Central Lateral Line and Auditory Pathways: A Phylogenetic Perspective

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SYNOPSIS. The phylogenetic origins of the lateral line electrosensory, lateral line mechanosensory, and auditory components of the octavolateralis system are unknown but each of these sensory modalities appears to have evolved early in vertebrate history. The octavolateralis terminal field occupies a large area of the dorsolateral wall of the medulla and among agnathids, cartilaginous fishes, non-teleost bony fishes and, with modifications, urodeles, consists of a dorsal electrosensory nucleus, a medial mechanosensory nucleus and a ventral octaval nuclear complex. This arrangement of medullary octaval nuclei, which differs from that of non-electroreceptive and electroreceptive teleosts, is considered the primitive plan and is retained in that phyletic line leading to tetrapods. Separate and parallel pathways are known, in elasmobranchs and a few teleosts, to ascend from each medullary lateral line center to the midbrain and presumably from midbrain to telencephalic levels via thalamic relays. There is no evidence, with the loss of lateral line senses among some amphibians and all amniotes, that the central neural pathways and nuclei are retained and used to process information from other sensory modalities. The anatomy of the central auditory system of fishes is unknown but is required for an understanding of whether auditory nuclei and pathways are retained during the fish-amphibian transition, or whether new ones arise, to process information from independently evolved peripheral receptors.

INTRODUCTION

The octavolateralis system consists of a lateral line subsystem that includes an array of mechanoreceptors and electroreceptors located in the skin, an octaval subsystem that comprises the mechanoreceptors of the membranous labyrinth or inner ear, and the sequences of neurons that carry information from the peripheral receptors of each subsystem to various levels of the central nervous system. The octaval component is universally present among vertebrates, while the lateral line mechanoreceptive component is found in all larval and most adult anamniotes. The electroreceptive component is likewise lacking in anamniotes, and, although widely distributed among anamniotes, is absent in certain groups (holosteans, most teleosts, and some amphibians). The phylogenetic origin of octavolateralis subsystems from a common ancestral source is unknown although ostracoderms apparently possess lateral line canals, an electroreceptive system, and an inner ear (Denison, 1966; Baird, 1974; Thompson, 1977) and all octavolateralis modalities appear established among Devonian gnathostomes (Orvig, 1971).

Historically, most studies of the evolution of the octavolateralis system have involved the peripheral apparatus. Similarities in the development and structure of the octaval and lateral line receptors formed part of the basis for considering these receptors to belong to a common "acousticolateralis" or octavolateralis system. Mechanoreceptors of the lateral line canals were hypothesized to have given rise to the electroreceptors and inner ear sense organs. The piscine ear was considered to be vestibular in function except among those teleosts that possess gas bladders (i.e.,...
pressure transducers) coupled to the labyrinth (van Bergeijk, 1967). Inner ear auditory receptors were thought to be the last peripheral octavolateralis component to evolve, occurring during the rhipidistian-amphibian transition with the appearance of a middle ear transmission apparatus and new receptors responsive to airborne sound. The change from aquatic to terrestrial living was accompanied by the loss of lateral line mechanoreceptors in many amphibian species, and it was hypothesized (Larsell, 1934) that the incoming fibers of the newly evolved auditory receptors synapsed upon a portion of the medullary lateralis center, thus transforming this phylogenetically old area into an auditory nucleus.

In contrast to these ideas, recent anatomical and physiological studies strongly indicate that each modality of the octavolateralis system is a separate system that evolved independently and in parallel within different vertebrate radiations. This is to say that the central neural pathways and centers which process information from lateralis and octaval receptors were established early in vertebrate history and are basic parts of the vertebrate body plan. Changes that have occurred through time involve adaptive modifications of primitive neural substrates to process inputs from diverse kinds and numbers of peripheral receptors, including the loss of certain peripheral receptors and the concomitant loss of central processing areas (e.g., the loss of the lateral line system in amniotes).

A basic special somatic sensory pathway involves a series of neuronal sequences from the primary neuron to the telencephalon via relay nuclei at each level of the neuraxis. In the auditory and lateral line systems medullary nuclei receive input from peripheral receptors and give rise to ascending lemnisci that terminate in the midbrain (these medullary nuclei may also project to the cerebellum and undoubtedly to the reticular formation). Information is relayed from the mesencephalon to the telencephalon via thalamic centers. Such thalamo-telencephalic projection systems, contrary to previous belief, are now known to exist among fishes (Schroeder and Ebbesson, 1974; Luiten, 1981; Echteler and Saidel, 1981) and are likely a general characteristic of the vertebrate brain.

The purpose of this discussion is to consider the main currently known features of the central ascending neuronal pathways of the mechanoreceptive, electroreceptive, and auditory components of the octavolateralis system and to present evidence that they are primitive constituents of the vertebrate central nervous system. The vestibular component of the octaval subsystem does not form long ascending lemnisci but more localized connections involved with postural reflexes and will be considered only as required in discussing the auditory component. Moreover, major consideration will be given to the octavolateralis system among those vertebrates within that phyletic lineage leading to tetrapods.

**Medullary Lateral Line and Octaval Patterns in Fishes**

Each octavolateralis subsystem is associated with a specific set of cranial nerves that terminate within a specialized part of the octavolateralis area of the medulla (Fig. 1). The electroreceptors and mechanoreceptors of the lateral line system are innervated by the anterior and posterior lateral line nerves. Among elasmobranches each anterior lateral line nerve possesses a dorsal root which carries electroreceptive information from the Lorenzian ampullae and terminates within a dorsally positioned longitudinal column of cells and neuropil called the dorsal nucleus. The ventral root of the elasmobranch anterior lateral line nerve and the posterior lateral line nerve innervate mechanoreceptors (canal neuromasts and free neuromasts or pit organs) and terminate within another dorsal cell and neuropil column called the medial nucleus (Boord and Campbell, 1977; Bodznick and Northcutt, 1980). The octaval or eighth cranial nerve innervates inner ear sense organs and terminates within a ventral column of cells and neuropil consisting of several nuclear subdivisions (Boord and Roberts, 1980; Northcutt, 1980). This arrangement of the octavolateralis peripheral nerves and three central...
nuclear columns occurs in representatives of Agnatha (petromyzontids), Chondrichthyes (elasmobranchs and holoccephalans), Dipnoi (lungfishes), Crossopterygii (coelacanths), Polypteriformes (bichirs and reedfish), and Chondrostei (sturgeons and paddlefish), although the neuroanatomical connections have not been experimentally confirmed in all cases. It is considered the primitive evolutionary pattern since it occurs in these early vertebrate radiations and can be used as a valuable diagnostic feature for comparative anatomical considerations (McCormick, 1982). Specifically, the presence of the dorsal root of the anterior lateral line nerve and the dorsal nucleus in a given species strongly suggests that it is electoreceptive. This suggestion has been confirmed physiologically in petromyzontids, polypteriforms, and dipnoans (Bodznick and Northcutt, 1981; Bullock et al., 1983). Conversely, arthrodires (placoderms) are believed to have possessed ampullae of the Lorenzinian type (i.e., electroreceptors); therefore, it is likely that a dorsal anterior lateral line nerve root and a dorsal nucleus were present in these close relatives of the cartilaginous fishes.

Electroreception appears to have evolved early in vertebrate history in a population ancestral to petromyzontids and cartilaginous fishes. Although retained in many vertebrate lines, including those leading to land vertebrates, it was lost in the later groups of actinopterygians (e.g., all living holosteans and most teleosts). The organization of the octavolateralis area of the medulla in these non-electroreceptive species differs from the primitive plan in that all lack the dorsal nucleus although the mechanosensory medial nucleus is retained. The electroreceptive sense has apparently evolved independently at least twice in teleosts—in the Osteoglossomorpha (mormyrids and the African notopterids) and in the Euteleosti (silurids and gymnotids). Electroreceptive teleosts comprise about 1% of all known teleost species. The peripheral receptors and central circuitry of the various teleost electroreceptive systems differ from the non-teleost electroreceptive systems and cannot be considered homologous (Boord and Northcutt, 1982; McCormick, 1982).

The medullary nuclei of the lateralis system of fishes are therefore organized into three different patterns as shown by non-teleost electroreceptive groups, non-electroreceptive groups, and electroreceptive teleosts (Fig. 2). The eighth nerve nuclei of fishes are also organized into three patterns, but the phylogenetic distribution of these patterns does not parallel those of the lateral line system. In all cases, the
FIG. 2. Patterns of variation of the primary lateral line areas of the medulla. The letters and symbols across the top indicate the presence or absence of various conditions with respect to the major lateral line centers as follows: A, lateral line area consists of the dorsal nucleus and the medial nucleus. A*, dorsal nucleus and medial nucleus present at least in larval stages. B, lateral line area consists of the medial nucleus. B*, medial nucleus present at least in larval stages. C, lateral line area consists of the medial nucleus and the newly evolved electrosensory lateral line lobe. O, lateral line subsystem absent.

Eight nerve nuclei form a column of cells and neuropil generally ventral to that of the lateral line nuclei. The pattern in lampreys, unlike that in any other vertebrate, is characterized by three aggregates of large cells (anterior, intermediate, and posterior octavomotor nuclei) that are included within a small-celled ventral nucleus (Larsell, 1967; Northcutt, 1979). It is uncertain whether agnathans possess inner ear auditory receptors in addition to their vestibular endorgans.

Four eighth nerve nuclei (anterior, magnocellular, descending, and posterior) occur among chondrichthyans, sarcopterigians, and non-teleost actinopterygians, and a fifth nucleus (tangential) is recognized in teleosts. Although fishes are believed to possess inner ear auditory receptors a separate and specialized medullary acoustic nucleus has not been conclusively identified. In mormyrids each inner ear receptor projects to parts of several octaval nuclei but the saccule, which is concerned with hearing, also projects to a separate and discrete area of the octaval complex (Bell, 1981a). This suggests that mormyrids, and perhaps other fish, may possess, like tetrapods, separate auditory and vestibular centers which are the targets of distinct auditory and vestibular nerves. However, the central terminations of inner ear receptors in fish may not follow this pattern because these receptors may be functionally heterogeneous, i.e., the same receptor may serve both auditory and gravistatic functions. Moreover, in different species of fish different endorgans may serve as the principal auditory receptor (Blaxter et al., 1981; Corwin, 1981; Platt and Popper, 1981).

MEDULLARY LATERAL LINE AND OCTAVAL PATTERNS IN AMPHIBIANS

All amphibians possess a lateral line subsystem, at least during larval stages, and an octaval subsystem. The lateral line subsystem contains mechanoreceptors and some species also possess an electric sense. The central organization of electrorreceptive and mechanoreceptive medullary centers is similar to that of primitive electrorreceptive non-teleostean fishes (Fig. 2). Larsell (1967) reported three anterior lateral line nerve roots in larval and aquatic adult urodèles,
and the dorsal root apparently carries electroreceptive input from ampullary organs to a dorsal neuropil region called the dorsal island of Kingsbury (Fritzsch, 1981). It is therefore likely, as Larsell suggested (1967), that the dorsal island of Kingsbury and the dorsal nucleus of primitive electroreceptive fishes are homologous. Ventrally positioned nerve fascicles from lateral line mechanoreceptors terminate ventral to the electroreceptive area in urodeles, presumably in the medial nucleus, and the octaval nerve terminates in a column of cells separate from the medial nucleus (Fritzsch, 1981).

According to Larsell (1967), anuran larvae possess a dorsal island of Kingsbury but adults, including aquatic species such as *Xenopus*, lack this structure and thus are presumably non-electroreceptive. Lateral line mechanoreceptive fibers in *Xenopus* terminate in the medial nucleus (Boord and Eiswerth, 1972). At least some larval apodans possess electroreceptors as well as mechanoreceptors (Hetherington and Wake, 1979) but the areas of termination of these receptors are unknown.

Larsell hypothesized that the amphibian medial nucleus was transformed into an auditory, or cochlear, nucleus with the loss of the lateral line mechanoreceptive system. However, in the premetamorphic bullfrog, a mechanoreceptive lateral line nucleus is situated medial to the octaval nucleus but disappears during metamorphosis with the loss of the lateral line and does not contribute to or transform into an octaval nucleus (Jacoby and Rubinson, 1983). It thus appears that the lateral line mechanosensory nucleus is lost with the loss of the peripheral system and has no counterpart (homologue) in amniotes.

Three nuclei are generally considered to form the column of cells receiving eighth nerve input in amphibians, a dorsal (acoustic) nucleus, a ventral nucleus and a caudal nucleus. In *Xenopus*, the eighth nerve projects to these nuclei but not to the medial (lateral line) nucleus. The octaval cell column is the only medullary component of the octavolateralis area in most adult anurans. In *Rana*, the dorsal (acoustic) nucleus receives input from the newly evolved inner ear auditory receptors (amphibian papilla and basilar papilla), while the other otic receptors (semicircular canals, utriculus, sacculus and lagena) project to the ventral and caudal nuclei (Gregory, 1972).

**Higher Order Auditory and Lateral Line Pathways**

Auditory and lateral line modalities are presumably represented at all levels of the brain but anatomical data on the ascending pathways and connections are available to a limited extent for only a few species. In amniotes, first order medullary acoustic nuclei and a second order cell group, the superior olivary complex, give rise to ascending lemnisci that largely terminate in a midbrain auditory center. This midbrain area projects to an acoustic area within the dorsal thalamus which in turn relays this information to pallial and, in some cases, striatal areas of the telencephalon. The nuclei which comprise the central auditory pathways are considered homologous among the three vertebrate amniote classes. The frog is the only amniote in which auditory pathways to the telencephalic level are known (Northcutt, 1980). Electroreceptive and mechanoreceptive lateral line pathways to mesencephalic levels are known among elasmobranchs and some teleosts (Knudsen, 1977; Bell, 1981b; Carr *et al.*, 1981; Braford, 1982; Finger, 1982; Maler *et al.*, 1982) and there is some information concerning these pathways beyond the midbrain (Braford and McCormick, 1979; Finger, 1980; Carr *et al.*, 1981; Boord and Northcutt, 1982; Finger and Bullock, 1982; Schweitzer, 1982).

Boord and Northcutt (1982) show in the clearnose skate that efferents from the electroreceptive dorsal nucleus and mechanoreceptive medial nucleus form separate channels en route to the torus semicircularis of the midbrain, where they terminate within separate nuclei of a lateral mesencephalic nuclear complex (Fig. 1). This complex includes lateral, dorsomedial, and ventromedial subdivisions; the lateral and dorsomedial subdivisions are electroreceptive and mechanosensory, while the other otic receptors (semicircular canals, utriculus, sacculus and lagena) project to the ventral and caudal nuclei (Gregory, 1972).
respectively. The ventromedial subdivision, on the basis of deoxyglucose metabolism and physiological evidence (Bullock and Corwin, 1979; Corwin and Northcutt, 1982), is presumed to be auditory but the ascending projections from medullary octaval nuclei have not yet been studied. In the teleost \textit{Cyprinus}, however, the auditory division of the torus semicircularis receives a bilateral projection from the anterior octaval nucleus. A diencephalic nucleus which presumably receives input from this toral area has been studied electrophysiologically (Echteler, 1981, 1982). An elasmobranch homologue of the auditory portion of the midbrain of other anamniotes and of amniotes remains to be discovered. The elasmobranch mechanosensory dorsomedial nucleus is considered homologous to the mechanosensory portion of the torus semicircularis of bony fishes, but the lateral nucleus of elasmobranchs is not homologous to the toral electrosensory zone of electroreceptive teleosts because electroreception was apparently re-evolved independently in teleosts (Boord and Northcutt, 1982).

The thalamus of elasmobranchs, like its counterpart in tetrapods, relays a variety of sensory inputs to the telencephalon (Schroeder and Ebbesson, 1974; Luiten, 1981). Electrosensory, acoustic, and visual responses have been recorded from restricted loci within telencephalic regions of sharks and rays (Platt et al., 1974; Bullock and Corwin, 1979). The main target for ascending electrosensory (and visual) input in skates is a subdivision of the medial pallial nucleus but the deep layers of the dorsal pallium (the central nucleus) cannot be excluded. The source of electrosensory input to these pallia appears to be the lateral posterior thalamic nucleus (Bodznick and Northcutt, 1984) which receives an input from the electrosensory lateral mesencephalic nucleus. Lateral line mechanosensory pathways to the telencephalon have not been demonstrated in sharks or skates but in a teleost (catfish, \textit{Ictalurus}) Finger (1980) shows that a ventral thalamic zone relays mechanosensory information to a central pallial nucleus of the telencephalon.

The organization of the higher order auditory pathways of frogs and amniotes is similar. Portions of the anuran midbrain torus semicircularis receive an acoustic input from the medullary dorsal acoustic nucleus and superior olive. This portion of the torus projects to a central thalamic nucleus and auditory information is then relayed, via the lateral forebrain bundle, to the ipsilateral striatum and possibly the medial pallium (Neary, 1974; Kicliter and Northcutt, 1975; Kicliter, 1979).

Concluding Remarks

Changes that have occurred during the evolution of the octavolateralis system in that phyletic line leading to the amniota involve the loss of the lateral line mechanoreceptors and electroreceptors and the appearance of specialized auditory receptors within the inner ear. There is no evidence that the central lateral line centers and pathways are retained among the amniotes. However, the otolithic labyrintheine receptors (maculae of the utricle, sacculus, and lagena) and macula neglecta of cartilaginous and bony fishes are retained in amphibians and amniotes. One or more of these endorgans has an auditory function among fishes but audition is primarily subserved by the newly evolved auditory papillae in amphibians, reptiles, birds and mammals. A goal of comparative anatomy is to understand how primitive or earlier derived central neural pathways have been altered to accomodate changes in the sensory periphery. How is the variability in the auditory periphery of fishes and amphibians reflected in the organization of the central auditory pathways? While auditory homologies are reasonably well-established among the amniotes, they are unknown among fishes and between fishes and amphibians. A piscine primary medullary auditory center has not been described although the central projections from individual labyrintheine sense organs are known for a few fishes; namely a moromyrid (Bell, 1981a), a cichlid (Meredith and Butler, 1982), and an elasmobranch (Barry, 1983). It is particularly difficult to delinate auditory projections of fishes because
inner ear maculae may function as both auditory and vestibular receptors (Corwin, 1981; Platt and Popper, 1981). Moreover, the same receptor may serve a different role in different fishes. It is believed that the saccular and lagena are auditory among most bony fishes although there are exceptions, e.g., the utricular macula is auditory in clupeids (Blaxter et al., 1981). The macula neglecta and saccular macula are the auditory receptors of cartilaginous fishes (Corwin, 1981) while the lagener macula plays a lesser or perhaps no role in audition.

Medullary auditory centers must exist because the evidence is overwhelming that fishes have an auditory sense and therefore the central course and connections of neurons carrying auditory information can be expected to differ from vestibular neurons. One anatomical approach that can be used to identify auditory centers at the level of the medulla of fishes is to determine the higher order connections of each of the primary octaval nuclei. For example, if one of the octaval nuclei is shown to have second order connections identical or similar to those of the amphibian dorsal (acoustic) nucleus, it could be considered either homologous to the dorsal acoustic nucleus, or a case of independent evolution of a similar pathway. Although the auditory pathways of fishes are currently unknown, at least three hypotheses can be considered in comparing the octaval nuclei of fishes with those of amphibians.

1. The primary auditory nuclei in fish are homologous to those in amphibians. This is a possibility even though the auditory endorgans are not identical among fishes and some of the auditory endorgans in amphibians have no counterparts in fishes. This hypothesis can fit a condition in which one or more of the labyrinthine sense organs of fishes function solely as an auditory receptor and project to a primary acoustic nucleus homologous to the amphibian dorsal (acoustic) nucleus. The particular endorgan which functions as an auditory receptor is irrelevant and may vary among fishes. In those species such as the Ostariophysi where the saccular and lagener maculae serve as auditory recep-

tors (Fay and Popper, 1980), neurons from these maculae would terminate within a specialized primary auditory area (which may include parts of one or more of the octaval nuclei), whereas fibers from vestibular receptors would have a separate terminal field. Among those species in which the utricular macula is auditory, utricular fibers would terminate within the same auditory area that receives saccular and lagener fibers in other fishes. Regardless of changes at the peripheral level, central structures are conservative and would receive auditory information over neurons from different otic endorgans of fishes. Fibers from the newly evolved auditory endorgans of amphibians would project to this same auditory area. The auditory nucleus of fishes would be homologous to that of amphibians, and these nuclei would have similar or identical central connections. This hypothesis could also fit a situation in which some or all of the otolithic endorgans have both auditory and vestibular functions. The neurons from these receptors would segregate centrally and terminate within separate auditory and vestibular nuclei.

2. The entire octaval cell column of fishes is a field homologue of the amphibian acoustic and vestibular nuclei; individual octaval nuclei are not comparable between fishes and amphibians. If the inner ear maculae of fishes have dual functions, this could be reflected centrally by the dual function of the octaval nuclei; there would be no specialized auditory and vestibular nuclei in fishes. The amphibian dorsal nucleus would arise by a reorganization of the octaval column of fishes. If this is the case, the efferent projections of each primary octaval nucleus of fishes would be expected to be similar to both auditory and vestibular secondary pathways of amphibians.

3. The auditory nuclei in fish are non-homologous to the dorsal (acoustic) nucleus of amphibians. According to this view, the independently evolved auditory receptors of amphibians would be paralleled by the appearance of new central auditory pathways. If the labyrinthine endorgans common to fish and amphibians are hypothe-
sized to be conservative in their central connections, then the appearance of new auditory endorgans in amphibians with projections separate from those of other labyrinthine endorgans implies that the amphibian dorsal (acoustic) nucleus has no direct counterpart in fishes. It is interesting to note that in *Rana* some of the cells of the ventral and caudal nuclei project to the mesencephalic torus semicircularis in parallel with the pathway from the dorsal nucleus (Wilczynski, 1981). If eighth nerve input to these cells originates from the saccular macula, which is both an auditory and vestibular receptor (Moffat and Capranica, 1976), this could represent a second ascending auditory pathway. If the saccular macula of fishes also projects to the torus semicircularis via a primary octaval nucleus, this might also be suggested that the difference in the organization of the octaval nuclei may be the result of a series of subsequent specializations. In addition, not only is there no one-to-one correspondence between the primary octaval nuclei of fish and amphibians, but these nuclei in amphibians and reptiles are also not readily comparable. In light of Lombard’s (1980) suggestion that certain peripheral auditory structures of the middle ear have evolved independently in amphibians and reptiles, it might also be suggested that the differences in organization of the octaval nuclei in amphibians and reptiles reflect the possibly independent evolution of auditory endorgans. Clearly, careful studies of the projections of the individual labyrinthine endorgans and of the higher order octaval pathways in fishes, amphibians, and reptiles will provide important clues to the resolution of these questions.

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