

## CHAPTER 3

# THE EVOLUTION OF BODY, BRAIN, BEHAVIOR, AND MIND IN JAWED FISHES

## Basic Affects and Phenomenal Awareness in Limbless Vertebrates

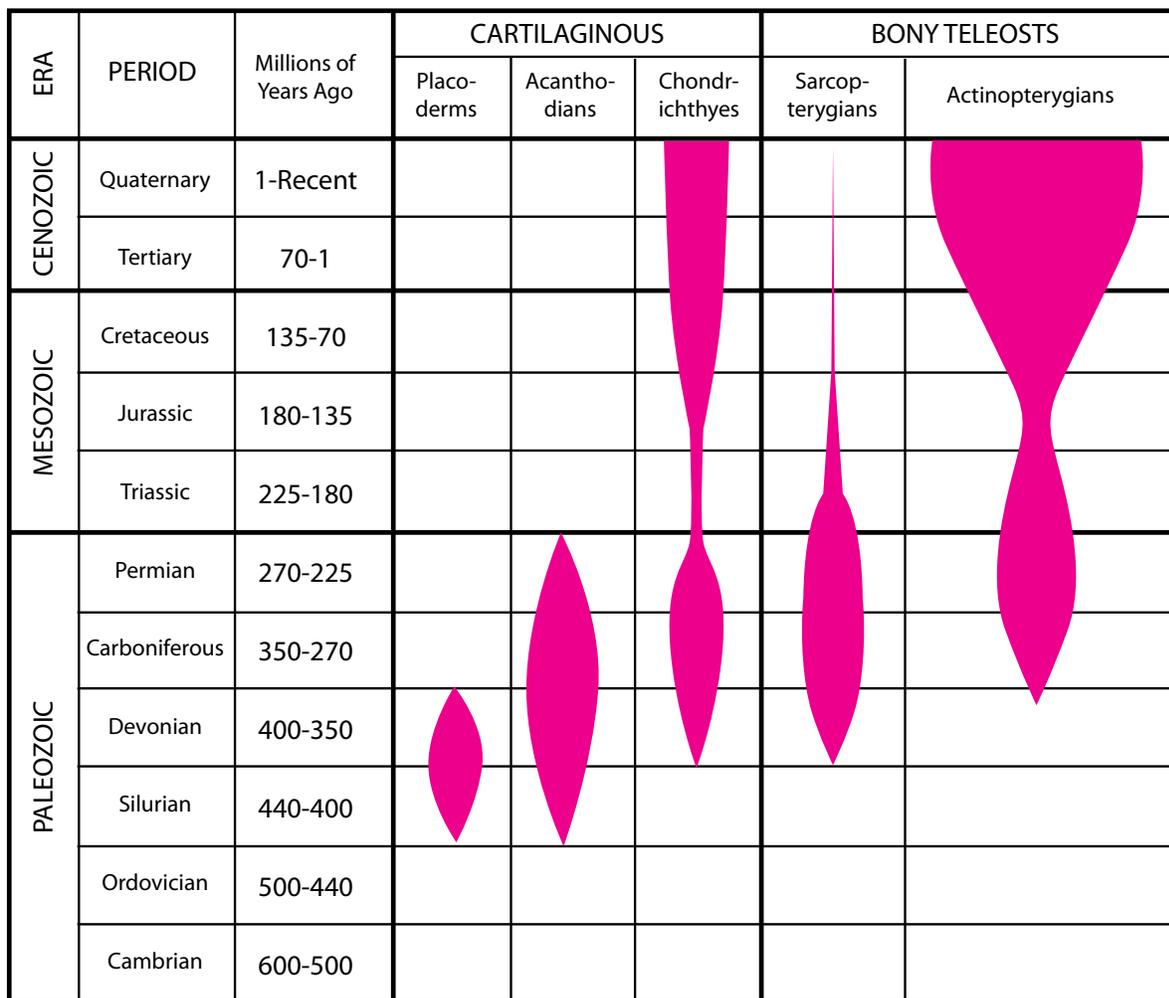
3.1	The Body, Brain and Behavior of Jawed Fishes: Our Piscine Neural Legacy .....	114
3.1.1.	Extinct and Extant Cartilaginous and Bony Fishes .....	114
3.1.2.	Somatic and Visceral Advances in Fishes .....	116
3.1.3.	Sensory Advances in Fishes .....	118
3.1.4.	Neural Advances in Fishes .....	122
3.1.5.	Piscine Contributions to the Evolution of our Head and Brain .....	136
3.1.6.	Our Piscine Neural Legacy .....	140
3.2.	Evidence for Basic Feelings and Emotions in Jawed Fishes:	
	Our Piscine Affective Legacy .....	140
3.2.1.	Do Fish have Feelings and Emotions? .....	140
3.2.2.	The Endocrinological Approach to the Study of Emotions .....	142
3.2.3.	Behavioral Studies of Emotional Expression in Fishes .....	144
3.2.4.	The Comparative Neurology of Emotions in Mammals and Fishes .....	151
3.2.5.	The Emotions of Fish and Our Piscine Affective Legacy .....	160
3.3.	Configural Perception, Memory, and Phenomenal Awareness in Fishes:	
	Our Piscine Perceptual Legacy .....	164
3.3.1.	Brain Mechanisms of Perception in Fishes .....	164
3.3.2.	Configural Perception, or Isomorphous Representation in Fishes .....	164
3.3.3.	Visual Mechanisms and Visual Perception in Fishes .....	165
3.3.4.	Phenomenal Awareness of the Visual World in Fishes .....	167
3.3.5.	Learning and Recognition Memory in Fishes .....	169
3.3.6.	Recollection Memory and Imagery in Fishes .....	173
3.3.7.	Short-Term Working Imagery in Fishes .....	175
3.3.8.	Phenomenal Awareness as Our Piscine Perceptual Legacy .....	179

### 3.1. The Body, Brain and Behavior of Jawed Fishes: Our Piscine Neural Legacy

**3.1.1. Extinct and Extant Cartilaginous and Bony Fishes.** The Silurian “arms race” among aquatic vertebrates led to the marginalization of jawless fishes and the increasing dominance of the faster, more agile and behaviorally more competent jawed fishes, the Gnathostomes (Romer, 1966; Carroll, 1988). Jawed fishes include the cartilaginous Placodermi, Acanthodians, and Chondrichthyes, and the bony lobe-finned Sarcopterygians and the ray-finned Actinopterygians (Fig. 3-1).

The cartilaginous Placoderms emerged during the Silurian period, about 440 m.y.a., and became extinct by the end of the Devonian about 350 m.y.a. The Acanthodians endured through the Carboniferous and Permian, until about 225 m.y.a. The Chondrichthyes emerged during the Devonian. By the Mesozoic era, the Chondrichthyes were becoming the dominant cartilaginous fishes. The surviving Chondrichthyes (Elasmobranchs) include about 440 species of sharks,

#### EVOLUTION OF JAWED FISHES (GNATHOSTOMES)



**Fig. 3-1.** The evolutionary history of extinct and surviving cartilaginous and bony fishes.

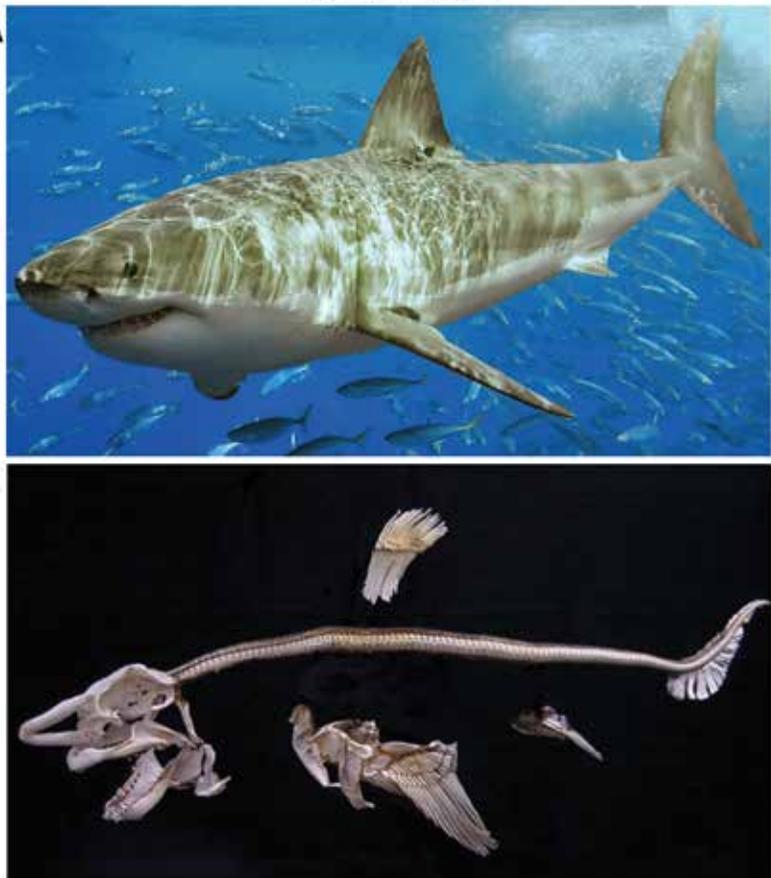
and several species of rays and skates. The bony, lobe-finned Sarcopterygians emerged about 400 m.y.a., flourished until the end of the Permian and, with the exception of Coelacanth and lungfishes, became extinct during the Mesozoic. The Sarcopterygians are considered ancestral to land vertebrates. Of the extant 25,000 species of bony fishes (teleosts), the great majority are ray-finned Actinopterygians. They began to evolve during the Carboniferous and became diversified and abundant since the Cretaceous period, about 145 m.y.a. They occupy all niches of the aquatic world, and range in size from miniscule to very large. The jawed Gnathostomes—the cartilaginous Chondrichthyes and bony Actinopterygians, had many advantages over the jawless Agnathans. The replacement of the notochord by an articulated cartilaginous or calcified vertebral column provides them with a strong and flexible girder to support a powerful trunk with hinged appendages; their powerful tail and fins aid them to swim fast and maneuver with great agility; their movable head with a strong jaw and teeth allows them to feed on whatever their habitat provides.

**EXTANT SHARKS.** Mature sharks of different species range in size from less than 20 cm (the dwarf lantern shark) up to 12 meters (the white shark; Fig. 3-2A). Some species feed on plankton, but most of them are carnivorous. The head of sharks contains paired laterally placed eyes, nostrils, and ear openings, and a series of canals that contain receptors sensitive to electromagnetism. All of them have a streamlined muscular body with articulated, cartilaginous vertebrae, but without a rib cage (Fig. 3-2B). Their body is covered with dermal denticles that reduce drag while swimming. They have well-developed dorsal and lateral fins, attached internally to the skeleton by connective tissue. Sharks can swim swiftly and make use, in various combinations, of their moveable head, undulating body and flapping tail to maneuver with great agility when attacking or fleeing. Some sharks have single or multiple rows of sharp teeth that are periodically shed and replaced. Some of them, like the great white shark, are powerful predators that will attack and kill seals and dolphins.

**A**

**B**

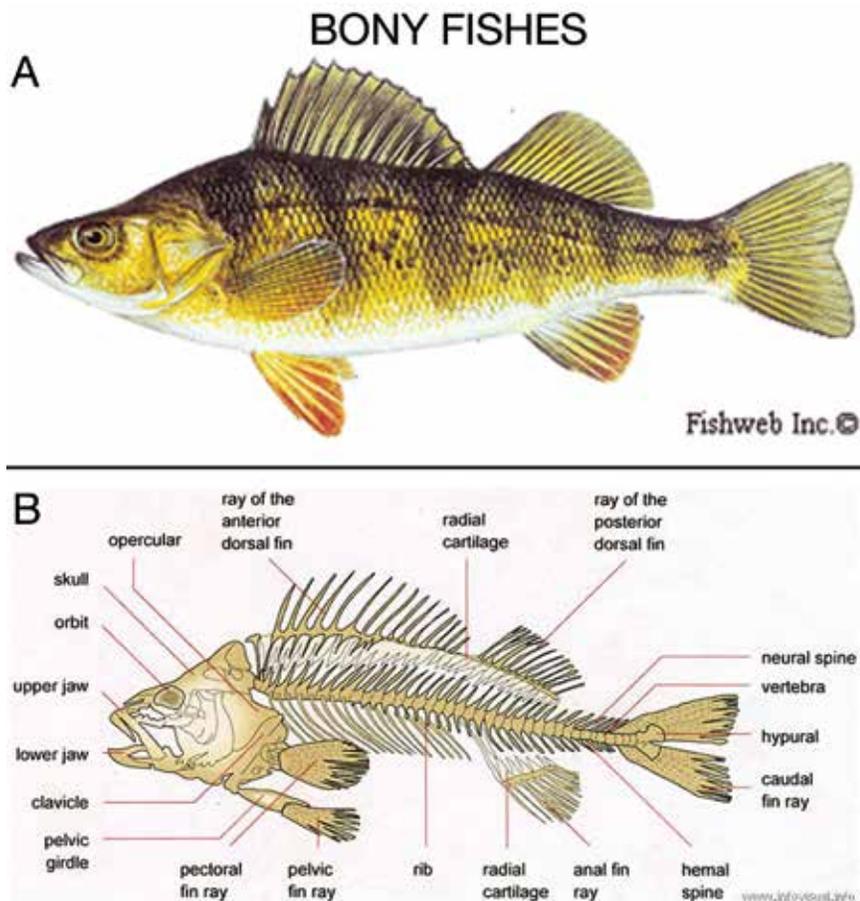
## SHARKS



**Fig. 3-2.** A. Swimming white shark. B. Cartilaginous skeleton of a shark. Note the lack of a rib cage (A. Modified, from whiteshark.jpg. B. From Canadian Shark Research Laboratory.)

**EXTANT TELEOSTS.** Most teleosts have a streamlined, muscular body (Fig. 3-3A) encasing a skeletal system consisting of a bony vertebral column and a rib cage that supports a variable number of fins with bony rays (Fig. 3-3B). The multitude of extant species of bony fishes are adapted to a great variety of aquatic habitats, exploiting different resources. Some bony fish live in brooks, lakes, swamps, and rivers, others in littorals, the open seas and oceans. A few live under rocks or in caves. There are bottom feeders that live off detritus, grazers that feed on the flora of coastal areas, and predators that cruise widely in search of prey. Some teleosts are small and timid that flee upon the least disturbance, others are large, powerful, and ferocious. Fish that live in murky or deep waters, where there is little light, rely mostly on smell and touch to locate nutrients, whereas surface-feeders that inhabit clear waters depend more on vision. Different species of fish use body undulation, tail flapping, and their oscillating fins to different extent and in different combinations to hover or cruise slowly while foraging, to dart swiftly and with agility to capture prey or avoid predators, and maintain their postural balance during these maneuvers (Rosenberger, 2001). Accordingly, there is considerable variability among fishes with regard to their sensory systems, neural organization, and behavior.

**3.1.2. Somatic and Visceral Advances in Fishes.** The evolution of the vertebral column represents a monumental advance in cartilaginous and bony fishes because that made possible



**Fig. 3-3.** A. A perch. B. Bony skeleton of a teleost. (A. Modified, from JPEG image. B. Modified, from infovisual.jpg.)

their growth in bulk relative to invertebrates, particularly those with an external skeleton that have to be shed to allow growth. Possession of a large body with powerful muscles is a progressive evolutionary trait because it benefits both the species and the individual. Large-bodied species, by virtue of their bulk, can displace smaller ones, and larger individuals can dominate smaller ones to occupy the best habitats, exploit the richest resources, and gain advantage in access to and selection of mates. Moreover, a large body can sustain a large brain, which lends the individual improved behavioral control. Growing a large body and sustaining its metabolic needs, of course, is challenging. It requires (i) a long, vulnerable period of growth and maturation; (ii) procurement of nutrients in large quantities; (iii) an efficient mechanism for the extraction of sufficient oxygen from water or air to supply increased need; and (iv) an efficient internal transport system to deliver the absorbed oxygen and the digested nutrients to distant tissues and cells.

**EVOLUTION OF THE PISCINE RESPIRATORY AND CIRCULATORY SYSTEMS.** Fishes primarily use their gills for respiration, extracting oxygen from the water, although some also get oxygen from the air and have lung-like organs. They also evolved an adequate circulatory system that is lacking in chordates. Moreover, the adoption of an active life style, exerted evolutionary pressure on fishes to separate in their circulatory system the fresh, oxygen-rich blood pool from the spent, oxygen-poor blood pool, and generate sufficient blood pressure (Burggren et al., 1997). Amphioxus lack a pumping heart, while tunicates have a simple tubular organ, composed of a single layer of striated muscle cells that propels blood by peristalsis (Randall and Davie, 1980; Withers, 1992). Pacemakers are located at the two ends of this tube and blood flow is reversed every minute or so, carrying alternately oxygenated blood from the gills to the viscera (visceral flow) and spent blood back to the gills (branchial flow) through a complex system of sinus channels (Anderson, 1986). This blood shuttling mechanism evolved in lampreys into a true circulatory system with a heart (hagfishes have several “heartlets”). However, the heart of agnathans is still primitive relative to teleosts, both in terms of cellular composition and anatomical organization (Davie et al., 1987; Burggren et al., 1997). The lamprey heart is composed of a sponge-like tissue formed by interlocking muscle bundles, called spongiosa. In teleosts, the ventricular spongiosa is encased in another myocardial tissue, the compacta. The compacta is supplied by its own blood vessels, the coronary circulation, and can develop much higher blood pressure than does the spongiosa. (In reptiles, birds and mammals, as an evolutionary advance, most of the heart is composed of compacta.)

When a fish swims, oxygen-saturated water enters through its open mouth and moves past the vascularized gill arches; at rest, a fish may suck water into its pharynx and pump it (Webster and Webster, 1974). When the oxygen content of the water is low, some fish use auxiliary mechanisms, such as cutaneous respiration, swallowing air, or breathing air with a primitive lung-like organ, the way lungfishes (*Dipnoi*) do. Air breathing, either as a supplement to water breathing or as the principal mechanism for gas exchange, has repeatedly evolved in several lines of fishes (Burggren et al., 1997). Lungfishes have pulmonary veins that directly connect their primitive lung with the heart; they also have their heart modified for improved separation of oxygenated and spent blood. However, the teleost heart has only two chambers, a single atrium and a single ventricle; therefore, the oxygen-rich blood coming from the gills and the oxygen-poor blood drained from the viscera and the brain are not efficiently

separated (Burggren et al., 1997). (Amphibians have a three-chambered heart; reptiles, birds and mammals a four-chambered heart with fully separated pulmonary circulation and systemic circulation.) Effective respiration and blood circulation was a prerequisite for the evolution of the expanding vertebrate nervous system because it is one of the body's most energy-consuming organs.

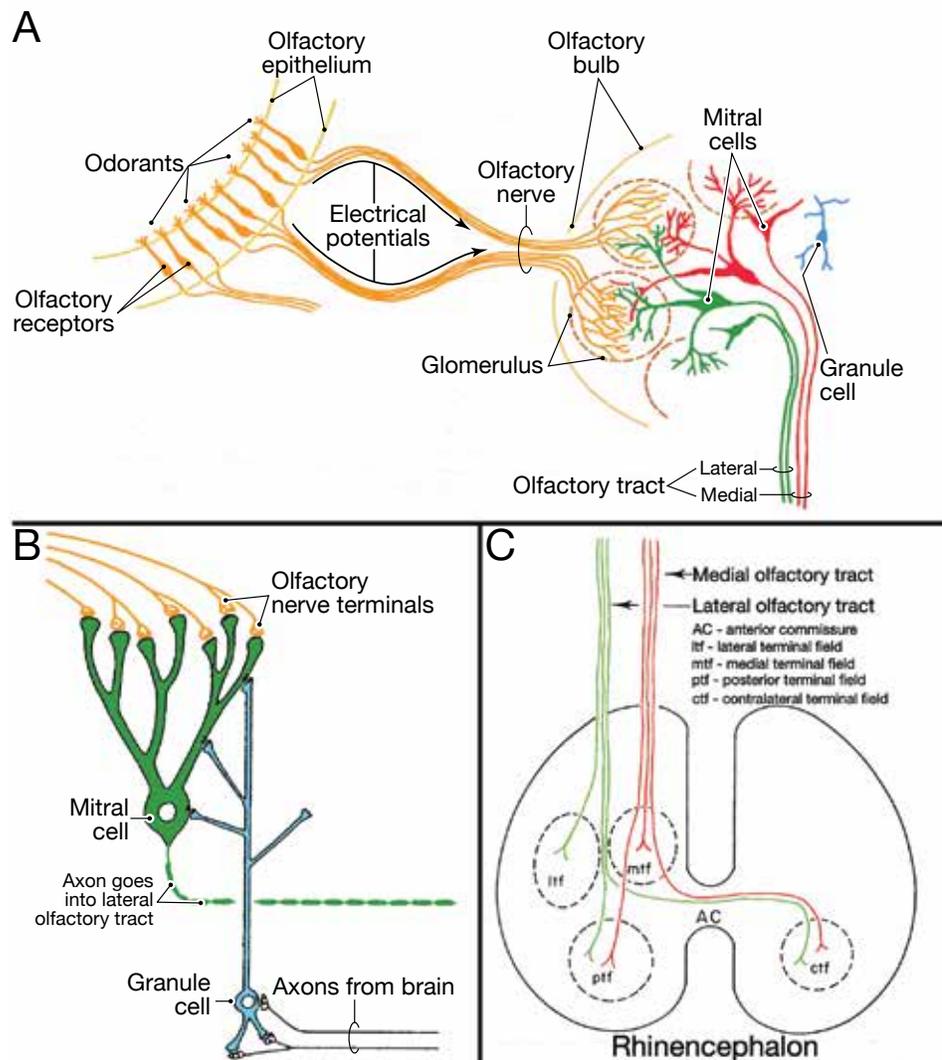
**THE EVOLUTION OF THE AUTONOMIC NERVOUS SYSTEM.** The coordination of respiration and circulation with variable metabolic needs in relation to ongoing activities is carried out in higher vertebrates by the two antagonistic components of the autonomic nervous system—the adrenergic sympathetic system promoting behavioral mobilization and the cholinergic parasympathetic system promoting regenerative functions. Amphioxus lacks an autonomic nervous system, and it is poorly developed in Agnathans, but both the sympathetic and parasympathetic systems are well developed in teleosts (Young, 1950; Pick, 1970). The teleost sympathetic nervous system is composed of a chain of peripheral nerve ganglia, roughly aligned with the individual cranial and spinal nerves. Preganglionic visceral efferent neurons originate in the brainstem and spinal cord; their axons synapse with postganglionic neurons in autonomic ganglia whose axons reach various tissues and organs—including the arteries of the head and gills anteriorly—the stomach, intestines, kidneys, swim bladder, urinary bladder, and genital organs posteriorly—and the cutaneous pigment cells (chromatophores) throughout the body periphery. (The importance of the latter in emotional expressions and communication of fish is described below). The major outflow of the parasympathetic nervous system is the vagus nerve and it plays an important role in regulating heart rate in fishes (Mott, 1957).

**3.1.3. Sensory Advances in Fishes.** In the following discussion of advances in the sensory mechanisms of fishes, our focus will be on teleosts. All teleosts have specialized sense organs that respond to chemical, mechanical, and optical stimuli and, excepting the lateral line organ that is absent in terrestrial vertebrates, their sense organs are structurally and functionally similar to those found in higher vertebrates, including humans.

**OLFACTION.** Volatile chemicals that emanate from distal sources are the stimuli that we sense subjectively as smell (olfaction), and water-soluble chemicals that contact the mouth we sense as taste (gustation). In many fishes, olfaction, mediated by nasal olfactory cells, plays an important role in the detection and localization of nutrients; gustation, mediated by oral taste buds, in the sampling, ingestion and swallowing of nutrients (Finger, 1983). Although both volatile and soluble chemicals are dispersed in water, fish can discriminate between the two. For instance, minnows trained to discriminate between odors (e.g., different musk solutions) and flavorful substances (e.g., glucose or quinine) lose their ability to make odor discriminations following removal of the olfactory bulb but continue to make gustatory discriminations (Strieck, 1924). Fish can detect three classes of odorants: amino acids (Sutterlin and Sutterlin, 1971; Suzuki and Tucker, 1971), gonadal steroids, and bile acids (Laberge and Hara, 2001). In the bottom-feeding catfish, volatile amino acids—like proline and arginine—induce barbel movements, searching and snapping (Valenticic and Caprio, 1994). The detection of steroids (and sex pheromones) is of great importance in the regulation of sexual behavior (Lastein et al., 2006; Hamdani et al., 2007). The role of bile acid sensitivity is not currently understood.

The teleost nasal cavity typically has two openings, an inlet anteriorly and an outlet posteriorly, and an epithelial cavity through which water passes as the fish swims forward. The olfactory epithelium is folded to form a variable number of lamellae, and it contains ciliated bipolar neurons and crypt cells (Fishelson, 1995; Hamdani and Døving, 2007). Each nasal cavity may contain as many as 5-10 million of these cells (Hara, 1986). The bipolar neurons have been implicated in food detection; the crypt cells in the detection of sex pheromones (Zippel et al., 1997). The external pole of ciliated bipolar neurons is the transducer mechanism stimulated by odorants, and the generated electrical potentials are transmitted to the olfactory bulb by the nerve fibers issuing at the internal pole (Fig. 3-4A). These axons gather in the olfactory *nerve* (nerve I), which has two branches that terminate in the glomeruli of the olfactory bulb and synapse there with the multipolar mitral cells (Fig. 3-4B). The mitral cell axons, in turn, form two branches of the olfactory *tract*, which terminate in the different nuclei of the olfactory brain, or rhinencephalon (Fig. 3-4C).

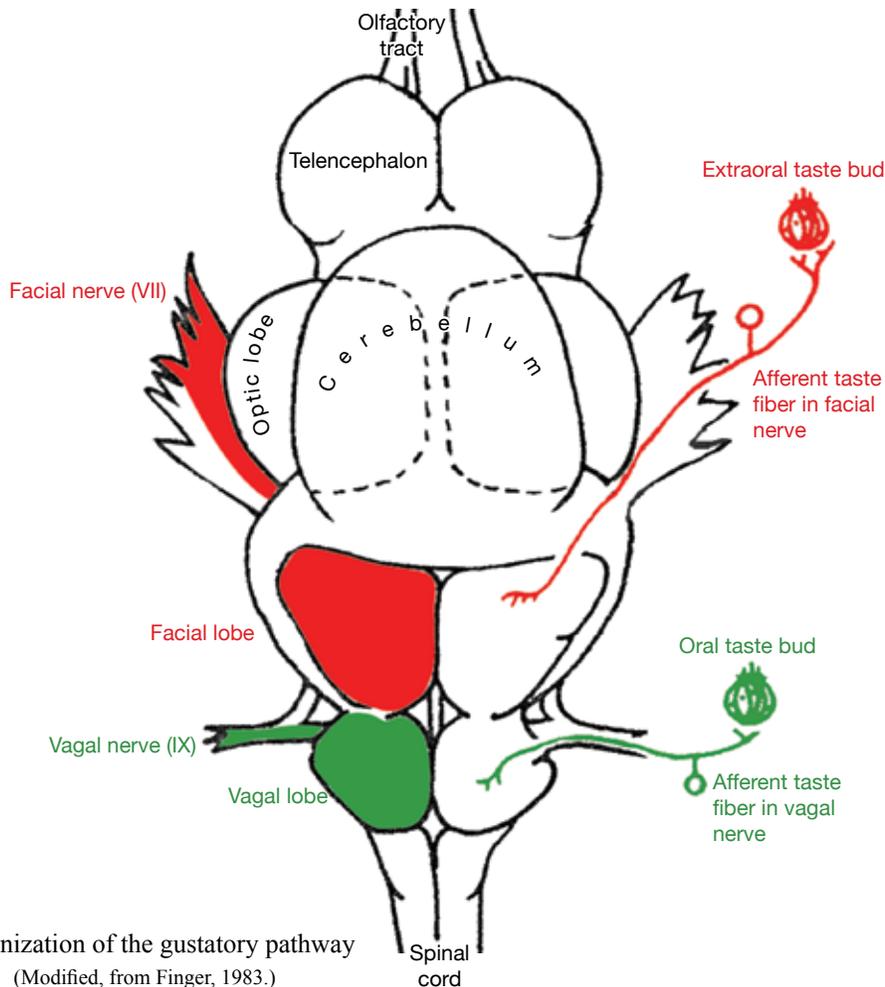
### Olfactory System of Teleosts



**Fig. 3-4.**  
**A.** Organization of the afferent pathway from the olfactory epithelium to the olfactory bulb.  
**B.** Cellular organization of the olfactory bulb.  
**C.** Nuclear organization of the rhinencephalon.  
 (A. Modified, from Evans, 1988. B. Modified, from Satou, 1990. C. Modified, from Oka et al., 1982.)

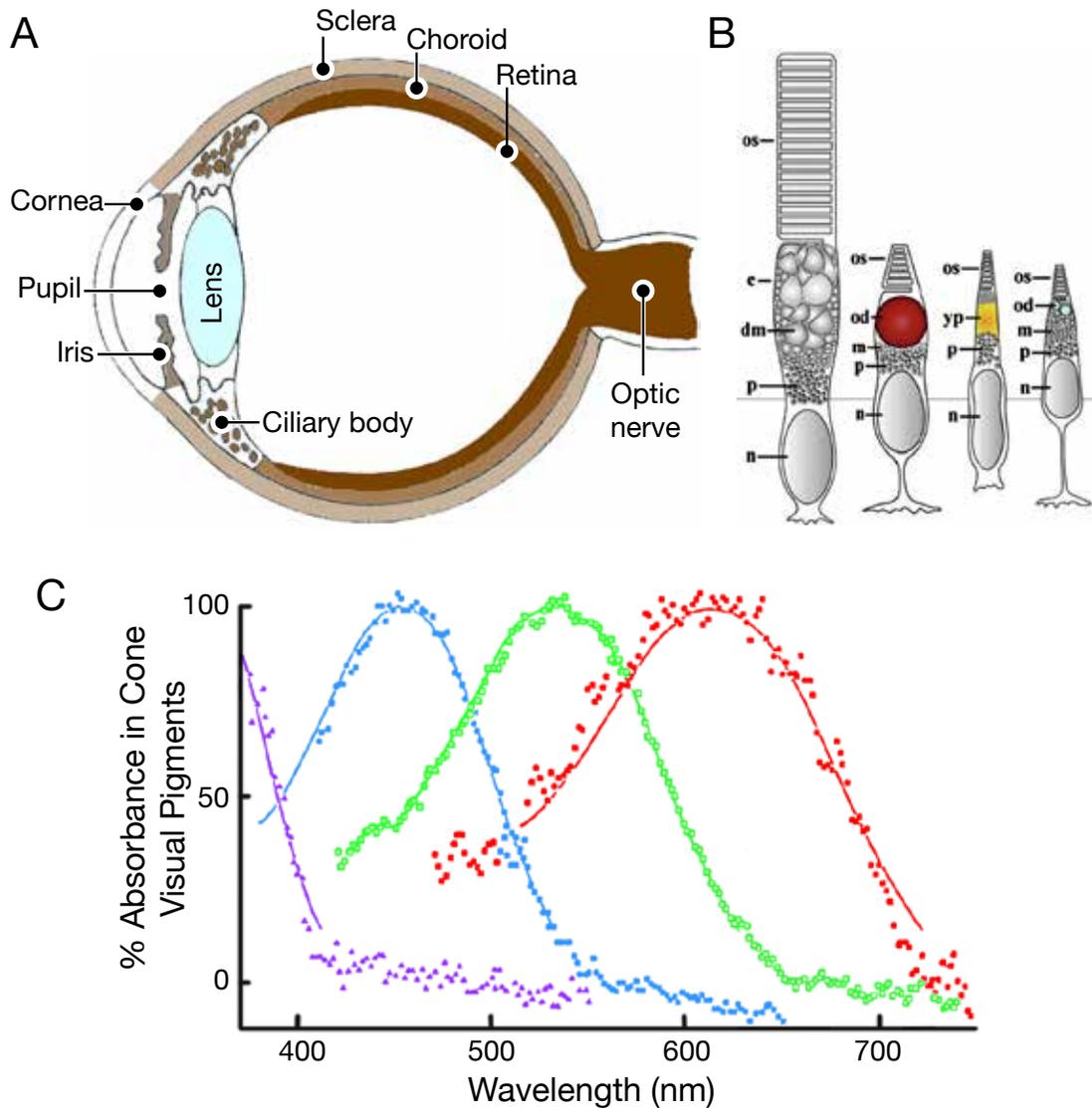
**GUSTATION.** Gustation plays an important role in food selection and swallowing in fishes (Finger, 1983). Taste buds that are morphologically similar to those found in mammals and man are present in the mouth of fish (oral taste buds) in high concentration as well as throughout the body surface (extraoral taste buds), particularly in bottom feeders (Atema, 1971; Bardach et al., 1971; Kapoor et al., 1975; Marui and Caprio, 1992; Hara, 1994; Finger, 2000). The taste buds contain dark and light cells with microvilli. The light cells synapse with nerve cell processes and are, accordingly, thought to be the sensory elements of gustation; the dark cells may be supporting elements. Gustatory information is conveyed to the CNS by fibers of the facial (VII), glossopharyngeal (IX), and vagal (X) nerves. There is some evidence that signaling the presence of nutrients by the extraoral taste buds is conveyed by the facial nerve to the facial lobe. Oral taste buds signal what should be swallowed or ejected via the vagus nerve to the vagal lobe (Fig. 3-5). We experience four basic taste qualities: sweet, bitter, salty and sour. Sweetness is the sensation elicited by dissolved carbohydrate nutrients in the water; bitterness by alkaloids that are often poisonous; saltiness reflects the sodium chloride concentration of the water; and sour taste depends on the pH of the aqueous medium. These sensations may be a piscine legacy of ours.

### GUSTATORY SYSTEM IN THE GOLDFISH



**Fig. 3-5.** Organization of the gustatory pathway in the goldfish. (Modified, from Finger, 1983.)

## FISH EYE, RETINA, AND SPECTRAL SENSITIVITY



**Fig. 3-6.** **A.** Structure of the eye in an active Brazilian freshwater fish. **B.** Four types of cones with different oil droplets in an Australian lungfish. (Abbreviations: **dm**, distended mitochondria; **e**, ellipsosome [hypertrophied mitochondria]; **m**, mitochondria; **n**, nucleus; **od**, oil droplet; **os**, outer segment; **p**, paraboloid [involved in glycogen metabolism]; **yp**, yellow pigment.) **C.** Wavelength absorbance spectrum of four cone visual pigments in the goldfish. (A. Modified, from Donatti and Fanta, 1999. B. Modified, from Bowmaker, 2008. C. Modified from Bowmaker et al., 1991.)

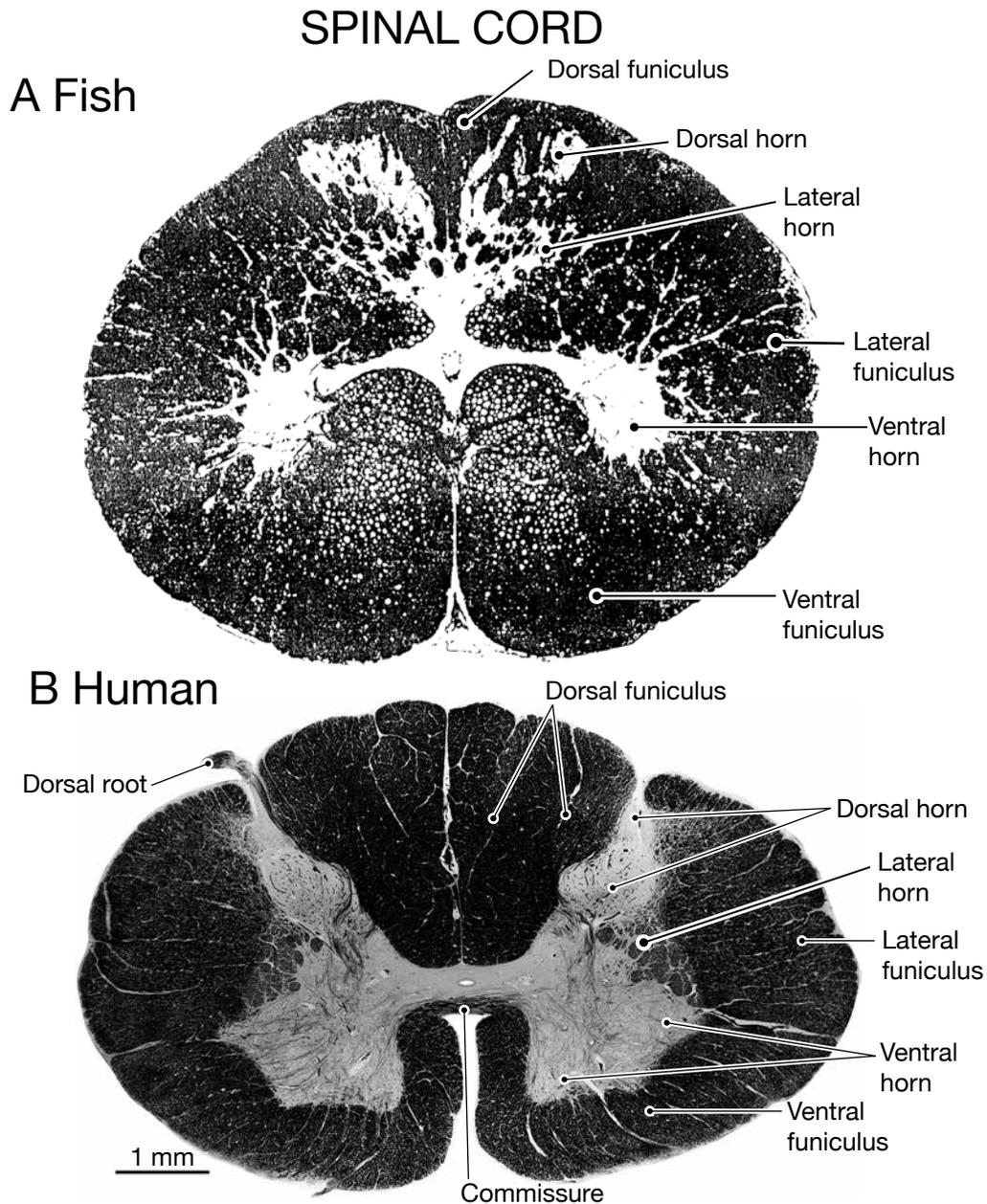
**VISION.** Most teleosts have a pair of well-developed eyes (Fig. 3-6A) with a large retinal screen that projects topographically organized images upon the paired optic lobes by way of the optic nerves. Laterally placed eyes, which provide a monocular panoramic view of the visual world, are common in fishes but some species have frontal eyes that provide binocular vision (Polyak, 1957). While in many respects the fish eye is similar to ours, there are some differences. For instance, distance accommodation is achieved by moving the lens backward or forward, as in a camera, rather than by changing the shape of the lens, and changes in pupillary size are sluggish (Guthrie, 1986).

The cellular composition and laminar organization of the fish retina is more elaborate than that found in lamprey, and similar to that of higher vertebrates (Collin and Collin, 1993; Donatti and Fanta, 1999). It consists of cell bodies of rods and cones, bipolar cells, amacrine cells and Müller cells, two layers of horizontal cells, and two types of ganglion cells. While lacking a fovea, there is an area centralis in the retina of some fish, densely packed with cones for detail vision (Levine et al., 1980). It has been estimated that, in the goldfish, about 220 thousand retinal ganglion cells send afferents to the optic tectum, which contains as many as 1-2 million processing neurons (Meek and Schellart, 1978). Species of minnows that inhabit clear water have twice as many optic nerve fibers (and hence ganglion cells) than minnows living in turbid habitats (Huber and Rylander, 1991, 1992). Naturalistic observations (Eibl-Eibesfeldt, 1970) and behavioral tests (Douglas and Hawryshyn, 1990; Kitschmann and Neumeyer, 2005) indicate that many species of fish are capable of acute color discrimination (Svaetichin, 1953; Tomita et al., 1967; Bowmaker and Kunz, 1987; Bowmaker et al., 1991; Collin et al., 1996; Hawryshyn and Hárosi, 1994; Bailes et al., 2006; Bowmaker, 2008). This is made possible by different types of cones with pigments that preferentially absorb light of different wavelength, or cones with different types of oil droplets as chromatic filters (Fig. 3-6B). Trout have pigmented cones with differential absorbance of electromagnetic wavelengths from ultraviolet, blue, green to red (Fig. 3-6C). In summary, the basic sensory mechanisms of our vision is a piscine legacy.

**HEARING.** The principal sensory mechanism in fish for the detection of mechanical stimuli in the environment is the lateral line system (Dijkgraaf, 1963; Bleckmann, 1986). Mechanical sensors embedded in this system respond to water flow, drag, vibrations, and contact with physical objects. While the lateral line system is absent in terrestrial vertebrates, its transducers, the ciliated hair cells with their 9+2 fiber organization, are similar to those found in the inner ear and vestibular apparatus of terrestrial vertebrates. The vestibular apparatus with its three canals is well developed in fish but the auditory apparatus is rudimentary. Fish lack an external ear, the middle ear ossicles, and a coiled cochlea. However, fish do respond to sound waves, and some species can localize the source of a sound with some degree of accuracy (Hawkins and Myrberg, 1983; Popper and Fay, 1993).

**3.1.4. Neural Advances in Fishes.** The central nervous system (CNS) of cartilaginous and bony fishes are archetypical of the brain organization of all vertebrates, including humans. As in higher vertebrates, so also in fish, the CNS is composed of two divisions, the spinal cord along the trunk and the brain encased in the head.

**THE SPINAL CORD.** The spinal cord has the same basic organization, with a central gray being surrounded by white matter, in fish (Fig. 3-7A) and man (Fig. 3-7B). The gray matter, which contains the cell bodies of spinal cord neurons, is clearly divisible in cartilaginous and bony fishes into three regions, the dorsal horn, the lateral horn, and the ventral horn. The dorsal horn is the target of somatosensory afferents entering the cord by way of the dorsal root, and the ventral horn is the site containing the somatomotor neurons whose efferents leave the cord by way of the ventral root. The lateral horn is linked with the visceral afferents and efferents of the autonomic nervous system (Altman and Bayer, 2001). It is of great significance that, unlike in lampreys and hagfish (Bullock et al., 1984), the axons of the spinal nerves are myelinated in true fishes (Waehneltd, 1990; Zalc, 2006). However, there are differences between the piscine



**Fig. 3-7.** The organization of the spinal cord in cross section in the stingray (**A**) and man (**B**). In such stained sections the white matter appears dark gray. (A. Modified, from Ariëns-Kappers, 1936. B. Cervical slice of Specimen Y132-61 from the Yakovlev Collection, an 11-month old infant.)

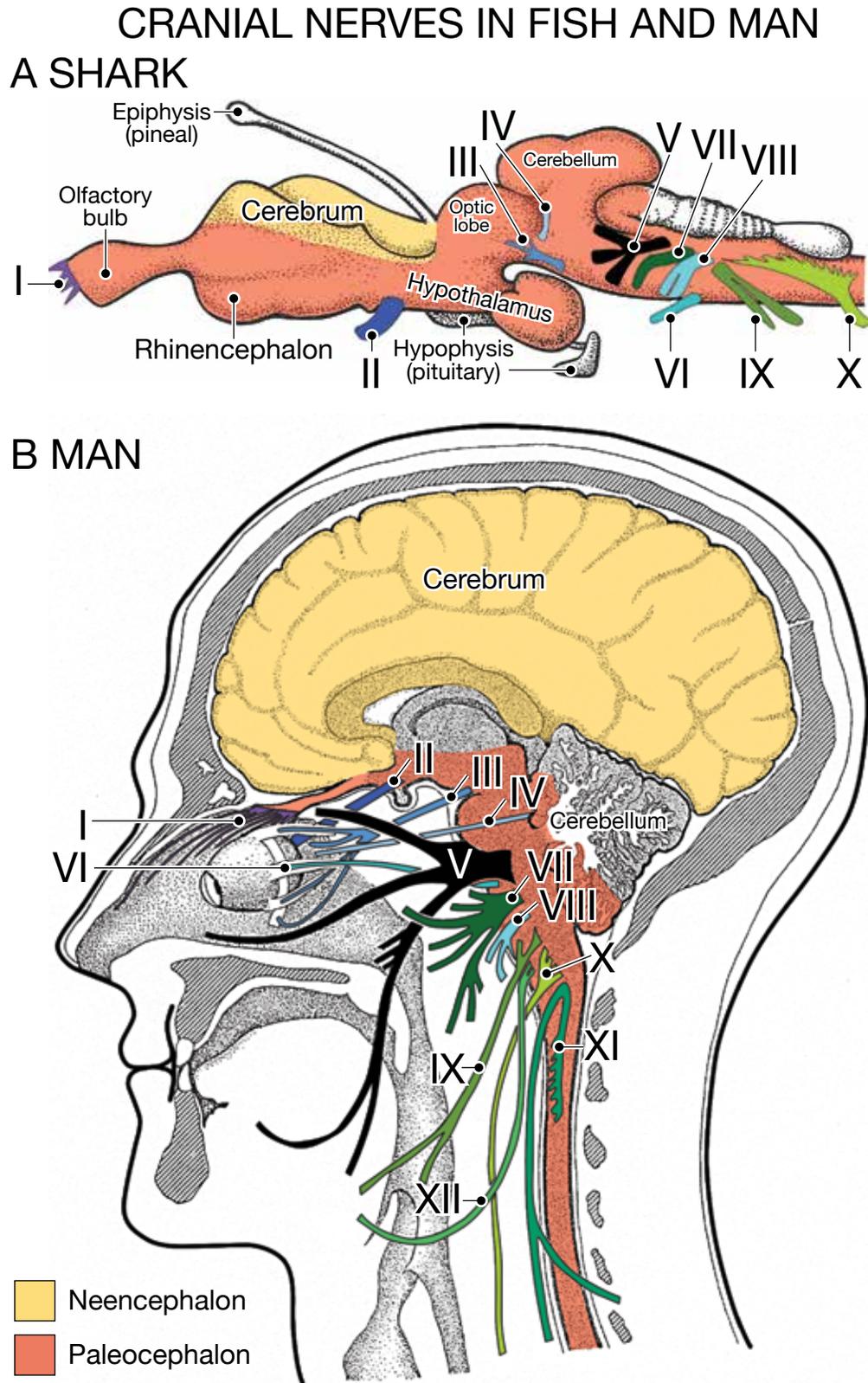
and human spinal cord. First, the dorsal, lateral and ventral horns are clearly separated in fish, and each has its own bridge (commissure) across the midline. In contrast, the gray matter in the human spinal cord forms a continuous structure with only one commissure. Second, the white matter, which contains local fibers and fibers that interconnect the spinal cord with the brain, has a different configuration in fish and man. Most obvious is the relatively small size of the dorsal funiculus in fish, which in humans is composed of the ascending afferents that convey information to the cerebral cortex. The lateral funiculus, which contains in primates

the fibers of the pyramidal tract responsible for the execution of volitional motor activities, also appears smaller in fish. We assume that the fish spinal cord contains a higher proportion of local (intra- and intersegmental) fibrous elements whereas the human spinal cord contains a higher proportion of fibers that interconnect it with the brain.

**THE CRANIAL NERVES.** The human brain is traditionally described as having 12 cranial nerves. Some of them are purely sensory, some mixed, others mostly motor. Except for the olfactory and optic nerves (I and II), which derive from the forebrain, the cell bodies of sensory nerves are located peripherally in the cranial nerve ganglia and their axons terminate in the hindbrain medulla. The cranial ganglia containing sensory fibers—the trigeminal (V), facial (VII), auditory-vestibular (VIII), glossopharyngeal (IX), and vagal (X)—are all present in cartilaginous (Fig. 3-8) and bony fishes. All the cranial motor nerves, except nerves XI and XII that control the tongue and neck muscles in higher vertebrates, are present in fish (Lázár, et al., 1992). The trigeminal nerve has three branches—the ophthalmic, maxillary and mandibular—innervating the eye, the upper, and lower jaw regions, respectively.

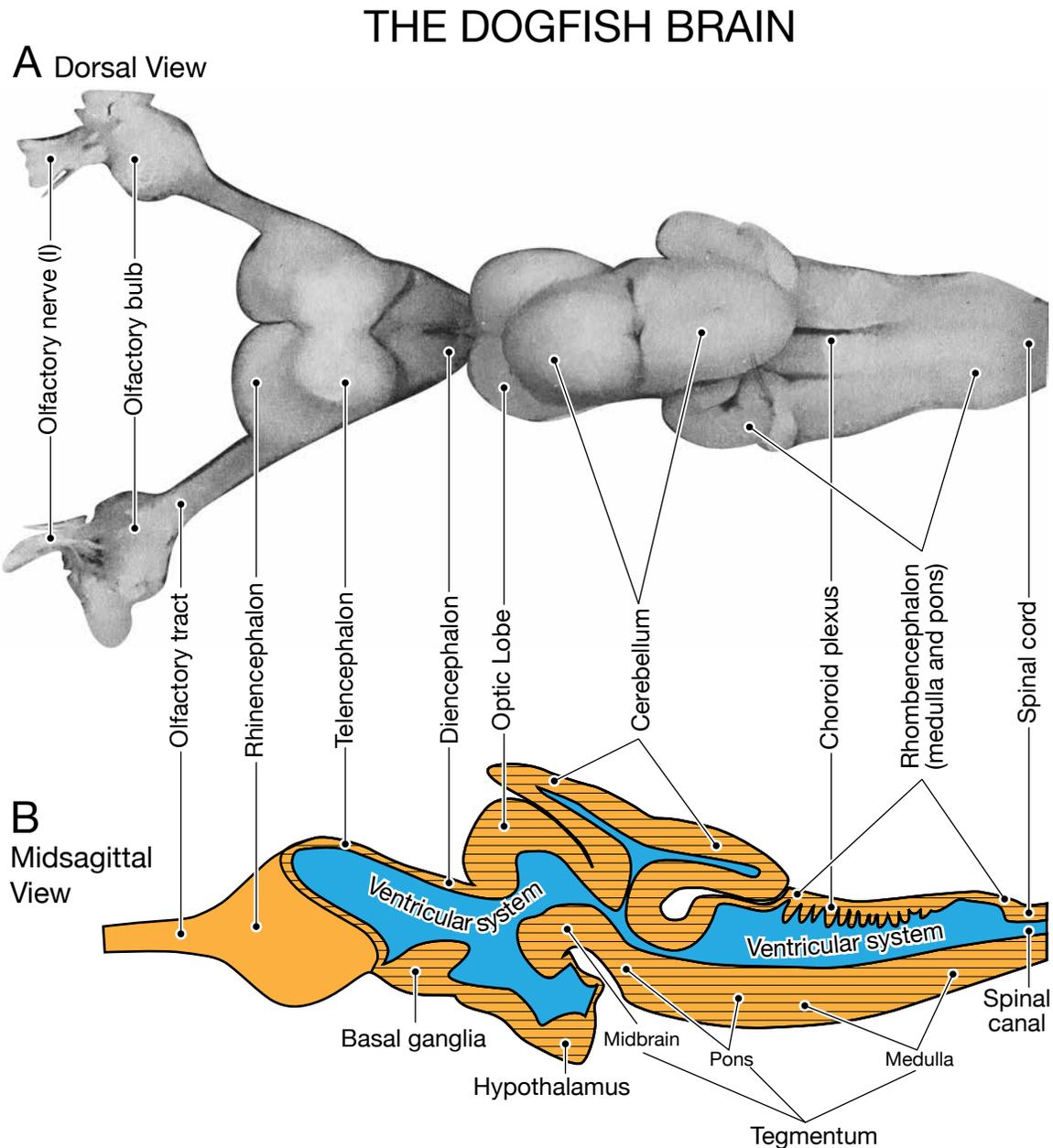
Recordings from single fibers of the trigeminal nerve indicate that they convey mechanical, thermal, and chemical stimuli and polymodal pain (Belousova et al., 1983; Sneddon, 2003). Gustatory afferents—which contact taste buds distributed in many fish not only in the oral region but also along the entire body—are present in the facial, glossopharyngeal, and vagus nerves, and terminate in the facial lobe and the vagal lobe of the medulla (Herrick, 1905; Biedenbach, 1973; Marui, 1977; Morita et al., 1980; Morita and Finger, 1985). The facial and vagal lobes are exceptionally large in bottom feeding fish, and in those living in murky water (Herrick, 1907; Finger, 1983, 1997; Huber et al., 1997; Wagner, 2001). It has been suggested that bottom-feeding catfish depend on the facial gustatory system to locate food, and on the vagal gustatory system to control ingestion (Atema; 1971; Kanwal and Finger, 1997). In different species of carps and minnows, large facial lobes are associated with “skin tasters,” whereas large vagal lobes with “lip tasters” (Evans, 1952). In the goldfish, the orobranchial portion of the vagal system controls the sorting of food in the mouth, the pharyngeal branch the chewing of palatable substances, and the abdominal branch regulates digestion (Goehler and Finger, 1992). It is noteworthy that in cave-dwelling fish species, the taste buds increase as the eyes degenerate (Varatharasan et al., 2009). Many fish also have large lateral line lobes associated with the octavolateral nerve (VIII), and several auditory nuclei in the medulla (McCormick, 1992). Vestibular components of nerve VIII terminate in the vestibular nuclei and higher-order auditory afferents reach the nucleus of the lateral lemniscus and the torus semicircularis in the midbrain (Kozloski and Crawford, 1998; Bass et al., 2001).

**THE BRAIN OF CARTILAGINOUS FISHES.** The brain of all fishes is composed of four divisions: telencephalon (forebrain), diencephalon (between-brain), mesencephalon (midbrain), and rhombencephalon (hindbrain). The latter has two components, the metencephalon (cerebellum) and myelencephalon (medulla). As seen from its dorsal aspect in an elasmobranch, the dogfish, the telencephalon has several components (Fig. 3-9A). Most anteriorly is the large olfactory nerve that terminates in the olfactory bulb. The latter is the source of fibers of the olfactory tract that terminate in the olfactory brain (rhinencephalon). More posteriorly is the small pallium (primitive cortex). As illustrated in the midsagittal plane (Fig. 3-9B), the telencephalon also

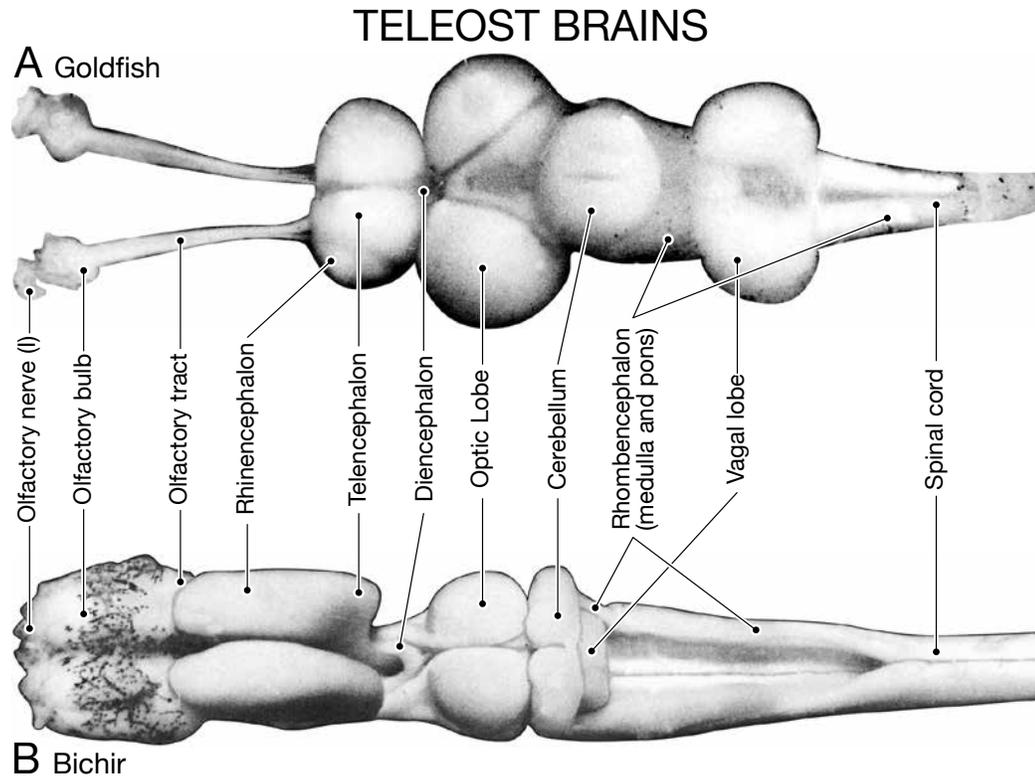


**Fig. 3-8.** The cranial nerves of the shark (A) and human (B). (A. Modified, from Romer, 1970)

has a ventral component, the basal ganglia. The diencephalon has two major components, the dorsal epithalamus, or habenula, which is connected with the pineal gland, and the ventral hypothalamus, which is associated with the pituitary gland. The mesencephalon consists dorsally of the stratified optic lobe (tectum), which is the target of the optic tract, and ventrally of the reticular formation (tegmentum) and some motor nuclei that move the eyes. The rhombencephalon consists of the dorsal cerebellum, a structure implicated in the sensory and feedback coordination of posture and locomotion, and of various lobes (or nuclei) that process the conveyed sensory input.



**Fig. 3-9.** The brain of an elasmobranch, the dogfish, viewed from the top (A), and as bisected along the midline (B). (A. Modified, from Schnitzlein and Faucette, 1969. B. Modified, from Sterzi, 1909.)



**Fig. 3-10.** Differences in brain morphology in the goldfish (**A**) and the bichir (**B**). The goldfish has a small olfactory bulb and rhinencephalon and a large vagal lobe; the opposite pattern is seen in the bichir. (Modified, from Schnitzlein and Faucette, 1969.)

**ORGANIZATION OF THE BRAIN OF BONY FISHES.** The brain is more differentiated in many teleosts than in elasmobranchs, and displays structural specializations in relation to the different niches to which the species is adapted. We illustrate these function-based differences by comparing the brain of the goldfish (Fig. 3-10A) and bichir (Fig. 3-10B). Goldfish, like carps in general, feed by sucking sand, gravel or mud from the bottom of lakes or rivers and sort the particles inside their mouths (Sibbing et al., 1986). Goldfish rely on the taste buds and the muscular apparatus of their palate and pharynx to sort the matter they ingest (Lamb and Finger, 1995). When they ingest a mixture of inedible and edible items they spit out the former and swallow the latter. When they ingest pellets flavored with quinine or caffeine (alkaloids that taste bitter to us), they promptly eject them. Similar observations have been made in bass (Linser et al., 1998). Relying on gustation in procuring food, the goldfish has a large vagal lobe. The oral taste buds, innervated by the vagus nerve, convey somatotopically organized gustatory input to the large and crisply laminated vagal lobe, a structure that accounts for nearly 20 percent of the entire brain of the goldfish (Finger, 2008). Efferents of the vagal lobe project to oropharyngeal motor neurons and these may control the oral sorting behavior (Finger, 1997; 2008; Kiyohara and Caprio, 1996). The bichir has a different life style. It is a nocturnal predator, hiding under a rock or in dense vegetation and attacks when a victim gets nearby. The predatory bichir has a large olfactory bulb and rhinencephalon but a small vagal lobe (Fig. 3-10B), suggesting that they rely on the sense of smell to detect and capture prey and use gustation less in food selection.

**THE PISCINE TELEENCEPHALON: PALLIUM AND BASAL GANGLIA.** The telencephalon of fish has a pallial and a ganglionic component, the former believed to be the primordium of the cerebral cortex (archicortex), the latter of the basal ganglia (archistriatum). Much of the piscine pallium is closely associated with the olfactory bulb. The olfactory bulb is an outgrowth of the forebrain and it is variably situated in different piscine species close to the olfactory epithelium or, as in fish with a long snout, some distance from it (compare Figs. 3-10A and B). The olfactory bulb is the end station of the olfactory nerves and its laminar organization is similar in fish and higher vertebrates (Sheldon, 1912). The first-order olfactory nerve fibers synapse in the olfactory bulb with mitral cells in spherical formations called glomeruli (Fig. 3-4). The mitral cells are the source of the second-order fibers forming the olfactory tracts. There are about 5-10 million fibers in the olfactory nerve (Hara, 1986) but the olfactory tract contains only about 100,000 fibers (Oka et al., 1982). This indicates considerable convergence, one similar to that found in higher vertebrates, and suggests signal integration within the olfactory bulb. The piscine olfactory system has a medial and a lateral component. Fibers arising in the medial and lateral regions of the bulb form the medial and lateral olfactory tracts, respectively (Satou et al., 1983). In turn, the medial olfactory tract projects to the medial and ventral telencephalon, preoptic area and the hypothalamus; the lateral olfactory tract projects to the dorsal and lateral telencephalon (Satou, 1990; Sas et al., 1993). Lesion experiments indicate that the medial olfactory system responds to pheromones, implicating it in reproductive functions (Stacey and Kyle, 1983; Resink et al., 1989); the lateral olfactory system responds to the odor of nutrients, implicating it in feeding behavior (Satou, 1990; Hamdani et al., 2001).

In many teleosts, the pallium surrounds a single median ventricle, rather than the paired lateral ventricles, as in higher vertebrates. In some phyla, the median ventricle fans out dorsolaterally where it is covered by a membrane rather than brain tissue. This pattern is referred to as the “everted pallium” (Nieuwenhuys, 1963; Nieuwenhuys and Meek, 1990). There have been many attempts to find homologies between the nonolfactory components of the piscine pallium and the mammalian cerebral cortex. It has been considered a primordium of the hippocampus or of a “general cortex.” The ganglionic components of the telencephalon have been homologized with such limbic forebrain structures as the septum and amygdala medially, and the basal ganglia laterally (Northcutt and Braford, 1980; Reiner and Northcutt, 1987; Schroeder, 1980; Braford, 1995; Portavella et al., 2004; Rink and Wulliman, 2004). While there is a multisensory input to the piscine telencephalon, including a visual one (Ebbeson, 1980; Luiten, 1981; Wulliman, 1998), there is no direct (“lemniscal”) thalamocortical relay system present, as in mammals, nor is there a direct corticofugal (“pyramidal”) motor outflow to the pons, medulla and spinal cord. The efferent tracts of the piscine telencephalon are the medial and lateral forebrain bundles (Schnitzlein and Crosby, 1967; de Bruin, 1980). The medial forebrain bundle originates in the ventral (presumably olfactory) telencephalon and terminates in the dorsal hypothalamus. The much larger lateral forebrain bundle originates in various regions of the nonolfactory forebrain. The latter has two components: a dorsal myelinated portion that terminates in the thalamus and midbrain, and a ventral unmyelinated portion that targets the hypothalamus (Schroeder, 1980). The homologies of the basal ganglia are uncertain.

**THE PISCINE DIENCEPHALON: THALAMUS AND HYPOTHALAMUS.** The diencephalon, defined as the brain region that surrounds the third ventricle, is relatively small in fish, except for the epithalamus (Schnitzlein, 1962) and hypothalamus (Crosby and Showers, 1969; Fernald and Shelton, 1985). The dorsal thalamus, which is so prominent in mammals, is poorly developed and while some thalamic nuclei have mammalian homologues, the identity of others is uncertain. Among the former are some midline thalamic nuclei; among the latter the nucleus rotundus and the nucleus glomerulosus. Components of the hypothalamus—such as the preoptic, supraoptic, suprachiasmatic, paraventricular and ventromedial nuclei, and the periventricular area—have been implicated in endocrine functions (Jorgensen and Larsen, 1967; Goosens et al., 1977; Maejima et al., 1994; Wullimann, 1998). These nuclei regulate such diverse visceral and housekeeping functions as metabolic energy balance and feeding; fluid and electrolyte homeostasis; drinking and micturition; sexual and reproductive maturation; growth and development; the circadian rhythm of sleeping and wakefulness; immune processes; and energy mobilization during stress, including offensive and defensive emotional expressions and behavior. This regulation is achieved with the aid of the sympathetic and parasympathetic branches of the autonomic nervous system and a complex endocrine network, including the pituitary gland (Halász, 2000).

**THE HYPOTHALAMO-PITUITARY ENDOCRINE SYSTEM.** The piscine hypothalamus is a highly vascularized brain region and contains most of the structures (“nuclei”) that are known to produce and store neurohumoral agents in higher vertebrates and man. These include the paraventricular and supraoptic nuclei, and the preoptic and periventricular areas. The paraventricular and supraoptic nuclei produce oxytocin and vasopressin, convey them to the pituitary gland and release them into the bloodstream to influence the activities of the vascular, gastrointestinal, and reproductive systems (Goosens et al., 1977). The preoptic nucleus and periventricular areas produce a series of hormones (or “releasing factors”), of which the following have been identified in fishes. (i) Thyrotropin-releasing hormone (TRH) (Jackson and Reichlin, 1974; Duarte et al., 2001), and (ii) growth hormone-releasing factor and somatostatin implicated in the regulation of morphogenesis and growth (Lin et al., 2000; Rousseau et al., 2001). (iii) Gonadotropin-releasing hormone (GnRH) that modulates the release of gonadal hormones (Maejima et al., 1994; Robinson et al., 2000; Andersson et al., 2001; Dubois et al., 2002). (iv) Pituitary prolactin implicated in reproductive processes (Segura-Noguera et al., 2000), and (v) prolactin-releasing hormone (Moriyama et al., 2002; Seale et al., 2002). (vi) Corticotropin-releasing factor (CRF) that modulates the release of adrenocorticotrophic hormone (ACTH) by the pituitary gland and glucocorticoid secretion by the adrenal cortex, and (vii) melanocyte-stimulating and melanocyte-inhibiting hormones (Duarte et al., 2001; Baker and Bird, 2002). In addition to the hypothalamus, other piscine brain regions also produce or store hormones. For instance, GnRH has been identified in the olfactory bulb, the medial olfactory tract, and the midbrain tegmentum of fish (Baby et al., 2000) and in areas of the telencephalon (Robinson et al., 2000; Gonzalez-Martinez et al., 2002). These sites may interact with the hypothalamus by way of hormonal or neural signaling. The medial forebrain bundle, the fornix and the dorsal longitudinal fasciculus of fish connect the hypothalamus with forebrain components of the limbic system: the septum, the amygdala and the piriform cortex (Crosby and Showers, 1969). Among the neurotransmitters of the CNS that influence production and secretion of releasing factors by the hypothalamus are norepinephrine (Lee et al., 2000), serotonin (Ekstrom and

Ebbesson, 1989), neuropeptide Y, and GABA (Trudeau et al., 2000; Senthilkumaran et al., 2001). This neurohumoral system, as we shall describe later, plays a major role in stress reactions, emotional expressions, and emotional behavior of fishes, much as it does in higher vertebrates and man.

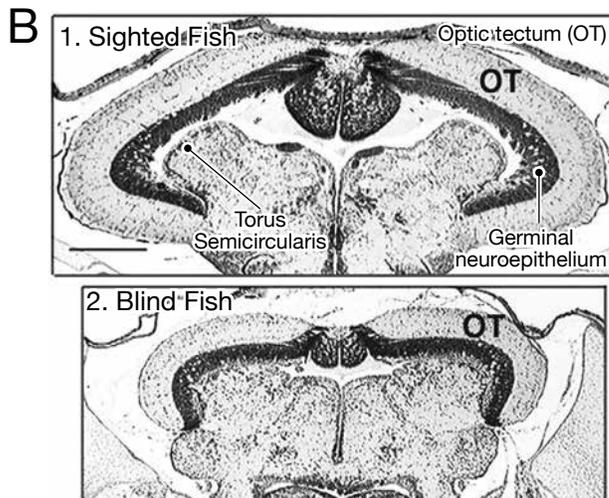
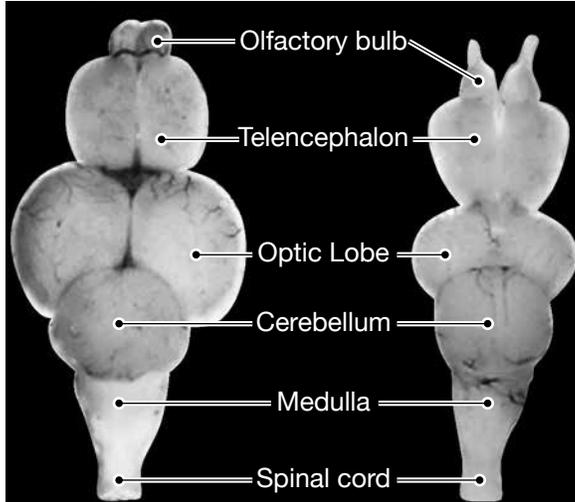
**THE PISCINE MESENCEPHALON: TECTUM AND TEGMENTUM.** The midbrain is one of the most differentiated regions of the teleost brain and may be its most important higher-order mechanism of behavioral control. It contains most components found in higher vertebrates, including the laminated tectum dorsally, the periaqueductal gray centrally, the reticular formation and red nucleus laterally, and the tegmentum ventrally. The two divisions of the piscine tectum are the paired optic lobes, known in mammals as the superior colliculus, and torus semicircularis, which may be the homologue of the inferior colliculus. Most of the optic nerve fibers that cross in the optic chiasm terminate in the upper layers of the contralateral optic lobe in a precise topographic, or retinotopic order (Schwassmann and Kruger, 1965). The optic lobe is well developed and highly laminated in most fish, particularly in surface-feeding fish that rely on vision to detect prey and predator, and recognize by their shape and markings social and mating partners (Pearson and Pearson, 1976; Schmidt, 1979; Demski and Beaver, 2001). The different layers of the optic lobe contain neurons with horizontally and vertically oriented dendritic arbors and axonal projections (Ramón y Cajal, 1909; Leghissa, 1955; Meek and Schellart, 1978; Schmidt, 1979). It has been estimated that, in the goldfish, about 220 thousand retinal ganglion cells send afferents to the optic tectum, which contains as many as 1-2 million processing neurons (Meek and Schellart, 1978). However, the optic lobe is the source of only 2-8 thousand myelinated efferent fibers. Evidently, there is considerable sensory integration in this principal visual center of the fish brain. In contrast to the superficial layers of the optic lobe, the deep layers have been implicated in motor functions. Electrical stimulation of the optic tectum in goldfish elicits eye rotation and body turning either towards the side of stimulation or away from it, depending on the exact site of stimulation and stimulus intensity (Salas et al., 1997; Herrero et al., 1998). These two responses are interpreted as visually directed orienting reactions and flight reactions, respectively. Additionally, some optic fibers project to the pretectum and the hypothalamus, and a few reach the thalamus. Their function is not known.

The size and complexity of the optic lobe differs in various piscine species. The regulation of optic lobe size is illustrated in *Astyanax mexicanus*, a species that exists in sighted and blind form, depending whether it lives in the open water or a cave (Soares et al., 2004). *A. mexicanus* reproducing in caves initially develop eye primordia but the lens and the retina degenerate in the dark and, in combination with the reduction in the number of optic nerve fibers, the growth of the optic lobe is retarded (Fig. 3-11A). The blind fish have substantially fewer optic lobe neurons than do the sighted fish. That difference—with 24,000 neurons in normal fish and 4,000 neurons in blind fish—is due to reduced proliferation of precursors of neurons in the tectal neuroepithelium, the germinal matrix of the optic lobe (Figs. 3-11B). The blind fish also fail to develop the skin pigmentation typical of sighted conspecifics.

The torus semicircularis, the homologue of the mammalian inferior colliculus is a less prominent component of the fish tectum (Fig. 3-11B). It is principally a target of auditory afferents

## OPTIC LOBE IN SIGHTED AND BLIND CAVEFISH

A 1. Sighted Fish      2. Blind Fish



**Fig. 3-11.** A. The brains of sighted (1) and blind (2) cavefish (*A. mexicanus*). Note the diminution of the optic lobe in the blind fish. B. Difference in the size of the germinal neuroepithelium in the sighted (1) and blind (2) cavefish. OT-optic tectum. (Modified, from Soares et al., 2004.)

(Page, 1970) and its neurons discharge in response to clicks (Crawford, 1997). The torus semicircularis, considered a higher-order auditory-visual integrative center (Schellart, 1983), has ascending connections with the optic tectum and several thalamic nuclei, and descending connections with premotor and motor nuclei of the brain stem and the spinal cord (Yoshimoto et al., 1999). Finally, the tegmentum and the reticular formation are recipients a large efferent outflow from the both the optic lobe and the torus. The discharge of tegmental neurons to visual and auditory stimuli (Page and Sutterlin, 1972) may reflect the involvement of this motor system in the mediation of sight- and sound-triggered behaviors.

**THE PISCINE CEREBELLUM.** Species differences in the size and complexity of the different paleocephalic lobes is particularly pronounced in the case of the cerebellum (Schnitzlein and Faucette, 1969). Among agnathans, hagfish lack a clearly identifiable cerebellum and the lamprey's cerebellum is, at best, very small (Figs. 2-25, 2-26). Among cartilaginous fish, the dogfish has a smooth cerebellum (Fig. 3-9), whereas the cerebellum of the skate and stingray is foliated. In bony fishes, the bichir has a small, smooth cerebellum; the cerebellum is larger in the goldfish (see Fig. 3-10). The cerebellum of mormyrids, which generate and communicate by

electric signals, is enormous and highly foliated, spanning the entire length of the underlying brain (Nieuwenhuys and Nicholson, 1969). The cellular organization of the cerebellum is a conserved feature of the vertebrate CNS (Altman and Bayer, 1997; Wullmann et al., 2011) and unlike most other rhombencephalic structures, it remains an expanding component of the mammalian (including human) brain. The great variability in the size and foliation of the cerebellum suggests an important principle of brain organization; namely, the plasticity

of the CNS in relation to the somatic organization and behavioral adaptations of the species. Although the CNS of all vertebrates has a similar basic design (Bauplan), that is not a fixed characteristic. Rather, the organization of the brain in different phyletic lines conforms to the somatic, sensory and motor organization of the species, and their life style in relation to the niches they occupy.

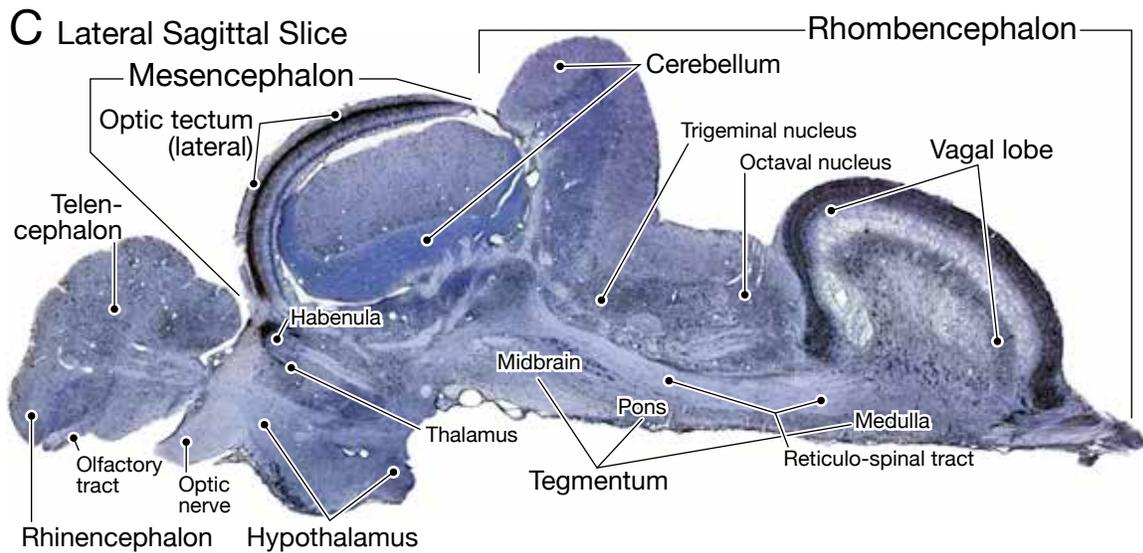
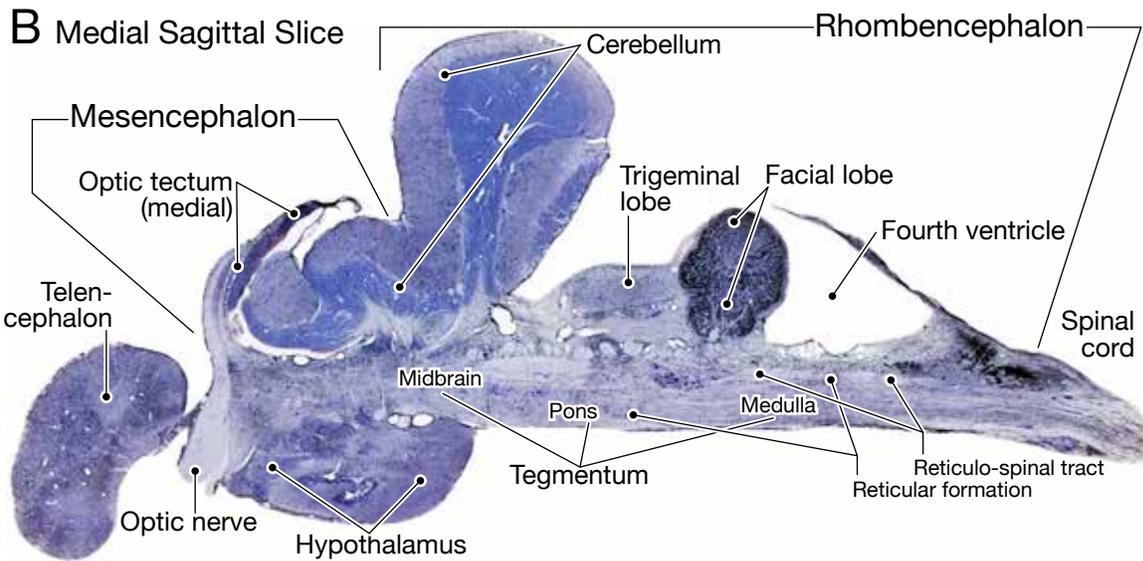
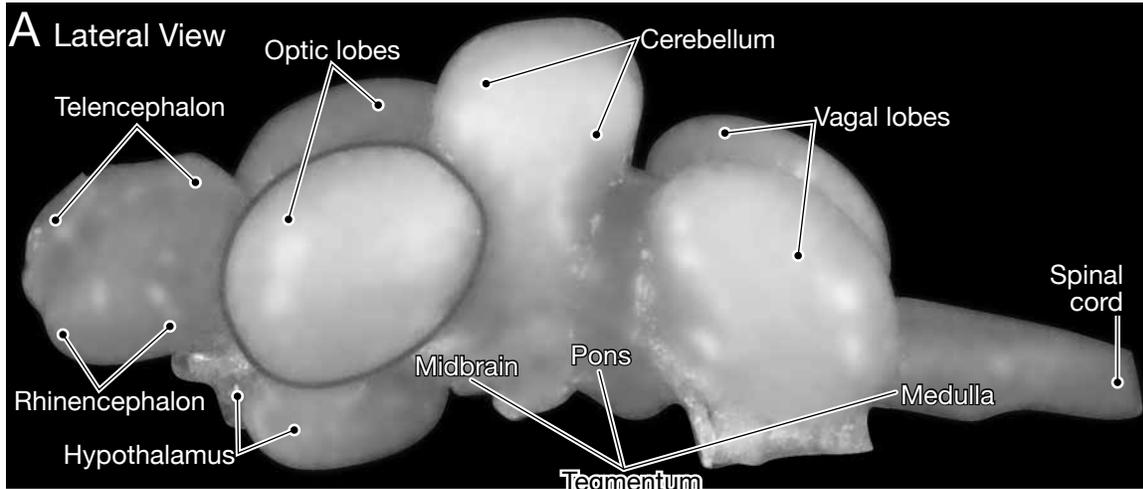
**ORGANIZATIONAL DIFFERENCES BETWEEN THE PISCINE AND THE HUMAN BRAIN.** The human brain is composed of the ancient paleocephalon, which is a piscine legacy, and of the neencephalon, a mammalian acquisition that has expanded progressively in the primate line as a superordinate neural system, and has climaxed in size and complexity in modern man (Fig. 3-8). As noted, some components of the piscine paleocephalon are fully preserved (and even elaborated) in the human brain, others have regressed. In contrast, the mammalian neencephalon is altogether absent in fish, although a small component of the telencephalic pallium may be its rudiment. To illustrate these evolutionary transformations we begin by examining the overall configuration of the goldfish paleocephalon (pp. 133-134), looking at it from the top (Fig. 3-12A) and the side (Figs. 3-12 D), and its histological organization in stained midsagittal (Fig. 3-12B), parasagittal (Fig. 3-12C), and horizontal (Fig. 3-12E) sections. The piscine telencephalon has two components: (a) the rhinencephalon (Fig. 3-12E), supplied by fibers of the olfactory tract (Fig. 3-12C, D) that come from the olfactory bulb (see Fig. 3-10A), and the poorly differentiated pallium. All elements of the piscine olfactory system have been preserved in man; however, they constitute, relatively speaking, a miniscule portion of the adult human brain. (The preserved components of the piscine paleocephalon in the human brain is illustrated in Fig. 3-16). Also preserved is the hypothalamus (Fig. 3-12A-C) with many of its neural and endocrine components that play a major role in the control of visceral and emotional functions. The thalamus, a large part of the human brain, is poorly developed in fish. The major components of the piscine mesencephalon, the tectum and tegmentum, have been preserved. However, whereas in fish the crisply laminated optic lobe is the target of the bulk of optic tract fibers, its homologue in the human brain, the superior colliculus, is the target only of a small complement of optic fibers. In man, the bulk of optic tract fibers terminate in the laminated dorsal lateral geniculate body of the thalamus, which relays the input to the visual cortex. This neencephalic system is absent in fishes. Similarly, while the reticulospinal system of the tegmentum (Fig. 3-12C) has been preserved, the major output line to the spinal cord in man is the corticospinal system, which controls volitional behavior, is absent in fish. Proceeding caudally, the goldfish brain contains four large and highly differentiated structures: the cerebellum, the trigeminal lobe (Figs. 3-12C, E), the facial lobe (Figs. 3-12B, E), and the vagal lobe (Figs. 3-12C, E). Each one is characterized by a unique and complex cytological organization. The cerebellum has been preserved and greatly expanded in the human brain but the others are far less conspicuous and form smaller “nuclei” that are targets of the trigeminal, facial and vagal nerves (Fig. 3-16B).

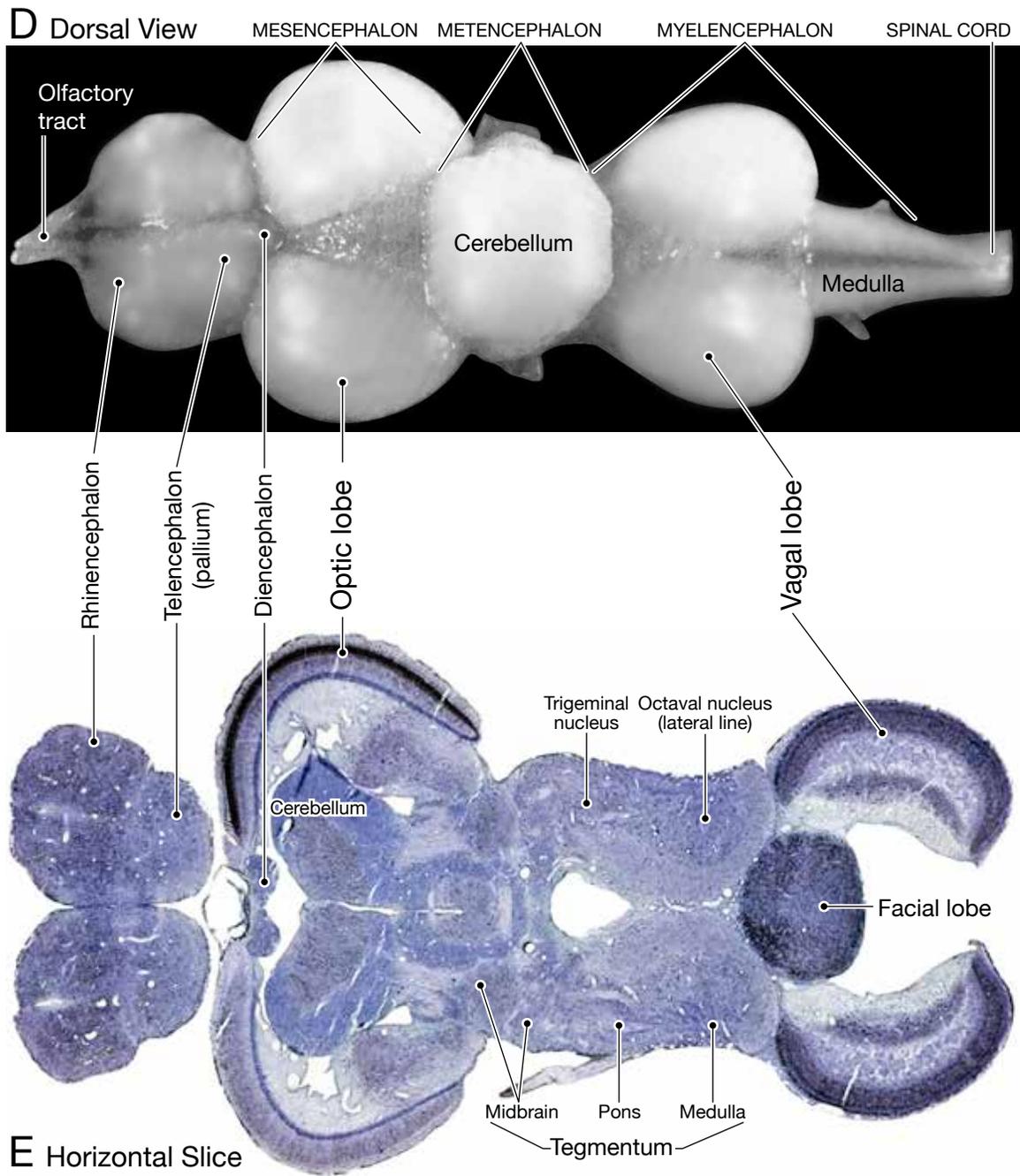
The large lobes of the piscine paleocephalon may be viewed as distinctive unimodal sensory processing mechanisms, as follows.

- The olfactory lobe (rhinencephalon) is the *nasal brain* that processes olfactory information about the distribution of odorants, mostly of organic origin.
- The optic lobe is the *ocular brain* that processes visual information emitted or reflected by distant objects .
- The cerebellum is the *vestibular-proprioceptive brain* concerned with spatial orientation and postural control.
- The trigeminal lobe is the *oral brain* processing multifarious information provided by the sensitive piscine lips.
- The facial lobe is the *palatal brain* that processes gustatory information about the quality of nutrients.
- The vagal lobe is the *pharyngeal brain* that regulates gastrointestinal and related internal functions.

**SEGREGATED PALEOCEPHALIC SENSORY PROCESSING MECHANISMS.** What is noteworthy about this piscine organizational system is the spatial *segregation* of the different lobes from one another and, judging by their distinct cytoarchitecture, different modes of information processing. This contrasts sharply with the spatial *unification* of the sensory systems in the mammalian neencephalon. In mammals, input from the visual, tactile and auditory senses are brought into close proximity in the relay nuclei of the thalamus, and are projected into adjacent cortical areas that have a comparable (six-layered) cytoarchitectonic organization and are intimately interrelated with one another by multimodal association areas. We suggest, that this change in neural organization—bringing together input from the different senses and processing them in a unitary way—constitutes a fundamental change in neencephalic information processing. It indicates a change from the brain providing discrete *unimodal* sensations about distinctive features of objects and events—their odor, taste, feel, color, shape, size, etc.—to constructing unified *multimodal* percepts that reflect their multifarious properties. Metaphorically speaking, it reflects a change from the times when decentralized dukedoms and principalities governed a nation independently from one another, employing different economical, social, and political rules and regulations, to the modern system of federated provinces and states run by a centralized government and its interconnected departments by a unified system.

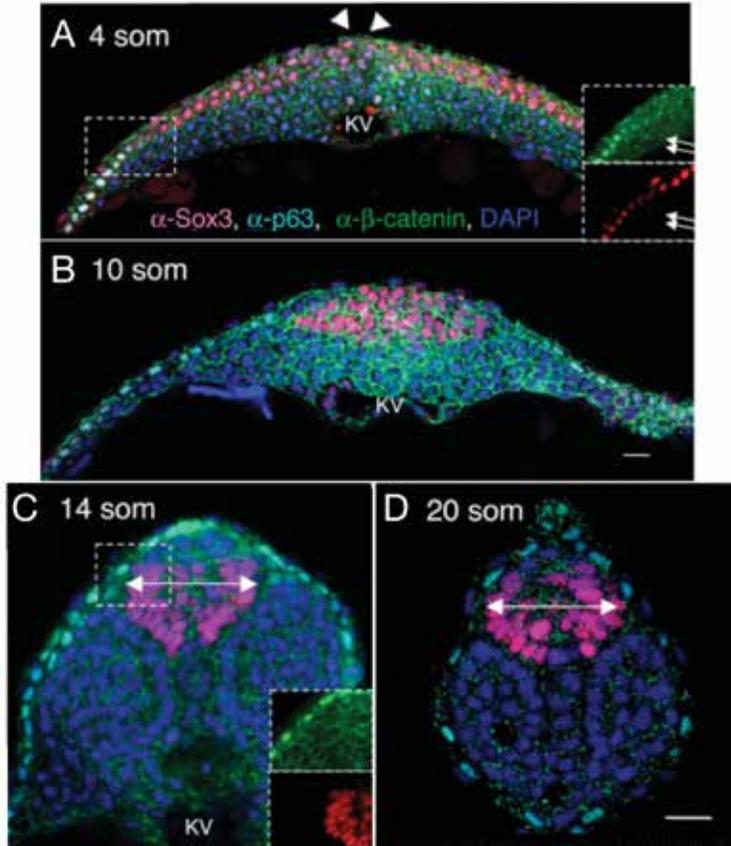
# THE GOLDFISH BRAIN





**Fig. 3-12.** Different views of the goldfish brain. **Facing page:** **A.** Photograph of the whole brain in lateral view. **B.** Photomicrograph of a stained section in the midsagittal plane. **C.** A stained section in the parasagittal plane. **This page:** **D.** Photograph of the whole brain in top view. **E.** Photomicrograph of a stained horizontal section. (A and D, modified from Raymond and Easter, 1983. B, C and E from Harvey Karten, BrainMaps.org.)

**3.1.5. Piscine Contributions to the Evolution of Our Head and Brain.** THE NEUROEPITHELIUM AND BRAIN DEVELOPMENT IN TELEOSTS. Neurulation has been studied in a teleost, the zebrafish, with a variety of techniques (Schmitz et al., 1993; Kimmel et al., 1994; Lowery and Sive, 2004, 2009; Clarke, 2009). According to a recent study (Harrington et al., 2010), putative precursors or neural cells appear in the dorsal ectoderm as early as the 4-somite stage (Fig. 3-13A), forming the neural plate. By the 10-somite stage, these neuroepithelial cells (NEP) coalesce in the mid-dorsal region (Fig. 3-13B). Then, between the 14-20 somite stages, NEP cells dip downward en masse to form a separate germinal tissue, the neural rod (Figs. 3-13C-D). This process, which involves the formation of tight junctions between the NEP cells, is regulated by a gene, *N-cadherin* (Hong and Brewster, 2006). The last step is the formation of a lumen in the center of the neural rod which thus becomes transformed into the neural tube, the closed NEP with its own internal fluid system. This process differs from that seen in higher vertebrates and man where the neural plate invaginates, forms the neural groove, and then fuses dorsally (Fig. 2-29). The choroid plexus, which is the source of the cerebrospinal fluid in the maturing and adult vertebrate brain, begins to form in the zebrafish about 2 days post-fertilization (Garcia-Lecea et al., 2008; Lowery and Sive, 2009). There is no evidence of a pial membrane encasing the neural tube and brain vesicles in zebrafish, suggesting an absence of a subarachnoid space or any other protective sheet, such as the dura, as in higher vertebrates. Finally, a notable feature of the fish brain is that the NEP persists through adulthood in most brain regions and produces new neurons (Zupanc, 2001).



**Fig. 3-13.** Formation of the neural plate and neural tube in the tailbud of zebrafish embryos between the 4- (A) and 20- (D) somite (som) stages. KV-Kupffer's vesicle. Arrowheads in A indicate medial extent of neural tissue. Insets in A and C: green stain=p63 cells; red stain=Sox3C cells; double arrows in A inset indicate cells co-expressing p63 and Sox3C. Lines with arrows at both ends in C and D indicate the width of the neural rod. Scale bar=20  $\mu$ m. (Modified, from Harrington et al. 2010.)

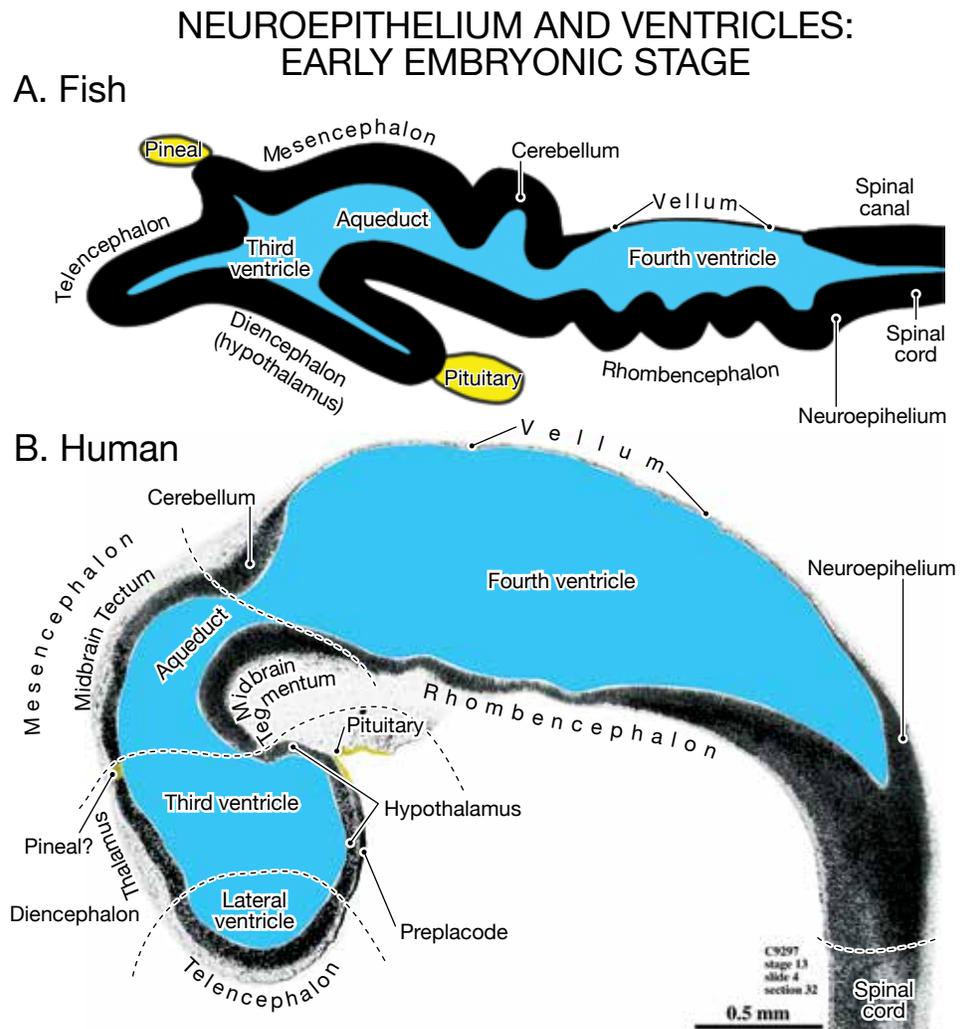
**THE NEURAL CREST AND THE PERIPHERAL NERVOUS SYSTEM.** The neural crest, first identified by His (1868) in humans, is composed of streams of cells that leave the NEP before its closure (Fig. 2-29) and migrate along definite paths into the interior of the body. The crest cells give rise to neurons of the spinal ganglia, the autonomic nervous system, the enteric nervous system, and such non-neuronal elements, as Schwann cells that myelinate peripheral nerves, pigment cells, and some other tissues (Hörstadius, 1950; Le Douarin and Kalcheim, 2009). There is no histological evidence for the existence of neural crest cells in primitive chordates, although a few marker genes associated with crest cells have been identified in them (Lacalli, 2001, 2004, 2008; Schlosser, 2005; Shimeld and Holland, 2005; Holland, 2009), but neural crest cells are present in jawless fishes (McCauley and Bronner-Fraser, 2003; Ota et al., 2007; Sauka-Spengler and Bronner-Fraser, 2008) and jawed fishes (Kimmel et al., 2001). Genetic studies in fish indicate that whereas the medial neural plate cells, which form the neural tube, express markers of *Pax* and *Msc* genes, the neural crest cells in the lateral border of neural plate express *Sox* genes (Holland, 2009). Notable among the novel vertebrate structures that neural crest cells produce in fish are the neurons of the spinal sensory ganglia and neurons of the parasympathetic and sympathetic ganglia. Being of neural crest origin, the vertebrate peripheral nervous system may be genetically different from the peripheral nerve network of such lower invertebrates as cnidarians (Section 2.3.2) and planarians (Section 2.4.2).

**THE PLACODES AND THE EVOLUTION OF THE HEAD IN TELEOSTS.** There is increasing evidence that components of the head that have evolved in fishes are derived from a distinctive germinal tissue, the placodes. While rostrocaudal polarization is a ubiquitous feature of all bilateral animals, and all of them have a frontal region studded with sensory cells that orient them as they move forward, they do not all have a differentiated head, defined as a movable body member furnished with paired nostrils, eyes and ears, a mouth, and a brain. So defined, amphioxus does not have a differentiated head (Fig. 2-21), and agnathans, like hagfish and lampreys, only have a primitive head, with simple sense organs, no jaws or a cranium (Fig. 2-24). It is in elasmobranchs and teleosts that the jaws and a cartilaginous or bony cranium have evolved. Embryological studies in fishes and higher vertebrates (Northcutt and Gans, 1983; Schlosser, 2005), including humans (Bayer and Altman, 2008), indicate that components of the cranial sense organs and other parts of the head derive from a special germinal tissue, the preplacodes.

The pluripotent germinal cells of the preplacode originate in the neural plate and leave it prior to NEP closure (Fig. 2-29). In the early embryonic human brain, these cells form a thickened epithelium, the preplacode, beneath the NEP where the cranial sense organs will develop (Fig. 3-14B). Subsequently, components of the preplacode segregate and form regional placodes. These generate the cells and tissues of such special structures as the olfactory epithelium (olfactory placode), the lens of the eyes (lens placode), a portion of the pituitary gland (hypophyseal placode), the inner ear with its neurons (otic placode), and neurons of the trigeminal, facial, glossopharyngeal and vagal ganglia (epibranchial placodes). As we noted earlier, there is no evidence for the existence of placodes in primitive (headless) chordates, with the possible exception of the hypophyseal placode (Section 2.5.6). While placodes are not easy to visualize with conventional histological techniques in lower vertebrates, they have been demonstrated with genetic markers in cartilaginous (O'Neill et al., 2007) and bony fishes

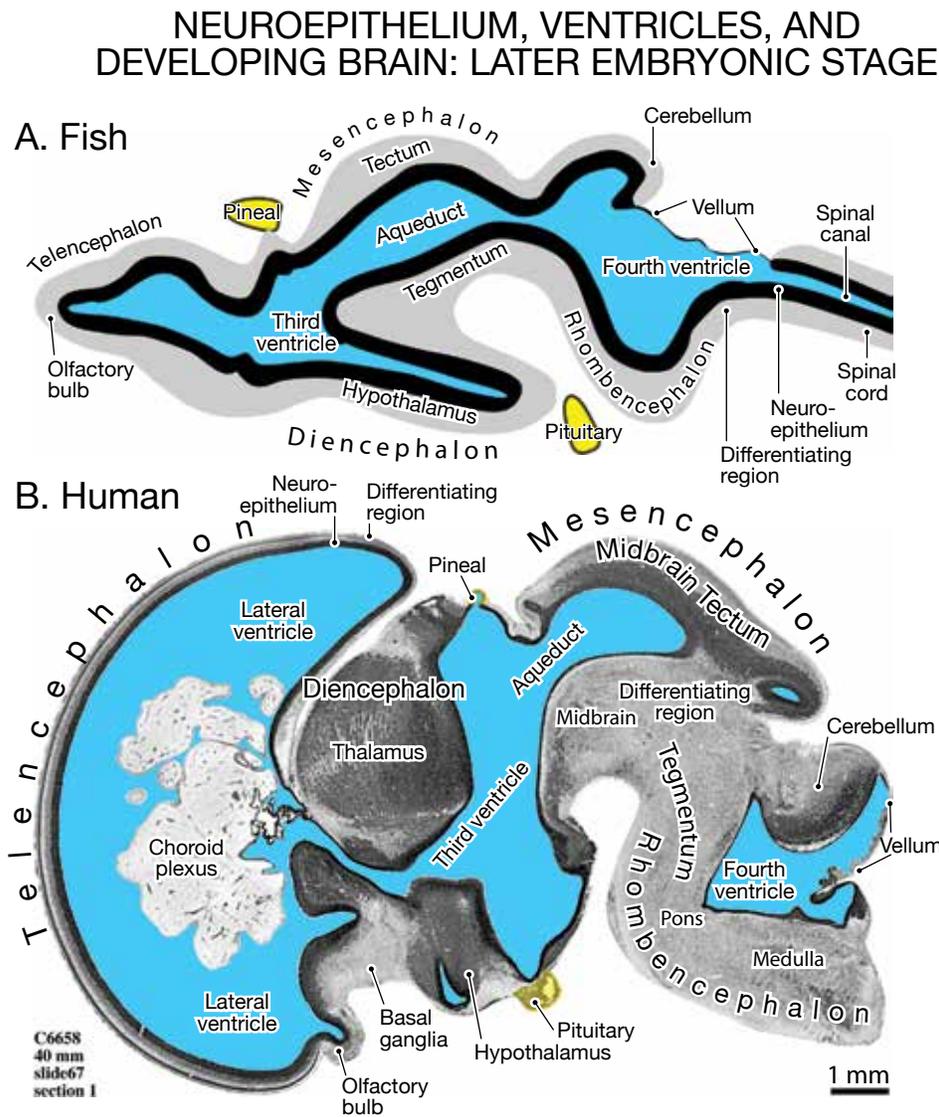
(Baker and Bronner-Fraser, 2001; Toro and Varga, 2007; Kwon et al., 2010; Modrell et al., 2011). The different placodes are specified by the up- or down-regulation of different genes and signaling molecules—among them various *Pax* genes, *Sox3*, *NeuroD*, and *Phox2*—during specific phases of embryonic development, and they generate the cranial and branchial tissues and organs that distinguish fishes from primitive chordates.

**SIMILARITIES AND DIFFERENCES BETWEEN THE PISCINE AND HUMAN NEUROEPITHELIUM.** The neurons of both piscine and human brain originate in the neuroepithelium (NEP) that surrounds the telencephalic, diencephalic, mesencephalic, and rhombencephalic ventricles. However, there are fundamental differences in NEP morphology between fish and man. First, during early embryonic development—the stockbuilding period when the precursors of neurons proliferate briskly but neuron differentiation and brain tissue formation has yet to commence—the mesencephalic and rhombencephalic vesicles are large in both but the telencephalic vesicle is larger in man (Fig. 3-14B) relative to fish (Fig. 3-14A). The same applies to the dorsal portion of the diencephalon. This suggests much greater growth potential



**Fig. 3-14.** Comparison of the relative size of the neuroepithelium (black) and the brain ventricles (blue) in fish (A) and human (B) embryos before the onset of neuronal differentiation. (B modified from Bayer and Altman, 2007.)

in humans for the cerebral cortex (produced by telencephalic NEP cells) and the thalamus (produced by dorsal diencephalic NEP cells) than in fishes. Second, during the next phase of embryonic development—when the proliferating cells start to leave the NEP and begin to differentiate to form the brain—that process is more advanced in the rhombencephalon and mesencephalon than in the telencephalon and diencephalon (Fig. 3-15B). That indicates that the phylogenetically older paleocephalon, the piscine component of the human CNS, matures before the phylogenetically more recent neencephalon. Third, the telencephalic NEP remains in an embryonic stage for a protracted period, acquiring more and more precursor cells before they form the cerebral cortex (Bayer and Altman, 2008). During embryonic development, the NEP cells divide along the bank of the ventricles filled with cerebrospinal fluid and, as we have argued, the embryonic human brain has “supraventricles” to accommodate the immense number of proliferating neural precursor cells. Evidently, from the outset of embryonic development the human forebrain is destined to become much larger relative to the rest of the brain than the fish forebrain.

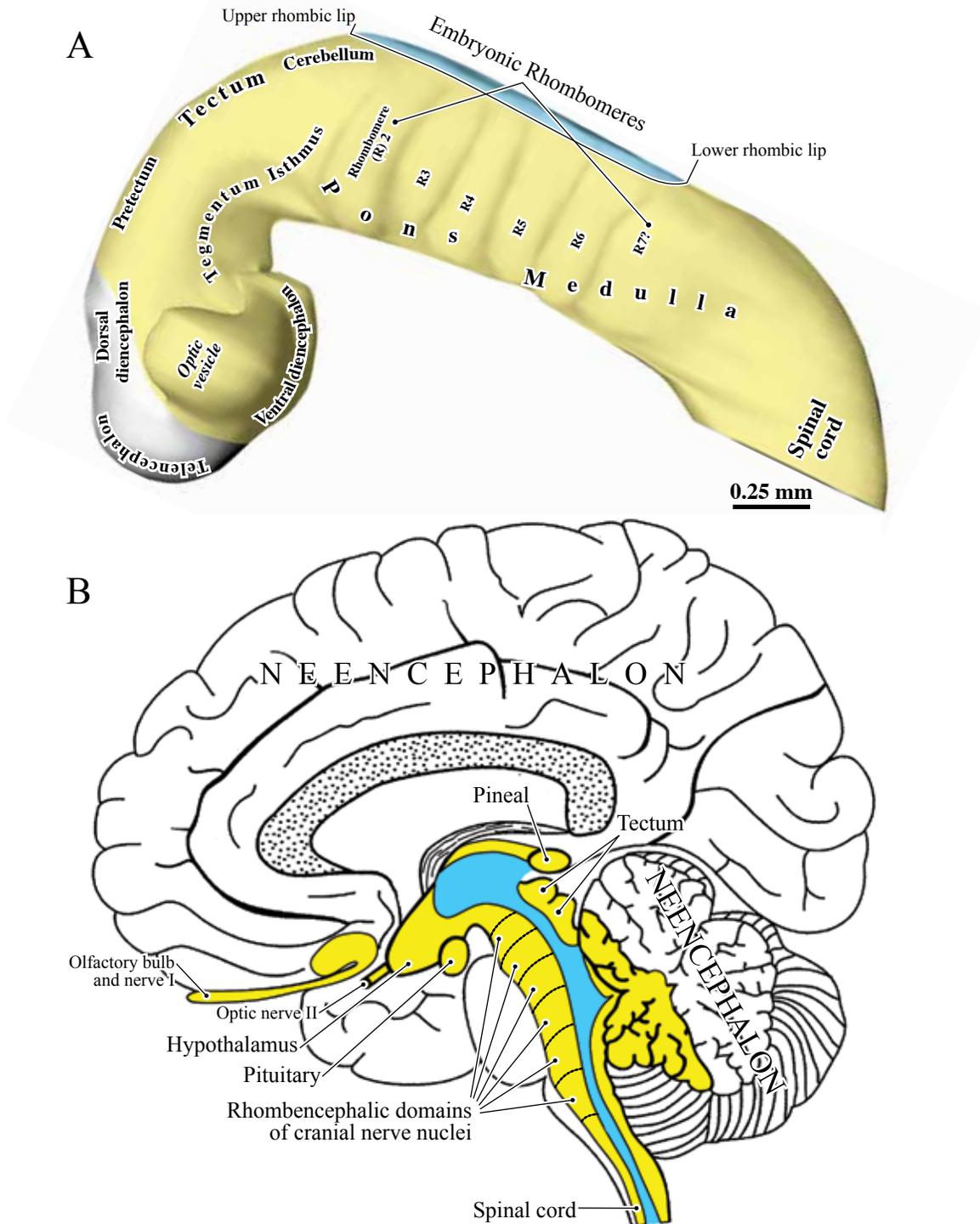


**3.1.6. Our Piscine Neural Legacy.** We owe jawless and jawed fishes for the basic organization of our cranial sense organs and the paleocephalic components of our brain. The olfactory system—the nasal epithelium, the olfactory nerve (nerve I), and olfactory bulb—have a similar organization in fish and man. The same applies to the basic components of our visual system, the eye and retina, and that portion of the optic tract (nerve II) that projects to the optic lobe, known as the superior colliculus in the human brain. The motor nerves III, IV and VI that innervate the extraocular muscles, which allow scanning and tracking of objects in the environment, have been identified both in cartilaginous and bony fishes. Fish also have well developed trigeminal (V), facial (VII), glossopharyngeal (IX) and vagal (X) ganglia and nerves, and related central structures (lobes) that have been implicated in gustatory, alimentary and related functions. Also present are the vestibular and auditory nerves (VIII) and their central nuclei, involved in postural coordination and sound processing. The hypothalamus is particularly significant among the brain structures that have evolved in fishes. Aided by a complex neurohumoral mechanism and the autonomic nervous system, much of it conserved in humans, the hypothalamus regulates the body's homeostatic functions and, as we describe below, emotional expressions and affective behavior. However, the available evidence indicates that while the core components of our brain, the paleocephalon, is well developed in fish, the neencephalon, particularly the cerebral cortex implicated in higher perceptual and cognitive functions, is at best rudimentary in these lower vertebrates. As an ontogenetic reflection of this phylogenetic trend, components of the paleocephalon—particularly the midbrain tectum and tegmentum, and rhombencephalon with the domains of the cranial nerve nuclei—develop in the human embryo far ahead of the neencephalic diencephalon and telencephalon (Fig. 3-16).

## **3.2. Evidence for Basic Feelings and Emotions in Jawed Fishes: Our Piscine Affective Legacy**

**3.2.1. Do Fish Have Feelings and Emotions?** When inferring feelings and emotions in others, we have an easier task with people like ourselves, and animals that we are familiar with, such as our dog, than with animals that live in a different milieu and are so different from us, such as fish. Humans often talk about how they feel. Of course, that is not always a reflection of what they experience, since verbalization often involves interpretations, rationalizations, denials and even simulations. Because of that, we tend to judge how people feel or what mood they are in not by what they say but by their emotional expressions, whether they smile or frown, laugh or cry, the tenor of their voice, changes in their body posture and movements, and the like. We judge whether dogs are happy or dejected, angry or fearful by their distinctive species-specific emotional expressions and behavior, such as their barking, tail movements, snarling, attacking or retreating. When it comes to lower vertebrates like fish, we have a problem in interpreting their affective state because their behavior is so unfamiliar to us, indeed, many people tend to deny that fishes have any feelings. We shall argue, however, that we share with fish a series of endocrine and physiological processes associated with emotional arousal and mobilization, and that we can use these manifestations in combination with their visible emotional expressions to infer their feeling state and mood.

## PALEOCEPHALON IN ADULT AND EMBRYONIC HUMAN BRAIN



**Fig. 3-16.** Development of components of the ancient paleocephalon in the early human embryonic CNS. **A.** Computer-aided 3-D reconstruction of a 4-week old embryonic human brain. **B.** Relative size of components of the paleocephalon in a midsagittal section of the adult human CNS. (A. Modified, from Bayer and Altman, 2007.)

**3.2.2. *The Endocrinological Approach to the Study of Emotions.*** Cannon (1915) reported almost a century ago that the panic reactions of a cat frightened by a barking dog (hissing, baring of canines, arching of the back, erection of hair, unsheathing of the claws, etc.) is associated with activation of the sympathetic and parasympathetic nervous systems and the release of adrenaline (epinephrine and norepinephrine) into the blood stream. Cannon went on to argue that autonomic activation and endocrine change play a major role in the regulation of other emotional reactions, such as pain, hunger, and rage. Subsequent studies in different species of mammals have established that in addition to adrenaline, a host of other hormones are involved in pain, hunger, anger, fear, and other emotional reactions, and that these are regulated by an extremely complex network of endocrine glands, the autonomic nervous system, and CNS structures, including the hypothalamus, the preoptic area, and the limbic system (Frankenhaeuser, 1975; Arimura, 2000; Halász, 2000). Among the endocrine reactions associated with emotional arousal are the release of CRH (corticotropin releasing hormone) and ACTH (corticosteroids) into the bloodstream which, upon reaching the adrenal cortex, cause the production and release of cortisol (a glucocorticoid). The adaptive significance of these endocrine changes during aroused emotional states is energy mobilization and an elevated supply of oxygen and nutrients to the skeletal muscles. In addition to the hormones that produce arousal, there are others that have the opposite stress-reducing and calming effect. Examples of such agents are melanin-concentrating hormone (Monzon and Barioglio, 1999) and neuropeptide Y (Britton et al., 2000).

**ENDOCRINE MECHANISMS AND STRESS REACTIONS IN FISH.** Many of these emotionally-implicated physiological and endocrine mechanisms are present in fishes. Much like mammals, fishes have a chain of sympathetic ganglia along the spinal cord targeting various visceral organs, and a parasympathetic (vagal) outflow to the heart (Pick, 1970; Nilsson, 1983). As in mammals, so also in fish norepinephrine- and dopamine-containing CNS efferents innervate the sympathetic ganglia. Monoaminergic and peptidergic efferents innervate the parasympathetic ganglia (Funakoshi et al., 2000, 2002). The adrenal cortex is represented in fish by clusters of chromaffin cells in the kidneys, and the adrenal medulla by interrenal cells (Henderson, 1997). Sympathetic stimulation causes the chromaffin cells to release epinephrine and norepinephrine, while parasympathetic stimulation induces the secretion of the stress hormone, cortisol (Gfell et al., 1997). In addition to this autonomic regulation, the hypothalamo-pituitary system secretes CRH into the portal circulation when fish are stressed and that triggers the secretion of ACTH into the systemic circulation (Wendelaar Bonga, 1997). The effects of these stress-induced endocrine reactions include enhanced oxygen uptake and transfer, increased blood glucose concentration, elevated CO<sub>2</sub> production, and the reallocation of energy resources from trophic functions (growth, reproduction and immune reactions) to behavioral mobilization (Wendelaar Bonga, 1997; De Boeck et al., 2001). For instance, intracerebral administration of CRH triggers a dose-dependent increase in swimming activity in chinook salmon, while a CRH antagonist reduces locomotor activity and the time that it takes fish to find cover in a novel environment (Clements et al., 2002). The CRH-produced hyperactivity is enhanced by concurrent activation of the brain serotonergic system (Clements et al., 2003).

**ENDOCRINE REACTIONS AND EMOTIONS IN FISH.** Do these stress-induced endocrine changes support the hypothesis that fish experience feelings and emotions? Favoring this assumption are

the parallels in the conditions under which fear- and anger-like endocrine changes occur in fish and mammals. When sea bream are captured, their blood level of cortisol and catecholamines increases several-fold and remains high for some time after confinement (Rotlant et al., 2001). This enduring change is associated with symptoms of depression, such as decreased appetite, immunosuppression, decreased growth rate, and increased mortality (Gregory and Wood, 1999). In the brook char, crowding in an aquarium elevates plasma cortisol levels (Vijayan and Leatherland, 1990). Some of these behavioral effects can be reproduced by chronic cortisol administration (Pickering and Pottinger, 1989).

Correlations between endocrine and emotional changes have been studied in trout. When trout are paired in a tank, fights ensue and, depending on the outcome, one fish becomes dominant and the other submissive (Abbott and Dill, 1989). Within minutes of such a staged fight, plasma cortisol levels rise both in the loser and the winner (Sloman et al., 2000). However, while cortisol concentration drops within hours to control levels in the winner, it keeps rising in the loser (Øverli et al., 1999). Apparently, the loser develops a state of chronic anxiety. This inference is supported by the observation that the increase in plasma cortisol level in the loser is proportional to its overtly expressed submissive behavior (Sloman et al., 2001). Likewise, cortisol-treated trout tend to become winners when paired with size-matched but untreated fish, and that treatment reduces the probability that a small fish will become subordinate to a larger fish (DiBattista et al., 2005). As in mammals, the “frustration” of a mid-size trout when threatened by a larger one often produces “displaced” aggression directed toward a smaller fish (Øverli et al., 2004). Finally, there is some evidence in trout for (i) episodic *fear*, the transient defensive response to a threatening stimulus; (ii) chronic *anxiety*, the more prolonged manifestation of stress under certain conditions, such as crowding; and (iii) *timidity*, as a genetically-based temperamental trait. Rainbow trout were separated into high-responding (HR) and low-responding (LR) individuals on the basis of their cortisol response to stress, and were subsequently bred selectively (Pottinger and Carrick, 1999). It was found that offspring of the LR trout tend to become submissive in staged fights with HR trout (Pottinger and Carrick, 2001). LR trout also displayed more locomotor activity when challenged by an intruder and were feeding less than HR trout (Øverli et al., 2002). Interestingly, this difference in aggression between the two lines occurs only when the animals are tested in an unfamiliar environment but not when they were tested in their home base (Schjolden et al., 2005). The inborn temperamental disposition is apparently influenced by epigenetic factors.

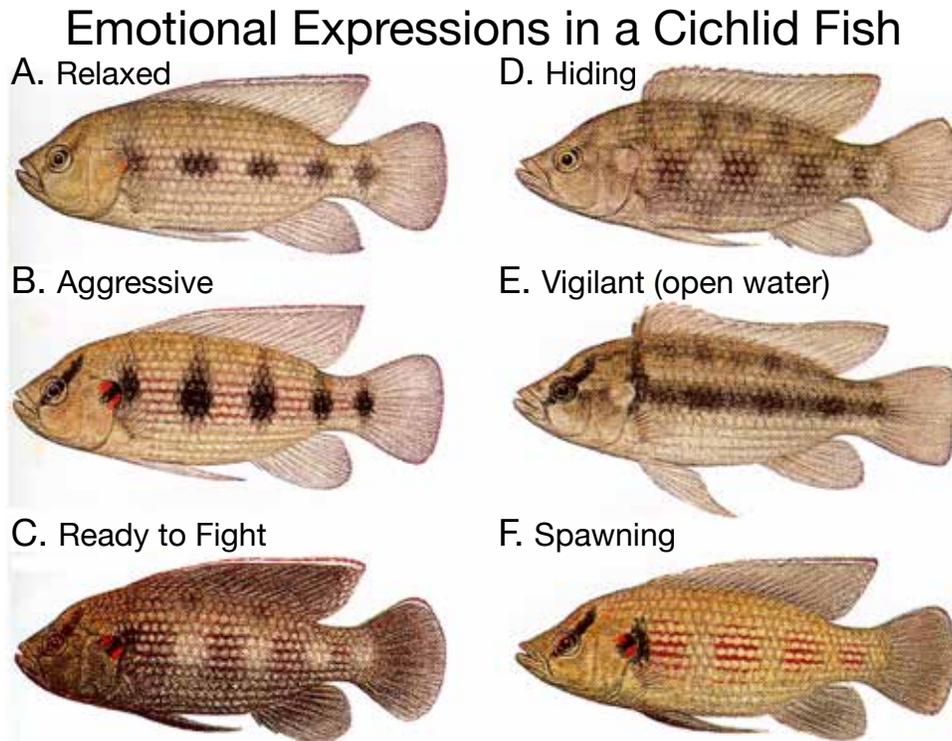
In addition to the shared endocrine mechanisms in agonistic behavior, there are also shared mechanisms in both fish and mammals in the affects regulating sexual and parental behavior. It has been known for some time that male goby engage in courtship behavior when exposed to water previously holding a gravid female (Tavolga, 1956). Of several internal body fluids taken from the gravid female, only ovarian fluids elicit this male behavior. Courtship behavior was abolished in males rendered anosmic. In different species of teleosts, courtship can be induced outside the breeding season by peripherally administered testosterone and related androgens (Rohr et al., 2001; Pall et al., 2002). Indeed, implants of androgens induce female goldfish to display male sexual behavior (Stacey and Kobayashi, 1996). Castration of the male abolishes seasonal courtship display but is restored upon implantation of testosterone and other steroids (Salek et al., 2001). The blood concentration of testosterone is 34 times higher in the

male stickleback during courtship than later when it takes care of its brood (Pall et al., 2002). Likewise, there is a decrease in the concentration of androgens in the mouthbrooding tilapia after the eggs are laid and parental behavior commences (Specker and Kishida, 2000).

**3.2.3. Behavioral Studies of Emotional Expression in Fishes.** Gross endocrinological and physiological manifestations may not be sufficient evidence to attribute specific affective states to others. We also have to consider concurrent emotional expressions and actions, and the context in which the visceral changes occur. Indeed, in daily life we use emotional expressions to infer the affective state of others. Seeing a person get red in the face and clenching his fist upon being insulted, we justly assume that he is angry, and that attribution is reinforced when that person strikes his adversary. Fish, likewise, display emotional expressions of anger by skin color changes and bodily movements that conspecifics respond to appropriately. Accepting that fish can be angered, what other affects may we attribute to them? Adhering to the principle of parsimony (Morgan, 1894), we can postulate only affective states for which we have behavioral evidence. We are justified to assume that fish suffer something like fear or terror when hooked because, as every fisherman knows, they struggle hard to escape. But may we attribute amicability, feeling of friendliness to fish that aggregate in shoals when feeding and form schools when they cruise or migrate? May we assume that when some species of fish display pair-bonding behavior, it is motivated by something akin to affection or love? May we assume that when fish guard the eggs they lay, and care for their young, like mouth brooders do, they are motivated by parental affection but parental affection is absent in species that abandon the eggs after spawning?

**EMOTIONAL EXPRESSIONS AS SPECIES-SPECIFIC COMMUNICATION OF AFFECTS.** We communicate our affective state to others by emotional expressions, informing them whether we are pleased or displeased, happy or sad, afraid or angry, surprised or disgusted, and so forth (Collier, 1985). For humans, facial expressions are the principal means of emotional communication. These expressions have universality across cultures (Darwin, 1872; Ekman, 1980), and are displayed in neonates (Landis and Hunt, 1939; Wolff, 1963; Hiatt et al., 1979; Izard et al., 1980; Ganchrow et al., 1983), indicating that facial expressions are species-specific reactions of innate origin rather than learned activities. This inference is supported by the observation that the facial expressions of happiness and sadness are indistinguishable in children born deaf and blind from those displayed by normal children (Eibl-Eibesfeldt, 1973). The facial expression of emotions is also well developed in higher primates, like apes and some monkeys (Kohts, 1935; van Hooff, 1972; Chevalier-Skolnikoff, 1973). Primates also use vocalization to communicate their feelings and emotions to conspecifics. For instance, Jürgens (1982) identified five different calls in squirrel monkeys: (i) purring-spitting—expressing aggressive assertiveness; (ii) groaning-shrieking—reflecting uneasiness and fear; (iii) clucking-yapping—warning about the approach of a predator; (iv) chirping-squealing—expressing submissiveness and plea for companionship; and (v) twittering-chattering—communicating pleasure and contentment. Again, there is evidence that these expressions are inborn traits. Squirrel monkeys reared from birth by mothers whose vocal cords were cut to prevent the young from learning the calls, vocalized normally and responded appropriately to calls emitted by conspecifics (Winter et al., 1973). Other mammals use different avenues to express their emotional state. The domestic dog, for instance, wags its tail when it is happy, and retracts its tail under its belly, much as

wolves do, when sad (Schenkel, 1948). Many fish use skin color changes to communicate their affective state to conspecifics. For instance, Wickler (1963) reported that male banded jewelfish, a cichlid, displays different skin markings when relaxed, when trying to establish a territory, when aroused to fight, when hiding in vegetation, when fleeing from some threat in the open waters, and when ready to spawn (Fig. 3-17). Obviously, we cannot directly ascertain whether a fish has feelings in the sense of subjective experience. But we face the same problem with all other beings, including our own kind. We cannot directly feel the pain, fear or joy of others, we infer these covert (private) affective states from their overt (public) displays or behavior, such as their emotional expressions and actions. But if it is true that affects play a role in fish behavior, what kind of emotions may we attribute to them? Below we provide behavioral evidence for the following putative affective states in fish: (i) the agonistic affects of fear, anger and hostility; (ii) the social affects of amicability and gregariousness; and (iii) the sexual affects of lust and amorousness. Some species of fish also display rudiments of parental emotions.

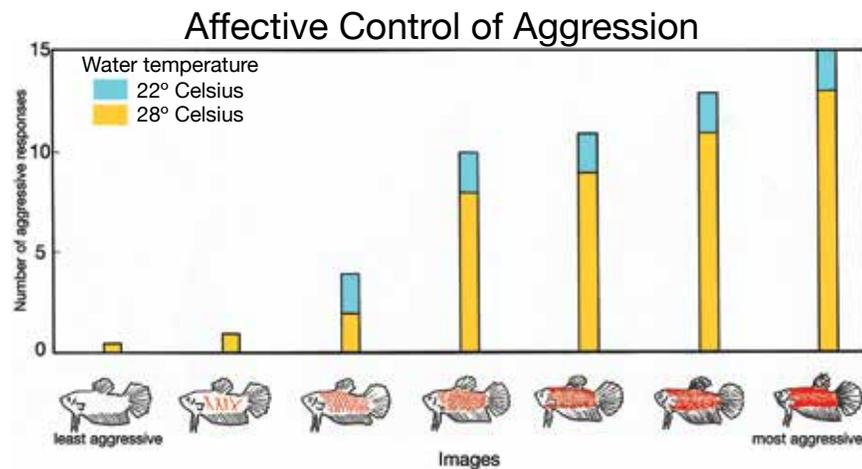


**Fig. 3-17.** Pigmentation changes in a cichlid (banded jewelfish) interpreted as emotional expressions of affective states. (Modified after Wickler, 1964; from Eibl-Eibesfeldt, 1970.)

**AGONISTIC DISPLAYS AND BEHAVIOR IN TERRITORIAL FISH.** Many fish acquire a home range or territory which they patrol and defend against intruders or competitors by offensive displays. These displays include, as already alluded to, changes in skin color from inconspicuous to obtrusive, the erection of gill covers, the spreading of fins, beating the tail as a menacing gesture, and such aggressive actions as snapping, biting, or butting the opponent (Eibl-Eibesfeldt, 1970). However, the holder of the territory or the intruder may terminate the fight by a display of submission. Submissive displays include fading of skin pigmentation, folding of the fins, and actions like retreating. In the male goby, the skin change is simple: it becomes darker when an intruding male enters in territory, and that aggressive signalling is followed

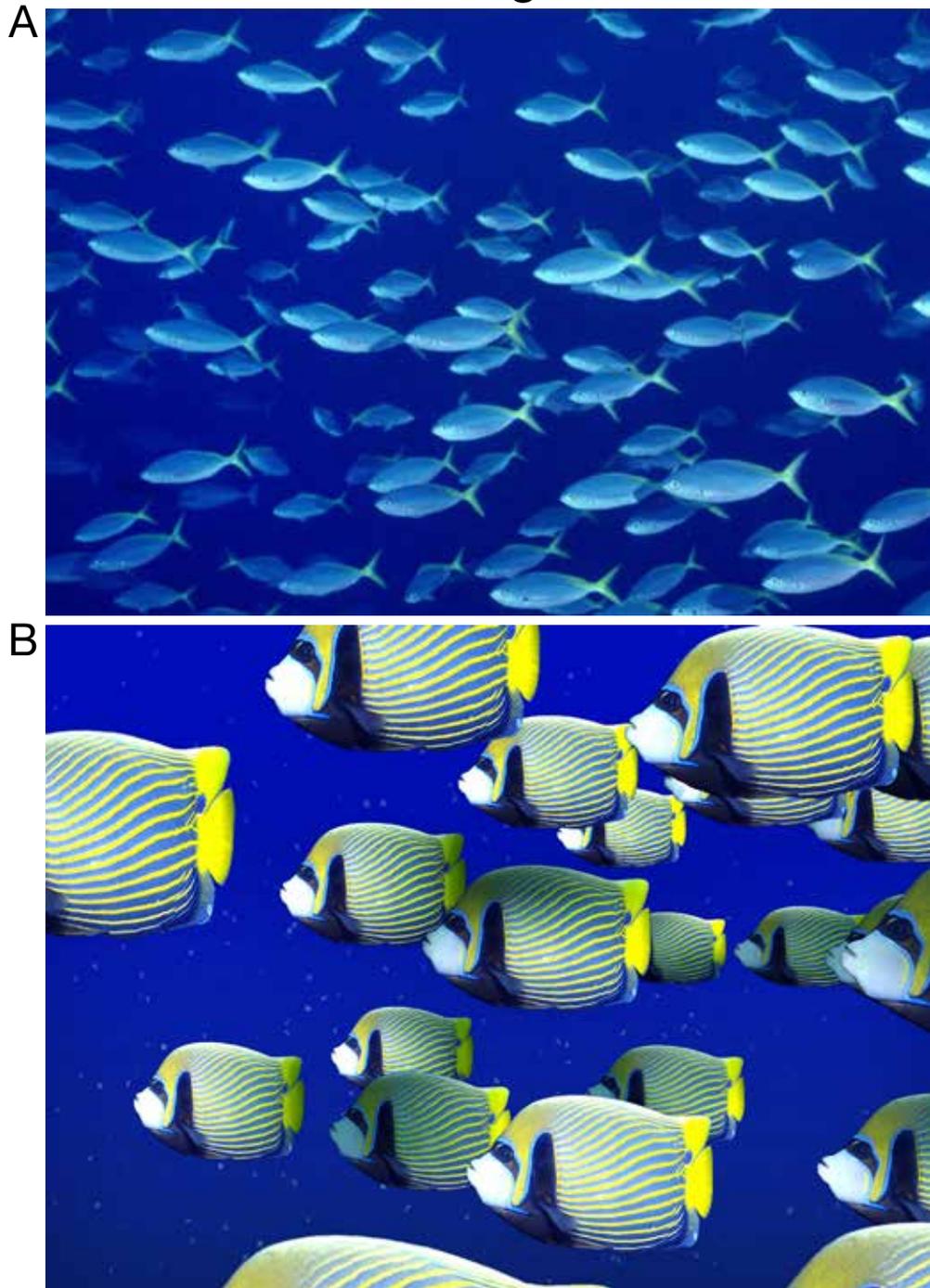
by attack if the intruder does not withdraw (Tavolga, 1969). Color changes as emotional expressions of dominance and submission are more complex in various species of cichlids. In one species (*Haplochromis*), the aggressive fish displays conspicuous vertical stripes, while the vanquished fish displays horizontal stripes (Albrecht, 1966). In another cichlid (*Aequidens paraguayensis*), the subordinate fish loses its color markings, whereas the markings of the dominant fish become more conspicuous in proportion to its level of arousal (Timms and Keenleyside, 1975). If a male Siamese fighting fish (*Betta splendens*) is placed in an aquarium already occupied by another male, a stereotypic sequence of aggressive reactions is triggered (Bronstein, 1998). That begins with the “intruder” approaching and then withdrawing several times from the territory holder. This maneuver may last for several minutes. Then the two start to fight, lounging at one another and biting. The combat may last several hours until one of them withdraws. This communicates defeat and leads to the establishment a dominance relationship between the two, the winner becoming the master of the territory. That hierarchic social relationship may endure for several days. Using artificial models of Siamese fighting fish, Lissmann (1932) found a linear relationship between increased levels of skin pigmentation and frequency of attacks by the challenged male (Fig. 3-18).

**Fig. 3-18.** Heightened frequency of attacks by Siamese fighting fish in response to artificial models with increased levels of body coloration. (Modified from Lissmann, 1932)



**THE GREGARIOUS BEHAVIOR OF SHOALING AND SCHOOLING FISH.** The majority of the 25,000 known extant species of fish form social aggregates, known as shoals and schools (Shaw, 1970; Radakov, 1973; Pitcher, 1988). Members of a shoal move randomly about in a loosely organized formation as they feed but swiftly join ranks to form a school when they proceed from one site to another, when a predator is detected, or some other threat is perceived. When schooling, all the fish line up parallel to one another and maneuver together in a tight formation (Fig. 3-19). Schools may vary in size from two or three fish to several millions of conspecifics. Although the fish act in unison, no leadership is evident. When the school turns to the right or to the left, individuals formerly on the flank become the leaders and vice versa. Schooling appears to be an inborn behavior (Shaw, 1970). Newly hatched minnows initially display an ambivalent approach-withdrawal relationship toward one another; then they intermittently swim in parallel; finally, when they reach about 10-12 mm in length, they swim continuously in unison. But this is not a learned behavior because if isolated fish are brought together when they are about 20 days old, they immediately start to swim in parallel.

## Schooling Fish



**Fig. 3-19.** Alignment of schooling fish. (A. From [www.giantpanther.com/wp-content/uploads/2011/02/School-of-Fish-III.jpg](http://www.giantpanther.com/wp-content/uploads/2011/02/School-of-Fish-III.jpg); B. from [www.phillaird.com/Images/Colorful\\_fish\\_school/Blue-and-Yellow-Fish-school.jpg](http://www.phillaird.com/Images/Colorful_fish_school/Blue-and-Yellow-Fish-school.jpg))

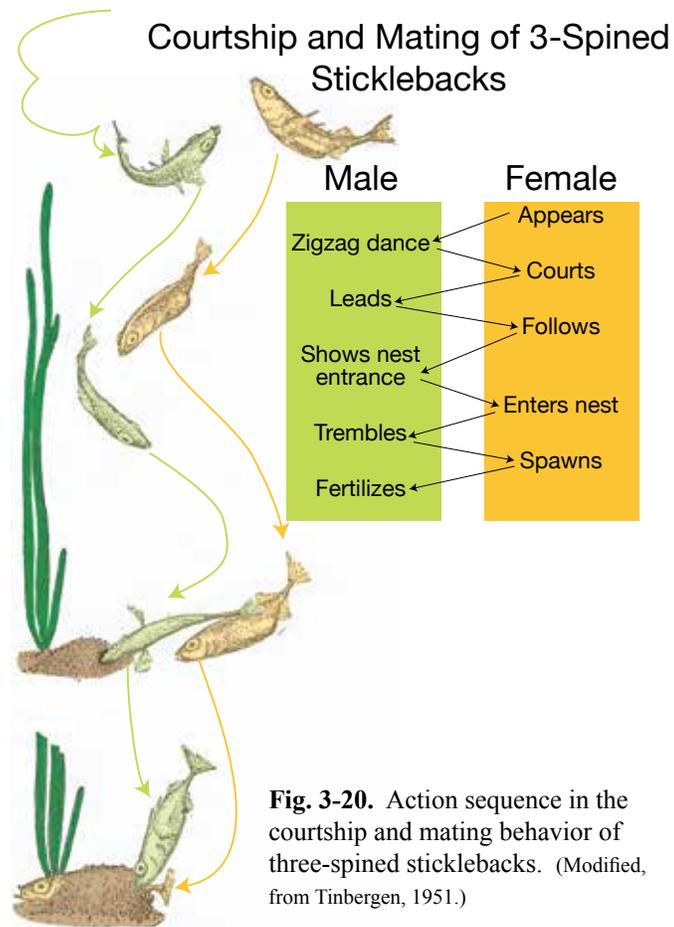
Experiments indicate that schooling is primarily guided by vision. A fish separated by a glass partition from the others, which abolishes olfactory and mechanical stimulation, persists in swimming in parallel with the others, changing direction and speed as they do (Pitcher, 1988). On the other hand, blinded fish do not school. Schooling aids the species by deterring predator attack by virtue of their large collective size and constantly changing configuration. Moreover, there is experimental evidence that foraging minnows moving in larger shoals locate a hidden food source faster than those foraging in smaller shoals (Pitcher et al., 1982) and flee faster from a predator model (Magurran et al., 1985). But schooling also has disadvantages because both predators, whether fish or birds, detect schools more easily than an individual fish and follow them more persistently, easily harvesting those on the periphery of the school. We suggest that a major factor in individual fish joining their kind is an emotional one: being surrounded by conspecifics with a particular coloration reduces anxiety. Indeed, it has been reported that an isolated minnow or goldfish becomes timid, spending most of its time hiding rather than feeding, but the same fish engages in progressively more foraging as it is transferred to larger shoals (Pitcher, 1988). Hence, the emotional benefit of schooling to the individual may be greater than its collective survival assurance.

In addition to this affiliative tendency, there is also evidence that fish communicate fear when danger is detected. When injured, minnows release a chemical alarm substance, and that induces all other minnows to go into hiding (Frisch, 1938). The chemically characterized alarm substance, a pheromone, functions as a species-specific antipredator signaling agent (Smith, 1982). Minnows in their natural habitat avoid traps marked with this substance (Mathis and Smith, 1992) as do sticklebacks marked with their own alarm substance (Chivers and Smith, 1994). The crucian carp swims rapidly to the bottom when exposed to extracts from the skin of injured conspecifics and hides wherever it can (Hoglund et al., 2005). Following administration of an anxiety-reducing drug (benzodiazepine) in a dose that does not produce sedation, causes minnows to display no alarm reaction when exposed to the pheromone (Rehnberg et al., 1989).

**COURTSHIP DISPLAYS AND SEXUAL BEHAVIOR IN BREEDING FISH.** Distinctive skin changes, either heightened pigmentation or pattern change, is widespread in many species of fish during the breeding season (Burnie and Wilson, 2001). For instance, Pacific sockeye salmon of both sexes have steel-blue heads and backs and silvery flanks before the reproductive season. When they return from the ocean during the summer to enter their home stream to breed, their heads turn bottle-green and their bodies become bright red. Pink salmon, normally metallic blue, become olive green or yellow when they begin their upstream migration, whereas Atlantic salmon develop a silvery sheen with blue backs and black spots along their flank. The exact role that these skin color changes play in the frenzy of salmon to reach their breeding ground is not well understood but their emotional arousal and powerful motivation is evident from their persistence in swimming against the river current, leaping over waterfalls or weirs, and abstaining all the while from feeding.

While the color change of migrating salmon endures through the breeding season, in other fish the color change is limited to bouts of courtship behavior. The skin of the unicorn fish that forages above coral reefs is normally an inconspicuous dark color. However, when a male encounters a female during the breeding season, within seconds it displays its conspicuous color markings: blue lips, a blue caudal fin, and light blue spots on its back and vertical stripes on its side (Eibl-Eibesfeldt, 1970). All these brilliant markings disappear as soon as the courtship display ends. The male haddock ready to mate uses not only its distinctive skin coloration but also specific bodily movements and vocal calls during its courtship display (Hawkins, 1986). With all its fins erect, the male approaches the gravid female and swims in tight circles underneath her while at the same time repeatedly emitting a clicking sound. As the female follows, a rasping call is emitted and the male mounts the female. This vocalization stops when the female releases her eggs into the water and, in turn, the male ejaculates its sperms. These displays evidently reflect the highly aroused state of the suitor which, we assume, is coupled with a corresponding affective experience of sexual ardor.

Fish that spawn in large groups tend to be promiscuous, others form a transient or enduring pair bond. In the latter, acceptance of a mate by the female is influenced by such factors as the size of the male, the extravagance of its decoration, its competitive aggression, and the intensity of its courtship display (Halliday, 1983). In gobies, the female may also display distinctive ornamentation during the breeding season, and male gobies engage in more intense courtship when confronting a colorful female than a drab one (Amundsen and Forsgren, 2001). An example of the affective regulation of sexual behavior in fish is the complex interaction of pair-bonded three-spined sticklebacks during the breeding season (Fig. 3-20), a pattern of behavior that must be hardwired because it is typical of all members of the species (Tinbergen, 1951). As a visibly gravid female cruises past a male's territory, the male starts a vigorous zigzag dance, displaying its conspicuous red mouth and belly. If the enticed female stays around, the male guides her to the entrance of the nest, and trembling over her induces her to lay her eggs. When the female departs, the eggs are fertilized by the male and it takes over the paternal task of fanning the eggs and guarding the nest against intruders. Even more complex is the courtship behavior of the Siamese fighting fish (Simpson, 1968). The sexually aroused male flares his gills and spreads his fins and tail when a female appears (Fig. 3-21). The skin of the female darkens and she twists her body as the male continues its display. The male starts to make bubbles, which float to the surface. Thereafter, the male wraps his body around the female and she responds by releasing several eggs. The male squirts the eggs with seminal fluid (milt). This sequence may be repeated several times and, once that ends, the male collects the eggs in its mouth and deposits them in the bubbles. The male guards the bubbles until the hatched free-swimming larvae leave the nests. This behavior suggests the emergence of parental affection in some species of fish.



## Courtship Display of Siamese Fighting Fish



**Fig. 3-21.** Courtship display of a *Betta splendens*. (From betta\_fish.jpg.)

**3.2.4. *The Comparative Neurology of Emotions in Mammals and Fishes.*** Support for the hypothesis of the involvement of emotions in piscine behavior comes from the evidence that components of the mammalian “emotional brain” and “limbic system” have evolved in fishes. As we describe below, several piscine brain structures—including the brainstem reticular formation, the hypothalamus, and the amygdala—play an important role in behavioral arousal and mobilization when responding to nociceptive stimulation; in ravenous eating when food deprived; in anger- and fear-like reactions when challenged or threatened; in amicable social relations with conspecifics; and amorousness when sexually stimulated.

*The Brainstem Reticular Formation and Affective Arousal in Mammals and Fishes.* The brainstem reticular formation has been implicated in mammals and man in the transition from somnolence to vigilance, and in emotional arousal and mobilization (Moruzzi and Magoun, 1949; Lindsley, 1951). The mammalian reticular formation is an extended field within the core of the neuraxis that stretches from the hypothalamus to the midbrain tegmentum and the medulla, and is composed of a heterogeneous population of neurons embedded in a matrix of ascending and descending fiber bundles (Brodal, 1957). Unlike the “specific” areas of the CNS—which receive modality-specific sensory messages and action-specific commands to discrete motor nuclei—the reticular formation is conceived of as a “diffuse” integrative system. It is the target of excitatory input from virtually all the senses of the body (interoceptive and exteroceptive) and the source of a “nonspecific,” ascending and descending modulatory output to nearly all regions of the CNS.

**THE MAMMALIAN RETICULAR FORMATION AND AFFECTIVE AROUSAL.** Interest in the function of the reticular formation was prompted in the late 1940s by two experimental findings. First, that its electric stimulation in cats produces a change from the synchronized cortical EEG activity, a pattern associated with relaxed wakefulness, to desynchronized EEG, a pattern reflecting behavioral arousal (Moruzzi and Magoun, 1949). Second, that its destruction produces somnolence or coma in cats (Lindsley et al., 1949) and monkeys (French et al., 1952). These observations gave rise the idea that the brainstem reticular formation is the activating mechanism of emotional arousal (Lindsley, 1951). Subsequent research disclosed the presence in the reticular formation and its neighborhood—in particular the raphe nuclei, the locus coeruleus, and the ventral tegmental area—of pools of neurons that synthesize and store monoamines (norepinephrine, serotonin and dopamine) and transport these neurotransmitters by axonal flow to distant sites, including the thalamus, the hippocampus, the amygdala, and the cerebral cortex (Dahlström and Fuxe, 1964; Ungerstedt, 1971; Moore, 1980). Although the exact mode of action of these transmitters at different CNS sites is unclear, there is experimental and clinical evidence that these monoamine pathways are part of a complex brain circuitry that controls affect and mood in human subjects (Whybrow et al., 1984).

**THE PISCINE RETICULAR FORMATION AND AFFECTIVE AROUSAL.** The reticular formation, distinguished by the presence of large reticulospinal neurons in fish, is one of the oldest components of the vertebrate CNS (Ariëns Kappers et al., 1936; Herrick, 1948). In the lamprey, reticulospinal neurons are targets of input from all the major sensory systems (Dubuc and Grillner, 1989; Deliagina and Pavlova, 2002; Viana Di Prisco et al., 2005) and the midbrain (El Manira et al., 1997; Zompa and Dubuc, 1998a,b; Brocard and Dubuc, 2003). It has therefore

been implicated in the cyclical alternation between sleep and wakefulness, and in prompting a swift escape reaction when danger is signaled by any one sensory source.

Wakefulness is the aroused state of sensory contact with the outside world and all higher animals alternate between that state and sleep, when they withdraw from such contact and try to rest. Diurnal animals usually sleep at night, and nocturnal animals prefer to sleep during the day. Although some fish—i.e., those that swim continuously to keep their gills oxygenated—may never sleep in the strict sense of the term (Kavanau, 1998), there is evidence that many do. For instance, a sleep-like state has been described in the diurnal zebrafish, consisting of a characteristic posture and elevated threshold to sensory stimulation (Zhdanova et al., 2001). Little is currently known about the regulation of the sleep-wakefulness cycle (the intrinsic circadian rhythm) in relation to the day-night cycle in fish, except for the involvement of melatonin, the hormone of the pineal gland, which plays a role in inducing sleeping in mammals and man. In free swimming flounder kept under a normal light regimen, the concentration of melatonin is much lower during the daytime than at night (Kulczykowska et al., 2001). When kept under constant illumination, this circadian rhythm is abolished.

More is known about the role of the piscine reticular formation in fear reactions. In the primitive lamprey, the axons of large reticular neurons (Mauthner and Müller cells) form the principal descending tract from the brainstem to the spinal cord, and are responsible for their swift flight response when subjected to intense stimulation (Orlovsky, 1970; Rovainen, 1978; Ronan, 1989; Deliagina et al., 2000). The reticulospinal Mauthner cells are similarly responsible for the fast flight response in teleosts (Retzlaff, 1957; Zottoli et al., 1987; Eaton et al., 2001). Hence, the reticular formation may serve fish as a sensitive but indiscriminate signaling mechanism to trigger escape when threatened in any way. The reticular formation is also involved in prompting swift reactions to specific stimuli. For instance, it has been shown that the visually guided prey-catching of zebrafish larvae—which promptly attack paramecia placed in their medium and ingest them in large numbers—is mediated by the optic lobe and two pairs of identified reticulospinal neurons that convey motor commands to the spinal cord (Gahtan et al., 2005). Following optic lobe lesions, zebrafish fail to detect and respond to paramecia. This tecto-reticulospinal network has also been demonstrated in trout (Bosch and Paul, 1993) and goldfish (Torres et al., 2005). In addition to the large reticulospinal neurons, smaller serotonergic and dopaminergic neurons that originate in the piscine brainstem, hypothalamus, and a few other regions of the fish brain (Ekstrom and Ebbeson, 1989; Funakoshi et al., 2000, 2002; Rink and Wulliman, 2002, 2004) may be involved in emotional arousal in fish. It has been reported that exposure of damselfish to a predator, alters serotonergic activity in the brainstem, hypothalamus and telencephalon (Winberg et al., 1993) as does fighting both in the winner and the loser (Winberg et al., 1996; Øverli et al., 1999). Moreover, differences have been noted in monoamine concentration and turnover in the brains of high-stress responsive (HR) and low-stress responsive (LR) strains of trout (Øverli et al., 2001; Schjolden et al., 2006).

*The Role of the Brainstem Central Gray in Pain in Mammals and Fishes.* It is of vital importance to all of us that our organs and tissues are protected from damage, and it is the experience of pain and suffering that motivates us to seek relief when hurt or injured. Pain,

which typically produces agitation and withdrawal, or reduced use of the affected body part, is mediated by a class of free ending nerves distributed in skin, muscle and viscera, known as nociceptors (Iggo, 1974). The typical nociceptive afferents are thin, unmyelinated nerve fibers that contain substance P as a neurotransmitter, and terminate in the superficial layers of the spinal cord dorsal horn and its homologue in the brainstem (reviewed in Altman and Bayer, 2001). Nociceptors, unlike the afferents conveying innocuous tactile stimuli, are slow-adapting neurons, that is, they persist in discharging and producing pain as long as the injurious stimulus is applied (Burgess and Perl, 1973).

**PERIAQUEDUCTAL MECHANISMS MEDIATING PAIN AND ANALGESIA IN MAMMALS AND FISHES.** The mammalian brain region specifically implicated in the production of pain, as well as its amelioration, is the midbrain periaqueductal (central) gray. Early studies indicated that rage reactions may be elicited in cats and dogs following removal of the entire forebrain (Bazett and Penfield, 1922; Bard, 1934). This gave rise to the idea that some spared midbrain or brainstem structure mediates pain. It was subsequently demonstrated that direct stimulation of the periaqueductal gray produces signs of suffering, rage, and emotional vocalization in cats (Delgado, 1955; Hunsperger, 1956) and monkeys (Jürgens, 1979), whereas destruction of the periaqueductal gray leads to attenuated sensitivity to nociceptive stimuli and reduced emotionality in rats (Liebman, et al., 1970; Edwards and Adams, 1974). There is also some evidence that different periaqueductal sites produce distinct types of somatic and autonomic responses to stressors or injury (Bandler, 1988; Keay and Bandler, 2004).

Interestingly, it has also been found in cats that, instead of triggering pain, electrical stimulation of the periaqueductal gray produces analgesia (Mayer et al., 1971; Liebeskind et al., 1973). There are also clinical reports that central gray stimulation in human patients produces either pain or analgesia (Nashold et al., 1969; Richardson and Akil, 1977; Boivie and Meyerson, 1982; Young et al., 1984). The analgesic effect of periaqueductal gray stimulation has been attributed to two mechanisms. First, the release of endogenous opiates—enkephalins and endorphins (Hughes et al., 1975; Hökfelt et al., 1977)—which silence nociceptive neurons of the brainstem in both animals (Atweh and Kuhar, 1977) and man (Hosobuchi et al., 1977). Second, the activation of serotonergic fibers (Deakin and Dostrovsky, 1978; Zeng et al., 1991). While injection of corticotropin-releasing hormone into the periaqueductal gray turns calm animals into agitated ones (Martins et al., 1997; Ku et al., 1998), the injection of opiates produces analgesia (Pert and Yaksh, 1974; Frenk et al., 1986). Because pain interferes with the ongoing vital activities of an animal, this dual mechanism allows an individual to avoid tissue damage either by passive withdrawal or active fighting or fleeing from its perpetrator.

Do fish suffer pain when injured? There is accumulating evidence that they do (Chandross et al., 2004). For instance, rainbow trout respond to injurious stimuli—pressure, excessive heat, and toxic chemicals—with similar physiological responses as mammals (Sneddon, 2003a). When a noxious substance is applied to the lip of a trout, the rate of its opercular beating accelerates and it stops feeding. Pain is mediated in fish by abundant A-delta fibers in the trigeminal nerve (Sneddon et al., 2003a). It is possible that the triggering of locomotion by stimulation of the periaqueductal gray in lampreys (Sirota et al., 2000) is due to the activation of this nociceptive center. Significantly, both substance P- and enkephalin-containing neurons

are present in the brainstem, diencephalon and telencephalon of salmon (Vecino and Ekstrom, 1990; Vecino et al., 1995) and zebrafish (Porteros et al., 1999). And, as in mammals, morphine administered to fish has an analgesic effect (Jansen and Greene, 1970; Ehrensing et al., 1982; Chervova, 1997; Sneddon et al., 2003b) and so does amphetamine and pentobarbital (Lett and Grant, 1989).

*The Role of the Hypothalamus and the Amygdala in Rage and Fear in Mammals and Fishes.* In a pioneering investigation, Goltz (1892) removed the cerebral hemispheres of a dog and found that while that operation produced severe cognitive deficits (for instance, the dog could not recognize his master or respond when called) the animal's emotional reactivity increased. When touched or slightly disturbed, the operated dog reacted with a full-blown expression of rage. The persistence of rage after decortication was confirmed by others in dogs as well as cats (Bard, 1928; Schaltenbrand and Cobb, 1930; Bard and Rioch, 1937). However, when a part of the brainstem was also extirpated in addition to the cerebral cortex, the rage reaction was abolished (Bard, 1934). The interpretation of these results was that the heightened rage reaction following decortication was due to the release of some lower-level emotional brain mechanism from neocortical inhibition.

**THE ROLE OF THE HYPOTHALAMUS IN RAGE AND FEAR IN MAMMALS.** Concurrently with the foregoing demonstrations, evidence was emerging that the hypothalamus is one of the neural centers of emotional behavior. The demonstration of the pivotal role of the hypothalamus in the mediation of autonomic reactions (e.g., Karplus and Kreidl, 1912) was confirmed and extended by Hess and his associates and interpreted as emotional manifestations (Hess, 1932; Hess and Brügger, 1943; Hunsperger, 1956). Hess and his associates showed that electrical stimulation of the anterior hypothalamus in freely moving cats produces not only autonomic manifestations of rage but also well-directed attacks, with unsheathed claws, on anyone situated nearby. More recently, maps have been produced of the specific hypothalamic and brainstem sites that, when stimulated, produce either fighting or fleeing, interpreted as anger and fear reactions (Wasman and Flynn, 1963; Romaniuk, 1965; Bandler, 1984, 1988; Siegel and Pott, 1988).

The hypothalamus is connected in all vertebrates with various fore- and hindbrain structures as well as with the pituitary gland. As we have noted earlier, it serves as the head ganglion of the autonomic nervous system and of the pituitary gland. The pituitary gland stores and releases various hormones and humeral factors that circulate in the blood stream and modulate the functions of various internal organs (Arimura, 2000; Halász, 2000; Chaudhri et al., 2006). With special reference to the role of the hypothalamus in rage and fear reactions, and in their amelioration, it has been shown that its stimulation in freely-moving animals produces chemical changes that accompany symptoms of anxiety, and that these symptoms can be triggered by the administration of corticosteroids (ACTH) and corticotropin releasing hormone (Kojima et al., 1995; Mohamed, 2001). In contrast, oxytocin has a calming (anxiolytic) effect. In mammals, oxytocin is produced at two different hypothalamic sites, and one of these is implicated in emotional reactions. The oxytocin produced by the magnocellular paraventricular and supraoptic nuclei, which is conveyed to the pituitary gland (neurohypophysis) by axoplasmic flow, produces such visceral reactions as uterine contraction and milk ejection. Oxytocin

produced by parvocellular neurons and released intracerebrally is associated with such reproductive functions as nest-building and caring for pups in virgin rats (Insel and Shapiro, 1992; Pedersen et al., 1992), and also with stress reduction and amicability in a social setting (Uvnas-Moberg, 1998; Engelmann et al., 1999; Neumann et al., 2000; Parker et al., 2005).

**THE ROLE OF THE HYPOTHALAMUS IN RAGE AND FEAR IN FISH.** We have described earlier the aggressive or rage behavior of fish when confronting an intruder into their territories. Fear reactions are just as ubiquitous. Fish living in open waters are in constant danger of predation and react to the slightest disturbance with a startle response and rapid flight. This escape response is controlled in teleosts by a pair of giant reticular neurons in the medulla, the Mauthner cells (Bartelmez, 1915; Zottoli et al., 1987; Eaton et al., 2001). However, if the Mauthner cells are destroyed, the escape response to disturbance persists (Gahtan et al., 2002). Apparently, there are higher-level flight circuits in the fish brain. According to one study, electric stimulation of the hypothalamus in freely moving bluegills triggers aggressive behavior, such as the attack of its own mirror image or chasing another bluegill (Demski and Knigge, 1971). There is some evidence for the role of hypothalamic neurohumoral agents in the fear and rage reactions of fish. The skin color changes of emotional expression in fish are produced by chromatophores, stationary or motile cells of different colors embedded in the skin (Fujii, 2000). The pigmentation change of defeated (anxious) arctic charr has been associated with an increase in the monoamine, ACTH, and melanin stimulating hormone (MSH) concentration of blood (Hoglund et al., 2000) and the regional activation of chromatophores is controlled by the hypothalamic release of MSH (Baker and Bird, 2002).

In addition to fleeing, many alarmed fish also secrete a substance that communicates danger to conspecifics. It has been discovered some time ago (Frisch, 1938) that injured minnows release a chemical substance into the water that induces conspecifics to seek shelter. Frisch called the chemical “alarm substance” (*Schreckstoff*). It has been found more recently that minnows avoid traps marked with this substance in their natural habitat (Mathis and Smith, 1992), and sticklebacks respond likewise to their own alarm substance (Smith, 1982; Chivers and Smith, 1994). The alarm pheromone is secreted by large epidermal cells (club cells) and it functions as a species-specific antipredator signaling agent. This simple chemical communication of danger to conspecifics has not been preserved in higher vertebrates; however, teleosts do display complex forms of defensive behavior and at least some of their neural and endocrine mechanisms have been preserved in humans as a piscine legacy.

**THE ROLE OF THE AMYGDALA IN FEAR AND RAGE IN MAMMALS AND FISH.** In addition to the hypothalamus, the telencephalic amygdala also plays a role in anger and fear reactions in mammals and man. Electrical stimulation of the amygdala in cats and rats evokes autonomic and somatic manifestations of defensive behavior and increased emotionality (Gastaut et al., 1952; Kaada et al., 1954; Roldán et al., 1974), and its destruction results in taming and reduced emotionality (Rosvold et al., 1954; Thompson et al., 1969; Kling, 1972; Miczek et al., 1974). In human patients, electrical stimulation of the amygdala may provoke either expressions of rage and uncontrollable violent behavior (Mark et al., 1972) or fear and anxiety (Halgren et al., 1978). The amygdala triggers these agonistic emotional responses by way of its neural and humoral connections with the hypothalamus and brainstem (Gray, 1973; Korte et al., 1992;

Davis, 1994; van Bockstaele et al., 1998). For instance, the injection of CRH into the central amygdaloid nucleus produces fearful behavior in rats (Ku et al., 1998; Wiersma et al., 1998). Notably, the emotional reactions produced by amygdaloid stimulation have a different temporal pattern than that produced by hypothalamic stimulation: it builds up gradually and fades away more slowly (Zbrozyna, 1972). Unlike the hypothalamus, the amygdala may be a higher-level (limbic) center for the modulation of anger and fear. That is suggested by reports that amygdaloid lesions interfere with avoidance learning in rats (Coover et al., 1973; Nagel and Kemble, 1976; Davis, 1992; LeDoux, 1993), cats (Ursin, 1965), and monkeys (Weiskrantz, 1956). Similarly, there is some evidence that aversive conditioning is associated with the functional activation of the amygdala in normal human subjects (Buchel et al., 1998; LaBar et al., 1998) and that amygdaloid lesions produce deficits in aversive learning paradigms (Bechara et al., 1995; LaBar et al., 1995). Another finding in patients with amygdaloid lesions has been the impairment in the ability to recognize the facial expression of fear in others (Tranel and Hyman, 1990; Young et al., 1996; Adolphs et al., 2001). Corroborating this, functional scanning studies in normal humans indicate that the amygdala is activated during the processing of fearful facial expressions (Morris et al., 1996) and other emotional displays (Garavan et al., 2001; Hamann and Mao, 2002). In monkeys, neurons have been identified in the amygdala that increase their firing rate in response to threatening faces (Gothard et al., 2007) and other emotional expressions, such as screams (Kuraoka and Nakamura, 2007).

As we noted earlier, there is a putative homologue of the amygdala in fish (Northcut and Braford, 1980; Schroeder, 1980; Braford, 1995). Little is known about the role of this particular region in the behavior of fish. Ablation of the telencephalon has been reported to reduce territorial fighting in the Siamese fighting fish (Noble and Borne, 1941; de Bruin, 1980), the stickleback (Segaar, 1961), and some other species (Hale, 1956; Fiedler, 1967; Aronson and Kaplan, 1968; Overmier and Gross, 1974; Schwagmeyer et al., 1977; de Bruin, 1980). Whether this is due to the elimination of the presumptive amygdala in fish remains to be determined.

*The Role of the Hypothalamus in Hunger, Appetite and Satiety in Mammals and Fishes.* The regulation of feeding is a very complex process and there is evidence for its affective control in mammals and, as we shall try to show, also in fish. In order to regulate when, how much, and what kind of nutrient to procure and consume, the individual has to monitor its changing energy and substrate needs (which we know subjectively as general and special hunger) and the desirable or hedonic properties of the available nutrients (appetite). And to prevent obesity, there must be mechanisms to suppress excessive food consumption (satiety). Ongoing research has established that a multitude of sensory, neural and hormonal mechanisms, both peripheral and central, are involved in this regulation. And while the process is not fully understood, the following is known (Anderson, 1994; Havel et al., 2000; Chaudhri et al., 2006). Olfactory and gustatory sensors selectively respond to the aroma and flavor of available food items; receptors in the gastrointestinal tract monitor the volume of the ingested nutrients; and different hormones and enzymes signal nutrient concentration in the blood stream and in different body organs, including the brain, as well as available energy reserves in the form of deposits of fat and glycogen. For instance, there is evidence for a direct monitoring of glucose levels (hypo- or hyperglycemia) in the blood stream, and its indirect monitoring by way of hormones

and other signaling molecules, such as blood levels of insulin, the concentration of which increases when feeding, and glucagon, the concentration of which increases when starved. Cholecystokinin (CCK) released from the duodenum in response to high nutrient metabolite concentration acts as a satiety signal by reducing hunger sensation in man, and leptin produced by fat cells reduces food intake, and its deficiency leads to obesity. Brain mechanisms are also involved. For instance, orexin produced by the hypothalamus is a powerful hunger- and appetite-inducing agent.

**BRAIN MECHANISMS THAT REGULATE FEEDING IN MAMMALS.** Studies carried out in the mid-1900s indicated that the feeding behavior of rats is regulated by two antagonistic hypothalamic sites, the lateral hypothalamic (LH) “feeding center” and the ventromedial hypothalamic (VMH) “satiety center.” Researchers found that destruction of the VMH makes rats obese (Hetherington and Ranson, 1942), and that this effect is not due to a metabolic abnormality but to overeating, or hyperphagia (Brobeck et al., 1943). In contrast to VMH lesions, LH lesions makes rats refuse to eat; they become aphagic (Anand and Brobeck, 1951). It was subsequently reported that if only unappetizing food is available to VMH-lesioned rats, they do not become obese; in fact, their weight falls below that of normal animals (Teitelbaum, 1955, 1957). This suggested that the operated animals eat excessively because they become more pleasure-seeking or hedonistic. Recent studies have shown that the VMH contains a large population of neurons that respond to the concentration of glucose in the blood stream and is a target of serotonergic and dopaminergic inputs involved in emotional arousal (King, 2006). In addition to LH and VMH, the hypothalamic arcuate and paraventricular nuclei, and other scattered sites with receptors for various gastrointestinal hormones, appear to play a role in the regulation of feeding (Havel et al., 2000; Chaudhri et al., 2006).

**THE PUTATIVE ROLE OF THE HYPOTHALAMUS IN HUNGER, APPETITE AND SATIETY IN FISHES.** Feeding behavior varies greatly in different species of fish. Some feed on plants, others are scavengers or detritus feeders, still others are predators, preying on invertebrates or other fish. Some species of fish are bottom-feeders, others are surface-feeders; some inhabit coral reefs or rocky coasts, others muddy and murky shores; some live in swift rivers, others in placid ponds or lakes; still others in dark caves. Among the predators, some lie in ambush until the prey comes within striking distance, others cruise far and wide in search or pursuit of prey. Feeding often requires complex behavioral activities. Seasonally and regionally changing food resources have to be located; choices have to be made when to eat to minimize the risk of exposure to predators; the available nutrients have to be selected in terms of their caloric contents and the animal’s changing substrate needs. Depending on the habitat they occupy and their dietary preferences, different species of fish rely on different sense organs to locate, select, ingest, and swallow food. Whereas diurnal surface-feeders rely more on vision to locate prey (Atema et al., 1980), bottom-feeders and nocturnal fish use olfaction (Hara et al., 1986; Valentincic and Caprio, 1994, 1997) or gustation (Atema, 1971; Lamb and Finger, 1995; Linser et al., 1998). We assume that most of these choices are made on the basis of inborn sensory discriminations and regulated by affective evaluations, what we call likes and dislikes.

The hypothalamus plays a major role in the regulation of feeding behavior in fish (Horn, 1998). While weight increase is less of a problem for them than it is for terrestrial vertebrates,

fish float in the water while land animals have to carry their full weight, fish do stop feeding in many situations, such as when they migrate, spawn or care for their brood. As in mammals, hypothalamic stimulation triggers eating behavior in fish (Demski and Knigge, 1971; Savage and Roberts, 1975). As in mammals, various hormones and humoral agents have been implicated in the regulation of piscine feeding. Among these are glucagon (Silverstein et al., 2001), cholecystokinin (Peyon et al., 1999), neuropeptide Y (Narnaware et al., 2000), galanin and beta endorphin (Lin et al., 2000b), corticotropin-releasing hormone (Bernier and Peter, 2001), and leptin and orexin (Volkoff, 2006). However, it is not known whether fish have a satiety center.

Hypothalamic orexin (hypocretin) was initially believed to promote either feeding in animals and man (Sakurai et al., 1998) or wakefulness (de Lecea et al., 1998). The latter hypothesis was supported by the evidence that depletion of orexins, or their receptors, produces narcolepsy (Burdakov and Alexopoulos, 2005). However, a more general affective role of orexin is suggested by the findings that it promotes behavioral arousal, vigilance, and behavioral exertion (Siegel, 2004; Spinazzi et al., 2006; Yoshida et al., 2006) as well as pain amelioration (Mobarakeh et al., 2005). It has also been implicated in stress-induced reward seeking and drug addiction relapse (Boutrel et al., 2005; Harris et al., 2005). Orexin appears to be a piscine heritage in terms of its chemistry, localization in the hypothalamus, and its neural connections (Faraco et al., 2006), and by facilitating feeding behavior (Lin et al., 2000; Volkoff et al., 2005) and behavioral arousal (Faraco et al., 2006). In summary, the close parallels in the neural and endocrine mechanisms that control appetite and feeding in fish and ourselves justifies the conclusion that not only the hormonal and neural mechanisms but also some of the affective regulatory processes are a piscine legacy.

*The Role of the Hypothalamus in Amorousness and Parental Affection in Mammals and Fishes.* In most animal species, sexual behavior is limited to the reproductive season when both sexes undergo profound endocrine, physiological and behavioral changes. Seasonal gonadal maturation—the production of sperms and ova—is coupled with the production and release of testosterone in males, and estrogen and progesterone in females, which trigger a series of somatic and behavioral transformations in the two sexes (Henderson, 1997). The somatic changes include the appearance of secondary feminine and masculine morphological characteristics. Conspicuous among the behavioral changes are the seeking and pursuit of females by the male, and its courtship activity, the function of which is to prompt ovulation and induce sexual receptivity in the females. There is ample evidence that the hypothalamus is involved in the affective instigation of these vital activities both in mammals and fish.

**THE ROLE OF THE HYPOTHALAMUS IN AMOROUSNESS AND PARENTAL AFFECTION IN MAMMALS.,** Two regions have been implicated in the affective control of sexual behavior in male mammals: the hypothalamus and its rostral extension, the preoptic area. In several mammalian species, electrical stimulation of these sites facilitates copulation by males (Malsbury, 1971; Perachio et al., 1979) and, correspondingly, lesions of the anterior hypothalamus and medial preoptic area abolish that behavior (Heimer and Larsson, 1966-1967, Giantonio et al., 1970; Hart et al., 1973; Hart, 1974). Facilitation of male copulatory behavior has also been observed following stimulation of the posterior hypothalamus and the midbrain tegmentum (Eibergen

and Caggiula, 1973). The medial forebrain bundle interconnecting these structures are also implicated in sexual behavior (Hitt et al., 1970; Eibergen and Caggiula, 1973). Furthermore, these regions have been shown to serve as “reward” sites, inducing electrical self-stimulation in rats (Olds, 1956; Caggiula and Hoebel, 1966; Caggiula, 1970), presumably because that produces pleasurable feelings or euphoria.

The hypothalamus also plays a major role in female sexual and maternal behavior in mammals. In several species, anterior hypothalamic lesions interfere with sexual receptivity (Sawyer and Robinson, 1956; Hitt et al., 1970; Pfaff, 1999). Oxytocin produced and released by magnocellular hypothalamic neurons induces uterine contractions during delivery, and vasopressin induces milk ejection and maternal behavior (Insel and Shapiro, 1992; Keverne and Kendrick, 1992; Pedersen et al., 1992). In addition, there are oxytocin-containing parvocellular neurons in the preoptic area, the bed nucleus of the stria terminalis, the amygdala, and the nucleus accumbens. The release of oxytocin by these brain structures ameliorates the female’s anxiety produced by male pursuit and contact during sexual behavior, and it facilitates maternal behavior. In the rat, the latter includes nest building, licking and grooming of the young, and their retrieval if they leave the nest (Pedersen et al., 1992).

**THE ROLE OF THE HYPOTHALAMUS IN AMOROUSNESS IN FISH.** In freely moving male goldfish, electrical stimulation of the preoptic area evokes courtship behavior and nest building (Demski and Knigge, 1971; Savage and Roberts, 1975). Sperm release is elicited by electrical stimulation along a path that begins in the preoptic area rostrally, and extends through the hypothalamus and the midbrain tegmentum to the medulla and the spinal cord (Demski et al., 1975). Similarly, courtship vocalization is evoked in toadfish by stimulating the preoptic area and ventral telencephalon, two sites that contain neurons that concentrate gonadal steroids (Fine and Perini, 1994). Correspondingly, preoptic lesions abolish spawning behavior in the killifish (Macey et al., 1974). In addition to the hypothalamus, sperm release is triggered by stimulating the ventral telencephalon (perhaps the amygdaloid primordium) and the adjacent forebrain bundle (Demski and Knigge, 1971). That the telencephalon plays an important role in courtship and nest building is suggested by several studies (Aronson, 1970). First, there is seasonal variation in the concentration of gonadotropin-releasing hormone in the brain of turbot (Andersson et al., 2001). Second, male sunfish discontinue their courtship behavior and nest building after surgical removal of the telencephalon (Hale, 1956). The same was observed in paradise fish (Schwagmeyer et al., 1977). Third, if the male without a telencephalon does build a nest, it is not properly constructed and the female cannot enter it to lay her eggs (Schönherr, 1955; Segaar 1961; Schwagmeyer et al., 1977; de Bruin, 1980). Olfactory bulb lesions had no such effect. These findings suggest that the amorousness displayed by fish during the reproductive season bears some similarities to that found in mammals.

However, parental care is absent in most fish and, hence, there is no justification for postulating parental affection. That holds in particular for fish that inhabit and breed in the open ocean and produce small floating (pelagic) eggs in prodigious numbers. For instance, the ocean sunfish lays up to 30 million eggs during the spawning season; the cod, 12 million; the haddock, 2 million eggs. The small pelagic eggs contain little yolk for nourishment but hatching occurs rapidly and the tadpoles move about freely and start feeding. Of course,

lacking parental protection, few of them survive. Fish that reproduce in the depth of oceans, and also those inhabiting shallow waters, and many freshwater species, typically have larger and fewer eggs, which sink to the bottom (demersal eggs). These may or may or may not be guarded or cared for. Salmon bury the 5,000 eggs they produce but beyond that, they do not care for them. Siamese fighting fish, which produce fewer eggs, place them in floating mucus bubbles and guard them until hatching. Sticklebacks that lay only 60 eggs, build a nest from plant debris, and ventilate and protect the eggs. Live-bearing fish produce even fewer eggs (Thibault and Schultz, 1978). Some cichlids are mouthbrooders, which is the most advanced form of parental care observed in fish. We may assume that in those fish that protect and care for their young, parental affection may operate in a rudimentary form.

**3.2.5 The Emotions of Fish and Our Piscine Affective Legacy.** Psychologists distinguish between basic, compound, and higher emotions (Arnold, 1960; Plutchik, 1980; Izard, 1991). (i) Basic emotions are those that are irreducible to others and are coupled with a distinctive, species-specific emotional expression. Humans laugh when happy and weep when sad, dogs wag or lower their tail. (ii) Complex emotions are an admixture of two or more basic emotions. For instance, thrill is a compound of fear and pleasure. The thrill of the hunter when facing a lion is an admixture of fear of the beast and the pleasure of being able to subdue it. (iii) Higher emotions are affects that are modified by other mental processes, such as memories, expectations, or ideas. Anxiety, for instance, is memory-based anticipated fear, such as returning to a site where one has been hurt previously, or it may be an imagined danger, as when flying in an airplane during a storm. Jealousy is an amalgam of anger and fear, together with an anticipation of loss of future pleasures. Shame may be a form of suffering occasioned by doing something that is perceived as stupid or dishonorable. We shall deal here only with basic emotions on the assumption that fish do not experience compound and higher emotions. Accordingly, we inquire what basic emotions may we attribute to fishes on the basis of such objective lines of evidence as autonomic and endocrine mobilization and emotional expression, and whether these traits have been conserved as our piscine legacy.

**THE FUNCTIONS OF BASIC EMOTIONS.** While we perform routine behavioral activities, such as walking, chewing or swallowing, automatically, choosing where to go and what to ingest typically requires mental guidance. That mental process may be affective or cognitive, that is, we make choices either impulsively on the basis of feelings of like and dislike or deliberately by thinking and reasoning. Affect-based behavioral guidance is the simpler and more spontaneous of these two mental processes. Cognitive judgments are based on individual experience, learning and deliberation, and can lead to a realistic (allocentric, objective) and nuanced assessment of prevailing conditions and circumstances. In contrast, affective responses are dichotomous, and self-centered (egocentric, subjective) valuations of what is instantly pleasing or displeasing, satisfying or frustrating, comforting or burdensome. Things that gratify homeostatic needs, relieve stress and strain, promote a sense of security and wellbeing, tend to generate positive affects—such as pleasure, joy, and feelings of wellness—and are accordingly chosen, pursued and embraced. Things that threaten safety, are hurtful or uncomfortable tend to generate negative affects—such as fear and anger, pain and malaise—are rejected, recoiled from and avoided.

The basic emotions are species-specific choice mechanisms that allow individuals to discriminate among things and conditions that are beneficial (feel good) and those that are detrimental (feel bad). A sweet and warm liquid, like mother's milk or a similar substitute solution tastes good upon first exposure to the suckling human newborn and it will ingest them; bitter or salty cold liquids taste bad and infants will reject them. Such ready-made affective valuations have evolved in all animals and have been conserved by genetic mechanisms because they promote the individual's fitness and, hence, they are passed on from one generation to the next as inherited traits. Importantly, there is more to basic affects than just inborn stimulus valuation and response selection. Affects are coupled with a motivating and energizing force. The basic affects of hunger and thirst arouse and mobilize the individual—young or old—to gratify the metabolic demands of its body; fear and anger protect it from situations that threaten its integrity; and pain and suffering guard it from injury and ailments. The basic affects are subjective experiences with conative force that have evolved in the animal world because they serve as “stick and carrot” behavioral guidance mechanisms. Positive affects make the individual pursue what it is genetically preprogrammed to acquire, embrace, or join; negative affects make it avoid what it is preprogrammed to shun, reject and recoil from. Hunger goads the individual and appetite lures it to satisfy its nutritional needs. However, because basic affects are ready-made responses, the sensory discriminations they mediate and the emotional behavior they generate are rough-and-ready mass actions—such as agitated fighting or depressed hiding—rather than nuanced, tailor-made actions based on cognitive assessment and deliberation.

**THE BASIC EMOTIONS OF MAN.** There is some disagreement about the number of basic emotions in humans. For instance, Plutchik (1980) lists eight basic emotions, Izard (1991) ten of them. Both authors list seven emotions by identical or cognate terms: (i) *fear*, (ii) *anger*, (iii) *joy* (pleasure), (iv) *surprise*, (v) *disgust* (loathing), (vi) *sadness* (distress), and (vii) *curiosity* (interest, anticipation). In addition, Plutchik lists (viii) *trust*. Izard, omitting trust, lists (viii) *contempt*, (ix) *shame*, and (x) *guilt*. If we consider shame and guilt to be higher emotions that involve cognitive processes (the “moral sentiments”), the two lists are in good agreement with eight basic affects, because *trust* listed by Plutchik ought to be paired with *mistrust*, and there is affinity between the latter and Izard's *contempt*. However, missing from both lists are several basic affects that we all experience in daily life. Notably, (xi) *pain* and *suffering* (which are the opposites of pleasure and joy), (xii) *hunger* and *appetite*, (xiii) *amorousness* (sexual desire, lust), and (xiv) *tenderness* (affection). Many psychologists do not view the latter as “emotions” because they are not associated with distinctive facial expressions, and view them as sensations with an affective tone. However, their inclusion into the category of basic affects is warranted because (a) all of them are associated with autonomic and endocrine mobilization; (b) all serve fundamental survival functions; and (c) all of them are “agitated” experiences when compared with such “calm” cognitive processes as perceiving, recollecting, thinking or reasoning.

**THE BASIC EMOTIONS OF FISH.** All the basic human emotions that we have listed serve specific organic functions and trigger specific behavioral activities. Therefore, turning to fish, we can attribute to them only those basic emotions for which there are organic and behavioral counterparts. We may attribute hunger to a food-deprived fish because anyone who has kept

fish in an aquarium on a rigorous diet knows how excited fish get before feeding time and how frenzied they become when they are fed. When a territorial fish raises its gills and fins, and attacks another fish placed into the aquarium, we may attribute anger to it. When a fish foraging in a lake flees when disturbed and hides in the vegetation, we may attribute fear to it. However, considering that most species of fish do not care for their brood, we cannot attribute parental affection to them, and because the social relations of schooling fish is so impersonal, we cannot attribute shame or guilt to them. On the basis of the evidence we have so far considered, we are justified in postulating five, organically based piscine affects.

1. *Pain* when injured, and *distress* when captured, confined or crowded. Pain protects fish from tissue damage and bodily injury. Distress induces them to improve living conditions. We may call these *prophylactic* affects.
2. *Hunger* when food deprived, and *appetite* and *disgust* in relation to the caloric and perhaps hedonic properties of available nutrients. These are the *dietary* affects.
3. *Fear* when sensing danger and threat, and *anger* when challenged by an intruder or adversary. These are the *defensive* affects.
4. *Amorousness* and *lust* which motivates males to approach and fertilize females. In some species of fish, parental affection motivates the female, the male or both to care for their progeny. These are the *procreative* affects.
5. *Amicability* motivates many species of fish to form shoals when foraging and move together in schools. These are the simple piscine *social* affects.

**THE RELATION OF BASIC EMOTIONS TO “INSTINCTS.”** The five basic emotions that we attribute to fish enable them to respond adaptively with ready-made actions and reactions to what fosters their survival as individuals and what hinders it. Newly hatched fish, without the benefit of learning from experience or training, select nutrients that are beneficial and ignore or reject substances that are useless or harmful. Traditionally, this type of inborn animal behavior is considered an “instinct,” a guiding mechanism that is contrasted with the higher faculty of experience- and education-based “intelligence.” In light of our current knowledge, the concept of instinct—the mysterious force implanted into the heart of beasts so that they can survive without the aid of mental processes—can be replaced by the scientific concept of genetically programmed affects. Inborn feelings and emotions empower inexperienced neonates, and adults among animals with limited learning abilities, to generate behavioral actions and reactions that satisfy their basic needs and wants. When an animal devoid of experience sets out to forage or hunt, persists in that pursuit until it finds food, and chooses what it will ingest and what it will reject, it is not guided by a mysterious instinct but by dietary affects—hunger, appetite, likes and dislikes—i.e., feelings and emotions produced by specific neural mechanisms.

**OUR PISCINE AFFECTIVE LEGACY.** When food deprived, we feel hungry; when threatened, we become frightened; when insulted, we get angry; and when sexually aroused we feel amorous. These affective states are associated with autonomic and endocrine reactions, and emotional

expressions and actions, and are regulated by specific brain mechanisms. The evidence that in fishes feeding, fleeing, fighting and sexual behavior are mediated by some of the same autonomic, endocrine and neural mechanisms as in humans, leads us to postulate that fishes experience similar affects, albeit they are communicated to conspecifics by different kinds of emotional expressions. Since so many of our genes, somatic traits, sensorimotor and neural mechanisms are a piscine legacy, we propose that the foundations of our feelings of hunger, fear, anger, and sexual ardor are a piscine legacy. This heritage is evident in the ontogeny of human affective development. Like the inexperienced tadpole that begins to forage soon after hatching, so also the feeding of the helpless human neonate is aided by inborn affective mechanisms. We assume that the human infant feels hungry when its stomach becomes empty, and it is that feeling that induces it to root and seek the mother's nipple. Succeeding with that, the infant avidly sucks and swallows the warm and sweet breast milk, presumably because that provides pleasurable feelings. The infant rejects cold milk or milk adulterated with quinine offered in a bottle because that must feel unpleasant or disgusting. We make these attributions because as adults, knowledgeable beings as we are, regulate much of our eating behavior on an affective basis. When we feel hungry, we stop whatever we may be preoccupied with and proceed to eat. When choices are available, we rely on our feelings of likes and dislikes what food items to select. When our stomach becomes full, it is the feeling of satiety that makes us stop eating. And when deprived of food for some length of time, the sensation of hunger turns into a passionate craving that overwhelms our entire consciousness. In unfortunate regions of our planet, this affect is familiar to millions.

Affects, aiding the survival of the individual and the species, have an evolutionary history much like cognition, concerned with getting to know the world. Only some of our basic emotions are a piscine heritage. As novel behavioral functions and abilities evolved in basal mammals, primates, and humans, these were accompanied by the evolution of corresponding basic affects that activate and energize them. Of all the basic emotions, hunger and lust may be phylogenetically the oldest. Hunger motivating feeding and amorousness motivating procreation are existential necessities. Individuals cannot survive without feeding, and the species becomes extinct without procreation. The other piscine emotions, anger and fear, are of a vital necessity only in an environment where there is competition, conflict, strife, and predation. In the case of our chordate ancestry, the filter feeders, like the extant amphioxus, could feed and reproduce in marginal niches without competing or fighting. Hence, anger need not have been part of their affective repertoire. When the disturbed amphioxus flees, it may experience rudiments of fear or maybe it just exhibits a simple reflex reaction. The extinct ancient agnathans, many furnished with heavy armors, evidently lived in a militant world, being pursued by aggressors and/or being themselves the aggressors. The violent tenor of life increased further as carnivorous jawed fishes evolved that pursued and fed on smaller fishes and other inhabitants of their aquatic milieu. It is in these fish that the agonistic affects have evolved, and the neural mechanisms mediating them remain part of our heritage.

### 3.3. Configural Perception, Memory, and Phenomenal Awareness in Fishes: Our Piscine Perceptual Legacy

**3.3.1. Brain Mechanisms of Perception in Fishes.** Sensations elaborated into perceptions is the mental process that acquaint animals with the features of the physical and animate world they live in, and the more veridical that acquaintance the greater their chances that they can survive and prosper in their environment. In mammals, including ourselves, perceptual processing is mediated by the neencephalon, the cortical projection and association areas that process sensory information conveyed by the thalamic relay nuclei. In fishes without a neencephalon, perception is mediated by paleocephalic structures, the olfactory, optic, facial and vagal lobes, and some other structures (Figs. 3-10, 3-12). It is a reasonable assumption that their perceptual world differs from ours. In our following analysis of the different *modus operandi* of the paleocephalon and neencephalon, we will focus on visual perception in fishes, mammals and ourselves, with occasional reference to some of the other sensory systems. We shall argue that even though the optic lobe provides fish with a fine-grained pictorial representation of the outside world, their visual perception differs substantially from ours because they lack the somatic and neural mechanisms that make possible the multimodal and cognitive integration of vision with information gained by our palpating and manipulative hands.

**THE OPTIC LOBE AND PISCINE VISUAL PERCEPTION.** The principal brain mechanism of piscine visual perception is the midbrain optic lobe. Following bilateral removal of the optic lobes (the homologue of the mammalian superior colliculus), goldfish lose the ability to recognize familiar objects by sight—such as food, obstacles and threatening objects—and tend to swim along the wall of the aquarium, apparently relying on other sensory mechanisms to orient themselves in space (Yager et al., 1977). Destruction of the optic lobe also abolishes the tendency of goldfish to swim with a rotating striped drum, although they track the stripes with their eyes, suggesting some residual pattern vision (Springer et al., 1977). In contrast, the forebrain appears to play minimal role in piscine visual perception. Its ablation (sparing the olfactory bulb) has no deleterious effect on the discrimination of simple visual stimuli, such routine activities as swimming, and rate of food consumption (Janzen, 1933; Nolte, 1932; Hosch, 1936; Zunini 1941; Bernstein, 1962; Overmier and Hollis, 1980; Savage, 1980). This contrasts with mammals, such as the rat (Lashley, 1935) or monkey (Klüver, 1933), in which visual pattern discrimination is abolished following ablation of the visual cortex.

**3.3.2. Configural Perception, or Isomorphous Representation in Fishes.** We have argued earlier (Section 2.2) that protozoans devoid of discrete sense organs but displaying goal-seeking behavior are guided and motivated by a putative subjective state, what we have called *protopathic sentience*. We characterized protopathic sentience as an inchoate dichotomous mental state—the experience of feeling “cozy” or “lousy”—without perceiving what particular external objects or events trigger these internal states. That is, protopathic sentience does not endow an animal with awareness of the features and properties of the external world. Multicellular organisms like a jellyfish with specialized sense organs and a peripheral nervous system, and a flatworm furnished with paired eyes and a small brain, may experience a higher form of subjective state, i.e., visual sensations and therefore we may attribute *qualeous sentience* to them. Qualeous sentience is exemplified by experiencing such

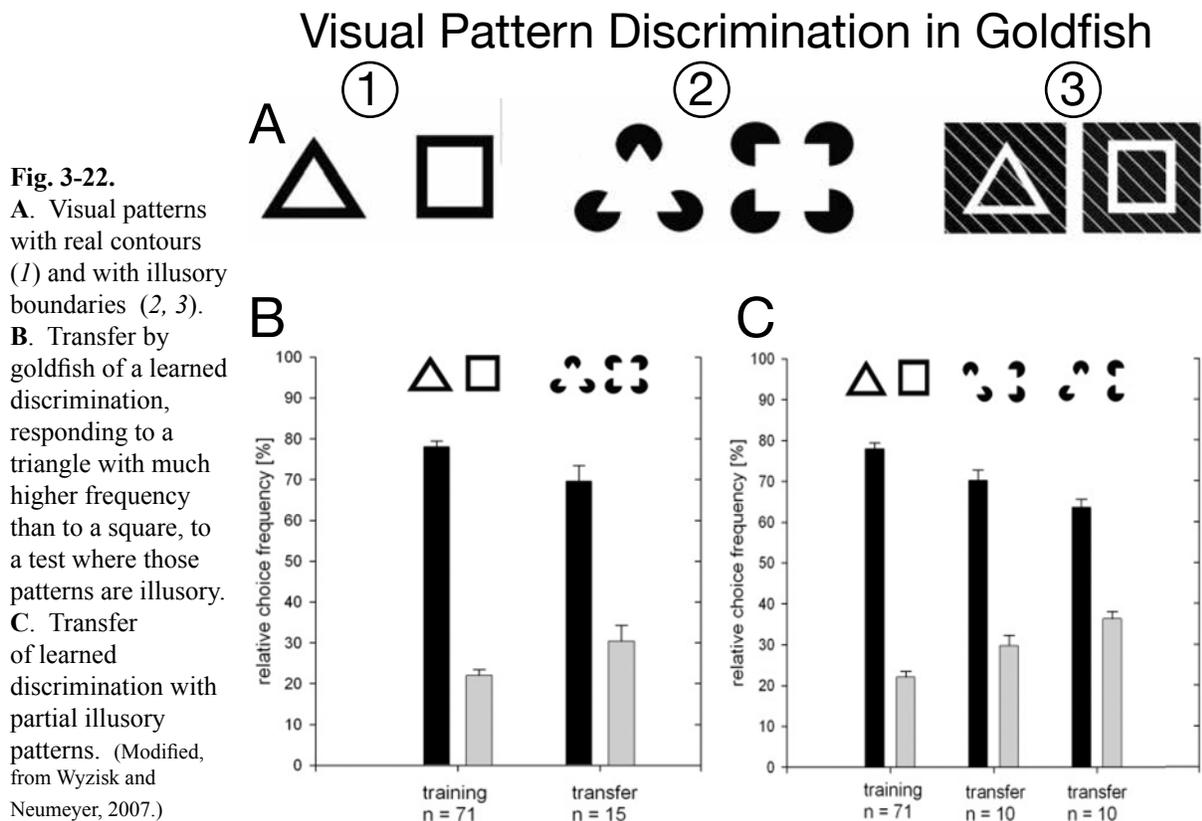
elementary sensations as a particular odor or taste, a gentle touch or a heavy blow, a dim or bright light, or red or blue visual expanse. Such sensations, as we know from personal experience, are accompanied by a feeling tone (affective valence) of a positive or negative sort. Some odors are pleasant, others unpleasant; some tastes are savory, others disgusting; some colors are soothing, others disturbing. In epistemological terms, qualeous sentience provides the subject with two experiences: first, qualitatively distinct impressions—a particular odor, taste, feel, color, etc.—and second, an affective tone—attractive, unattractive, hurting, soothing, etc. Significantly, what is experienced is not an isomorphous representation (image, portrait, or model) of external reality but a code that signals goings-on in the environment and their existential relevance. Qualeous sensations do not model external reality—the form, size, texture or structure of different objects. They are vivid impressions of one kind or another, that allow the prompt and unmistakable discrimination of salient stimuli. One wavelength of electromagnetic radiation is sensed as “red,” another as “green”; one chemical as “sweet,” another as “bitter,” and so forth. But as was clearly argued by the founders of modern science (Galileo, Newton) and philosophy (Locke, Hume), these sensed features—called “secondary qualities”—do not exist in the outside world. The realistic representation of external objects and events in awareness is made possible by the perception of “primary qualities,” such as shape, size, motion, and number. This advance, the faculty of *configural perception* (pattern recognition), evolved in our phylogeny, in fishes. Thanks to the evolution of bilateral, highly differentiated, and topographically organized sensory input and brain processing mechanisms, fishes obtain an isomorphous portraiture of the phenomenal features objects and events in the external world.

**3.3.3. Visual Mechanisms and Visual Perception in Fishes.** As described earlier (Section 3.1.3), most species of fish have complex eyes with a differentiated optical apparatus, a large photosensitive retinal surface, and a topographically organized integrative nerve center, the stratified optic lobe (Figs. 3-11, 3-12). These mechanisms provide fish with the faculty of visual pattern discrimination. That ability is of great importance to surface feeders and those inhabiting clear waters, because it enables them to visualize landmarks as they swim about in search of food, discriminate prey and predator, and forage and cruise in the company of their own kind. Different species of fish are distinguished by a particular shape and distinctive markings distributed over their body surface, such as dots, patches or stripes of a particular color. These markings play a pivotal role in kin recognition as they form schools (Breder, 1951; Katzir, 1981) and engage in courtship displays and dominance contests (Lissmann, 1932; Tinbergen 1951; Stacey and Chiszar, 1978; Guthrie, 1986). The display of these markings is often enhanced by visible body movements or dances. Fish apparently also build a topographic representation (spatial map) of their home range and follow different routes, as safety requires, to distant feeding and breeding sites. “Site fidelity,” the disposition and ability of fish to return to their homes when displaced is a widespread phenomenon (Gerkins, 1953; Minakawa and Kraft, 2005).

**PATTERN PERCEPTION.** The first mechanism that makes possible pattern discrimination in fish, as in other vertebrates, is the complex eye with a laminated retina, a structure where there is a complex synaptic interaction among photosensitive transducer cells (rods and cones), first-order bipolar cells, intercalated amacrine cells, and second-order ganglion cells. As a result,

the retina conveys information to the optic lobe not only about changing levels of illumination but also about the shape and texture of objects regardless of their brightness (Guthrie, 1986; Sakai and Naka, 1988a, b). However, the visual pattern discrimination of fishes appears to be inferior to that of birds and mammals. Experiments with artificial models indicate that a few prominent visual features, like the color patch of the male or the silhouette of the female's swollen belly, rather than fine configurational details trigger aggression in male fighting fish (Lissmann, 1932) and induce courtship behavior in the three-spined stickleback (Tinbergen 1951). In the swordfish, in which females show a preference for males with an elongated "sword," that preference is abolished by enlarging the image of a swordless model (Rosenthal and Evans, 1998). Tinbergen (1951) proposed that these species-specific discriminations are based on innately recognized "key stimuli" that operate as "releasers." But there is experimental evidence that fish can learn to recognize visual patterns that are not part of their hard-wired behavioral repertoire.

In pioneering experimental studies, Herter (1930, 1953) demonstrated that minnows can be trained to distinguish circles, squares, triangles, crosses, etc., as well as figures of the same shape but different sizes. Of course, in their natural environment fish often have to discriminate objects that lack clearly delineated boundaries or are partially occluded by other objects. Relevant, therefore, is the recent demonstration that fish trained to discriminate such geometric figures, transfer their learned discriminations to corresponding figures created with illusory contours (Wyzisk and Neumeier, 2007; Sovrano and Bisazza, 2009). Human subjects trained to discriminate a triangle and a square with clearly outlined contours (Fig. 3-22A1) retain that learned discrimination when the square and triangle is created by visual illusion



(Figs. 3-22B, C), irrespective whether that is produced by luminosity differences or some other means (Kanizsa, 1987). This feature of visual perception has been demonstrated in fish with full (Fig. 3-22B) and partial (Fig. 3-22C) illusory figures. Importantly, however, there is also some evidence that prominent features of the geometric figures (curves, acute angles, knobs) rather than subtle details help fish make these learned pattern discriminations (Northmore et al., 1978).

**DEPTH AND DISTANCE PERCEPTION.** Judging by the acuity and agility displayed by many species of fish in their three-dimensional world—darting with great speed to capture distant prey, avoiding obstacles in their path, diving or jumping out of the water when pursued—they must possess well-developed depth and distance perception. In one experiment, goldfish were trained to discriminate two equidistant objects that differed in size, being rewarded with food or access to peers when selecting the arbitrarily designated object as the positive cue (Douglas et al., 1988). Following this training, the distance of the objects was changed so that both the small and the large object produced a retinal image of the same size. The fish continued to select the target to which they were originally trained, indicating that their visual perception obeys the principle of size constancy. While in birds and mammals with medial eyes (e.g., eagles, monkeys, humans) size constancy is aided by binocular cues, fish with laterally placed eyes (unless they rapidly bob their heads) must rely principally on monocular cues. Among the monocular cues of our depth perception (as when we look at the world with one eye covered) are familiarity with the relative size and texture of objects, and such variables as occlusion, linear perspective, and aerial perspective. Relative size refers to the fact that when we identify an object we take into consideration the fact that the retinal field subtended by a familiar object decreases or increases in proportion of its assessed distance. Distance estimation is aided by the perceived textural detail of a familiar thing; the less crisp it is, the farther it is likely to be situated. Occlusion refers to the fact that things situated farther tend to be obscured by things closer to the observer, and linear perspective to the increasing convergence of lines that frame things located at increasing distances. Aerial perspective refers to the growing haziness (or blueness) of an object or scene the farther it is located from the viewer. We do not currently know which of these monocular cues fish rely upon but they must use at least some of them to obtain a realistic 3-D representation of the world they live in. Significantly, because monocular cues are physical invariants, their assessment may be based on automatic computations rather than mentally-aided deliberations and judgments.

**3.3.4. Phenomenal Awareness of the Visual World in Fishes.** Although fish are capable of visual pattern and distance discrimination, that does not mean that piscine and human perceptions are identical. A fundamental difference, we propose, is that piscine visual perception is *phenomenal*, fish are aware of the surface features of objects they see, but our visual perception may also be *substantive*, that is, we can become acquainted not only with the appearance of things but also with their structural properties. The argument is as follows. Because fish can visually discriminate innocuous fish from dangerous predators and a predator displaying a relaxed posture from one readying itself to attack, can track the movement of conspecifics when shoaling and schooling, and identify potential mates when courting and mating, they are evidently capable of configural perception. However, without palpation and manipulation (touching, stroking, lifting, pulling, squeezing, tearing, etc.), the unimodal

visual input that a fish receives and processes by the optic lobe provides only information about an object's surface features not its substantive properties. Lacking a prehensile tongue and, in particular, limbs with dexterous digits, fish do not get the extra information that we regularly obtain about the structural characteristics of things—such as their weight, strength, composition, pliability, coarseness, slipperiness, and so forth.

To obtain a representation of something as a substance with multimodal properties requires the ability to concurrently focus several senses on that target and centrally amalgamate that information to form a unitary percept. Of course, fish use several senses to orient themselves in their environment and discriminate different objects. They do not bump into one another while swimming close to one another, they do not crash into rocks when carried by waves, and the like, presumably because mechanical sensors of their lateral line system provide echo signals of the presence of other objects and their properties. They must also smell the object seen from a distance, then can touch it with their lips as it gets closer, and taste it when ingested. However, there is no evidence that fish effectively integrate all these *successive* inputs into a single multimodal *simultaneous* percept. As we noted earlier, the brain mechanisms processing these different sensory inputs are largely segregated from one another (Fig. 3-12) and while connections undoubtedly exist, the conduction delay precludes instantaneous integration. To paraphrase Sjölander (1993), the hunting fish starts out by chasing a distant prey as a “visual fish,” which closer up becomes an “olfactory fish,” and then, upon ingestion, turns into a “gustatory fish.” Fish do not examine objects in their environment as, say, a dog does when it encounters a novel object—pawing, sniffing, biting and shoving it, pouncing on it, shaking it, and trying to tear it apart, and certainly not as primates do as they palpate and manipulate everything that they come into contact with. On the basis of this behavioral difference, we propose a fundamental distinction between the simpler form of isomorphous *unimodal, phenomenal perception*, which we attribute to fish, and the more advanced *multimodal, substantive perception* that we attribute to mammals in general and primates in particular.

Lacking multimodal perceptual integration has behavioral consequences. Consider, for instance, the behavior of a Siamese fighting fish when it faces its own image in a mirror and attacks it as if it were an “intruder.” The experiment can be repeated many times but the animal fails to realize that it is fighting a phantom rather than a genuine competitor. The behavior of mammals is quite different, as illustrated by a personal observation. A young dog, whose life history was well known from infancy, was taken to a new residence and for the first time faced its own image in a large mirror reaching the floor. The puppy became agitated, barked at the “stranger” and then tried to play with it. This behavior persisted for a while, abated within a few days and, henceforth, the puppy (and later as an adult) never pays attention to its visage upon entering that room. The image appears to be of no greater interest to it than the decorations on the adjacent walls. The interpretation of this observation is that for a dog the picture of a dog does not endure as the representation of a real animal unless it is confirmed to be a real creature by added sensory information, perhaps its odor, its warmth, and whether it responds appropriately when challenged. (As we shall see later, at a still a higher level of perceptual organization than that is present in dogs, as in apes and young children, the mirror image is recognized as one's own reflection.) The calm that is maintained by dogs looking at a television program depicting dogs in action, and their agitation when a real dog appears

in the room, supports this interpretation. The transformation of the image of a thing into a substantive representation requires multimodal integration but fish do not seem to possess that aptitude. We consider phenomenal perception as the first stage in the veridical representation of the external world, and some of the organic mechanisms mediating it are a piscine legacy of ours. However, the current evidence indicates that multimodal perceptual integration and substantive awareness is mediated in mammals by a higher-level integrative neural system, the neencephalon, which is absent in fish.

**3.3.5. Learning and Recognition Memory in Fishes.** Although much of fish behavior has the character of stereotypic species-specific activity, which suggests inborn reflexive and affective coordination, there is ample observational evidence that much of what fish do in their natural habitat is dependent on mnemonic processes. It requires learning to become familiar with the layout of one's particular habitat, to find the shortest and safest routes to distant sites to feed and mate, and then find one's way back home to rest. There is also a wealth of experimental evidence that fish can be trained to make perceptual discriminations and acquire new behavioral routines. Learning presumes mnemonic processes either in the form of mindless conditioning and habit formation or as the recollection of previous experiences in the subjective sense of the term.

We are familiar with two basic forms of subjective memory: recognition and recollection. *Recognition memory*—perceiving something as familiar—involves a perceptually-prompted retrieval of information stored in the brain and its melding with the current impression. We recognize Sarah as a familiar person with certain traits because we have met her before and match our current impression with the retrieved memory image of her visage and behavior. In that process, which modifies and enriches what is currently given to the senses, the contribution of the memory image is not segregated from the total configuration (Gestalt) of the percept. *Recollection imagery* is different from recognition memory both functionally and experientially. The recalled imagery is typically not triggered by an external event but by some internal process (need, desire, thought), and it becomes manifest in subjective experience as a faint copy of something from the past, a flashback or a vision. Recollection imagery may serve the individual as a search image in pursuit of a desired object or a landmark along one's route, or some anticipated or sought-after end state or goal. From the perspective of ease of learning, recognition memory is far simpler than recollection imagery. We know from personal experience, as well as from experiments, that it is far easier to recognize a previously encountered object, place or person than it is to recollect (visualize, bring to mind) what they look like. Hence the issue whether fish possess recognition memory as well as recollection imagery has to be examined separately.

*Types of Learning in Fishes.* Experimentally demonstrated learning ability in fish includes avoidance learning, appetitive and aversive conditioning, simple instrumental learning, and such spatial learning as mastering a simple maze or solving a detour problem. Avoidance learning by fish was reported over a century ago by Triplett (1901) who found that perch ceased to attack minnows, on which they prey, when they were separated in an aquarium by a glass partition and have bumped into it several times. Henceforth, the perch abstained from attacking the minnows even when the glass partition was removed, although they attacked

new prey, such as worms. Aversive conditioning, which involves pairing a visual stimulus with punishment, was reported in various species of fish (Frolov, 1928; Bull, 1957; Harlow, 1939). In Harlow's study, goldfish were first tested with various stimuli to which they did not respond overtly. Then a previously ignored gentle touch triggered flight after it was repeatedly paired with a shock. Subsequent tests showed that the goldfish also responded thereafter with flight to neutral stimuli that were never paired with the shock. This reaction has been interpreted as learned sensitization, a form of anxiety produced by previous aversive experience.

Among learning tasks mastered by fish are the following: learning visual pattern discriminations (Herter, 1930, 1953; Wyzisk and Neumeyer, 2007; Sovrano and Bisazza, 2009), as already described; finding routes through a maze (Churchill, 1916; Welty, 1934); proceeding to a visible but inaccessible target by taking a detour (Russell, 1931); and operating simple devices modeled on Skinner boxes (Haralson and Bitterman, 1950). Recent naturalistic studies indicate that fish learn to effectively navigate in the environment they inhabit (Braithwaite, 1998; Warburton, 1990; Odling-Smee and Braithwaite, 2003), recognize conspecifics and kin (Griffiths, 2003), and improve their foraging and hunting skills with age (Laland and Williams, 1997; Warburton, 2003). The question we examine next is whether these instances of learning can be parsimoniously explained as mediated by mindless association processes (conditioning) or are there indications for the involvement of subjective memory, such as recognition and recollection. We begin with a brief examination of spatial learning and social learning by fish.

**SPATIAL LEARNING: RATS MASTERING MAZES.** For over a century, mazes with long or short routes to a goal box (a site baited with some reward), with blind alleys along the way, have been used as experimental tools to study spatial learning in rats. Behavioral theorists sought to explain the great proficiency of rats in solving maze problems as the product of a trial-and-error process, the mindless consolidation of the sequence of correct (reward facilitating) turns and elimination of incorrect (reward retarding) turns (Hull, 1943). However, suggestive evidence emerged, that when rats learn to navigate through a maze, they acquire a mental image of its layout because, when some alleys were blocked, rats switched and used other suitable alleys to reach the goal box. In a seminal study, Tolman et al. (1946) trained two groups of rats in a four-arm maze, situated in a room with ample extra-maze cues. One group of rats, the "response learners," had to consistently take the same turn (say, to the right) to get to the baited arm, regardless which arm they were started from. The other group, the "place learners," had to find the same spatial location (say, the north arm), irrespective which arm they were started from. The experiment showed that place learning was a far easier task for rats than response learning. Tolman (1932, 1948) concluded that rats acquire a "cognitive map" of the layout of the maze and that that putative mental representation aids them in mastering the task.

**SPATIAL LEARNING BY FISH.** In their daily life, fish alternate between patrolling their home base and venturing afar to feed and mate. The first requires recognition of features and landmarks of one's particular habitat; the second, the recollection of sites previously visited, how to get there, and how to get back home. There is experimental evidence that, like rats, fish can master maze problems. Thorndike (1911) found that individual killifish learn how to find the shortest route to a feeding site by swimming through a series of openings in a partition.

Similarly, Russell (1931) reported that three-spined sticklebacks learn how to get quickly into a bottle placed into the aquarium to access food placed there by swimming through the bottle's narrow neck and then get out of it rapidly. In this task, the fish had to learn two things: first, to inhibit the natural tendency to move forward to directly access the visible incentive and avoid bumping into the bottle and, second, how to take the shortest roundabout route (detour) to reach the target. Like rats, goldfish tested in a maze display place learning; upon being transferred to a new starting position, they spontaneously choose the appropriate route to the target area (Rodríguez et al., 1994; Salas et al., 1996). What cues might fish use to build such a map-like spatial representation of their environment? Schluessel and Bleckmann (2005) trained stingrays to locate food in a four-arm maze in a manner similar to that used with rats by Tolman. The food was always located in the same arm but one group of stingrays (the response learners) had to start from the same location, while the starting arm for the other group (the place learners) was varied from trial to trial. The results indicated that whereas the place learners used an "allocentric" strategy and turned in the appropriate direction when started from a novel starting position, the response learners were handicapped by having mastered an "egocentric" turning response.

It is known from maze studies that rats utilize a variety of intramaze and extramaze cues to avoid blind alleys and find shortcuts to the goal box (Restle, 1957). Intramaze cues may be olfactory, auditory, tactile or visual—the odor, sound, texture, and markings on the floor and walls of the different arms at choice points. Extramaze cues may be an overhanging light bulb at one end of the room, a window at another end, and the like. The elimination of intramaze and extramaze cues, separately or in combination, makes the rat's task far more difficult. With regard to what fish face in their natural habitat, the "intramaze" cues might be local features of their resting site, and the "extramaze" cues such global landmarks as the distant landscape, the direction of sunset or sunrise, and so forth. In a recent pilot study, individual fish were isolated in a small central tank within a larger tank that contained conspecifics (Sovrano et al., 2002). The isolation tank had covered escape holes in different locations, some of which would open upon pressing, allowing the experimental fish to rejoin its peers. The results indicated that the successful fish learned to rely both on a global landmark (geometric position of the escape hole) and a local signpost (color of one of the walls) to solve this problem.

**THE HOMING OF SALMON.** The best known naturalistic example of spatial learning in fish is the behavior of migrating salmon (Hasler et al., 1978). Many species of salmon spawn in freshwater tributaries where gravid females deposit their eggs in gravel pits and the males then fertilize the eggs. The parents die soon thereafter and the hatched young stay together and feed in the stream for a year or longer. As they mature, their skin color changes and they commence their downstream migration to a lake or sea. They may stay there for about 2 years, some of them traveling as much as several thousand kilometers as they visit distant foraging sites. Once fattened, their skin color changes again and they begin their return journey to the ancestral breeding ground, overcoming many obstacles along the route. How is this feat accomplished? Hasler et al. (1978) used a combination of field and laboratory techniques to answer this question. Two groups of young salmon were raised in tanks with water from Lake Michigan. For the experimental group, a minute quantity of an artificial odor, either morpholine or phenethyl alcohol, was added to the water. The control fish were raised in the

same water without the added odorant. During the spawning season, two tributaries of Lake Michigan (the “home streams”) were scented with either morpholine or phenethyl alcohol; 16 other tributaries were left unscented. The salmon were then released in lake Michigan, and a survey of all the streams showed that over 90 per cent of the fish raised in the scented tanks returned to their respective “home stream” while the control fish were randomly scattered in the other streams. Laboratory experiments in a four-armed maze with cascading water baited with different scents gave similar results. Evidently, the fish become imprinted on some chemical in the streams where they have spent their youth, perhaps some distinctive amino acid (Shoji et al., 2000), and return to those sites when ready to breed.

**SOCIAL LEARNING AND KIN RECOGNITION.** Much of animal learning is socially facilitated. The young’s affiliation with their parents, kin and elders provides them with the opportunity to benefit from their experience (Galef, 1988; Heyes, 1994). Social attachment is facilitated by an early form of learning, called imprinting. Imprinting was originally studied in birds (Lorenz, 1935). Newborn precocial birds, such as ducks that can walk soon after hatching, display a disposition to follow their mother as she moves about in search of food, water, and resting sites. If incubator-raised ducklings first encounter some other moving object, be it a bird, a person or a decoy, they follow that object and become attached to it (Lorenz, 1950; Hess, 1973). This selective attachment, the transformation of an unspecified innate “releaser” into the image of some specific being or object, has a profound effect on the bird’s long-term behavior, such as its social affiliation and later mate choice (Immelman, 1972).

Kin recognition in fish is attested to by their schooling behavior, as discussed earlier. Kin recognition may be based on visual cues and/or chemical signaling. Zebrafish recognize kin by visually-mediated differences in skin pigmentation (Engeszer et al., 2004). Imprinting may be the underlying mechanism. In an experimental study, individual juvenile zebrafish from two kin groups were tested in a two-choice apparatus for their preference of the maze arm that contained water from the kin aquarium and one with water from a non-kin aquarium (Mann et al., 2003). The results showed that, on the basis of some olfactory cue, the fish were attracted to the arm containing kin-baited water. In catfish, kin recognition is mediated by dispersal of an identified chemical, phosphatidylcholine, in their skin mucus (Matsumura et al., 2004). However, there is no evidence for individual recognition in schooling fish. In large schools of thousands of members, changes in the group’s direction of movement, as when they maneuver collectively to avoid a predator, the identity of those individuals who lead and those that follow changes constantly (Shaw, 1978; Parrish et al., 2002). In contrast, some pair-bonding species, such as cichlids, do give indications of individual recognition (Keenleyside, 1991). And in cooperatively breeding cichlids, not only the parents but also the helpers that participate in brood care may be recognized as individuals (Hert, 1985; Balshine-Earn and Lotem, 1998). In summary, although fish behavior is fundamentally stereotypical in character, learning plays an important role in some facets of their behavior.

**COGNITIVE LIMITATIONS: SERIAL REVERSAL LEARNING.** The function of learning is to utilize past experience and empower the individual to modify its behavior as environmental conditions change. However, if a learned behavior becomes indelibly ingrained, as is the case with imprinting, what is learned may lead to behavioral rigidity rather than flexibility. Hence,

the ability to unlearn a no longer useful habit is also important. A test designed for this is reversal learning (Mackintosh, 1974). In its simplest form, an animal is trained to enter an arm of a Y- or T-maze painted one color, say green, by getting a reward and abstain from entering the unrewarded red arm. After the animal has mastered this discrimination, the task is reversed: the green becomes unrewarded and the red arm is rewarded. The animal is motivated to inhibit the old response and learn a new one. Typically, animals fail initially, as they tend to persevere in the old habit. However, after several such reversal tasks with different sets of stimuli, advanced animals, such as monkeys, learn the rule: “win-stay, loose-switch” and, once they comprehend this, make the correct choice on the second trial within a session (Warren, 1965). Rats do less well on such serial reversal tasks (Pubols, 1957; Bitterman et al., 1958), and fish (Gonzalez et al., 1964; Behrend et al., 1965; Behrend and Bitterman, 1967; Woodward et al., 1971) apparently fail to make much progress even after as many as 25 serial reversals (Fig. 3-23). This failure illustrates the cognitive limitations of fish.

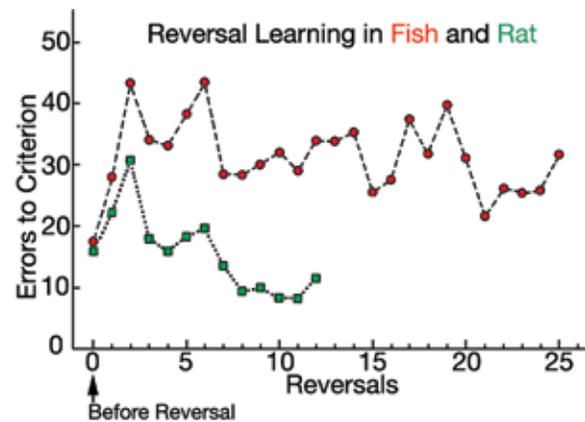


Fig. 3-23. Errors committed in successive discrimination trials by fish and rats. (Modified, from Sutherland and Mackintosh, 1971.)

**3.3.6. Recollection Memory and Imagery in Fishes.** Most of the examples of learning that we have so far considered could be mediated by recognition memory. Social learning typically involves little more than recognizing peers and joining them in whatever they happen to be doing: foraging, migrating, fleeing, mating, hiding, and the like. But there is suggestive evidence that in some instances learning by fish may be based on recollection. When a fish learns to follow a particular path to a feeding site, is it possible that it is aided by a *search image* for the desired food and a *guide image* how to reach that target by a roundabout route?

*Forming and Changing of Habits by Fishes.* In a naturalistic setting, Helfman and Schultz (1984) examined how coral reef grunts acquire the social tradition of staying together in one location during the day and collectively moving to a particular foraging site at twilight. A group of grunts that had an established foraging site were transferred to a distant location containing a resident population. The transplanted grunts immediately followed the residents at twilight to the new foraging site, abandoning their old tradition. This behavior may be interpreted as a simple form of recognition-based social facilitation, the newcomers accepting the guidance of the experienced residents. However, when residents were later removed, the new tradition was preserved by the transplanted grunts. In this situation, the newly acquired habit cannot be attributed to social facilitation but suggests the acquisition by the new residents of a novel search image and spatial map. In a laboratory study, some guppies were transferred to a group of conspecifics that were trained to take a particular route to a specific feeding station (Laland and Williams, 1997). After five days in their company, the transferred guppies began to follow the same route as did the resident fish. And when the original residents were thereafter removed from the group, the untrained guppies retained what they have learned from them

and followed the new route to the new feeding station. What started out as a simple following behavior—doing what the majority does—became a new behavioral pattern, implying that at least some individuals of the transferred fish acquired a new spatial map to reach the new target. New habit formation is apparently based on a combination of social facilitation and individual learning by some group members. The acquisition of the habit to approach a feeding area by way of a difficult access route was facilitated in guppies by the introduction of trained fish (Swaney et al., 2001). When given a choice, untrained guppies transferred to a new site tend to follow experienced conspecifics rather than inexperienced ones, and familiar conspecifics rather than unfamiliar ones (Lachlan et al., 1998). Nonetheless, the acquisition of a new tradition may also be achieved without social facilitation. When an entire population of blue-headed wrasse was removed from a particular locale, the transplanted wrasse found new breeding sites, and that tradition was thereafter preserved over several generations (Warner, 1998).

*The Role of Recollection and Imagery in Mammals and Fishes.* Is there an objective way to distinguish whether an animal masters a new habit through an insentient physiological process, such as imprinting or associative learning, or by relying on a mediating mental process, such as an anticipatory image (expectation of some outcome), a search image (looking for a particular object), or a guide image how to reach the goal (cognitive map)?

**RECOLLECTION IN MAMMALS.** In a pioneering study by Tinklepaugh (1928), a monkey looked on as the experimenter placed banana under one cup and lettuce under another cup. After a short delay, the monkey was allowed to reach for one of the cups and could consume whatever it found. Preferring the banana, the monkey quickly learned to consistently reach for the cup hiding the banana. In the next phase of the experiment, a banana was placed under one of the cups, but during the delay period the banana was surreptitiously replaced with lettuce. Lifting the preferred cup, the animal refused to remove the lettuce and kept searching for the banana. This behavior is difficult to explain without postulating that the animal had an *anticipatory image* of the desired reward and, when allowed to make a choice, relied on that *mental representation* to get what it desired. Subsequent studies that we describe in detail later, showed that rats will run through a maze faster when rewarded in the goal box with a preferred food item than when rewarded with a less favored item (Crespi, 1942; Zeaman, 1949). And when they are trained to master the maze by obtaining the preferred item but, upon reaching the goal box, they find a less favored item, their performance suddenly deteriorates (Elliott, 1928). This change in performing a learned behavior is most easily explained if we assume that the rat is guided by a recollected anticipatory mental image when it masters a maze and is frustrated when it fails to get what it expects.

**RECOLLECTION IN FISHES.** Do fish similarly anticipate a particular reward when trained to perform a learned task? Lowes and Bitterman (1967) trained two groups of goldfish to make an instrumental response (swim to and strike a button) with one group receiving 40 worms as a reward, the other 4 worms. Like mammals, the fish getting the larger reward moved faster to the feeder than did the fish getting the smaller reward. However, in contrast to mammals, fish that initially received 40 worms but later found only 4 worms displayed no change in performance. Similarly, Gonzalez et al. (1972) trained goldfish to swim to a feeder, one group

receiving 40 worms, the other only a single worm. While the fish getting the larger reward swam faster to the target than those getting the smaller reward, there was no change in their performance when the reward was subsequently drastically reduced. Do fish fail to display frustration when the incentive is reduced because their behavior is not guided by a search image or because that search image is too vague to represent magnitude?

We opt for the latter interpretation because there is both experimental and observational evidence for recollection-based anticipatory behavior in fish. In one experiment, groups of golden shiners were fed daily at a feeding station during the beginning, middle, and end of an artificially maintained 12-hour day/night cycle (Laguë and Reeb, 2000; Reeb and Laguë, 2000). Most fish displayed *anticipatory* behavior by gathering in front of the feeder at about the time they were regularly fed there. Another study tested whether cichlid angelfish could learn to associate two variables, i.e., time and place of feeding (Gomez-Laplaza and Morgan, 2005). Food was delivered over a 3-week period in one corner of the tank in the morning and in another corner in the afternoon. Groups of angelfish learned to gather near the feeder at the appropriate time and place. Is social facilitation aiding this performance? Importantly, although pearl cichlids do need social facilitation, isolated angelfish can also master such a task (Barreto et al., 2006). Similar results were obtained in food restricted tilapia (Delicio and Barreto, 2008).

The most compelling evidence for fish relying on a guiding search image and an anticipatory goal image has been observed in gobies in their natural habitat. Aronson (1951) reported that intertidal gobies, which tend to stay in small pools during low tide, accurately jump from one pool to the next when their pool begins to dry out or when disturbed, and thus succeed in escaping by reaching the sea. How can gobies do that when they cannot see the location of the pools as they jump from one to the next? Aronson's (1971) subsequent analysis indicated that gobies accomplish this by exploring the region during high tide and forming a "cognitive map" of the exact location of the deeper sites. Moreover, gobies retain the memory image of the exact location of these pools for over a month. When transferred to region where they had no opportunity to explore the features of their new environment at high tide, they failed to jump from pool to pool at low tide. In summary, there is evidence that at least some fish can use recollection imagery to regulate their foraging strategies in relation to the time of the day or find an escape route when their pool dries out.

**3.3.7. Short-Term Working Imagery in Fishes.** The next issue we wish to examine is whether fish use short-term memory in situations where the making of a choice requires recollection of a preceding cue or instruction, what Baddeley and Hitch (1974) called "working memory." And, if they use working memory, how long does the imagery persist?

**STUDIES OF WORKING MEMORY IN MAMMALS.** In a pioneering experiment, Hunter (1913) trained animals to find a reward by selecting among several compartments the one cued by a lit bulb. In the second phase of the study, the cueing bulb was lit for a brief period but the animal was constrained by a glass enclosure from responding until some time has elapsed. This procedure sought to answer two questions. First, can the animal find the correct compartment by recollecting where the bulb was lit earlier, i.e., can the animal use a persisting memory image to

solve a behavioral task? Second, how long can the delay be extended to make a correct choice; i.e., how enduring is that memory image? The results showed that rats could solve the delayed reaction task if the delay did not exceed 10 seconds. Raccoons succeeded with a delay up to 25 seconds, and dogs with delays as long as 5 minutes. Because the animals often kept their body pointed toward the correct compartment during the delay period, critics argued that the test does not support the hypothesis that the animals use a memory image (“ideation”) unless reliance on postural orientation can be ruled out. Later experiments showed that without overt orientation, rats, cats, and monkeys succeeded with delays of several minutes to several hours, and apes with delays up to two days (reviewed by Maier and Schneirla, 1935).

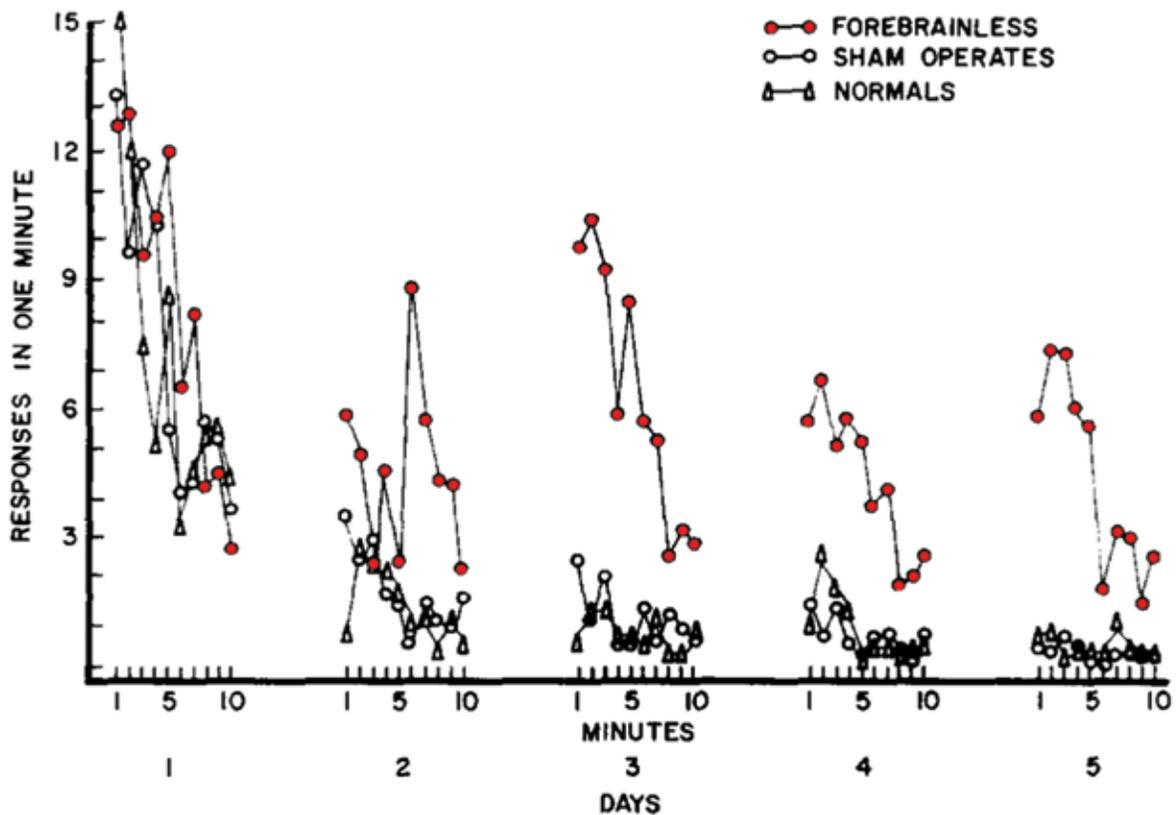
In another type of delayed reaction test, a monkey is seated in front of an experimental apparatus fitted with a tray that contains several wells (Harlow, 1949). As the animal looks on, a piece of banana is put into one of the wells, and then all the wells are covered with distinctive objects to cue which well is baited. An opaque screen is now lowered for some length of time and when it is raised, the monkey is allowed to uncover one of the wells. If the monkey reaches for the correct well as its first move it can collect its reward, if it fails to locate the correct well, the trial is terminated. Monkeys can solve this problem with delays of several minutes, suggesting that they can remember the correct cue by relying on a persisting memory image over that period. Still another procedure to study the persistence of a memory was designed specifically for rats. It consists of a central platform and eight arms extending from it as spokes of a wheel (Olton and Samuelson, 1976). Food is placed in recessed wells at the end of every arm and the rat is allowed to freely explore all the arms. Traditional association theory (Thorndike, 1911; Hull, 1943) predicts that upon finding food in the first arm that was visited, the rat should return to the same “reinforced” site. In fact, rats proceed successively to unvisited arms and explore most (if not all) of the unvisited arms on their first trial. Rotation of the radial maze indicates that this efficient foraging strategy is achieved by using extramaze cues (location of door, windows, furniture, etc.) in the laboratory rather than recognizing the visited arm by some nonspatial cue (such as an olfactory trail). If extramaze spatial cues are absent, rats tend to adopt another foraging strategy, such as always visiting the arm adjacent to the one previously visited (Suzuki et al., 1980). In either case, the rat’s effective foraging behavior cannot be explained without postulating that it can recollect (retain in its working memory) what it has done on the preceding trial until all the possible storage sites have been explored.

**CAN FISHES USE SHORT-TERM WORKING IMAGERY TO SOLVE PROBLEMS?** A few studies bear upon the issue whether fish rely on working imagery in their foraging behavior. In one of them (Schiller, 1948), fishes had to swim around an opaque partition to obtain a food reward. The results indicated that they were successful in this detour task if the bait was out of sight for no longer than a few seconds. More direct studies used an eight-arm maze modified for fish. Siamese fighting fish (Roitblat, et al., 1982), and sticklebacks and wrasse (Hughes and Blight, 1999) were found to visit previously unvisited arms above chance level after prolonged training but nowhere with the efficiency of rats. Fish needed extramaze cues to do that, without extramaze cues, the fish developed a stereotypic strategy of visiting every third arm. Some evidence has been presented that fish (specifically, cave fish) avoid their own odor when given a choice of visiting a site scented with their own odor and one without it (Paglianti et al.,

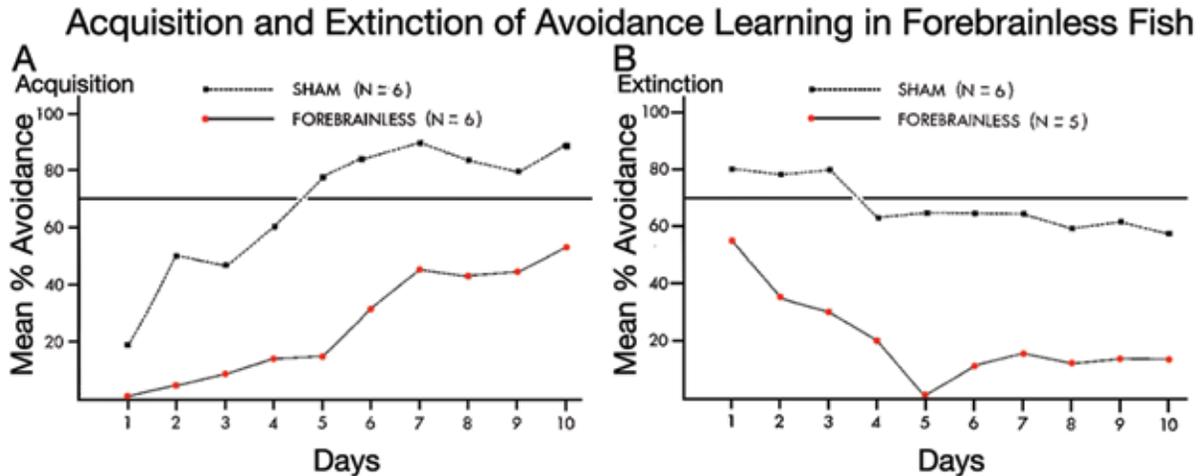
2006). That odor memory for site already explored is retained for about 6-18 hours, and is lost thereafter (Ceccolini et al., 2010). In summary, these experiments suggest that fish may use working imagery to a limited extent to aid foraging, but the duration of their short term memory and its efficiency is far below that of a primitive mammal, like the rat.

**THE FOREBRAIN'S ROLE IN MEMORY CONSOLIDATION IN FISHES.** While short-term memory is retained in goldfish after telencephalic ablation, as they learn by the end of brief daily sessions to refrain from snapping at a visible but inaccessible prey, memory consolidation is interfered with, as there is little retention of what they have learned from one day to the next (Peeke et al., 1972). Normal goldfish rarely snap at a visible but inaccessible shrimp by the second day of testing whereas forebrainless fish keep biting at a high rate at the beginning of the fifth day (Fig. 3-24).

### Short-Term and Long-Term Memory in Fish



**Fig. 3-24.** Snapping at a visible but inaccessible prey (shrimp) by normal, sham-operated, and forebrain-ablated goldfish. There is poor retention of habituation from one day to the next in the forebrainless fish. (From Peeke et al., 1972.)



**Fig. 3-25.** A. Deficit in the acquisition of an avoidance response in forebrain-ablated relative to sham-operated goldfish. B. Extinction of the avoidance response in the forebrain-ablated fish when shock delivery is terminated. (From Hainsworth et al., 1967.)

Similar deficits have been obtained in other learning tasks in goldfish and some other piscine species (Hainsworth et al., 1967; Kaplan and Aronson, 1967; Aronson and Kaplan, 1968; Savage, 1969; Overmier and Gross, 1974; Rooney and Laming, 1988; Overmier and Hollis, 1990). For instance, normal and sham-operated goldfish learn much faster and with greater consistency to shuttle from one compartment to another to avoid getting shocked than do forebrain-ablated fish (Fig. 3-25A). And unlike fish with intact forebrains, they do not retain what they have learned without reinforcement by repeated shocks (Fig. 3-25B). And while forebrainless fish can master a maze task based on a simple turn strategy (motor conditioning), they show deficits when they have to use a more complex place learning strategy, which requires the formation of a cognitive map of the maze (Salas et al., 1996; López et al., 2000a). These findings suggest that the piscine telencephalon plays an appreciable role in mnemonic functions.

What specific regions of the piscine telencephalon mediate these mnemonic functions? According to one study, restricted medial telencephalic lesions (but not lateral lesions) produce as severe deficits in learning an avoidance task by goldfish as does the removal of the entire telencephalon (Portavella et al., 2004). In contrast, lateral telencephalic lesions produce deficits in spatial learning but not in the avoidance task (Portavella and Vargas, 2005). According to another study (Rodríguez et al., 2002), dorsal and medial telencephalic lesions produce cue learning deficits in goldfish, whereas lateral telencephalic lesions (in line with the previous report) produce memory impairment in a spatial learning task, but not in a cue learning task. However, there are also discrepant reports. According to Saito and Watanabe (2004), dorsomedial lesions of the caudal telencephalon, but not dorsolateral lesions, produce deficits in relearning a maze task in goldfish but there was no deficit when the fish relied on a cue to find food. A subsequent analysis indicated further that the spatial learning deficits were evident after dorsomedial lesions only if the goldfish were prevented to rely on extramaze orienting cues (Saito and Watanabe, 2006). Notwithstanding this discrepancy—one set of

studies implicating the lateral telencephalon as the crucial mechanism of spatial learning, the other a dorsomedial site (the presumed rudiment of the hippocampus)—the evidence that the piscine telencephalon mediates mnemonic functions appears to be well established.

**THE FOREBRAIN'S ROLE IN BEHAVIORAL INTEGRATION IN FISHES.** A different approach to assess the role of the forebrain in fish behavior has been the examination of the relationship between the relative size of the forebrain in relation to the habitat they occupy. Species of fish inhabiting complex spatial environments, such as coral reefs, tend to have larger forebrains than do other species (Kotrschall et al., 1988; Bauchot et al., 1989). As we noted earlier (Section 3.3.1), the forebrain plays little role in the mediation of visual perception. Following its ablation, fish swim about, feed and gain weight much like normal fish do. However, fish manifest changes in behavioral integration following forebrain ablation, as exemplified by a reduction or abolition of territorial fighting, courtship behavior, and nest building (Noble and Borne, 1941; Schönherr, 1955; Hale, 1956; Segaar 1961; Fiedler, 1967; Aronson and Kaplan, 1968; Schwagmeyer et al., 1977; de Bruin, 1980; Overmier and Hollis, 1990). There are also changes in their schooling behavior. Whereas normal minnows do not allow a strange fish to join their school, operated animals do not display this “xenophobia” (Berwein, 1941). These findings suggest the possibility that instead of memory for specific events (episodic memory), the piscine telencephalon plays a significant role in the gradual improvement of behavioral performance (procedural memory).

**3.3.8. Phenomenal Awareness as Our Piscine Perceptual Legacy.** According to the available comparative-psychological evidence, jawed fishes are endowed with the ability to discriminate discrete objects in the external world on the basis of their distinctive configuration (shape, texture, size, etc.). This is in contrast to primitive invertebrates, such as a hydra or jellyfish, or primitive chordates, like amphioxus, that lack the sensory and neural mechanisms for that ability. They must have elementary visual sensations, but without topographically organized bilateral eyes and dedicated brain mechanisms to process the conveyed information, they cannot perceive the pattern and spatial location of whatever they see. In contrast, fish with bilateral eyes, and a topographically organized retinal surface and optic lobe, possess the mechanisms to perceive what objects look like. That advance from having only *anisomorphous sensations* (seeing light and dark points and diffuse expanses) to having *isomorphous representations* (pattern perception) of the external world is our piscine legacy. Fish are not just lured, irritated, or warned about salient events in their environment by amorphous stimuli, they also perceive the *phenomenal features* of the objects, beings, scenes and events that gratify or frustrate their needs and wants. However, this does not imply that fish are aware of the *substantive properties* of the things they perceive. They lack extremities with prehensile digits to palpate, manipulate and examine what they perceive, hence their awareness does not extend to an appreciation of the multifarious properties that characterize tangible objects. And because of their cognitive limitations, their awareness is not like our explicit, reflective consciousness of what transpires around us. Their awareness of the external world must be an implicit one, something like our semiconscious appreciation of what we are doing as we carry out some routine activity, like chewing softly or vigorously depending on the texture of the food, increasing or decreasing our grip as necessary when we hold on to something, or avoiding obstacles along our path as we walk or drive.