
11

Sensory Cranial Nerves

INTRODUCTION

The sensory cranial nerves of the brainstem fall into three distinct categories: the dorsal cranial nerve sensory components of the trigeminal nerve that carry somatosensory sensation for the head, the ventrolateral placodal nerves that carry taste, and the dorsolateral placodal nerves that carry the lateral line and octaval senses. As discussed in Chapter 9, each of these three categories represents a developmentally distinct component of the neuromeric segments. The sensory cranial nerves of the forebrain are discussed in later chapters.

DORSAL CRANIAL NERVES: SENSORY COMPONENTS FOR GENERAL SOMATOSENSORY SENSATION

One of the most dramatic advances in the evolution of the head was the transformation of the first arch of the visceral skeleton into components of the jaws. Although the jaws continued to play a role in respiration by regulating the flow of oxygenated water to the gills, they also greatly altered the way that the animals fed and many aspects of their mode of living. Jawed fishes were able to become more active predators. The ability for predation had important consequences for subsequent evolutionary changes such as improved fins and tail propulsion for more rapid maneuvering to approach prey or to avoid predators, changes in body form to reduce drag, and camouflage to deceive prey or to deceive predators. The central nervous system evolved concurrently with these changes by providing the sensory input and motor control that made these behaviors possible.

Somatosensory Innervation of the Head

The cranial nerve that is most closely associated with the development of the jaws is the trigeminal nerve (V). This nerve is derived from the nerve that supplies the first (mandibular) visceral arch (of the second head segment). Closely allied to the trigeminal nerve is the dorsal facial nerve (VII_D), which is derived from the nerve that supplies the second (hyoid) visceral arch (of the third head segment). These two nerves provide much of the sensory innervation from the skin and muscles of the head. These sensations include pain, temperature, touch, and proprioception.

The trigeminal nerve carries the sensory neurons from the jaws and elsewhere on the head as well as the motor neurons that control the deep muscles of the head, that is, the jaw muscles. The dorsal facial nerve carries sensory neurons from the skin of the head and face as well as from the muscles in anamniotes, but in amniotes, relatively few of these somatosensory fibers are found in VII_D. The majority of the somatosensory fibers from the head enter the brainstem via the sensory roots of V.

The trigeminal system is best developed in animals with a prominent snout, such as alligators, birds, and other animals, such as pigs, in which the snout is used for exploration and manipulation. The presence of vibrissae (whiskers) on the snout is also associated with an expansion of the trigeminal system. Vibrissae are important for tactile exploration and to provide an indication that the snout is about to bump into something. Many species of birds have a few rather untidy-looking feathers that stand out at the base of the bill. These feathers may be the avian equivalent of vibrissae and might possibly serve as air-speed indicators.

The trigeminal nerve has three great branches in mammals. The **ophthalmic branch** innervates the skin of the head region, the nonvisual parts of the eye including the muscles, and

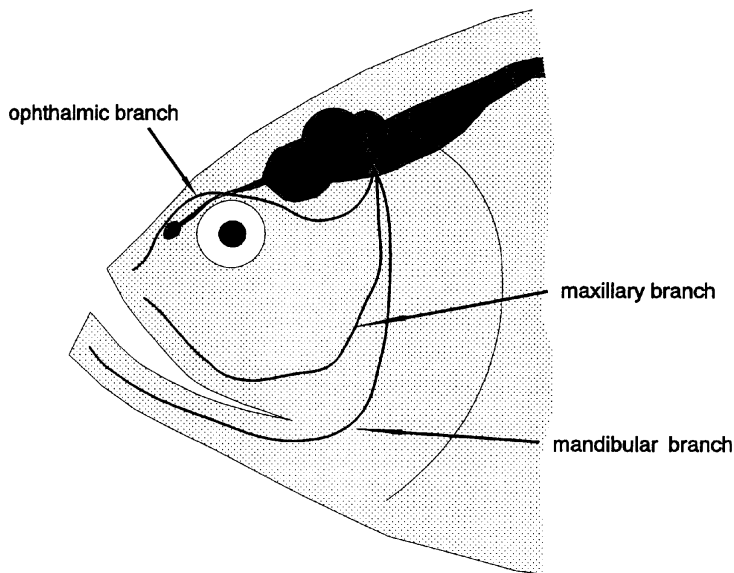


FIGURE 11-1. Distribution of the branches of the trigeminal nerve in a bony fish.

the snout. The **maxillary branch** innervates the upper jaw (the maxilla) including the upper teeth, the roof of the mouth, and the upper lip. The **mandibular branch** innervates structures of the lower jaw (mandible) including the lower teeth, the tongue, the floor of the mouth, and the lower lip.

Similar branches of the trigeminal nerve are present in nonmammalian vertebrates (Fig. 11-1), but in many of these groups, a separate profundus nerve has been identified that corresponds to the ophthalmic branch of the trigeminal nerve in mammals. The profundus nerve may represent the dorsal nerve of the first head segment (see Chapter 9). In *Latimeria*, the profundus nerve innervates the mucosal walls of a series of rostrally located tubes that contain the lateral line receptors. The profundus nerve probably carries pain and temperature information from the walls of the tubes. The lateral line receptors themselves are innervated by the anterodorsal lateral line nerve, which we will discuss below. Some other special adaptations of the trigeminal nerve, such as infrared (IR) detection in snakes, which we will discuss below, also involve the ophthalmic, or profundus, part of the trigeminal nerve.

Central Terminations of the Trigeminal Nerve

The central terminations (Fig. 11-2) of the axons of the trigeminal nerve are rather consistent in vertebrates. The fibers of the maxillary, mandibular, and ophthalmic branches terminate in the **descending nucleus of the trigeminal nerve** (descending V) in the somatic afferent column, along with somatosensory axons entering from other cranial nerves. Descending V is continuous at its caudal end with the dorsal horn of the spinal cord and appears to serve an equivalent function for the head. The sensory trigeminal axons also terminate in the pons, in an expansion of the somatic afferent column called the **principal nucleus of the trigeminal** (principal V). In both the principal V and descending V, the terminations of the axons remain segregated according to their source. In other

words, a spatial map of the arrangement of structures in the head is maintained in the trigeminal nuclei.

The trigeminal nerve is not the only source of somatosensory input to the brainstem. In addition to the trigeminal nerve, general somatosensory fibers can arrive at the descending nucleus of V by way of three other nerves: the dorsal facial (VII_D), the dorsal glossopharyngeal (IX_D), and the dorsal vagus (X_D) nerves. In all cases, however, the destination of the somatosensory fibers in VII_D , IX_D , and X_D is the same, the descending nucleus of V. Their inputs are conveyed to the same dorsal thalamic and telencephalic sites, in somatotopic order, as the inputs of the trigeminal nerve itself.

The Mesencephalic Division of the Trigeminal System

An additional component of the trigeminal system remains to be described. This is the mesencephalic division, which is one of the most unusual components of any sensory system. It is a very consistent feature and can readily be identified in every class of vertebrates with the exception of agnathans. The unusual characteristic of this sensory nerve (the **mesencephalic root of V**) is the location of its cell bodies, which are known as the **mesencephalic nucleus of the trigeminal nerve**, or mesencephalic V (Fig. 11-3). All dorsal cranial nerves, with the exception of the mesencephalic root of V, have their cell bodies outside of the central nervous system in ganglia. The cell bodies in these ganglia are derived from neural crest. The cells that form mesencephalic V are likewise derived from neural crest, but unlike other neural crest cells, they do not migrate ventrolaterally. Rather than being in a ganglion or close to the other cells and fibers of the trigeminal system, these cells lie in the dorsomedial part of the midbrain, in or adjacent to the tectal commissure, which is a broad band of axons that connects the right and left tectal hemispheres. This arrangement may be a remnant of an earlier stage in the evolution of the brainstem when such internal ganglion cells may have been more common.

Similar cells are seen in the spinal cord and/or medulla of many aquatic vertebrates. The latter are called **Rohon-Beard cells** and were discovered in lampreys by Reissner in the mid-1800s. It was Sigmund Freud, however, who while still a medical student, identified these cells as unmigrated spinal ganglion cells. In lampreys, these cells are present in the spinal cord and also along the entire extent of the medulla; they may be serially homologous to the mesencephalic V cells of jawed vertebrates.

The mesencephalic root of V carries proprioceptive information (for position sense) from the jaw muscles and the connective tissue surrounding the teeth. In mammals and amphibians, mesencephalic V also carries proprioception for the extraocular eye muscles, that is, the muscles that move the eyes. In contrast, in fishes and birds, the proprioceptors in the extraocular muscles are innervated by trigeminal axons that terminate in descending V. In sharks, the fibers of mesencephalic V do not respond to stimulation of muscle receptors; rather, they respond to stimulation of the skin around the mouth and displacement movements of the teeth. The majority of the mesencephalic V fibers terminate in motor V and so would appear to play an important role in the regulation of jaw open-

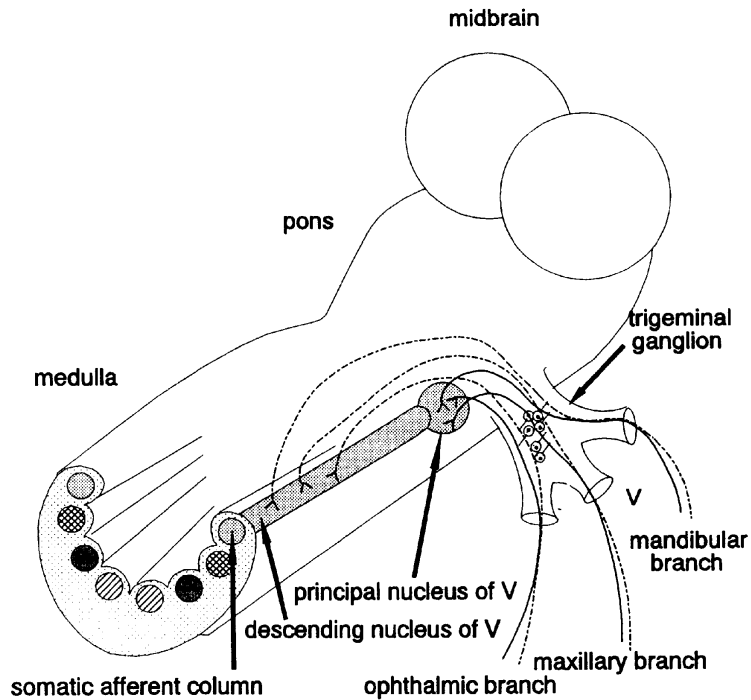


FIGURE 11-2. Central terminations of the afferent somatosensory fibers of the trigeminal nerve.

ing and closing and perhaps in the adjustment of jaw pressure.

Secondary Connections of the Trigeminal Nuclei

The majority of research on the secondary connections of principal V and descending V has been done in mammals and birds. The general organizational pattern of efferents from the trigeminal nuclei is that only the axons of the mesencephalic root of V terminate directly in the motor nucleus of V, which controls the contraction of the jaw muscles (see Chapter 12). In this case, a sensory neuron terminates directly on a motor neuron, forming a two-neuron (monosynaptic) reflex arc, which is the simplest type of neural network. In contrast, the efferents of principal V and descending V affect activity in motor V and motor VII_D indirectly by way of their terminations in the reticular formation, which in turn sends axons to the motor nuclei. The reticular formation often serves to coordinate the activity in related motor nuclei, such as motor V, motor VII_D, and the three motor nuclei that control the eye muscles. Such coordination of jaw and eye muscles is important in feeding behaviors, especially in predatory animals.

Another secondary connection of the trigeminal system is a bundle of axons that ascends from descending V and principal V to a somatosensory nucleus in the dorsal thalamus. From the dorsal thalamus, axons pass up to the telencephalon and terminate in the somatosensory cortex or pallium. The somatotopic organization that exists in principal V and descending V persists throughout the entire pathway so that at the level of the telencephalon, the cells that are responsive to stimulation of various points on the head, snout, jaws, and mouth are arranged in separate groups.

An unusual variation on the general vertebrate pattern is found in birds, in which the target nucleus of principal V is not in the dorsal thalamus but in the telencephalon. This telencephalic cell group in birds is called **nucleus basalis**. It sends its efferents to a somatosensory telencephalic pallial area in a topographically organized fashion. Whether nucleus basalis is a homologue of the trigeminal, somatosensory, dorsal thalamic nucleus of mammals has not yet been resolved.

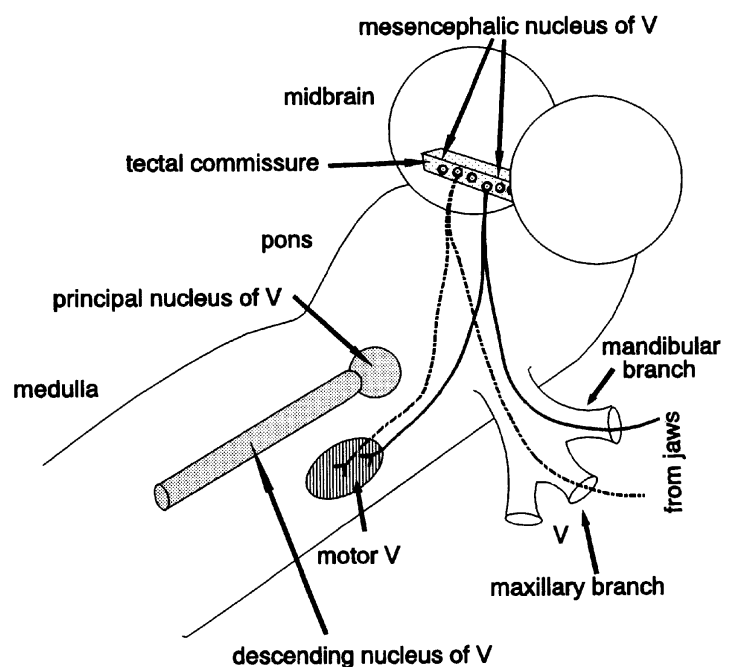


FIGURE 11-3. Connections of the mesencephalic nucleus of the trigeminal nerve.

Specialized Adaptations of the Trigeminal Nerve

A remarkable adaptation of the trigeminal nerve has occurred in two families of snakes: the boids (pythons and boa constrictors) and the crotalids or pit vipers (rattlesnakes, water moccasins, bushmasters, fer-de-lances, etc.). Both families have developed sensory pits on the head (Fig. 11-4). In the boids, the pits are principally on the lips; the pit vipers possess a prominent sensory pit below each eye. In both cases, the sensory pits are lined with photoreceptors that are sensitive not to the light that is visible to our eyes but to invisible IR radiation.

Infrared radiation is emitted by all objects that have warmth and especially by mammals and birds, which maintain a high body temperature. Such warm bodies are easily detected by IR sensors in the absence of all visible light. One study of the rattlesnake's IR detection sense reported that the snake could detect a temperature difference of 0.003°C from the background, which is roughly the amount of heat radiated by a human hand at a distance of one-half meter.

The IR detectors transmit their information to the brain via the maxillary branch of the trigeminal nerve. These neurons terminate in a special cell group: the **lateral trigeminal nucleus**, which is not found in non-IR detecting snakes. The nucleus is located lateral to descending V in the somatic afferent column. A similar, but independently evolved, lateral trigeminal nucleus has been reported in the vampire bat, which also detects IR radiation.

Recent physiological studies of the lateral trigeminal nucleus in rattlesnakes indicate that the neurons in this cell group possess many of the characteristics of cells in the visual system: small receptive fields and excitatory and inhibitory interactions that could serve to sharpen edges and provide a basis for the detection of motion and its direction. Of course, we have no idea what the rattlesnake's subjective experience of stimulation of its IR detectors is like, but the available evidence points to it being something very like vision.

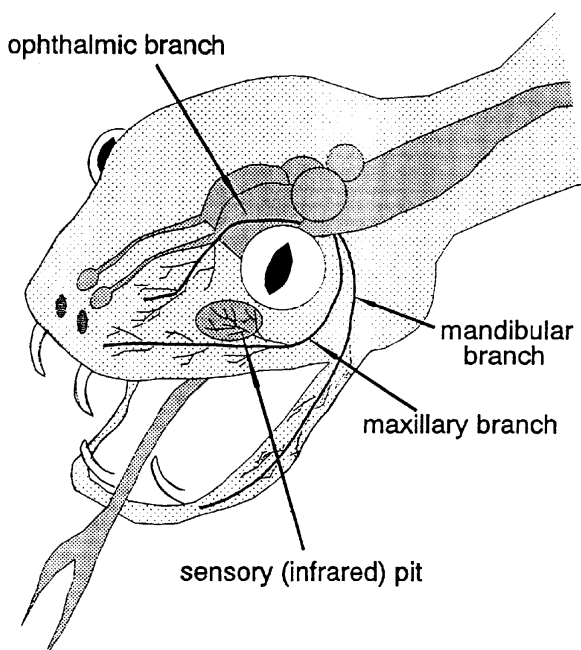


FIGURE 11-4. Distribution of the branches of the trigeminal nerve in a rattlesnake.

In the crotalids, the lateral trigeminal nucleus sends its efferents to a special group of cells in the reticular formation: the **nucleus reticularis calor** (i.e., the reticular nucleus of warmth). This reticular nucleus sends its efferents to the tectum, which is the region of the midbrain in which various maps of the surrounding environment, such as visual and auditory, are stored. The efferents of the boid lateral trigeminal nucleus project directly to the tectum. Tectal maps will be discussed in greater detail when we describe the tectum in a later chapter.

Another quite remarkable adaptation has recently been reported in the platypus. These monotreme (egg-laying) mammals have a prominent snout that resembles the bill of a duck. The "duckbill" of the platypus, rather than being keratinized as are bird bills, is leathery. Contained within the snout are rod-like structures that are mechanoreceptors and ampullary receptors similar to the electroreceptors of the lateral line system in aquatic anamniotes. These electroreceptors are capable of detecting the compound muscle-action potentials of the well-developed tail musculature of shrimp, on which platypuses feed. Similarly, mechano- and electroreceptive structures have been found on the beak of echidnas (spiny anteaters). Although the central termination of these receptors has not yet been determined, their location on the snout would seem to implicate the trigeminal system, and mechano- and electrosensory evoked potentials have recently been recorded in the somatosensory cortex in the platypus.

A third specialized adaptation of the trigeminal nerve may have occurred in birds and be related to magnetoreception. Some recent work suggests that some of the trigeminal neurons are responsive to magnetic stimuli; the neurons may be sensitive to the electromagnetic alignment of particles of ferromagnetic material (magnetite) that are present in the ethmoidal region of the skull. This system may thus contribute to migratory, homing, and orientation abilities.

VENTROLATERAL PLACODAL CRANIAL NERVES: TASTE

Some of the earliest vertebrates, derived from ancestral chordates, were adapted to life as filter feeders in an aquatic environment, probably very much the way that larval lampreys and some jawed fishes survive today. These animals filter food particles or small prey from the water column that is pulled in by the suction action of the branchial muscles. The filtration is done by sticky mucus or by the gill rakers acting as a sieve. The trapped particles or prey are washed into the digestive tract, and the excess water is expelled along with respiratory gasses. Some fishes are bottom feeders that suck up mouthfuls of bottom sediment, extract the edible morsels, and eject the remainder, and some predatory fishes suck in mouthfuls of water that carry the prey into their mouths. All of these methods of feeding require mechanisms for differentiating between the edible and the inedible, between objects that produce illness and those that do not, and between more favored and less favored foods. These mechanisms are the chemical senses of gustation (taste) and olfaction (smell). In this chapter, we will discuss gustation. Olfaction, which is used not only for feeding but also for social recognition, orientation, territorial marking,

and courtship, is a more complex subject and will be discussed in Chapter 29.

The receptors for gustation are taste cells located in groups on small peg-like projections known as **taste buds**. An animal's sensitivity to taste stimuli depends on the number of taste buds. The greater the number of taste buds, the higher is the probability that a stimulus molecule will be detected.

In fishes, taste buds are located not only in the mouth and in the throat, but sometimes on the lips, on the surface of the head, and on the body skin. Many species of bony fishes have taste buds on the tips of their pectoral fins, which permits them to sample the taste qualities of the bottom sediment. The "whiskers" that give the catfish its name (technically known as **barbels**) are studded with as many as 20,000 taste buds and serve a similar, bottom-tasting function. In addition, the catfishes and the cyprinids, which includes the common goldfish, have in excess of 150,000 taste buds all over their body surface. Although we find it difficult to imagine what this skin-tasting sense is like, it probably gives the fish a taste map of the surrounding environment, just as the electrosense gives certain fishes an electrical image of nearby objects and organisms and the IR sense provides an IR picture to certain snakes.

In tetrapods, all of which have tongues, the taste buds are located on the tongue as well as in the mouth and throat. Amphibians, diapsid reptiles, and turtles have considerable numbers of taste buds, which suggests that their taste sensitivity is rather good. Birds, on the other hand, have relatively few taste buds compared to the other tetrapods and would appear to make less use of this sense.

The Gustatory System

The number of taste qualities that animals can detect is relatively few. The most commonly reported are sweet (sugars), salty (salts), sour (acids), and bitter (alkaloids). In addition, some taste neurons have been reported to be excited by certain amino acids and pure water. Because human taste sensitivity is limited to sweet, sour, salty, and bitter, we cannot imagine what amino acids or pure water taste like. Sensations in the mouth that are produced by chemical irritants such as pepper and various "hot" spices and seasonings are not transmitted either by the gustatory or by the olfactory nerves. These are somatic sensations just like pain and temperature and are carried by fibers of the maxillary and mandibular divisions of the trigeminal nerve (V) to the trigeminal nuclei in the somatic afferent column.

The Gustatory Nerves and the Nucleus Solitarius

The taste cells have no axons; instead, axons of gustatory fibers of the ventrolateral facial (VII_{VL}), ventrolateral glossopharyngeal (IX_{VL}), and ventrolateral vagus (X_{VL}) nerves detect changes in excited taste cells and transmit this information to the common target of taste axons no matter by which nerve they enter the brain: the gustatory nucleus (a rostral division of nucleus solitarius), which is at the rostral end of the visceral afferent column of the medulla (Fig. 11-5).

The nucleus solitarius consists of two divisions with their boundary being roughly at the level of the entrance of the

vagus nerve. The rostral division of nucleus solitarius is the region that receives the gustatory fibers from VII_{VL}, IX_{VL}, and X_{VL}, and is now recognized as a separate nucleus: the gustatory nucleus. This is a ventrolateral, epibranchial placodal afferent system rather than a visceral afferent system as previously believed. The caudal division of nucleus solitarius is the general visceral component of the visceral afferent column and receives fibers via the dorsal glossopharyngeal (IX_D) and the dorsal vagus (X_D) nerves from the viscera of the body, such as the digestive, circulatory, and respiratory systems. While not involved in the perception of taste, the visceral afferents of IX_D and X_D carry input that, along with taste afferents, affects feeding behavior.

A somatotopic organization exists in the gustatory nucleus such that the gustatory nerves from the different regions of the head (and the body in those animals with skin taste buds) enter the nucleus in approximately the same order as they are located in the body, that is, axons from more rostral regions of the mouth (or body) enter the more rostral portions of the gustatory nucleus. A similar, topographic arrangement has been found in the terminations of axons from the general viscera in the caudal division of nucleus solitarius. Axons from the various internal organs terminate in the caudal nucleus solitarius in the same order as the organs are arranged in the body.

Secondary Connections of the Gustatory Nucleus and Nucleus Solitarius

The pathways taken by efferent axons from the gustatory nucleus and the caudal division of nucleus solitarius have been studied in some detail in mammals, especially rodents and primates. In primates, the efferents of the gustatory nucleus follow the typical routes of the sensory systems of cranial nerves that terminate in the lower brainstem. From the target cell group of the primary axons of the cranial nerve, secondary axons ascend to the dorsal thalamus to end on tertiary cells whose axons in turn end in the telencephalon. The secondary gustatory fibers terminate on cells in the dorsal thalamus that are situated close to the cells that receive the secondary somatosensory fibers. The dorsal thalamic gustatory cells send their axons to one or more regions of the telencephalon—gustatory isocortex and areas in the ventral part of the telencephalon. As in the dorsal thalamus, the telencephalic gustatory cells are not far from the somatosensory cells.

An important additional nucleus in this system is the **parabrachial nucleus**, which is located in the dorsal pons. The medial part of this nucleus receives projections from the gustatory nucleus and is sometimes referred to as the **pontine taste area** (PTA). It contains a topographic representation of the gustatory receptors on the tongue. In rodents, the gustatory part of the parabrachial nucleus serves as an intermediary between the gustatory nucleus and the gustatory dorsal thalamus and also projects directly to gustatory isocortex. In primates, the parabrachial nucleus appears to be more involved with the caudal, visceral division of nucleus solitarius. In both primates and rodents, the parabrachial nucleus also sends many axons to ventral forebrain structures such as the hypothalamus and the amygdala, which lies in the basal part of the telencephalon. The gustatory pathways are shown in Figure 11-6.

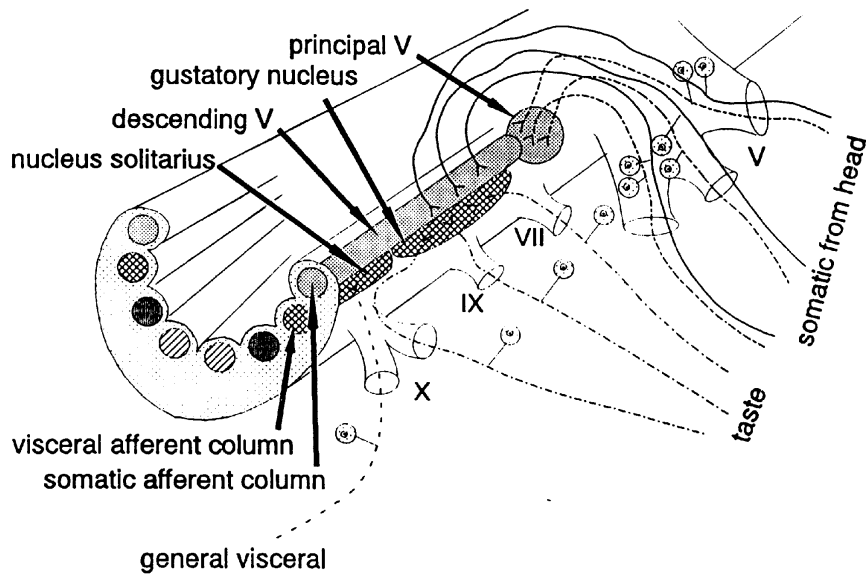


FIGURE 11-5. Diagram of the terminations of gustatory and tactile cranial nerves.

The cells of the caudal, visceral division of nucleus solitarius send some of their axons to the dorsal motor nucleus of the dorsal vagus (X_D) nerve. This nucleus, which is part of the visceral motor column, is the source of parasympathetic axons that distribute to the viscera of the thorax (chest) and abdomen and other brainstem motor nuclei that control salivation. Nucleus solitarius also projects to a more ventral nucleus in the brainstem: **nucleus ambiguus**. There is probably a stronger input to nucleus ambiguus from the gustatory nucleus than from the more caudal, viscerally related nucleus solitarius. Nucleus ambiguus gives rise to general somatic efferent axons in the dorsal glossopharyngeal, dorsal vagus, and accessory nerves that innervate the muscles of the pharynx (throat).

Cyprinid and Silurid Gustatory Specializations

Although taste is very well developed in fishes in general, two suborders of ray-finned fishes have become highly special-

ized for the use of the gustatory sense; these are the cyprinids, which include the carps, minnows, chubs, and goldfishes, and the silurids (or catfishes). As we discussed previously, these animals not only have mouth, throat, and skin taste buds, as do other species of fishes, but they have evolved a vast system of taste receptors over virtually the entire body surface. Along with this expansive gustatory surface, a system of elaborately organized central structures has developed that rivals the most complex neural organizations seen in any central nervous system.

Both groups of fishes are bottom feeders, and the mechanisms that they have evolved are highly sophisticated adaptations for the separation of food particles from inedible bottom sediment. In goldfishes, for example, two, opposing surfaces in the oropharynx (mouth and throat) manipulate bottom sediment in such a way as to separate the edible and tasty particles from those that are inedible or unpalatable. These surfaces are the **palatal organ**, which is a muscular structure attached to the roof of the mouth, and the surface of the gill arches. Both of these structures are studded with thousands of taste buds, which are innervated by branches of the ventrolateral vagus (X_{VL}) nerve. The gustatory branches of X_{VL} terminate in the gustatory nucleus, just as in other vertebrates, but what is so unusual in cyprinids and silurids is that the gustatory nuclei of the right and left sides have "ballooned" out to form rather prominent lobes on the caudal brainstem. They are known as the **vagal lobes** (or more properly the glossopharyngeal-vagal lobes because the axons of the ventrolateral glossopharyngeal (IX_{VL}) nerve in addition terminate in their rostral ends). The internal structure of the vagal lobes consists of a series of nine layers of neurons with a complex organization. In addition to a topographical organization of mouth structures in the vagal lobe, taste axons from each of the specialized structures terminate in specific layers. For example, axons innervating the taste buds of the palatal organ project to layer six; those innervating the taste buds on the gill arches project to layers two and four; layer nine receives both palatal and gill arch axons. The general visceral afferent axons from IX_D and X_D terminate in a separate, visceral afferent nucleus.

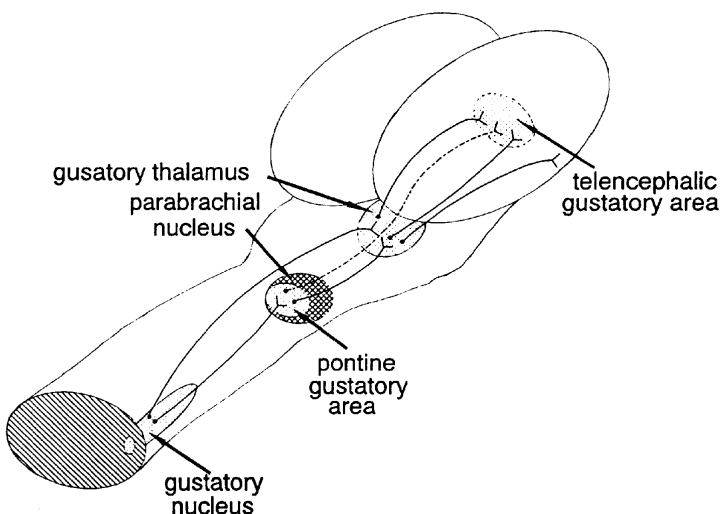


FIGURE 11-6. Ascending gustatory pathways in mammals.

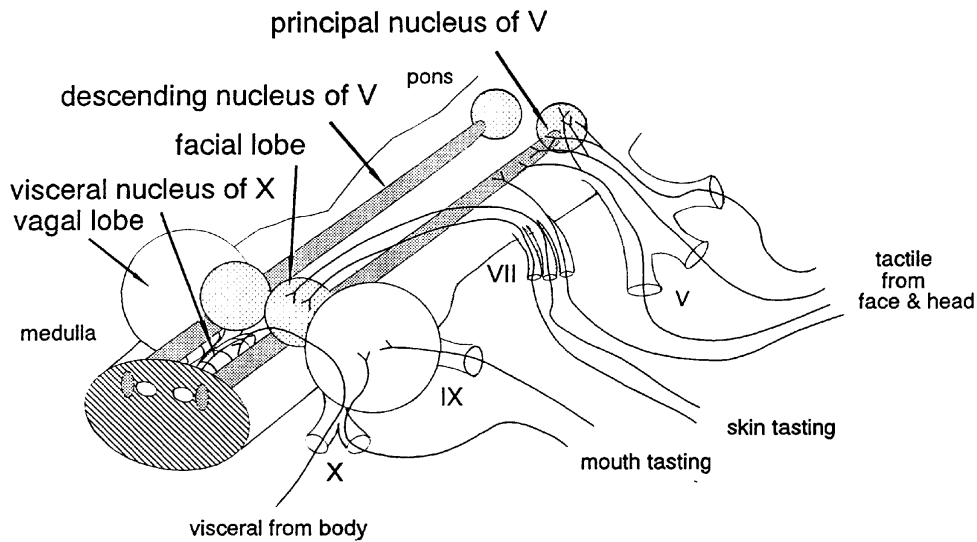


FIGURE 11-7. Afferent tactile and gustatory pathways in cyprinids and silurids.

In addition to the paired vagal lobes, these fishes have a second pair of lobes, called the **facial lobes**, which lie rostromedial to the vagal lobes. As the name implies, the facial lobe receives the gustatory axons of the ventrolateral facial (VII_{VL}) nerve. In catfishes, this nerve is quite elaborate with branches from the upper lip, the lower lip, the anterior palate, the pectoral fin, which also is used for bottom tasting, and a branch known as the recurrent branch because it “runs back” towards the tail. The recurrent branch serves the vast number of taste buds on the body surface. A topographical organization is found in the facial lobe with the more rostral structures being represented in the rostral portion of the lobe. The vagal and facial lobes and their relationship to the trigeminal system are shown in Figure 11-7.

Some of the efferents of the vagal and facial lobes (Fig. 11-8) are involved in the coordination of various feeding and

postural reflexes. The vagal lobe projects to those general somatic efferent motor nuclei of the caudal brainstem that control the palatal organ and other muscles of the oropharynx. The facial lobe projects to a nucleus located near the border of the medulla and spinal cord, called the **spinotrigeminal funicular nucleus**, which provides a point of interaction between gustatory information and tactile information from the head and the body.

The major efferent projections of the facial and vagal lobes are ascending. Both lobes project to a nucleus located in the pons called the **superior secondary gustatory nucleus**. The superior secondary gustatory nucleus projects to an area in the caudal part of the diencephalon called the **preglomerular nuclear complex** (see Chapter 20) and to the hypothalamus. The preglomerular gustatory nucleus also receives direct projections from

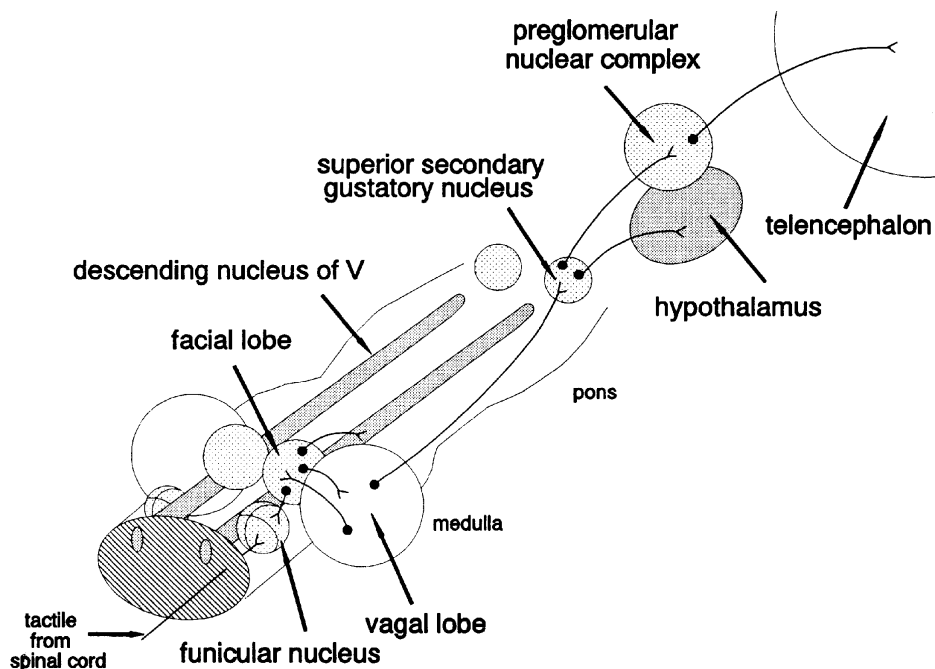


FIGURE 11-8. Ascending gustatory pathways in cyprinids and silurids.

the vagal and facial lobes; it relays gustatory information to an area in the telencephalon. The hypothalamic projection most likely provides the visceral and endocrine control cell groups in the hypothalamus with information about what has been tasted in the mouth. The superior secondary gustatory nucleus appears to be the homologue of the gustatory portion of the parabrachial nucleus, that is, the pontine taste area, of mammals.

In summary, we can see that the sense of taste has been developed to a superb degree in the cyprinids and silurids. At the peripheral end, the distribution of receptors on the body surface, fins, lips, and in the mouth provide the animal with a highly detailed taste map of the environment as well as the means for detecting food items and rejecting inedible or noxious objects. These processes are made possible by an extraordinary group of central structures: complex lobes with individual layers that receive very specific inputs and are organized topographically. The extreme development of the vagal lobe/facial lobe complex in these fishes is an excellent illustration of one of the ways that the nervous system responds to adaptive pressures for the increased use of a neural system.

A great deal of effort has been expended to work out the details of the vagal lobe/facial lobe system in cyprinids and silurids. We have good reason to believe that this research will greatly enhance our understanding of the way taste information (and other sensory information as well) is processed in the central nervous system of all vertebrates. One way to understand a biological system is to study it in an animal that is specialized for its use.

DORSOLATERAL CRANIAL NERVES: LATERAL LINE AND OCTAVAL SYSTEMS

In aquatic vertebrates, the dorsolateral series of placodes gives rise to multiple nerves that fall into as many as four main sensory categories:

- Mechanosensory lateral line.
- Electrosensory lateral line.
- Auditory.
- Vestibular sense.

In terrestrial vertebrates, the lateral line system is absent, and only the senses associated with the eighth nerve, that is, the auditory and vestibular senses, develop.

In the aquatic environment, the visual, auditory, and chemosensory systems aid in the detection of the presence of other animals. The lateral line system is an additional important detector of other animals. It functions over a greater range of environmental conditions than the other sensory systems—in calm, clear, illuminated water as well as in turbid, murky water and in darkness. The lateral line sensory system has two major components in many vertebrates: a mechanosensory system and an electrosensory system.

The mechanosensory lateral line allows an aquatic animal to perceive other moving animals at a distance. Current-like movements of the water caused by the motion of other animals (predators, prey, conspecific sexual partners, or other members

in a school) are detected by the lateral line neuromasts and/or pit organs (see Chapter 2), the mechanosensory receptors. Behavioral studies have shown that such detections are responded to and are thus important to the animal. On the other hand, water displacements caused by the animal's own movements can be detected by the mechanoreceptors, but reactions to these stimuli are suppressed by other neural mechanisms. Motor control and related feedback mechanisms, rather than the lateral line, are used to regulate locomotory behavior.

The electrosensory lateral line is used for a wide range of functions. It is often used to detect and identify prey, whether the prey is another free-swimming animal or an animal concealed on the bottom under a layer of sand or mud. The electrical profile of such animals can be located and identified by the ampullary or tuberous receptors (see Chapter 2) of the lateral line electrosensory system. In the variety of fishes that can produce electrical signals—an electric organ discharge, or (**EOD**)—the electrosensory system plays an important role in social interactions, including the recognition of individual conspecifics within a social hierarchy.

The auditory and vestibular senses are common to aquatic and terrestrial vertebrates. Auditory receptors respond to pressure waves with accompanying particle motion, that is, to sound. The frequency of the waves and the location of their source are analyzed within the auditory system. Vestibular receptors are involved in maintaining equilibrium and respond to gravitational and other accelerational cues that allow for orientation of the body within the three spatial dimensions.

The Lateral Line System

The mechanosensory lateral line system is widely distributed in aquatic anamniotes. It was apparently present in the earliest vertebrates, as it has been identified in agnathans, cartilaginous fishes, bony fishes, lungfishes, the crossopterygian *Latimeria*, and aquatic amphibians. The mechanosensory lateral line system is thus a ubiquitous feature of anamniote vertebrates, and its evolutionary history is more conservative than that of electroreceptive lateral line systems.

An electroreceptive lateral line system has been evolved independently at least several times. Electroreception appears to have been evolved in the ancestral vertebrate stock of at least lampreys and jawed vertebrates, since morphologically similar electroreceptive systems are known to be present in lampreys, cartilaginous fishes, lungfishes, the crossopterygian *Latimeria*, and many amphibians. Among nonteleost bony fishes, a similar electroreceptive system is present in reedfishes and sturgeons. Electroreception appears to have been lost in the common ancestral stock of the Holostei (gars and the bowfin) and the Teleostei, however. It was then reevolved independently three or four times. These convergent electroreceptive systems are present in two different groups of ostariophysans, silurids and gymnotids, and in two different groups of osteoglossiforms, the mormyrids and notopterids.

The receptors for the mechanosensory lateral line usually lie within canals that are arrayed over the surface of the head and body. Figure 11-9 shows the distribution of the mechanosensory lateral line canals on the head of the coelacanth *Latimeria*, as well as the so-called rostral organ that contains electroreceptors in this species. The mechanoreceptors and electrore-

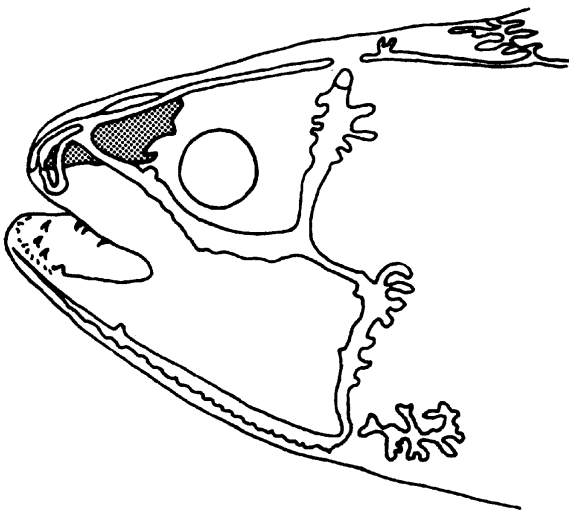


FIGURE 11-9. Drawing of the mechanoreceptive lateral line canals and the putative electroreceptive rostral organ (stippling) in the coelacanth *Latimeria*. Rostral is toward the left. Adapted from Northcutt (1986).

ceptors are innervated by up to six separate nerves, the **anterodorsal, anteroventral, otic, middle, supratemporal, and posterior lateral line nerves**. Not all vertebrates with the lateral line system have all six nerves. The urodele amphibian *Ambystoma*, for example, has five lateral line nerves (Fig. 11-10), lacking an otic lateral line nerve.

In the medulla, the mechanoreceptive lateral line fibers terminate primarily in two structures (Fig. 11-11), the **eminentia granularis** of the cerebellum and part of the **lateralis column**. In bony fishes, the lateralis column consists of a large

nucleus that forms most of the column's rostrocaudal extent, called **nucleus medialis** or **nucleus intermedius**. The more caudal nucleus in the column, **nucleus caudalis**, also receives mechanosensory input. In cartilaginous fishes, the mechanoreceptive cell group is similarly called the medial (or intermediate) octavolateralis nucleus, and in amphibians, it is called nucleus intermedius.

The position of the column of nuclei that receive mechanoreceptive lateral line inputs is relative to one or two other cell columns present in the medulla. The mechanoreceptive nuclei generally lie dorsal and/or lateral to a cell column, the octaval column, which receives input from the eighth nerve [Fig. 11-12(A)]. In electroreceptive nonteleost bony fishes, the mechanoreceptive lateral line column additionally lies lateral or ventrolateral to the cell column that receives the electrosensory lateral line input [Fig. 11-12(B)], called **nucleus dorsalis**, while in electroreceptive teleosts, the mechanoreceptive lateral line column is medial or ventromedial to the electroreceptive area, called the **electrosensory lateral line lobe** (Fig. 11-13). In cartilaginous fishes, this cell column is called the **dorsal octavolateralis nucleus**. In electroreceptive amphibians, the mechanosensory nucleus intermedius lies ventral to the electrosensory column, which is called nucleus dorsalis.

The ascending projections that arise from both the mechanosensory and electrosensory lateral line nuclei travel with octaval fibers in the **lateral lemniscus**. This pathway is bilateral but projects predominantly to the contralateral side. The lateral lemniscus terminates in a part of the roof of the midbrain called the **torus semicircularis** in most anamniotes but is referred to as the **lateral mesencephalic nucleus** in some sharks and as a group of several nuclei—the **lateral mesencephalic complex**—in other sharks. Within the midbrain roof, the zones of

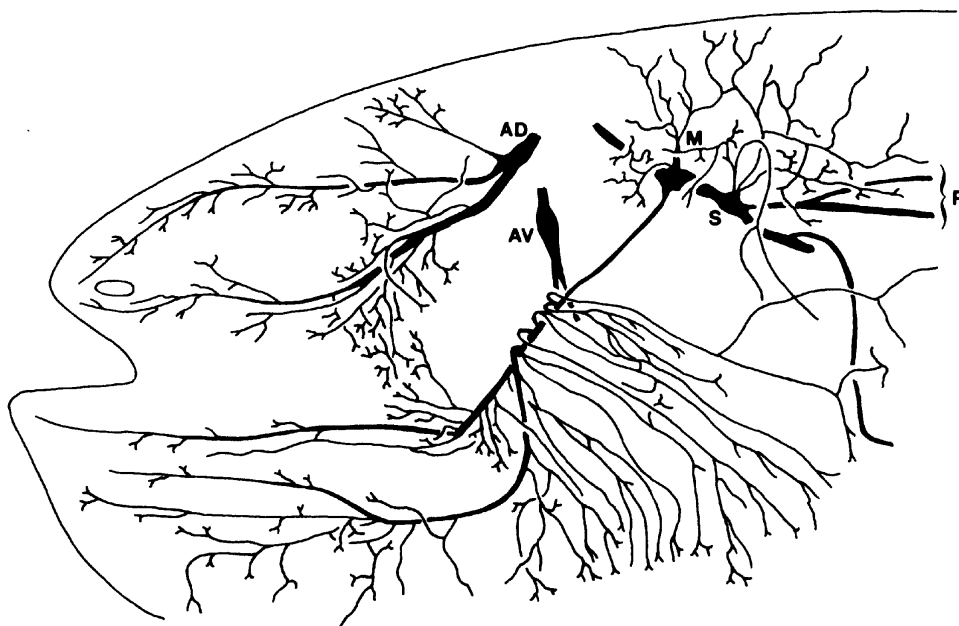


FIGURE 11-10. Drawing of the major branches of the five lateral line nerves present in the axolotl, *Ambystoma mexicanum*, which lacks an otic lateral line ramus. Rostral is toward the left. Abbreviations: AD, anterodorsal lateral line nerve; AV, anteroventral lateral line nerve; M, middle lateral line nerve; P, posterior lateral line nerve; S, supratemporal lateral line nerve. Adapted from Northcutt (1992).

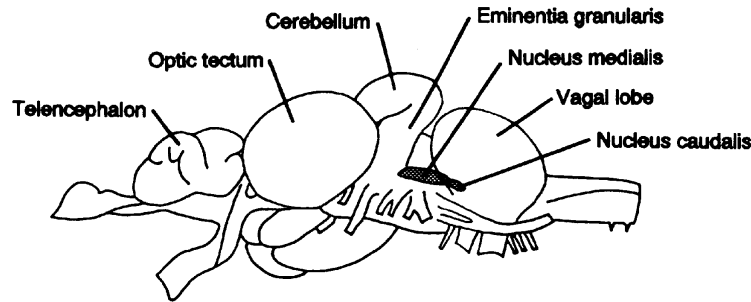


FIGURE 11-11. Lateral view of the brain of a goldfish (*Carassius auratus*) with the position of the lateralis column projected onto it. Adapted from Puzdrowski (1989). Used with permission of S. Karger AG.

termination of the mechanosensory, electrosensory, and octaval fibers remain separate (Fig. 11-14). Within each of the lateral line sensory systems, a spatial map of the input is also maintained. From the midbrain, lateral line input is relayed through the **preglomerular nuclear complex** in the caudal diencephalon in bony fishes (see Chapter 20), or its putative homologue in cartilaginous fishes, to the telencephalon.

The Octaval System

The octaval system consists of the auditory and vestibular rami of the eighth cranial nerve and their central structures and connections. These two rami are present in all vertebrate groups, but substantial evidence exists showing that at least part of the peripheral auditory receptor apparatus has been independently evolved in fishes and among tetrapods. Similarities in the central nervous parts of these systems allow for the possibility that at least some of the auditory nuclei and pathways were maintained through periods of change in the peripheral

receptor apparatus. Thus, some of the octaval nuclei may be homologous among the various groups of vertebrates, particularly at midbrain and more rostral levels, but some of the relationships of the various medullary octaval nuclei in different vertebrate groups remain open to question.

In most vertebrates, vestibular and auditory fibers terminate within various parts of the brainstem, including the cerebellum, reticular formation, and the **octaval column** in the medulla. The octaval column is the main auditory region involved in relaying the input to more rostral parts of the brain. Where a lateral line system is also present, the octaval column lies ventral to it, as referred to above.

In agnathans, the eighth nerve terminates within the octaval column but not in any other brainstem sites. In lampreys, the octaval column has three nuclei, two of which, the **ventral** and **octavomotor** nuclei, receive the bulk of the eighth nerve fibers. In hagfishes, the eighth cranial nerve projections are primarily confined to a single area, called the **ventral nucleus of the area acusticolateralis**.

In agnathans and jawed fishes, at least some of the octaval endorgans are thought to process both auditory and vestibular information. In fishes, the nerves from all of the octaval endorgans primarily terminate within the octaval column, which com-

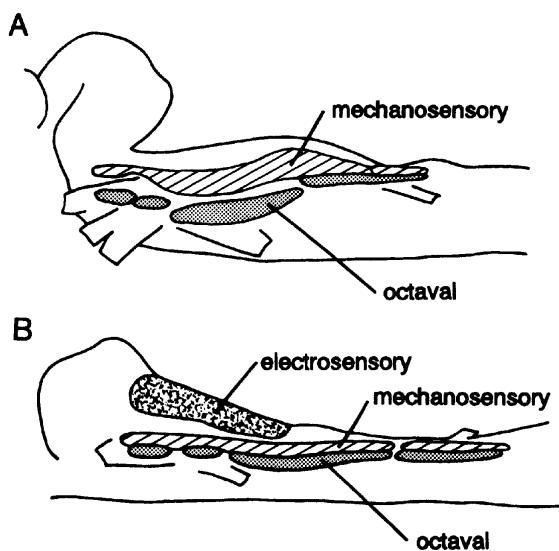


FIGURE 11-12. Projection onto a lateral view of the brainstem of nuclei receiving (A) mechanosensory (diagonal lines) and octaval (fine stippling) projections in the bowfin (*Amia*) and (B) electrosensory (random stippling), mechanosensory (diagonal lines), and octaval (fine stippling) projections in a sturgeon (*Scaphirhynchus*). Adapted from McCormick (1989). Used with permission of Springer-Verlag.

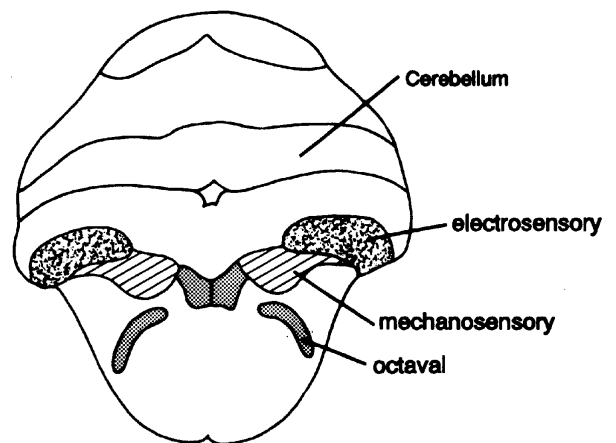


FIGURE 11-13. Drawing of a transverse section through the brainstem of the osteoglossomorph fish *Xenomystus* showing the relative positions of the electrosensory (random stippling), mechanosensory (diagonal lines), and octaval (fine stippling) nuclei. Adapted from McCormick (1989). Used with permission of Springer-Verlag.

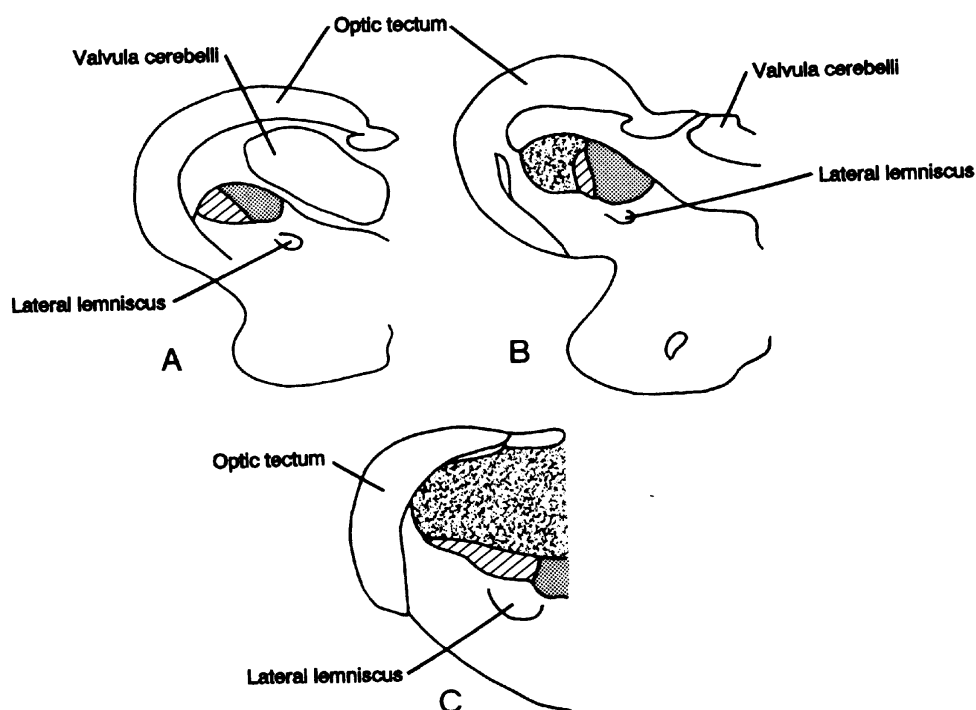


FIGURE 11-14. Drawings of transverse hemisections through the brainstem in three ostariophysan fishes: (A) *Cyprinus*, (B) *Ictalurus*, and (C) *Eigenmannia*. The areas of termination of ascending projections in the torus semicircularis are shown for electrosensory (random stippling, as in Figs. 11-12 and 11-13), mechanosensory (diagonal lines), and octaval (fine stippling) pathways. Adapted from McCormick (1989). Used with permission of Springer-Verlag.

prises at least four nuclei, the **anterior, magnocellular, descending, and posterior nuclei** (Fig. 11-12). Auditory input that is relayed through the octaval column to more rostral levels is primarily routed through the dorsal parts of the anterior and descending nuclei. Auditory input is relayed to the roof of the midbrain—the torus semicircularis in most anamniotes and the lateral mesencephalic nucleus or complex in cartilaginous fishes. The fibers ascend via the lateral lemniscus in a primarily contralateral pathway, as do the lateral line projections (Fig. 11-14). Just as a spatial map is maintained in the lateral line system, a tonotopic representation is maintained in the auditory pathway. In bony fishes, an auditory pathway from the midbrain to the dorsal thalamus, and thence to the telencephalon, has been traced. Auditory responses have been recorded in the telencephalon of sharks, although the anatomy of the ascending pathway remains to be studied.

In amphibians, two patterns of octaval nuclei in the medulla exist. One of these patterns is seen in nonanuran amphibians, in which an octaval column is present ventral to the lateral line sensory zone. This column can be divided into three nuclei that correspond to the anterior, magnocellular, and descending nuclei of fishes. The dorsal parts of these nuclei primarily receive auditory input, while the ventral parts primarily receive vestibular input.

The second pattern is present in anurans. In most adult anurans, the mechanosensory lateral line system is absent, and two columns in receipt of octaval input are present. The dorsal column contains one nucleus, the **dorsolateral nucleus**, which receives auditory input. The ventral column contains up

to four nuclei: the **anterior, lateral octaval, medial vestibular, and caudal nuclei**. Auditory inputs are primarily confined to the dorsal parts of these nuclei and vestibular inputs to their ventral parts. The dorsolateral nucleus is the main nucleus for relay of auditory information to more rostral parts of the brain. The most prominent rostral projection is via the lateral lemniscus directly to the torus semicircularis and thence, via the dorsal thalamus, to the telencephalon. Pathways that relay auditory information to the torus semicircularis through secondary medullary nuclei, particularly a nucleus called the **superior olivary nucleus**, are also present.

In nonmammalian amniotes, the cochlear nerve terminates primarily in two medullary nuclei, a laterally lying **nucleus angularis** and a medially lying **nucleus magnocellularis**. Nucleus magnocellularis projects bilaterally to **nucleus laminaris** (Fig. 11-15), which is a third nucleus that lies between the two cochlear receptive nuclei. Nuclei angularis and laminaris give rise to bilateral pathways that project directly to the roof of the midbrain and also indirectly to it via relays through other brainstem nuclei, including the **superior olivary nucleus** and a nucleus embedded within the lateral lemniscal fibers, called the **nucleus of the lateral lemniscus**. In all amniotes, the auditory part of the roof of the midbrain projects, via the dorsal thalamus, to the telencephalon.

In the ancestral stock of mammals, bony elements of the jaw were incorporated into the middle ear, which allowed for the conduction of higher frequency sounds to the oval window and the auditory receptive neural apparatus, the cochlea. This change is correlated with the presence of additional, phylo-

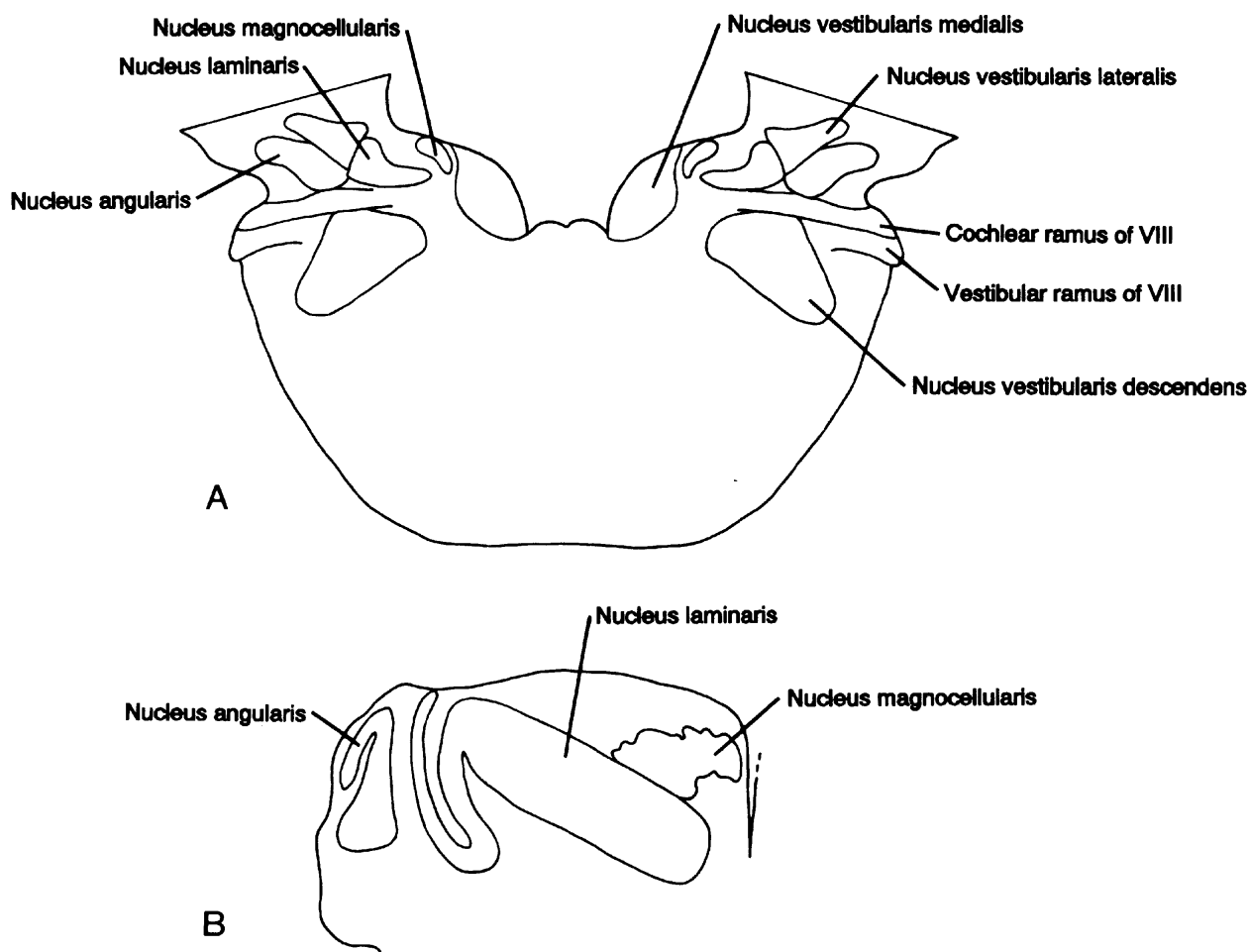


FIGURE 11-15. (A) Drawing of a transverse section through the brainstem of a bird (*Columba livia*) showing the position of octaval nuclei. Adapted from Karten and Hodós (1967). Used with permission of the Johns Hopkins University Press. (B) Drawing of a horizontal hemisection through the auditory nuclei in the brainstem of a barn owl (*Tyto alba*). Adapted from Carr and Boudreau (1991).

genetically new nuclei in the auditory brainstem of mammals. A number of the major nuclei present in mammals, however, are thought to be homologous to auditory nuclei in nonmammalian amniotes.

Of the cochlear nuclei present in mammals, the **anteroventral cochlear nucleus** appears to be homologous to the nucleus magnocellularis of nonmammalian amniotes, while the **posteroventral** and **dorsal cochlear nuclei** appear to be homologous as a field to nucleus angularis. The **medial superior olive** in mammals appears to be homologous to nucleus laminaris of nonmammalian amniotes, while the mammalian **lateral superior olive** is the homologue of the superior olivary nucleus of nonmammals. Ascending pathways, directly and indirectly to the midbrain roof, and thence via the dorsal thalamus to the telencephalon, similar to the ascending auditory pathways in nonmammalian amniotes, are present in mammals.

The vestibular nerve is relatively conservative among tetrapods, terminating in vestibular nuclei that lie in the same region of the medulla as the auditory nuclei. Two vestibular nuclei, a **superior** and a **lateral**, have been reported in anurans, with a possibility of two additional nuclei. In reptiles, four nuclei have been described: **dorsolateral**, **ventrolateral**, **ventromedial**, and **descending**. The most complex organization of

the vestibular nuclei has been found in birds, which have six: **descending**, **medial**, **rostral**, **tangential**, **dorsolateral**, and **ventrolateral**. In mammals, **superior**, **lateral**, **medial**, and **inferior vestibular nuclei** have been identified. The vestibular nuclei project to the cerebellum, some of the other motor cranial nerve nuclei, and the spinal cord. They also give rise to ascending projections to a region related to the somatosensory part of the dorsal thalamus.

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