INTEGRATION
Nervous and Sensory Systems

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The most refined methods of anatomical analysis cannot reveal the things that are of greatest significance for understanding the nervous system. Our primary interest is in the behavior of the living body, and we study brains because these organs are the chief instruments which regulate behavior.

Herrick 1948:5

Introduction

The nervous system, consisting of the brain and its cranial nerves and the spinal cord and its nerves (fig. 6.1), underlies all vertebrate behaviors. Vertebrates detect environmental cues filtered through their various senses and send these signals centrally via peripheral nerves. This information is processed by either relatively simple spinal reflexes or more complex brain circuitry, and commands are sent back through peripheral nerves to drive muscles and glands in some presumably adaptive manner. An adaptation is defined here as a feature that contributes to the survival of an individual or to the survival of its offspring (Liem and Wake 1985).

For most anurans, the tadpole neural circuitry is remodeled abruptly at metamorphosis. Sensory systems, muscle groups, and glands are reworked during the transition from aquatic, essentially limbless, swimming larvae to, in most cases terrestrial, quadrupedal, saltatory adults. During this remarkable transition, the nervous system must shift its ability to process and integrate the information received and the systems being affected between two very different types of organisms. This transition means that in addition to the usual and important questions of neural structure and function, the tadpole nervous system requires a further level of analysis; unlike that of most other vertebrates, the nervous system of the aquatic tadpole must be considered within the context of its rapid metamorphosis into the nervous system of a terrestrial frog. In this light, three questions concerning the neurobiology of tadpoles are addressed. (1) What portion of a tadpole's nervous system reflects what a tadpole actually uses? (2) Which systems must be reworked at metamorphosis? (3) What tadpole neural tissues are developed for later use by the adult? Also, interspecific variations in the behavior and ecology of tadpoles reflected in their neuronal organization and function must be considered.

The general neurobiology of anuran tadpoles is less well known than that of either anuran embryos or adults. For example, Spemann discovered the mesodermic induction of ectoderm to neuroectoderm in anuran embryos (Hamburger 1988). Adult anurans were used in the discoveries of the workings of the neuromuscular junction (Birks et al. 1960) and the rules underlying neuronal specificity within the visual system (e.g., Constantin-Paton et al. 1983; Reh et al. 1983; R. W. Sperry 1963). An excellent review of the neurobiology of amphibians, including adult structures, is provided by Wilczynski (1992). More recently, studies of tadpoles have provided an understanding of the growth of the cerebellum (e.g., Hauser et al. 1986a, b, and Uray
1985), the formation of and variation in the spinal cord (K. Nishikawa and Wassersug 1988, 1989; Nordlander 1984, 1986), and sexual differences within the nervous system (Gorlick and Kelley 1987).

The information contained in this chapter largely results from research on species of Rana and Xenopus with most other information based on species of Bufo and Hyla. The details of the organization of higher brain centers are known only for adults and are presented as a starting point for understanding the brain of tadpoles. To avoid the pitfalls of generalizing about “the tadpole,” I point out known phylogenetic and ecological variations. I introduce the nervous system and the organization of the tadpole brain and then examine the organization and function of the spinal cord and brain, discuss the various sensory systems used by tadpoles, and summarize the organization of the tadpole nervous system with a brief consideration of the changes that it undergoes during metamorphosis.

An Overview

The nervous system can be divided into (1) peripheral (PNS) versus central (CNS) systems, with the CNS divided further into the brain and spinal cord (figs. 6.2–6.3); (2) somatic (external or voluntary) and visceral (internal or involuntary) systems; (3) sensory, integration, and motor systems; and (4) neurons and their more numerous supportive glial cells. Neural processing begins with information acquired through the sense organs. External sensory systems detect the types and intensities of energy present in the environment and translate this information into neuronal signals. Sensory systems act as filters for the reception of types of stimuli with adaptive value while presumably eliminating those that are less important. Internal sensory systems monitor the visceral environment and insure that the animal’s physiological mechanisms are operating within their limits of tolerance.

The brain, which receives sensory information and transmits motor commands either through cranial (CN) or spinal (SN) nerves (figs. 6.2–6.3), is divided into a forebrain (proencephalon), midbrain (mesencephalon), and hindbrain (rhombencephalon; fig. 6.4; also see D. Black 1917). The forebrain is divided into an anterior telecerebellum and a posterior diencephalon (fig. 6.4), which function in receiving olfactory and terminal nerve information and integrating sensory inputs and motor outputs. One region of the diencephalon, the hypothalamus, regulates hormone production and involuntary autonomic responses. The midbrain consists of a dorsal, sensory tectum and a ventral, motor tegmentum (fig. 6.4). The midbrain integrates first-order (primary) visual inputs with higher order inputs from the lateral line, auditory, and vestibular systems. The hindbrain includes the cerebellum and medulla oblongata (fig. 6.4), and the combination of the mid- and hindbrains forms the brain stem. The area receives primary inputs from all of the sensory systems except the terminal nerve and olfaction, including vision, acousticolateral, gustatory, and general sensations, and sends motor commands to the muscles and glands of the head, cervical region, and viscera. The reticular formation of the brain stem is involved with integrating sensory inputs and with overall arousal. The cerebellum mediates motor learning and coordination.

The spinal cord is both a relay center and controller of reflexive behaviors and receives sensory information from specialized touch, temperature, pain, and postural receptor organs through its dorsal nerve roots. The spinal cord either directly provides the motor output to the muscles of the trunk, tail, and developing limbs (reflex behavior; see Shiriakov and Shupliakov 1986 for the anatomy of these connections) through its ventral roots or first relays these sensations to the brain and then transmits the brain commands back to the muscles. Within the brain stem and gray matter of the spinal cord, sensory centers tend to be dorsal, autonomic
centers are lateral and intermediate, and motor centers are ventral (fig. 6.5B).

In addition to neurons, the vertebrate brain contains glial cells of three basic types: astrocytes, ependymal cells, and oligodendrocytes. Glial cells are thought to provide the skeleton of the brain, to provide nutrition to neurons, and, in some specialized cases, to guide developing neurons as they migrate to their final position. Oligodendrocytes form the myelin sheaths that encircle neuronal axons.

The autonomic nervous system regulates involuntary body functions and assures that an organism is operating within its physiological limits. The sympathetic and parasympathetic components typically act antagonistically. The sympathetic system is energy expending and considered the "fight or flight" component; it halts gut peristalsis, tightens gut sphincters, dilates pupils, and increases heart rate (Pick 1970). The parasympathetic system is energy conserving and effects the opposite results. The most structurally visible features of the autonomic nervous system are the paired sympa-

thetic trunks, each a series of ganglia that extend from anterior to posterior and parallel to the spinal cord (fig. 6.6; Taxi 1976). Sympathetic ganglia receive preganglionic fibers that travel through communicating rami from the spinal nerves (fig. 6.7; W. M. Davis and Nunnemacher 1974 and Schlosser and Roth 1995). About one quarter of the fibers in a spinal nerve are preganglionic parasympathetics (fig. 6.8; Vance et al. 1975). Preganglionic fibers enter the sympathetic trunk and may course either anteriorly or posteriorly.
through two or three ganglia prior to synapsing on postsynaptic neurons. Postsynaptic neurons leave the sympathetic trunk and follow the major arteries to visceral organs. Presynaptic neurons may also synapse distal to the sympathetic trunk in visceral plexuses (figs. 6.6–6.7). For example, the solar plexus in anurans is formed by branches emanating from sympathetic ganglia 3, 4, and 5 that supply the stomach and adjacent parts of the alimentary canal (see C. A. Brown et al. 1992). The sympathetic ganglia and nerves of all vertebrates develop from neural crest cells. Neurons of the parasympathetic system leave the central nervous system either via cranial nerves or through the sacral parasympathetic system. Parasympathetic fibers from the laryngeal ventralis branch cranial nerve CN X provide parasympathetic innervation of the smooth muscles of the lungs, heart, and stomach.

Oka et al. (1989) observed parasympathetic neurons by backfilling CNs V, VII, IX, and X branches with cobalt lysine. Parasympathetic cell bodies form an almost continuous column through the brain stem dorsal to the corresponding motor neurons of the same cranial nerves. Heathcote and Chen (1991) detailed the development of the parasympathetic cardiac ganglion in *Xenopus laevis*. The sacral parasympathetic system functions in reproduction and for this reason may not be well developed in tadpoles.

**Spinal Cord**

The spinal cord occupies the neural canal within the vertebral column and is round or oval in cross section (figs. 6.7–

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**Fig. 6.4.** Lateral (left) and dorsal (right) views of the tadpole brain.
Abbreviations: Forebrain: TEL = telencephalon and DI = diencephalon; midbrain: TEC = tectum and TBG = tegmentum; and hindbrain: CB = cerebellum and MO = medulla oblongata.

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**Fig. 6.5.** Cross sections of the brain stem. (A) The brain stem has an inside (ventricular) and outside (pial) surface, and the dorsal, verticalalar plates are separated from the ventral, horizontal basal plates by the sulcus limitans in the lateral ventricular wall. (B) Cranial nerve and brain stem functional components are arranged into four longitudinal columns. (C) The cellular organization of the brain stem. Asterisk indicates position of sulcus limitans, and dotted lines separate longitudinal columns. Abbreviations: AP = alar plate, BP = basal plate, P = pial, SA = somatic afferents (sensory), SAL = stratum albulum (major area of fiber tracts), SE = somatic efferents, SEP = stratum ependymale cells, SGR = stratum griseum (major cell body layer), SSP = stratum subependymale cells, V = ventricular, VA = visceral afferents, and VE = visceral efferents (motor).
from the cord progressively more anterior than they exit the neural canal (fig. 6.9). Nerves exit the neural canal between the vertebrae, except for SN 10 and 11 (if present), which exit via foraminae in the coccyx. The morphology of the spinal cord and spinal nerves and their relationships to tail myotomes through metamorphosis have been studied by K. Nishikawa and Wassersug (1988) for both Rana and Xenopus. Spinal nerves range from 23 to 29 pairs primitively (e.g., ascaphids and discoglossids), and reductions have occurred independently at least seven times during anuran evolution. The posterior end of the spinal cord, termed the filium terminal, in R. catesbeiana and R. pipiens (Chesler and Nicholson 1985) contains a functional neuropile supported by a large number of glial cells (H. Sasaki and Mann 1981).

Tadpoles have a ventral root in the position of SN 1 that is apparently homologous to CN XII in other vertebrates and is designated here as such. All other spinal nerves have a dorsal root with a large ganglion (M. R. Davis and Constantine-Paton 1983 and Wilheim and Coggeshall 1981) and a ventral root that fuses with the dorsal root distal to the ganglion (fig. 6.7). Peripheral to this junction, a small branch of the spinal nerve passes dorsally to innervate the skin and muscles of the dorsal trunk. The large ventral branch of each spinal nerve innervates ventral and lateral skin muscles of the trunk and tail. The ultrastructural development of ventral roots has been studied by Nordlander et al. (1981). A ramus communicans containing preganglionic

Fig. 6.6. The sympathetic trunk showing ganglia 2–10 and the coeliac (gut) plexus of an adult Rana esculenta. Ganglia 8 is split in the specimen drawn, and the ventral rami of spinal nerves 3–6 are indicated. Abbreviations: CP = coeliac plexus, Gan = ganglion, and SN = spinal nerve. Redrawn from Taxi (1976) with modifications of the original figure suggested by Dr. Taxi; reprinted by permission of Springer-Verlag and Taxi.


Variation in the morphology of the cord along its length depends on the type and number of its connections. The spinal cord, especially its white matter, is wider nearer the brain than at thoracic or posterior levels so that the cord tapers anteriorly to posteriorly (fig. 6.3). Imposed upon this tapering, the spinal cord is wider at the cervical and lumbar levels to accommodate the sensory and motor neurons that form the brachial and lumbar plexuses in the limb regions (K. Nishikawa and Wassersug 1988 and Sutherland and Nunneley 1981, Hyla and Eleutherodactylus). Lateral motor pool neurons increase in number with development of the limbs in the tadpole.

The spinal cord supplies each body segment with a pair of spinal nerves (figs. 6.7 and 6.9; K. Nishikawa and Wassersug 1988) numbered according to the vertebral level at which the pair exits. Proceeding down the cord, spinal nerves arise

Fig. 6.7. A schematic representation of the organization of the spinal cord. The left side of the illustration shows dorsal and ventral horns composed of dorsal, intermediate, and ventral gray matter; and the white matter (fiber tracts) is peripheral. The right side shows the types of spinal fibers and their locations, including the sympathetic trunk and a sympathetic plexus. Symbols (dorsal to ventral): gray dotted = somatic afferents bringing general pain, pressure, temperature, and touch sensation from cutaneous receptors as well as afferents from muscle spindles through the dorsal ramus, gray solid = afferent fibers bringing visceral feedback; black solid = preganglionic sympathetic fibers to ganglia in the sympathetic trunk and visceral plexuses; black dashed = postganglionic fibers to visceral organs to control autonomic functions; and gray dashed = somatic efferents to voluntary muscles through the ventral ramus. Redrawn from Noden and De La Hunta (1985); reprinted by permission of Williams & Wilkins Co., Noden, and De La Hunta.
Fig. 6.8. Fiber types in the anuran spinal cord. The left side of the illustration shows dorsal sensory fibers and a dendritic tree from an axial motor neuron from the right side; on the right there are three motor neurons that send axons ventrally to the periphery. The ventromedial cell represents an axial motor neuron of the medial cell group (M), and the more lateral cells represent limb motor neurons from the lateral cell group (L). The transition between white matter and gray matter is shown by a dashed line. From Székely and Csóka (1976) after Székely (1976); reprinted by permission of Springer-Verlag and Székely.

sympathetic fibers extends from each ventral branch to the sympathetic nerve trunk.

Most anuran tadpoles have more than 20 pairs of spinal nerves (K. Nishikawa and Wassersug 1989), which reduce to about 10 pairs after metamorphosis. In Rana, SNs 2 and 3 join a connecting ramus to form the brachial plexus (e.g., Oka et al. 1989). Spinal nerves 7 and 8 form the lumbar plexus, and SN 7 gives off a branch (the iliohypogastric) to muscles of the lateral and ventral body wall. Spinal nerves 7 and 8 may fuse with SNs 9 and 10. The organization of neurons into nerve trunks from SNs 8 and 9 to the glutaeus muscle in Bufo marinus adults was studied by D. R. Brown et al. (1989). The ventral branches of the spinal nerves between the brachial and lumbar plexuses give off branches to the lateral and ventral body wall musculature and to the skin. In anurans branches of SNs 9 and 10 form a plexus that innervates the bladder, cloaca, oviducts (in adult females), and lymph hearts.

Developmentally, prior to the formation of the spinal ganglia, peripheral sensation is provided by large, dorsal Rohon-Beard cells (fig. 6.10; Bixby and Spitzer 1982; Hughes 1957; Spitzer and Spitzer 1975). These cells are first present in the spinal cord at gastrulation (Lamborghini 1980), increase in numbers that peak in tadpoles, and are then reduced and eventually lost at metamorphosis (Decker 1976; Eichler and Porter 1981; Lamborghini 1987).

In the sensory spinal cord each nerve from the dorsal root courses centrally into the dorsal horn of the gray matter and divides into a medial and lateral division (e.g., Antal et al. 1980; see fig. 6.8 for general appearance of incoming sensory fibers). The lateral division consists of a small-diameter fiber that appears to terminate in the dorsal horn. The medial division consists of a large-diameter fiber that enters the dorsal funiculus and splits into ascending and descending collaterals. The ascending collateral courses cranially into the brain stem, where it continues into the stratum album (fig. 6.5C). Axons in this tract terminate in the hindbrain vestibular nuclei (spinovestibular fibers), the reticular formation (spinoreticular fibers; figs. 6.11–6.12), and in the diencephalon.

In anurans, cells from the dorsal root ganglion also project directly into the cerebellum (Székely et al. 1980). In the spinal cord these fibers ascend in the ipsilateral dorsal funiculus (Gonzalez et al. 1984; Joseph and Whitlock 1968; Van Der Linden and Ten Donkelaar 1987; Van Der Linden et al. 1988), enter the cerebellum, and synapse directly on Purkinje cells (Ebbesson 1976). In the cerebellum these dorsal spinocerebellar fibers mingle with fibers of the ventral spinocerebellar tract (a component of the ventral white matter). The anuran spinal cord differs from that of all other vertebrates except turtles (Künzle 1983) in having this direct projection from the dorsal root ganglia into the cerebellum. The function of this projection is not known.

In the ventral spinal cord, the dendrites of motor neurons

Fig. 6.9. Schematic view of the posterior spinal cords in Xenopus laevis and Rana catesbeiana tadpoles. The solid bars indicate the position of the cell bodies of motor neurons. Note that the spinal nerves (SN) exit the cord progressively more posteriorly than the position of their cell bodies and that the spinal cord extends more posteriorly in Xenopus. Redrawn from K. Nishikawa and Wassersug (1988); reprinted by permission of Wiley-Liss, a subsidiary of John Wiley & Sons, Inc., and of Nishikawa.
described the reticulospinal, rubrospinal, tectospinal, and trigeminoospinal tracts; and characterized two smaller projections, one from the posterior ventral nucleus of the midbrain and one from the interstitial nucleus of the medial longitudinal fasciculus. A. Roberts and Alford (1986) described the role of descending neurons in producing fictive swimming in *Xenopus*.

In the ventral spinal cord, the number of motor neuron cell bodies is matched to the number of muscle motor units (McLennan 1988; Prestige 1967, 1973; Rubin and Mendell 1980; D.C. Sperry and Grobstein 1983). There is a developmental overproduction of motor neurons, and cells that do not establish connections or the proper type of connections with motor units eventually die (Ferns and Lamb 1987; Hughes 1961; Kett and Pollack 1985; Lamb 1981; McLennan 1988). The result appears to be an appropriate matching of motor neuron number and size with motor unit numbers and sizes (D.C. Sperry 1987). The organization of cervical spinal cord motor nuclei differs between anurans and caudates (D.B. Wake et al. 1988).

The development of spinal motor neurons and the mechanisms these cells use to match motor unit numbers is an active area of research (e.g., Farel and Benelmann 1985, 1986; Lamb 1981; Lamb et al. 1989; McLennan 1988; D.C. Sperry and Grobstein 1983). Nordlander (1986) described the normal development of motor neurons in the tail of *Xenopus* tadpoles, and D.C. Sperry and Grobstein (1985) examined the effects of hormonal manipulation on lumbar motor neuron numbers and cell sizes in *Xenopus*. Van Mier et al. (1985) studied the development of motor neuron dendrites in first- and second-order cells within the ventral horn. C.L. Smith and Frank (1988a, b) and Van Mier and Ten Donkelaar (1988) examined the peripheral specificity of sensory connections in the developing spinal cord of *R. catesbeiana*.

**Brain**

**Hindbrain (rhombencephalon)**

The hindbrain consists of the medulla (caudal portion of the brain stem), isthmus (connection between the medulla and the midbrain), and cerebellum. The spinal cord grades into the medulla so that in gross appearance it is difficult to determine exactly where the spinal cord ends and the hindbrain begins (figs. 6.3–6.4).

The organization of the brain stem (hindbrain + midbrain) is generally the same as the spinal cord, with sensory elements located dorsally and motor elements ventrally (fig. 6.5). The vertically oriented sensory portion of the brain stem is termed the alar plate, and the horizontally oriented motor portion is termed the basal plate (fig. 6.5A). The division between these two areas is termed the sulcus limitans and is visible along the wall of the IVth ventricle (fig. 6.5A). The brain stem can be divided further into longitudinal columns that represent functional similarity (fig. 6.5B). The somatic motor column lies along the midline, somatic sensory portions lie along the lateral border, the visceral motor column is in a mediocentral position, and the visceral sensory

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Fig. 6.10. The spinal cord in a young tadpole. Abbreviations and symbols: L (no stipple) = developing interneurons, M (dark stipple) = developing motor neurons, and R-B (dorsomedial black) = Renshaw-Beard cells. The developing central canal (central open space) is delineated by germinal zones (light stipple). Developing ascending and descending fiber tracts (irregular stipple) are located laterally. Redrawn from A. Roberts and Clarke (1982); reprinted by permission of The Royal Society of London and Roberts.
Fig. 6.11. A series of transverse sections through the tadpole brain. In each section, key nuclei and tracts are shown on the left, and gross histological appearance is shown on the right. Some structures may be located slightly anterior or posterior to the sections shown. Abbreviations: APL = lateral portion of the amygdala, APM = medial portion of the amygdala, CB = cerebellum, DP = dorsal pallium, DS = dorsal striatum, FLM = medial longitudinal fasciculus, HD = dorsal habenula, HV = ventral habenula, HY = hypothalamus, IL = lateral lemniscus, I Line = terminal area for primary lateral line afferents, LPD = lateral dorsal pallium, LPV = lateral ventral pallium, LS = lateral septum, M = Mauthner cell, MP = medial pallium, MS = medial septum, nuc CB = nucleus of the cerebellum, OC = optic chiasm of CN II, POA = preoptic area, PM = profundus mesencephali, RF = reticular formation, SPC = spino-cerebellar tract, ST = solitary tract, TBS = tectobulbar and tectospinal tract, TE = tectum, TO = torus, VS = ventral striatum, VTN = ventral thalamic nucleus, III = nucleus of CN III, VI = nucleus of CN VI, Vm = motor nucleus of CN V, VIII = terminal area for auditory and vestibular primary afferents, IXm = motor nucleus for CN IX, and Xmx = motor nucleus for CN X. Redrawn from Nieuwenhuys and Opdam (1976); reprinted by permission of Springer-Verlag and Nieuwenhuys.
column is lateroventral (fig. 6.5B). This guide can be used to determine the approximate locations of first- and second-order nuclei and their tracts (Nikundiwe and Nieuwenhuys 1983 and Opdam et al. 1976).

Histologically, four laminae within the brain stem are superimposed upon these organizational columns (fig. 6.5C). A medial lamina of cells termed the ependymal layer lines the fourth ventricle (figs. 6.5A, C). These small cells send a single neurite covered with numerous short appendages radially into more lateral laminae. Laterally adjacent to the ependymal layer, the subependymal layer is completely free of cells but contains the radial neurites of the ependymal cells in the brain stem. The stratum griseum contains the majority of the cell bodies. These cell bodies can be either large or small with large cells frequently grouped into clusters. The stratum albumen is the most peripheral and is a continuation of the peripheral fiber tracts of the spinal cord. Axons within the stratum albumen send collaterals or terminal axons into the stratum griseum. The stratum albumen also contains the terminations of ependymal cells and some cell groups embedded within the fiber layers. Among amphibians, the brain stem of anurans is considered to be more differentiated than that of caudates. Nikundiwe and Nieuwenhuys (1983) used cell staining techniques to characterize the nuclei of the brain stem in *Xenopus*, and these authors describe seven primary efferent (motor) nuclei, 13 primary afferent (sensory) nuclei, 7 reticular formation nuclei, and 15 "relay" nuclei (see Opdam et al. 1976 for an interpretation of the brain stem organization in *Rana*).

The brain stem receives or sends fibers from all of the cranial nerves except CN 0 (= terminal nerve) and CN I (= olfactory nerve) which project into the telencephalon. In the brain stem the division between the mid- and hindbrain occurs posterior to the level of CN IV (figs. 6.3). The somatic sensory column (SA, somatic afferents; fig. 6.5B; see longitudinal organization above) is located dorsolaterally and receives inputs from—proceeding back to front—the posterior division of the lateral line nerve (nPLL), CN VIII, the anterior division of the lateral line nerve (nALL), and the sensory component of CN V (fig. 6.12). Within the acoustico-vestibulo-lateral line complex, the vestibular nucleus is most ventral, the two acoustic nuclei are central, and the lateral line nucleus is dorsal. The nuclei for the general and special visceral afferents (VA; fig. 6.5B) are located within the midlateral brain stem and consist of components of CNs V, VII, IX, and X. In general, these nuclei contain diffuse assemblages of cells and are not easily recognized (Nikundiwe and Nieuwenhuys 1983; Opdam et al. 1976). The nuclei for the general and special visceral efferents (VE; fig. 6.5B) occupy the medioventral brain stem. The general visceral efferent is the parasympathetic innervation (carried by CNs III, IV, IX, and X). The special visceral efferent component consists of the neurons projecting to muscles derived from branchiomeres (carried by CNs V, VII, IX, X, and XI). These visceral motor nuclei form a continuous column through the brain stem (Ebbesson 1976; Nikundiwe and Nieuwenhuys 1983; Oka et al. 1989; Opdam et al. 1976). The most medial brain stem column contains the somatomotor cell bodies (SE, somatic efferents; fig. 6.5B) that innervate the tongue (CN XII) and the extraocular eye muscles (CNs III, IV, and VI; fig. 6.12). Stussie et al. (1983) reported that the hypoglossal nerve (CN XII) in *Rana pipiens* contains a dorsomedial and a ventrolateral subnucleus.

The reticular formation is located in the ventromedial portion of the brain stem (fig. 6.11G) and, although not shown completely here, projects from the midbrain through the hindbrain and into the cervical spinal cord. Its cells and fibers are diffuse. The reticular formation receives collaterals.
from brain stem nuclei and tracts involved in reflex arcs. The superior olive (fig. 6.12) is located within the basal plate and receives neurons from the dorsal octaval nucleus (CN VIII; Fuller and Ebbesson 1973) and the midbrain tegmentum (Wilczynski and Northcutt 1977). The olive sends fibers to the midbrain torus semicircularis (Nikundiwe and Nieuwenhuys 1983 and Opdam et al. 1976). The nucleus isthmi (fig. 6.12) may be involved in processing binocular inputs in adults and in tadpoles with overlapping visual fields. Most tadpoles do not have binocular vision and the function of this nucleus in tadpoles with lateral eyes is not clear. The nucleus isthmi is reciprocally connected to the midbrain tectum (Groahstein and Comer 1983; Udin et al. 1992; Wilczynski and Northcutt 1977).

Among fiber tracts the medial longitudinal fasciculus (figs. 6.11E, F, G) is a phylogenetically old feature of the vertebrate brain stem. This tract contains reticulospinal, vestibulomesencephalic, and vestibulospinal axons and mediates the vestibulo-ocular reflex. The lateral Lemniscus (fig. 6.11F) carries second-order auditory and lateral line nerves from their primary nuclei to the midbrain torus semicircularis. (Wilczynski 1988; Will 1988). Senn (1972) detailed the development of these and other brain stem structures in *Rana temporaria*.

Mauthner neurons (fig. 6.11G) are the largest axons in the brain stem and appear to initiate the startle response of tadpoles, although other cells may also contribute (R. K. K. Lee and Eaton 1989). Mauthner neuron connections have been described in *Bombina, Bufo terrestris, Hyla cinerea*, *Kaloula pulchra*, *Polyplectodes leucospalax*, *Rana esculenta*, *Scaphiphis boltroviski*, and *Xenopus laevis* (Will 1986). Mauthner cell dendrites are contacted by fibers from the CNs VIII and V, lateral line neurons, and midbrain neurons (Cioni et al. 1989; Will 1986). The spinal motor neurons that receive input from the Mauthner cells in larval amphibians are the earliest to develop (Blight 1978; Nordlander et al. 1985). Stefanelli (1951) reported that Mauthner cell degeneration is related to tail resorption at metamorphosis even in species with aquatic adults, while Moulton et al. (1968) and Will (1986) revealed the persistence of Mauthner cells in adult anurans.

The sensory and motor connections of CN XII (fig. 6.11H; Stuesse et al. 1983) of *Rana pipiens* originate from two nuclei located medially and laterally within the cauda medulla. Motor fibers from the medial nucleus project to the extrinsic tongue muscles in adults. Motor fibers from the lateral hypoglossal nucleus innervate the sternohyoid muscle. Sensory fibers arise mainly from the tongue, and in the brain stem, they travel posteriorly in the dorsolateral fiber tract to thoracic levels. The development of these motor and sensory connections in tadpoles probably depends on the extent of tongue development.

The central projections of the CN IX–X complex (fig. 6.12) were mapped by Stuesse et al. (1984; adult *Rana catesbeiana*) and Simpson et al. (1986; adult *Xenopus laevis*). Motor fibers of CN IX arise in the brain stem from a small ventrolateral nucleus, and those of CN X originate from a slightly more posterior nucleus (Stuesse et al. 1984). Afferents from CNs IX and X enter the dorsal roots of the respective nerves and descend in two tracts, either the solitary tract (fig. 6.12) or the spinal tract of CN V and the dorsolateral tract of the spinal cord. In *Xenopus*, CNs IX and X fibers are within the three roots of the IX-X complex and within the nPLL (Simpson et al. 1986). The most anterior of these IX-X roots (root 1) contains sensory fibers that terminate in the solitary tract and on lateral line efferents. Root 2 contains somatosensory fibers that terminate in the posterior medulla and anterior spinal cord and motor fibers from CNs IX and X. Root 3 contains motor fibers to the laryngeal muscles and efferents to the viscera. The results of these studies confirmed the same general conclusions of Rubinson and Friedman (1977) on *Rana catesbeiana*, *R. pipiens*, and *Xenopus muelleri*.

Lateral line, acoustic, and vestibular afferents terminate in different areas of the somatic sensory column (figs. 6.11–6.12; Fritzsch 1988; McCormick 1988; Will 1988; Will and Fritzsch 1988). Herrick (1948) and Larsell (1934) proposed that lateral line target neurons receive auditory fibers at metamorphosis. Fritzsch et al. (1984) and Jacoby and Rubinson (1983) did not support this hypothesis based on modern tract-tracing techniques. Lateral line fibers project into an intermediate nucleus, while auditory fibers project to a distinct nucleus located more laterally and ventrally (Fritzsch et al. 1984). According to Altman and Dawes (1983), some anterior fibers in the posterior division of the CN LL (nPLL) may be cutaneous afferents that project to the spinal cord in a manner similar to that of CN V. Within the lateral line system, second-order neurons project to the contralateral midbrain torus semicircularis (figs. 6.11–6.12) via the lateral lemniscus (fig. 6.11F).

Efferent neurons (not shown) project from the brain stem back to receptors and prevent hair cells from firing. These fibers originate from a CN VIII nucleus located ventrally and medially within the medulla (Fritzsch 1981a; Russell 1976). Primary afferents from the amphibian and basilar papilla (fig. 6.13, see auditory system) project into one or two nuclei at the dorsolateral edge of the alar plate (figs. 6.11–6.12; Altman and Dawes 1983; Fritzsch et al. 1988; b; Jacoby and Rubinson 1982). Rubinson and Skiles (1975) suggested that primary auditory afferents also project directly to the superior olivary nucleus. Second-order projections from the primary auditory nucleus project to the superior olivary nucleus (Rubinson and Skiles 1975) and the midbrain torus semicircularis (fig. 6.12; Nikundiwe and Nieuwenhuys 1983; Opdam et al. 1976; *Rana*; Wilczynski 1988).

Sensory fibers from neurons innervating the semicircular canals, utricle, saccule, and lagena project into the medullary vestibular complex (fig. 6.13). Sensory vestibular fibers also project directly into the cerebellum (Altman and Dawes 1983). Efferents from the brain stem to the vestibular end organs arise from the same nucleus as lateral line efferents, and single efferent neurons may send axons to both the lateral line and vestibular systems (Clas et al. 1981). Based on second-order projections, the vestibular complex can be divided into anterior and posterior divisions (not shown). In *Rana*...
pippens the anterior portion projects to the nuclei of CNs III, IV, and VI and contributes to the vestibulo-ocular reflex; posterior efferents form the vestibulospinal pathway (Montgomery 1988).

The trigeminal nerve is composed of a motor nucleus that innervates the muscles of mastication (fig. 6.12), a midbrain (mesencephalic) sensory nucleus that mediates masticatory forces, a principle sensory nucleus, and a spinal sensory tract that is an anterior continuation of the spinal dorsolateral column (Nikundiwe and Nieuwenhuys 1983, Xenopus; Opdam et al. 1976, Rana). These last two trigeminal nuclei mediate somatosensation from the head.

The mesencephalic and motor trigeminal nuclei are involved in a reflex arc. Resistance to jaw closure in both tadpoles and adults is relayed through receptors to cells in the mesencephalic trigeminal nucleus (see Kollros and McMurray 1956 for cellular details of this nucleus) that project to motor trigeminal neurons and prevent further jaw closure. S. Lewis and Straaznicky (1979) examined the development of these neurons. Motor trigeminal cells formed embryonically are responsible for buccal movements in both the tadpole and the adult. Alley and Barnes (1983) and Barnes and Alley (1983) found that the same cells that innervate the tadpole muscles innervate the adult muscles, despite the facts that adult muscles first arise at metamorphosis and that the tadpole and adult muscle groups subserve different feeding behaviors. These authors indicated that trigeminal motor neurons are recycled and respecified during metamorphosis. Omerza and Alley (1992) showed that about 80% of motor axons supplying adult muscle fibers originate from tadpole neuromuscular junctions.

Cerebellum

The cerebellum is perhaps the easiest neuronal structure to recognize because of its location (figs. 6.11F—6.12), highly regular cellular organization, and stereotyped inputs. The cerebellar cortex is composed of an external molecular layer, a thin layer of large Purkinje cells, and an internal granular cell layer (e.g., Herrick 1948; Larssel 1967; Sotelo 1976; Székely et al. 1980). Deep to the cortex, cerebellar nuclei (fig. 6.11F) serve as relay centers for afferent and efferent cerebellar fibers (Gonzalez et al. 1984; Montgomery 1988). The cerebellum receives inputs from the spinal cord, vestibular nuclei, lateral line system, and other hindbrain nuclei (Grover and Grüsser-Cornehls 1984; Larssel 1925; Sotelo 1976). Neurons in the dorsal root ganglia of the cervical and lumbar regions project directly to the cerebellum (Joseph and Whitlock 1968; Székely et al. 1980). These fibers terminate in a somatotopic pattern. A second type of spinocerebellar projection, arising from secondary cells in the spinal cord, is present in both dorsal and ventral spinocerebellar tracts (Van Der Linden et al. 1988) and terminates as mossy fibers in the cerebellar granular cell layer. Climbing fibers originate in the medulla at the location of the inferior olive. Efferents from the cerebellar nuclei project to the contralateral cerebellar nucleus and to the spinal cord. Cerebellar efferents also project bilaterally to the basal plate of the medulla and to the midbrain (Montgomery 1988).

The cerebellum functions in motor learning and coordination (Freeman 1965) and in anurans consists of the corpus, paired auricles, and a nodulus. The cerebellum does not fully mature until metamorphosis (e.g., Gona et al. 1982; Kollros 1981). The appearance of the corpus cerebellum in tadpoles is associated with the development of the tail musculature and the spinocerebellar tracts. The cerebellum auricles, which may receive and process lateral line inputs, are more fully developed in tadpoles than adults (Larssel 1967). The protracted development of the anuran cerebellum has made this structure a useful model for researchers interested in pattern formation within the nervous system (e.g., Hauser et al. 1986a, b; Uray 1985; Uray and Gona 1979, 1982; Uray et al. 1987, 1988).

Midbrain (mesencephalon)

The midbrain is the anterior continuation of the brain stem and is divided into a ventral tegmentum, which continues the ventral motor columns, and the dorsal tectum, which continues as the medullary sensory columns (figs. 6.4 and 6.11). The terminal nuclei include CNs III and IV and nucleus ruber (fig. 6.12; Nikundiwe and Nieuwenhuys 1983). The nuclei of CNs III and IV (along with the hindbrain CN VI and perhaps CN V) send motor fibers to the extraocular muscles (Straka and Dieringer 1991). In the tegmentum these nuclei are located dorsomedially. Cranial nerve III emerges from the brain stem ventrally, and CN IV emerges dorsally. Both nuclei receive vestibular fibers from the medullary vestibular nucleus. The torus semicircularis receives second-order lateral line (Plassman 1980; Will et al. 1985) and second- and third-order auditory inputs (Feng and Lin 1991; Potter 1965), which it processes and sends to the tectum. The torus semicircularis also receives ascending inputs from the spinal cord (Ebbesson 1976), reticular formation, hypothalamus (Neary and Wilczynski 1977), and reciprocal
connections from the contralateral torus (Nikundiwe and Nieuwenhuys 1983; review by Northcutt 1980). The nucleus ruber forms reciprocal connections with the cerebellum (Larson-Prior and Crute 1992).

Three additional tegmental nuclei have been identified. The nucleus profundus (fig. 6.12) receives fibers from the superior olive (Rubinson and Skiles 1975), but its function is unknown. The optic nucleus receives bilateral connections projecting from each retina (Levine 1980). The mesencephalic nucleus of CN V contains large sensory neurons that mediate masticatory forces. More cells occur in the trigeminal mesencephalic nucleus of tadpoles than in adults and during metamorphosis a large number of these cells die (Kollros 1984, *Rana pipiens*; Kollros and Thiese 1985, *Xenopus laevis*). The midbrain tectum is located dorsal to the tegmentum (figs. 6.4 and 6.11E) and receives first-order inputs from retinal ganglion cells and third-order inputs from the lateral line and auditory systems (Ebbesson 1970; Keating and Gaze 1970; Lowe 1986). The tectum integrates sensory inputs with motor commands (Elephantid 1988a, b, lateral line system, *X. laevis*). Tectal inputs were considered by Wilczynski and Northcutt (1977), and Lowe (1987) showed that single cells within the tectum respond to both lateral line and visual inputs. Vestibular and auditory signals also reach the midbrain tectum. Auditory and lateral line information terminates in the torus semicircularis before being relayed to the tectum (Feng and Lin 1991; Pettigrew 1981; Wilczynski 1981). The torus is homologous with the mammalian inferior colliculus, and the tectum is a homolog of the superior colliculus.

The tectum is the best-studied structure in the anuran brain. Retinal ganglion cell axons of tadpoles project to the contralateral tectum in an ordered fashion, an arrangement that facilitates the study of neuronal connections (e.g., Constantine-Paton and Capranica 1976; Dubs and Constantine-Paton 1990; Reh et al. 1983). The formation of order within the nervous system is itself an important question. Recent papers on this subject involving anurans include Constantine-Paton (1987), Constantine-Paton et al. (1983), Fujisawa (1987), Grobstein et al. (1980); Levine (1980), Montgomery and Fite (1989), Reh et al. (1983), and Straznicky and Tay (1982). Details of the salamander tectum in the context of visual behavior were presented by G. Roth (1987), and Lázár et al. (1991) demonstrated differences in the pattern of tectal lamination between *Rana esculenta* and *Xenopus laevis*. Anterior tectal projections in the tectothalamic tract and the postoptic commissure (Lázár et al. 1983; Vesselinov et al. 1971) will be considered with the forebrain. Posterior tectal efferents project to the nucleus isthmi (fig. 6.12) and in turn connect bilaterally back to the tectum (Grobstein and Comer 1983; Gruberg and Udin 1978; Udin and Fisher 1985). Other posterior tectal projections include tectobulbar (bulb refers to the medulla) and tectospinal fibers which may be responsible for generating or transmitting motor commands (Lázár et al. 1983). The pretectal nucleus lentiformis (not shown) receives contralateral retinal inputs as well as inputs from the tectum and tegmentum in *Rana pipiens* (Montgomery et al. 1985). Montgomery et al. (1982) examined the mesencephalic nuclei responsible for the optokinetic response in *R. pipiens* adults.

**Forebrain**

The telencephalon and diencephalon (fig. 6.4) integrate sensory inputs and initiate motor outputs. The telencephalon appears to integrate sensory information beyond that found in the thalamic nuclei (Ebbeson 1980; Northcutt 1981). The telencephalon receives anterior inputs from the olfactory bulbs (CN I) and terminal nerve (CN 0) and posterior inputs from the visual, auditory, and somatosensory systems by way of thalamic (diencephalic) relays (Klifert 1979; Northcutt 1974; Wilczynski and Northcutt 1983a). The diencephalon includes the epithalamus, consisting of the habenula and the pineal gland; the hypothalamus, which controls homeostasis and drives such as hunger and thirst (fig. 6.11); and the thalamus, which functions primarily as a relay nucleus. Stensouër (1987) described the effects of forebrain ablations on the behavior of tadpoles.

The terminal nerve (CN 0), of unknown function in anurans, is associated with the olfactory nerve (Herrick 1909; Hofmann and Meyer 1989; also Szabo et al. 1990). Hofmann and Meyer (1989) reported that the terminal nerve in *Bufo marinus* and *Xenopus laevis* projects to the forebrain medial septum, preoptic nucleus, and the hypothalamus. The olfactory bulbs (CN I) located distal to the anterior telencephalon are connected to the brain via olfactory tracts. The targets of these tracts are the main olfactory bulb and the accessory olfactory bulb (fig. 6.14; Scalia et al. 1991a, b). The main olfactory bulb, accessory olfactory bulb, and the anterior olfactory nucleus are interconnected ipsilaterally. The main olfactory bulb and anterior olfactory nucleus project to the contralateral medial wall of the telencephalon. Ipsilateral main olfactory bulb fibers also terminate near the origin of the brain stem medial longitudinal fasciculus. The accessory olfactory bulb projects to the lateral cortex of the contralateral telencephalon via the lateral forebrain bundle. The amygdala, a nucleus associated with the olfactory system (fig. 6.14), projects to two nuclei within the ipsilateral hypothalamus and a nucleus posterior to the ipsilateral nucleus isthmi (fig. 6.12; Kemali and Guglielmotti 1977). Scalia et al. (1991a, b) provided detailed descriptions of the main and accessory olfactory bulb projections in *Rana pipiens*. Ji and Holley (1992) described the olfactory bulb outputs in *R. ridibunda*, and Burd (1992) and Byrd and Burd (1991) described olfactory development in *Xenopus laevis*.

The posterior telencephalon is divided into four areas around each lateral ventricle (figs. 6.11 and 6.14). The dorsal part of the posterior telencephalon is divided into medial and lateral pallial areas. The septal area lies ventral to the medial pallium, and the striatal area lies ventral to the lateral pallium and lateral to the septum. The amygdala lies in the posterior striatum. The septum and striatum are synaptic stations where olfactory fibers join with fibers from the diencephalic thalamus and the midbrain. The telencephalon connects with posterior brain areas through the medial and lateral forebrain bundles (fig. 6.14). The medial forebrain bundle contains ascending and descending connections that
bers include inputs from the ipsilateral amygdala, the ventral thalamus, and adjacent preoptic areas. The striatum projects through the lateral forebrain bundle most heavily to the contralateral anterior endopeduncular nucleus, ventral thalamus, and preoptic area (Wilczynski and Northcutt 1983b).

Neary and Northcutt (1983) recognized two habenular nuclei within the epithalamus, two hypothalamic regions (preoptic area and infundibulum), three thalamic regions (dorsal, ventral, and tuberculum), and a transitional pretectal area in the diencephalon of adult *Rana catesbeiana*. The epithalamic habenula (fig. 6.11D, E) connects to the septum, hippocampus, hypothalamus, and thalamus (Kemali 1974; Kemali and Guglielmotti 1977) and is proportionally larger in animals with a well-developed forebrain. M. J. Morgan et al. (1973) described the left-right asymmetry in the habenulae of adult *R. temporaria*. The habenula plus the interpeduncular nucleus form the inner ring of the limbic system, which may be the highest correlate of the anuran brain. Herrick (1948) suggested that this structure controls feeding.

The epithalamus also contains the pineal organ (epiphysis), which has a small projection (best developed in anurans within amphibians) to the dorsomedial surface of the epithalamus (fig. 6.15). These fibers contain the frontal and pineal tracts (parietal nerve) and enter the pretectal region in the posterior part of the epithalamus. In the lateral and ventral walls of the diencephalon, the thalamus forms a web of connecting fibers with all contiguous parts of the brain and serves as an important center for sensory correlation. For example, the optic nerves primarily project to the optic lobes of the midbrain, but along their course collaterals fibers are given off to the thalamus (Fite et al. 1977) where they synapse with fibers from other sensory systems (Neary and Northcutt 1983). J. C. Hall and Feng (1987) considered the anatomy and physiology of the thalamic auditory region in adult *Rana pipiens* and presented evidence for parallel circuits.

Posteroventrally within the diencephalon, the bilobate hypothalamus (fig. 6.11E) is divided into preoptic and tuberoinfundibular regions. The preoptic nucleus is connected to the ventral thalamus and the ventral lobe of the hypophysis (pituitary). Neurons within the preoptic area and ventral hypothalamus respond to conspecific mating calls (Allison 1992, *Hyla cinerea*). The tuberoinfundibular nucleus is connected to the hypophyseal portal vessels. The general functions of the hypothalamus include activating the brain stem reticular formation; controlling the autonomic nervous system, metabolism, and pituitary gland; correlating gustatory, visceral, and olfactory inputs; and regulating feeding rates and water balance (Saraz and Netsky 1981).

The hypothalamus and pre-optic area receive fibers from most regions of the forebrain, but telencephalic olfactory inputs and medullary gustatory inputs appear to predominate. Efferent fibers project to motor centers, the brain stem reticular formation, thalamus, forebrain, and olfactory limbic centers. The hypothalamus does not receive fibers from the major somatosensory pathways. In nonmammalian vertebrates, fibers of the optic tract that terminate directly in the

join septal olfactory and limbic centers with the midbrain tegmentum and diencephalic preoptic and hypothalamic regions. Specific connections here include descending fibers from the septum that project to the ventral thalamus, preoptic area, and anterior hypothalamus. The lateral forebrain bundle connects the striatum with the posterior brain and contains afferents from thalamic nuclei, which in turn receive inputs from the midbrain torus and tectum (Wilczynski and Northcutt 1983a). Other lateral forebrain bundle fi-

![Diagram of brain regions](image-url)
preoptic area and hypothalamus may mediate color changes in the skin. The specific connections of the preoptic area of the hypothalamus (Neary and Northcutt 1983; fig. 6.14) that project to the pituitary are associated with the medial forebrain bundle, medial pallium, lateral amygdala, and infundibulum; see Fire (1985) for data on the pretectal area. The lateral forebrain bundle is the main afferent pathway for visual signals into the forebrain (Klitscher and Northcutt 1975). Information about the visual world, especially moving objects and changes in general illumination, is processed by telencephalic neurons.

The pituitary gland lacks neurons and is composed of glial astrocytes and pituitocytes (Gerschenfeld et al. 1960). Within the pituitary, the neurohypophysis is located ventral to the hypothalamus and connected to it via a fiber tract called the infundibulum, and the adenohypophysis is located in a diverticulum in the roof of the mouth.

**Sensory Systems**

The sensory capabilities of generalized tadpoles include: audition and vestibular functions, mechanoreception through the lateral line system, olfaction, taste, vision, and miscellaneous senses (e.g., photodetection through the pineal complex and somatosensation—pain and postural sensation, temperature, and touch). For each system, the material will be presented in the sequence: receptor structure and function, peripheral innervation, first-order connections within the brain or spinal cord, development, and patterns of phylogenetic and ecological variation.

**Auditory System.**

The anatomy, development, evolution, and physiology of the anuran auditory system have been well studied (e.g., Fritzsch et al. 1988a; Villy 1890; Wever 1985). The role of audition in spacing, courtship, and isolating mechanisms contributing to speciation is well known for adults (Fritzsch et al. 1988a; McCormick 1988; Ryan 1986, 1988; J. J. Schwartz and Wells 1983). It is important to realize that the mode of transfer of pressure waves (sounds) to the inner ear (Jaslow et al. 1988) is different in tadpoles than in adults. In adults, sound impinges on the tympanic membrane where pressure differentials are transformed into mechanical movements. The middle ear transmits these vibrations to the inner ear via (fig. 6.13) the plectrum (attaches to the tympanum), columella (the connecting bone), and operculum (links columella to the oval window, which in turn connects to the inner ear). In some anurans the columella has been lost (Truel 1973, 1979). Motions of the oval window create movements of the perilymphatic fluid that generate movements of the endolymphatic fluid. The endolymphatic fluid stimulates the hair cells of the sensory neuroepithelia and the basilar and amphibian papillae.

Tadpoles hear despite lacking middle ear bones and a tympanum. Sound pressures are transmitted to the inner ear via a bronchial columella, which grows from the round window (a connection between the middle and inner ears) toward the ipsilateral bronchus and lung at about the time of opercular closure (Witschi 1949, 1956). In the process of growing, the columella pierces the dorsal aorta (see Boatwright-Horowitz and Simmons 1997). According to Capranica (1976) and Witschi (1949), this unusual arrangement may isolate the columella from other tissues and permit it a greater degree of movement. The columella attaches to the lung and bronchus, which vibrate in response to changes in water pressure.

The inner ear of tadpoles and adults contains two auditory receptive areas, the amphibian papilla and basilar papilla (fig. 6.13; E. R. Lewis and Lombard 1988). Amphibians are unique in this regard because most other vertebrates have one auditory receptive area epithelium (e.g., saccula in fish, basilar papilla in reptiles, and cochlea in birds and mammals; Wever 1973). The surface morphology of the amphibian papilla of *Rana catesbeiana* is described by E. R. Lewis (1976) and R. Lewis and Lombard (1988). The basilar and amphibian papillae are tuned to different frequencies which tend to be specialized to an animal's acoustic environment. The number of hair cell receptors within these papillae varies interspecifically and with size intraspecifically. Typically, large animals have large papillae that contain numerous hair cells.
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(Capranica 1976). The basilar papilla is the generalized auditory organ. Its hair cells receive only afferent innervation and respond to frequencies above 500 Hz. The amphibian papilla is sensitive to both low- and high-frequency stimuli.

During metamorphosis of *Bufo regularis*, the walls of the dorsal aorta, the bronchial columnella is resorbed, and the oval window, operculum, and tympanic columnella form. At metamorphosis the cartilage for the plectrum is visible and the tympanic membrane is visible as a crescent-shaped structure (Capranica 1976).

Auditory fibers from the basilar and amphibian papillae travel in CN VIII (acousticovestibular nerve) and terminate in the auditory nucleus in the brain stem (Boord et al. 1970; Capranica and Moffat 1974; Larsell 1934; Matecz 1979; McCormick 1982). Acoustic fibers within CN VIII are organized by the frequency of the stimulus they carry. The auditory system in anurans has been considered in detail by Fritzsch et al. (1988a).

Shofner and Feng (1984) examined the developing basilar and amphibian papillae with both light and scanning electron microscopy and described an increase in the size of the sensory epithelium and the addition of hair cells as the animal grows. Capranica (1976), Fritzsch et al. (1988a, b), Sedra and Michael (1959), and Witschi (1949, 1956) detailed the changes in the auditory apparatus through larval development and metamorphosis in *Bufo* and *Rana*. Mudry and Capranica (1980, 1987), Mudry et al. (1977), Neary (1988), and Neary and Wilczynski (1986) described auditory pathways in the forebrain of adult *Rana*. See Fritzsch (1988) for a description of the evolution of the auditory system in anurans.

**Vestibular System**

The vestibular system consists of three orthogonally oriented semicircular canals plus a utricle, a saccule, and a lagena that function together in orientation and maintenance of body position in space (fig. 6.13; E. R. Lewis and Lombard 1988). As with the lateral line and auditory systems, the sensory mechanism is fluid (endolymphatic fluid in the vestibular system) motion across an epithelium of mechanoreceptive hair cells. The sensory epithelia of the three semicircular canals are contained in ampullary bulges within the canals, while utricular and saccular hair cells project into an otolithic membrane. The semicircular canals detect angular acceleration or rate of body turning and tilting and are oriented in orthogonal planes with respect to each other (e.g., E. R. Lewis and Lombard 1988; Precht 1976). Each of the semicircular canals emerges from the elongate utricle. The anterior vertical semicircular canal detects motion in an anterolateral-posteromedial plane, the posterior vertical canal detects motions in an anteromedial-posterolateral plane, and the horizontal canal detects horizontal movements. The anterior vertical canal of one side of the tadpole is oriented in the same plane as the contralateral posterior vertical canal. The utricle and saccule monitor linear acceleration and gravitational pull. The utricular macula is oriented horizontally and is crescent-shaped around a central structure termed the striola. The hair cells are polarized in a direction radial to the striolar curve and, taken together, are responsive to movements through 360°. Type I hair cells with long stereocilia that extend to the tip of the kinocilium are found along the striola. Type II hair cells with a long kinocilium and short stereocilia are found along the sides of the striola.

The saccular macula is oriented nearly vertically and faces posterolaterally. The striola is curved and the hair cells, considered together, are sensitive to 360°. Outside the striola, kinocilia are directed outward and inside they face inward. Most saccular hair cells resemble the utricular Type II cells. The posterior protrusion from the saccule is termed the lagena and has a ciliary pattern resembling the utricle. Afferent neurons are bipolar cells. Axons terminate in the vestibular nucleus (e.g., R. E. Dunn 1978). Hair cells also receive efferent fibers. Caston and Bricht-Berthout (1985) described connections of vestibular afferve to the horizontal semicircular canal in *Rana esculenta* and showed that the efferents both inhibit and facilitate the afferent response. These authors reported that neurons within the vestibular nucleus respond both to motion through the vestibular nerve and light pulses from the midbrain tectum. Van Bemmelen (1959) described a reflexive vestibular behavior that allows Xenopus tadpoles to maintain a stable position in the water column.

**Lateral Line System**

The lateral line system of aquatic anamniotes consists primarily of mechanoreceptive and electroreceptive end-organs (Bullock et al. 1983). Anurans retain mechanoreceptors (= neuromasts; Fritzsch 1981b) but have lost their electroreceptive subsystem. Mechanoreceptive neuromasts are sensitive to local water displacements (i.e., the large-scale movements of water molecules) rather than changes in water pressure (small local movements of water molecules that vibrate around a relatively fixed point); to which the auditory system is most sensitive. The lateral line system of tadpoles consists of three main lines each on the trunk and head (fig. 6.16A; Escher 1928; Kingsbury 1985; Lannoo 1987; Shelton 1970, 1971; M. Uchiyama et al. 1991). Tadpoles with midventral spiracles have a symmetrical arrangement of the neuromasts, but those with sinusiradial spiracles often have asymmetrical arrangements perhaps because of developmental interference caused by the spiracle (Lannoo 1987). Hair cells are the actual displacement detectors of neuromasts (fig. 6.16B; Flock 1968; Flock and Wersäll 1962; Jande 1966; I. J. Russell 1976; M. Uchiyama et al. 1990, 1991).

Hair cells contain a ciliary bundle (the “hairs”) at their external surface that consists of a single kinocilium (fig. 6.16C) located at the edge of the bundle and numerous stereocilia. This anatomical polarization corresponds to a directional sensitivity. Displacements of the cilia in the direction of the kinocilium depolarize the cell while displacements in the opposite direction hyperpolarize the cell. Depolarizations increase the rate of firing of the cell, and hyperpolarizations prevent the cell from firing (Flock 1968; review by I. J. Russell 1976). Typically, adjacent hair cells are oriented oppositely so that a stimulus that depolarizes one hair cell will...
hyperpolarize the other. Neuromasts are innervated by multiple neurons, and hair cells that are oriented similarly are innervated by fibers of the same neuron.

Neuromasts are usually elongated, and their direction of maximum sensitivity corresponds to the long axis of the oval. Sensitivity in directions other than the main axis is proportional to the cosine of the angle from the main axis (Flock 1965). Unlike other tadpoles, pipid larvae have round neuromasts; such structure makes their axis of sensitivity difficult to determine (Lannoo 1987). In contrast, aquatic pipid adults have linear neuromasts (Shelton 1970, 1971). Typically, neuromasts within a line are oriented in the same direction (fig. 6.16A; Göner 1963; Lannoo 1987; Shelton 1970). Dorsal trunk neuromasts are most sensitive to displacements in a dorsoventral direction, and middle and ventral trunk neuromasts are most sensitive to anterior-posterior displacements. On the head, supraorbital and infraorbital lines are the most sensitive in directions tangential to the margin of the eye. As these lines run onto the snout, neuromasts change orientation to become anterior-posteriorly sensitive. The angular line is most sensitive to dorsoventral displacements while the two hyoid lines combine to be sensitive to both dorsoventral and anterior-posterior displacements (Lannoo 1987).

As generalized, pond-dwelling tadpoles grow, primary neuromasts formed embryonically divide to form secondary neuromasts (fig. 6.16B; Lannoo 1987; Russell 1976). All secondary neuromasts derived from a single primary neuromast are aligned in the same direction as the primary neuromast and compose a receptor unit (after Zalkow 1984; previously termed steth or plaque, Lannoo 1987, 1988; I. J. Russell 1976).

Hair cells within neuromasts are innervated by bipolar primary afferent neurons whose cell bodies are located in ganglia (Shelton 1970; Van Der Horst 1984). Neuromast afferents course through branches of either the anterior (nALL, head) or posterior (nPLL, trunk) lateral line nerve. Once in the brain, all lateral line afferents bifurcate to send one collateral anteriorly and one posteriorly within the medullary nucleus medialis (Altman and Dawes 1983; Boord and Eisworth 1972; Fritzsch et al. 1984; Jacoby and Robinson 1983; Lowe and Russell 1982; Matecz and Székely 1978). Neuromasts also are innervated by efferent fibers whose cell bodies are located in the ventral medulla (Will 1982). Efferent axons course through the lateral line nerves. Single efferent cells may send axons to the lateral line, auditory, and vestibular systems (Claas et al. 1981). The efferent system appears to hyperpolarize hair cells, which prevents neuromast function and precludes overstimulation (e.g., during swimming; I. J. Russell 1976). The lateral line system may be responsible for maintaining the spacing between individuals in schools of *Bufo* tadpoles. Diminishing the sensitivity of neuromasts through exposure to streptomycin, which is toxic to hair cells, alters the orientation of individuals and the distance between tadpoles of *Xenopus laevis* (Lamm et al. 1982). In adult *Xenopus*, Elephandt (1988a, b) found that the oriented response to water displacements diminishes with the surgical ablation of neuromasts.

Neuromast receptor units vary in number of organs, number of hair cells per organ, and their position relative to the epidermal surface. These morphological features correlate well with the particular habitat of a tadpole (Lannoo 1987) and presumably are adaptive. Generalized pond tadpoles have a large number of units composed of three to five secondary neuromast organs that are positioned flush with the epidermis. In contrast, stream and arboreal tadpoles have fewer receptor units composed solely of primary neuromasts that are positioned below the epidermal surface. In general, reductions in the number of receptor units occur within lines rather than through the elimination of whole lines, although *Ascopus* tadpoles appear to have lost their oral line (Lannoo 1987). Considerable variation in neuromast features is found within the genus *Osteoglossus* (Hylidae). Older tadpoles of the bromeliad-dwelling *O. brumae* (see Thompson 1996 for information on the habitat and ecology of these tadpoles) have receptor units composed of single (primary) neuromasts, while congeneric, pond-dwelling tadpoles (O. dominiensis and *O. septentrionalis*) have receptor units containing multiple secondary neuromasts (Lannoo et al. 1987).

The lateral line system develops embryonically from pre- and postotic plaques (R. G. Harrison 1904; Lannoo and Smith 1989; S. C. Smith et al. 1988, 1990; Stone 1922, 1933; see J. F. Webb and Noden 1993). These plaques give rise to primordia that migrate in anterior and posterior directions to form the neuromast organs and their innervation (review by Lannoo and Smith 1989). Primordia from preotic plaques migrate anteriorly to form the cranial lateral
line component, and postotic primordia migrate posteriorly to form trunk and tail components. At least three precocial and three postotic placodes give rise to individual nerve branches and their ganglia (Northcutt 1989; S. C. Smith et al. 1988). Neuromasts derived from precocial placodes are innervated by branches of the nALL, while neuromasts from postotic placodes are innervated by the nPLL. Winklbauer and Hausen (1983a, b, 1985a, b) developed and tested a model for the formation of the supraorbital neuromast line in *Xenopus*. They proposed that stem cells are allocated randomly to neuromasts as they are dividing. Each stem cell divides seven times before becoming terminal; terminal cells become hair cells. Therefore, the number of hair cells per neuromast depends on the numbers of stem and terminal cells allocated per neuromast. The generality of this model to other species, and in fact to other lines of neuromasts within *Xenopus*, has not been determined.

**Olfactory System**

The olfactory system of anurans is divided into two parallel subsystems termed the primary or main olfactory system (MOS) and the secondary or accessory olfactory system (AOS). In the MOS, the olfactory afferents innervate receptors located in the sensory epithelium of the nasal capsule and terminate on target neurons in the main olfactory bulb (MOB; fig. 6.14). The ultrastructure of the olfactory bulb and its neurons is described in K. H. Andres (1970) and Burton (1985). Neurons from the MOB project into the lateral cortex of the telencephalon (Kemali and Guglielmotti 1987; Northcutt and Royce 1975; Scalia 1976; Scalia et al. 1968, 1991a, b). Neurons from the AOS afferents form the vomeronasal nerve, which innervates olfactory receptors in the sensory epithelium of the vomeronasal organ and projects to the accessory olfactory bulb (AOB; fig. 6.14). Neurons in the AOB project to the amygdaloid nucleus on the lower surface of the telencephalon (Kemali and Guglielmotti 1987; Scalia 1976). The AOS is well developed in anurans and caecilians but poorly developed in most salamanders. The degree of development of the AOS is positively correlated with the development of Jacobson’s organ, which is absent in neotenic salamanders. The amygdaloid nucleus is correspondingly well developed in anurans and caecilians, as is the striatum (see Forebrain).

The sensory epithelia of the MOS and AOS are similar to each other and to the nasal epithelium of other vertebrates (fig. 6.17). Cilia on the external surface of the olfactory epithelium originating from the olfactory neurons are interposed by an almost continuous sheet of microvilli (fig. 6.17). Below the surface of the epithelium, the olfactory neurons become grouped into olfactory file containing hundreds of unmyelinated axons that form a compact olfactory nerve (Burton 1985). The main olfactory and accessory olfactory nerves course separately into the anterior portion of the olfactory bulb where their synapses form olfactory glomeruli. Each glomerulus is a spherical group of terminals from numerous primary olfactory neurons that contacts the dendrites of mitral cells, the principle postsynaptic neurons. Each mitral cell appears to contact more than one glomerular dendrite. The axons of the mitral cells form the effluent projections of the olfactory bulbs.

The olfactory system develops from an ectodermal placode in *X. laevis* (Klein and Graziaedi 1983). Whether the

![Fig. 6.17. Developmental series (left to right) and organization of the olfactory epithelium. Note the ciliated cells separating the dark olfactory neurons. From Klein and Graziaedi (1983); reprinted by permission of Wiley-Liss, a subsidiary of John Wiley & Sons, Inc., and of Klein.](image-url)
olfactory system of pipoids, with their aquatic tadpole and adult stages, is representative of all tadpoles remains to be determined. Likewise, the embryonic differentiation of olfactory placode tissue into principal and accessory systems remains to be described, although there is likely phylogenetic and ecological variation in the olfactory system of tadpoles. There are known variations in the structure of the internal nares and associated skin folds (Wassersug 1976a). Pond, stream, and arboreal tadpoles probably are sampling fundamentally different olfactory environments and using their olfactory systems to mediate different behaviors. For example, pond tadpoles appear to recognize kin via olfaction (chap. 9).

Gustation
In adult anurans, taste buds are located on papillae or protrude only slightly from the mucosal surface and are scattered over the floor and the roof of the buccal cavity and the dorsal surface of the tongue. Taste buds in the roof and floor of the buccal cavity are nonpapillary, while those on the tongue occur on fungiform papillae. Each taste bud papillary disc, which can contain up to 700 receptor cells depending on the species, is innervated by 5–10 myelinated nerve fibers (C. B. Jaeger and Hillman 1976). Taste buds are innervated by CNs VII and IX. The facial nerve innervates the roof and floor of the buccal cavity, while the glossopharyngeal nerve innervates the tongue. To my knowledge, taste buds have not been described in tadpoles but are assumed to be present.

Visual System
The visual system of anurans is well known (Fite 1976). What is not known is the extent that tadpoles, some of which are nocturnally active, rely on visual cues. The extraocular eye muscles of tadpoles appear to be the same as those in adult frogs but less developed (Nowogrodzka-Zagóriska 1974). Adult frogs also have levator bulbi muscles innervated by CN V which lift the eyes back into position after they have assisted in pushing food into the esophagus.

Amniotes focus images on the retina by changing the shape of the lens. Amphibians and fishes focus by changing the distance between the lens and retina—proximally for far vision and distally for near vision. Because the refractive index of water and the vitreous humor are similar, tadpoles have less need for accommodation than do adults. The cornea is divided into an inner and an outer layer that fuse at metamorphosis (reviewed by Kollros 1981). The retina receives and processes light energy with two basic receptor types, three kinds of interneurons, and ganglion cells that project into the brain (figs. 6.18–6.19). The vertebrate retina has a number of features that are unusual from the perspectives of mechanical design and neural processing. First, the sensory surfaces of the photoreceptors face backward so that light must pass through the ganglion cells and their axons and the interneuron layer before reaching the receptors. Second, photoreceptors are stimulated by darkness; light hyperpolarizes and inhibits rods and cones. Third, the neurotransmitter released from the photoreceptors hyperpolarizes one bipolar cell type while depolarizing the second bipolar cell type. Fourth, photoreceptors carry and process information without generating action potentials.

Rod and cones are composed of three segments (fig. 6.18). An outer distal segment consists of a series of stacked disks containing the photoreceptor pigment (Corless and Fetter 1987 and Corless et al. 1987a, b, Rana pipiens). The inner segment contains many mitochondria, the nucleus, and ribosomes. The synaptic terminal occurs proximally and transmits the receptor signal to the interneurons, which is the first step in sending visual information to the brain. The
anuran retina contains green (sensitivity peak at 433 nm) and red rods (502 nm; fig. 6.18; Donner and Reuter 1976; J. Gordon and Hood 1976; W. R. A. Muntz 1962a, b; W. R. A. Muntz and Reuter 1966). Green rods are sensitive to violet and blue light and are known to occur only in anurans and caudates. Green rods are important in light adaptation and provide inputs that contrast with those from cones. Red rods appear important in dark adaptation. Anurans possess a dichromatic cone system of color vision. Single cones have a peak frequency sensitivity between 575 and 580 nm, and double cones are most sensitive at 502 nm (Hailman 1976). As photons excite these visual pigments they become bleached; a chemical change in the permeability of the receptor membranes affects the transmission of neural signals. In tadpoles, adult retinal pigments are preceded by their corresponding 3-dehydroretinal pigments (i.e., porphyropsin rather than rhodopsin; Donner and Reuter 1976). The developmental shift in the spectral preference in tadpoles was studied by R. G. Jaeger and Hailman (1976). Amphibians usually lack a macula, an area of high visual acuity. For a discussion of the intricate biochemistry underlying phototransduction, see Donner and Reuter (1976) and J. Gordon and Hood (1976).

Rods and cones differ in their sensitivities. In general, rods are able to detect lower light levels than cones but are poor at spatially and temporally resolving this light. This is because the large photoreceptor outer pigment is more likely to be hit by photons, but this size compromises spatial resolution. Also, rod photoreceptor pigment stacks are less polarized and therefore more sensitive to reflected light, and rods converge onto bipolar neurons. The slower response of rods to photostimulation compared with cones limits their temporal resolution. In the retina the majority of synapses occur in the inner (IPL) and outer plexiform layers (OPL; fig. 6.19). The thin IPL is where rods and cones synapse, and the thick OPL is where the amacrine, bipolar, and ganglion cells synapse (Dowling 1976; J. Gordon and Hood 1976). Rods and cones send information to the ganglion cells either directly through bipolar interneurons or indirectly via amacrine, bipolar, and horizontal interneurons. Information from the photoreceptors is sent to either on-center or off-center bipolar cells (fig. 6.19). Bipolar cells are connected by inhibitory horizontal cells. When one cell is excited it inhibits the surrounding cells of the same polarity (e.g., on-center cells inhibit surrounding on-center cells). This arrangement increases contrast and sharpens edges. Bipolar cells connect to ganglion cells directly or indirectly through amacrine cells (fig. 6.19); which mediate interactions between the on-center and off-center systems and have several other specialized functions (Donner and Reuter 1976).

Ganglion cells transmit information from the retinal cells centrally into the brain through CN II—the optic nerve and tract. The retina (technically part of the brain) in *Rana p. piaenis* contains about 450,000 ganglion cells, 5–7 times as many bipolar cells and 2–3 times as many photoreceptors. Several types of ganglion cells are classified on the basis of the types of information they carry; B. D. Frank and Hollyfield (1987a, b) described seven classes in *R. p. piaenis*. Stirling and Merrill (1987) detailed the functional morphology of a ganglion cell type that transmits the off-center response. Gaze and Grant (1992) described the patterns of retinal cell death during ontogeny of *Xenopus laevis*. The retina projects principally to the contralateral midbrain tectum, although a small ipsilateral projection that appears at metamorphosis may also exist in adults (M. Schütte and Hoskins 1993). Other retinal fibers project bilaterally to the diencephalic thalamus and pretectal visual centers (these nuclei in turn project to the tectum). The brain also sends neurons centrifugally to the retina. This small projection (30–40 neurons, *Rana*) originates from the telencephalic lamina terminalis near the olfactory nuclei (fig. 6.14) and courses through the preoptic area and into the optic tract to the retina. While the number of afferent fibers in the optic tract increases during ontogeny, the number of efferents remains constant (H. Uchiyama et al. 1988).

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**Fig. 6.19.** Connections of anuran photoreceptors within the retina. Abbreviations: AC = amacrine cell, BC = bipolar cell, HC = horizontal cell, GC = ganglion cell, IPL = inner plexiform layer, off cent = off-center ganglion cell, on cent = on-center ganglion cell, and OPL = outer plexiform layer. Redrawn from Bailey and Gouras (1988). Copyright 1985 by Elsevier Science Publishing Co., Inc.; reprinted by permission of Elsevier, Bailey, and Gouras.
The literature on the visual orientation and feeding behavior of anurans has been dominated by studies on adult frogs (Ingle 1976; Maturana et al. 1960). From a phylogenetic perspective (review by Grüsser and Grüsser-Cornelius 1976), the retinas of adult anurans respond to cues from stationary objects, those of bufonids respond to cues from moving objects, and hyliids respond to intermediate stimuli. These visually guided behaviors correspond to ecological activity patterns (sit-and-wait vs. mobile predators) and result from differing proportions of retinal neuronal classes. Interestingly, the tadpoles of the species reviewed by Grüsser et al. (1976; Bufo bufo, Osteopilus septentrionalis, Rana esculenta, and R. pipiens) were all generalized pond dwellers (Orton 1944). This begs the question of whether the retinal morphology of these tadpoles reflects their common lifestyle or the more variable lifestyles of their respective adults. Retinal cell number increases with growth in tadpoles. Beach and Jacobson (1979a, b) and P. Grant et al. (1980) examined the patterns of cell proliferation in the retina of Xenopus. S. Grant and Keating (1986) studied the metamorphic and postmetamorphic maturation of the retina and the midbrain optic tectum. Dunlop and Beazley (1981) described the increasing number of ganglion cells in tadpoles through adults in Helotoperus eyrei, where a visual streak is present in adults but not tadpoles; Bork et al. (1987) described the growth of optic fibers in the retina of Xenopus, and Cullen and Webster (1979) described the metamorphic changes that occur in the myelin sheath of optic nerve axons in Xenopus.

Miscellaneous Senses

Adult frogs, and apparently tadpoles, are sensitive to pain and touch through free nerve endings in the epidermis and dermis (reviews by Catton 1976 and Spray 1976). Cutaneous nerves, among the 60–80 myelinated neurons arising from each spinal nerve, can be grouped into two functional categories: those less than 3 μm, which are also the slowest conducting fibers (0.8–5 m/s) that transmit temperature and pain impulses, and those greater than 5 μm with conduction velocities greater than 7 m/s that transmit phasic and tonic pressure information. In addition to small fibers with slow conduction velocities, pain and temperature receptors are characterized by a long latency from stimulus to discharge and by an action potential of long duration.

The pineal organ (epiphysis) is a small projection attached to the dorsomedial surface of the epithalamus (fig. 6.15) which, within amphibians, is best developed in anurans. These fibers enter the pretectal region in the posterior portion of the epithalamus. The cytology of the pineal is described by Van de Kamer (1965). This organ functions in detecting features of ambient light, such as seasonal variation in photoperiod and perhaps the strength and inclination of sunlight, that mediate physiological functions such as breeding and overwintering (Bagnara 1965; Binkley et al. 1988). Locomotor activity is altered by a sudden drop in light intensity detected by the pineal organ (R. G. Foster and Roberts 1982). Hendrickson and Kelly (1971) described the development of this structure. Frogs (D. H. Taylor and Ferguson 1970) and tadpoles (Justis and Taylor 1976) can orient relative to a shoreline when allowed only pineal input.

In most anuran tadpoles and adults, the peripheral portion of the pineal organ is termed the frontal organ (= strumorgan; reviewed by Adler 1976). The skin with reduced pigmentation overlying the frontal organ is called the brow spot. Eldred et al. (1980) showed that the central projections of the frontal organ are similar to the ordinary pineal projections and are widespread, including the amygdala, pretectal region, and the central gray of the mesencephalon and diencephalon.

Muscle spindles are stretch receptors that provide information about the location and position of the limbs, trunk, and tail. Spindles are reflexively connected to motor neurons through a pathway termed the stretch reflex, which serves to maintain muscles at their functionally appropriate length (e.g., E. G. Gray 1957; reviewed in Otoson 1976; Gans and De Gueldre 1992) presented some data on the physiology of larval muscles.

Metamorphosis

The changes that occur in the nervous system of anurans during metamorphosis and the effects of thyroxine in driving these changes are summarized in Hughes (1976) and Kollos (1981). Some conclusions can be drawn about how the nervous system accommodates the tadpole and adult stages. First, the tadpole nervous system comprises features (e.g., lateral line system and posterior spinal cord) that are exclusively larval traits lost at metamorphosis. Second, the tadpole has nervous elements (e.g., limb motor neurons and the corpus of the cerebellum) that apparently are not important in tadpoles but will become functional in adults. Third, the tadpole nervous system includes cells (e.g., motor trigeminal cells) that perform one function in tadpoles and are reworked at metamorphosis to perform a new function in adults. Finally and perhaps most remarkably, a majority of the cells, especially in higher order nuclei, are not known to change during metamorphosis. These cells may function appropriately within the demands of both the tadpole and adult worlds.

The brains of tadpoles are not all alike. Variation appears to be common even within the limited number of tadpoles that have been studied. Orton's (1944) tadpole types offer a starting point for comparative neurobiologists interested in the ecological and phylogenetic bases (but see chap. 4) of neuronal variation in these animals, and the diversity described in chapter 12 provides the mileposts for such investigations. Despite enormous efforts by many researchers to provide basic information about the organization and functioning of the anuran nervous system, we are only now beginning to understand how tadpoles integrate nervous system development and differentiation, and how it is altered to fit the demands of different environments. Learning by tadpoles and how this is modified at metamorphosis is poorly studied (e.g., Munn 1940a, b; Punzo 1991; Strickler-Shaw and Taylor 1991; Youngstrom 1938).
Summary

There are two significant generalizations that can be drawn from a review of the nervous and sensory systems of anuran tadpoles. Few taxa have been examined, but there are many variations exhibited even among this small number. Future studies of a more ecologically and phylogenetically diverse assemblage will most certainly turn up other interesting patterns. The second generality arises from the profound and abrupt remodeling of the neural circuitry at metamorphosis (also chap. 5). In a life cycle that includes a profound metamorphosis from an aquatic larva to a terrestrial adult, questions about adult influences on tadpole nervous system morphology must be considered in addition to the more obvious questions of neural structure and function in tadpoles. Several conclusions can be drawn. First, tadpole nervous systems have elements (e.g., lateral line system) that typically function only in tadpoles. Second, tadpole nervous systems have other elements (e.g., limb motor neurons) that are not important to tadpoles but are important in adults. Third, other elements (e.g., trigeminal motor neurons) are re-worked at metamorphosis to perform new functions in adults. Fourth, the majority of neurons are not known to change during metamorphosis. This latter uniformity is remarkable when one considers the differences between a swimming, herbivorous tadpole and a hopping, carnivorous adult frog. Finally, the brains of tadpoles are not all alike; there is no such thing as “the tadpole brain” even within the limited number of species that have been studied. Despite enormous efforts by many researchers, we are now only beginning to understand tadpole nervous systems.

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