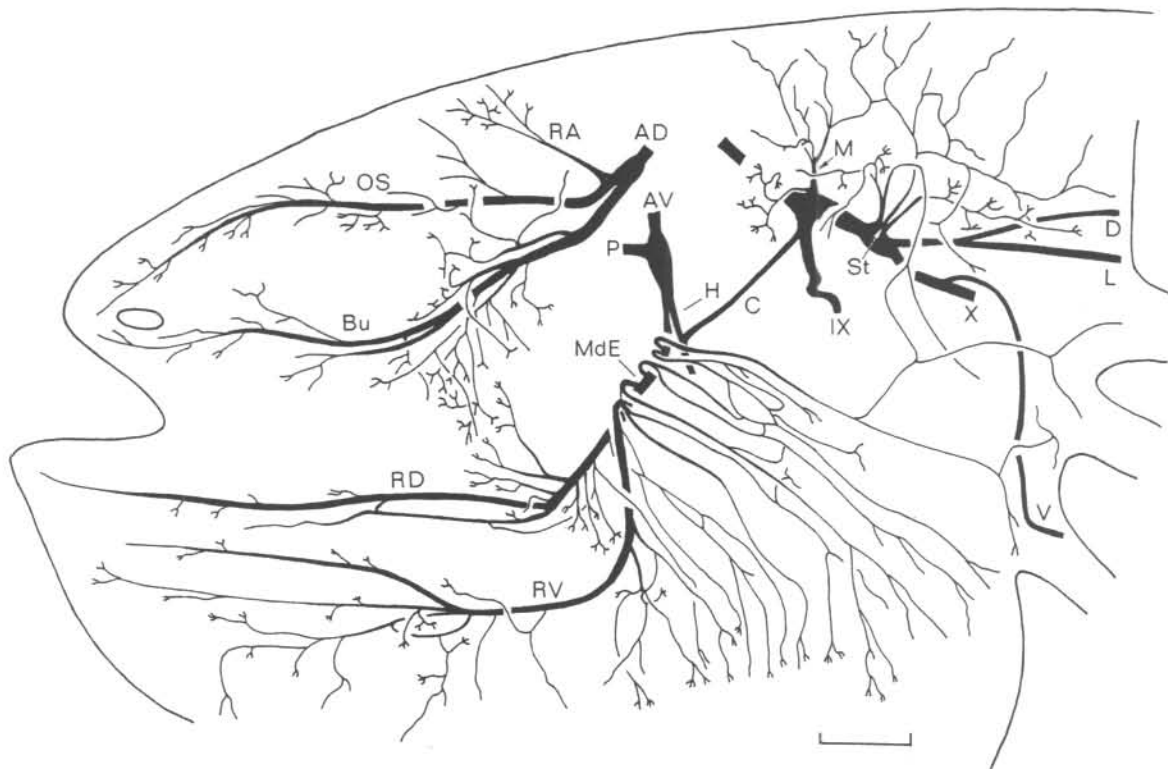


Figure 3. Reconstruction of the lateral line nerves in an axolotl based on camera lucida drawings of Sudan-Black and Winkelmann and Schmit preparations. AD, anterodorsal lateral line nerve; AV, anteroventral lateral line nerve; Bu, buccal ramus of AD; C, commissural ramus of AV; D, dorsal ramus of posterior lateral line nerve; H, hyoid ramus of facial nerve; L, lateral ramus of posterior lateral line nerve; M, middle lateral line nerve; MdE, external mandibular ramus of AV; OS, superficial ophthalmic ramus of AD; P, palatine ramus of facial nerve; RA, anterior ramule of AD; RD, dorsal ramule of MdE; RV, ventral ramule of MdE; ST, supratemporal ramus of posterior lateral line nerve; V, ventral ramus of posterior lateral line nerve; IX, glossopharyngeal nerve; X, vagal nerve. Bar scale equals 2 mm.

with the ganglion of the facial nerve, but the ganglionic cells of the anteroventral lateral line nerve can be clearly distinguished from those of the facial nerve, as they are approximately twice as large, and their cytoplasm is heavily pigmented. An anteroventral lateral line nerve, separate from the facial nerve, exists in many other anamniotes (Northcutt, 1989; Puzdrowski, 1989; Song and Northcutt, 1990), and two separate nerves exist through late embryonic stages of axolotls (unpublished observations). The lateral line fibers that innervate the lower jaw and cheek region of axolotls are thus believed to constitute a cranial nerve separate from the facial nerve.

The anteroventral lateral line nerve of axolotls and other ambystomatid salamanders (Coghill, 1902) exhibits an additional ramus, termed the commissural ramus, which passes caudally to fuse with the glossopharyngeal nerve immediately distal to the combined ganglionic complex of the glossopharyngeal and vagal nerves (Fig. 3). Application of horseradish peroxidase to the commissural ramus (unpublished observations) retrogradely labels ganglion cells of the anteroventral lateral line nerve and their centrally coursing axons. These fibers can be traced into the dorsal octavolateralis nucleus of the medulla, which only receives fibers of sensory cells that innervate ampullary organs. These results suggest that the commissural ramus contains caudally directed peripheral fibers of anteroventral ganglionic cells that innervate ampullary organs located ventral to the postotic line. In order to test this hypothesis, I have injected horseradish peroxidase directly into these ampullary organs and, in fact, have thereby labeled ganglionic cells of the anteroventral lateral line nerve. Thus peripheral fibers of this cranial nerve appear to pass caudally, where they anastomose with rami of other cranial nerves in order to innervate postotically located ampullary organs. Additional studies are currently underway to examine the developmental relationships of these organs and their innervation.

Primitively, a third lateral line nerve, termed the otic nerve, can be recognized in many fishes. It consists of a distinct ganglion, located ventral to the ganglion of the antero-dorsal lateral line nerve, and it innervates neuromasts of the otic canal (Northcutt, 1989). Axolotls do not possess neuromasts in a comparable topographical position and show no obvious trace of an otic ganglion or nerve.

The postotic cranial nerves of axolotls and

other ambystomatid salamanders are extremely complex (Fig. 3). A single ganglionic mass occurs lateral to the caudal medulla, from which issue 10 major rami in addition to the commissural ramus of the anteroventral lateral line nerve. Application of horseradish peroxidase or other tracers to these rami indicates that five separate rami innervate lateral line receptors (unpublished observations). Ganglionic cells located in the rostral end of the ganglionic complex innervate pit organs of the middle pit line, whereas a more caudally located population of cells in the ganglionic complex innervates the neuromasts of the postotic line in addition to all trunk neuromasts. The neuromasts of the postotic line are innervated by fibers within the supratemporal ramus, whereas those on the trunk are innervated by dorsal, lateral and ventral rami (Fig. 3).

An analysis of the innervation of postotic and trunk lateral line organs in fishes (Northcutt, 1989; Puzdrowski, 1989; Song and Northcutt, 1990) indicates that, primitively, at least three separate lateral line nerves occur postotically: a middle lateral line nerve that innervates the middle pit line and the neuromasts of the temporal canal, a supratemporal lateral line nerve that innervates the posterior pit line and neuromasts in the supratemporal and post-temporal canals, and a posterior lateral line nerve that innervates all trunk neuromasts.

The experimental observations in axolotls are consistent with the interpretation that the postotic ganglionic complex represents the fusion of the ganglia of three separate lateral line nerves (middle, supratemporal and posterior) as well as the glossopharyngeal and vagal nerves. Examination of the development of the postotic ganglia of axolotls, presently underway in my laboratory, clearly indicates that axolotls initially possess separate lateral line and branchiomic ganglia that fuse late in development. Thus axolotls exhibit evidence of five separate lateral line nerves, but they appear to have lost the otic lateral line nerve as well as those rami of the supratemporal nerve that innervate the pit organs of the posterior pit line, and they secondarily fused all ganglia of the postotic cranial nerves.

This new and hopefully more complete analysis of the distribution and innervation of the sensory organs of the lateral line system of axolotls establishes the groundwork for a detailed re-exploration of the ontogeny and developmental mechanisms of this system in ambystomatid salamanders.

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Axolotl Newsletter Number 19

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