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Sensory Biology of Elasmobranchs

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12.1 Introduction

Sharks have become practically legendary for their sensory abilities. Some of the recognition is deserved, and some is often exaggerated. Accounts of sharks being able to smell or hear a single fish from miles away may be fish stories, but controlled measurements of elasmobranch sensory function have revealed that these animals possess an exquisite array of sensory systems for detecting prey and conspecifics, avoiding predators and obstacles, and orienting in the sea. This sensory array provides information to a central nervous system (CNS) that includes a relatively large brain, particularly in the rays and galeomorph sharks, whose brain-to-body weight ratios are comparable to those of birds and mammals (Northcutt, 1978).

Sensory system performance can be quantified in many ways. In the end, elasmobranch biologists wish to know, "How 'good' is elasmobranch hearing … smell … vision?" in a given behavioral or ecological context. To answer this basic question, sensory performance can be scaled in two general ways: *sensitivity*, which involves the minimum stimulus detectable by the system; and *acuity*, which is the ability of the system to discriminate stimulus characteristics, such as its location (direction of a sound or odor, resolution of a visual image, etc.) and type (frequency of sound, odor chemical, color of light, etc.). These parameters apply to all senses in one way or another and help to make comparisons across phylogenetic lines.

This chapter reviews the anatomy, physiology, and performance of elasmobranch senses within the context of sensory ecology and behavior. Special emphasis is placed on information that has come to light since publication of Hodgson and Mathewson's 1978 volume on elasmobranch senses (Hodgson and Mathewson, 1978a). Generalizations across all elasmobranch species are difficult and unwise, for with nearly 900 extant species, and only a fraction studied for their sensory capabilities, much still remains to be discovered about the diversity of sensory system function in elasmobranchs.

12.2 Vision

> "My nose is sufficiently good. My eyes are large and gray; although, in fact, they are weak to a very inconvenient degree, still no defect in this regard would be suspected from their appearance."
>
> **— Edgar Allan Poe, "The Spectacles" (1844)**

Poe could have been writing about the eyes and nose of a shark, for prior to the 1960s the perception, both scholarly and popular, was that vision in sharks was poor compared with the other senses, especially olfaction. Sharks' sense of smell was thought to be so much more important than vision and other senses that sharks were commonly called "swimming noses," even though visual scientists (e.g., Walls, 1942) recognized that elasmobranch ocular anatomy was highly developed. Sensory research in the 1960s and subsequent decades began to alter our understanding of shark visual capabilities. Several comprehensive reviews can be consulted for detailed research findings on elasmobranch vision (see Gilbert, 1963; Gruber and Cohen, 1978; Hueter and Cohen, 1991). This section summarizes what is known about the visual systems of sharks, skates, and rays with an emphasis on special adaptations for elasmobranch behavior and ecology.

12.2.1 Ocular Anatomy and Optics

Elasmobranch eyes are situated laterally on the head in the case of selachians and on the dorsal surface of the head in batoids, although the more benthic sharks (e.g., orectolobids, squatinids) have more dorsally positioned eyes and the less benthic rays (e.g., myliobatids, rhinopterids, mobulids) have more laterally positioned eyes, obvious adaptations for pelagic vs. benthic habits. Eye size in elasmobranchs is generally small in relation to body size but relatively larger in juveniles and in some notable species, such as the bigeye thresher shark, *Alopias superciliosus*.

In all elasmobranchs the two eyes oppose each other, which allows for a nearly 360° visual field, especially in the case of swimming sharks utilizing a laterally sinusoidal swimming pattern. Limited eye movements are observed in some species, primarily to compensate for swimming movements and stabilize the visual field (Harris, 1965). Binocular overlap is small, and blind areas exist directly in front of the snout or behind the head when the animal is still. The sizes of these blind areas depend on the configuration of the head and the separation of the eyes, but typically the forward blind area extends less than one body length in front of the rostrum.

The ocular adnexa are well developed and more elaborate than in most teleosts, although the upper and lower eyelids in most elasmobranchs do not move appreciably or cover the entire eyeball (Gilbert, 1963). Benthic shark species such as orectolobids have more mobile lids, which serve to protect the eyes while burrowing. Some shark species, especially the carcharhinids and sphyrnids, possess a third eyelid, the nictitating membrane, which can be extended from the lower nasal corner of the eye to cover the exposed portion of the eye (Gilbert, 1963). This membrane functions to protect the eye from damaging abrasion and may be extended when the shark feeds or comes into contact with another object. It does not naturally respond to bright light, although it can be conditioned to do so (Gruber and Schneiderman, 1975). Some other sharks not equipped with a nictitating membrane, including the white shark, *Carcharodon carcharias* (Tricas and McCosker, 1984) and the whale shark, *Rhincodon typus* (Hueter, pers. obs.), use the extraocular muscles to rotate the entire eye back into the orbit to protect it from abrasion during feeding and other activities.

The outer layer of the elasmobranch eye (Figure 12.1) comprises a thick cartilaginous sclera and a gently curving, transparent cornea, the fine structure of which includes sutural fibers that resist corneal

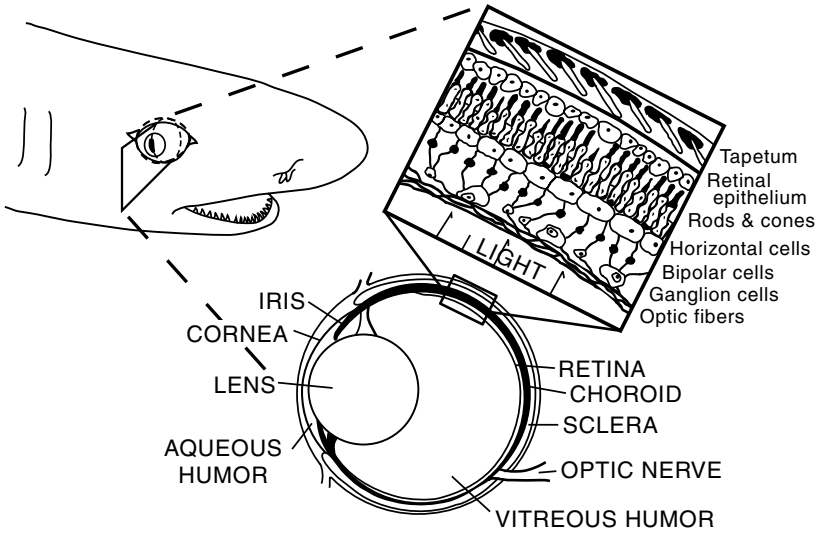

FIGURE 12.1 Cross section through a shark eye showing ocular and retinal anatomy. Tapetum lucidum shown in non-occluded state exposing reflective plates for greater visual sensitivity under scotopic conditions. (Modified from Hueter, R.E. and P.W. Gilbert. 1990. In *Discovering Sharks*. S.H. Gruber, Ed., American Littoral Society, Highlands, NJ, 48–55.)

swelling and loss of transparency in challenging chemical environments (Tolpin et al., 1969). Unlike teleosts, most elasmobranchs have a dynamic iris that can increase the size of the pupil in dim light or decrease it in bright light. Depending on species, the shape of the pupil can be circular (e.g., most deep-sea sharks, which have less mobile pupils for the more constant, low-light conditions), vertical slit (e.g., *Carcharhinus* spp., *Negaprion brevirostris*), horizontal slit (e.g., *Sphyrna tiburo*), oblique slit (e.g., *Scyliorhinus canicula, Ginglymostoma cirratum*), or crescent-shaped (e.g., many skates and rays). Mobile slit pupils are typically found in active predators with periods of activity in both photopic (bright light) and scotopic (dim light) conditions, such as the lemon shark, *N. brevirostris* (Gruber, 1967); a slit pupil that can be closed down to a pinhole is thought to be the most effective way to achieve the smallest aperture under photopic conditions, because a circular pupil is mechanically constrained from closing to a complete pinhole (Walls, 1942). In skates and rays, the combination of a U-shaped crescent pupil with multiple pupillary apertures under photopic conditions provides optical benefits including enhanced visual resolution, contrast, and focusing ability (Murphy and Howland, 1991).

The elasmobranch cornea is virtually optically absent underwater due to its similarity in refractive index to that of seawater (Hueter, 1991), leaving the crystalline lens to provide the total refractive power of the eye. Elasmobranch lenses are typically large, relatively free of optical aberration, and ellipsoidal in shape, although the spiny dogfish, *Squalus acanthias,* and clearnose skate, *Raja eglanteria,* have nearly spherical lenses (Sivak, 1978a; 1991). In the juvenile lemon shark, *N. brevirostris*, the principal power (D_p) of the lens is nearly +140 diopters (D), about seven times the optical power of the human lens (Hueter, 1991).

Some elasmobranch lenses contain yellowish pigments that are enzymatically formed oxidation products of tryptophan, similar to lens pigments found in many teleosts and diurnal terrestrial animals. These pigments filter near-ultraviolet (UV) light, which helps to minimize defocus of multiple wavelengths (chromatic aberration), enhance contrast sensitivity, and reduce light scatter and glare under conditions of bright sunlight (Zigman, 1991). They may also help to protect the retina from UV damage in shallow benthic and epipelagic species. Zigman (1991) found yellow lens pigments in coastal and surface-dwelling species such as the sandbar shark, *Carcharhinus plumbeus*, the dusky shark, *C. obscurus*, and the tiger shark, *Galeocerdo cuvier*, but interestingly not in another carcharhinid and shallow-water shark, the lemon shark, *N. brevirostris*, or in the shallow-dwelling nurse shark, *Ginglymostoma cirratum*. Both lemon and nurse sharks inhabit tropical waters where UV damage to the eye could be a problem, so the ecological correlations are unclear, and there may be other factors dictating the presence or absence of these lens filters. Nelson et al. (2003) described a related UV-filtering mechanism in the corneas of scalloped hammerhead sharks, *Sphyrna lewini*, in which the degree of UV protection by the cornea increased with duration of exposure to solar radiation.

Accommodation is the ability to change the refractive power of the eye to focus on objects at varying distances. Without accommodative ability, the focal plane of the eye is static, and in the absence of other optical adaptations, the image of any object in front of or behind that plane will be out of focus on the retina. Elasmobranchs that accommodate do not vary lens shape as humans do, but instead change the position of the lens by moving it toward the retina (for distant targets) or away from the retina (for near targets). The lens is supported dorsally by a suspensory ligament and ventrally by the pseudocampanule, a papilla with ostensibly contractile function (Sivak and Gilbert, 1976). Evidence of accommodation in elasmobranchs has been inconsistent across species, and many of the species studied have appeared to be hyperopic (far-sighted) in the resting state of the eye (Sivak, 1978b, 1991; Hueter, 1980; Hueter and Gruber, 1982; Spielman and Gruber, 1983), which is problematic.

Hueter et al. (2001), however, discovered that unrestrained, free-swimming lemon sharks (*N. brevirostris*) were not hyperopic and could accommodate, in contrast to previous findings for the same species under restraint (Hueter, 1980; Hueter and Gruber, 1982), suggesting that the hyperopia and absence of accommodation measured in many elasmobranchs under restraint is an induced, unnatural artifact resulting from handling stress. Eliminating this artifact, it is possible that most elasmobranchs would be emmetropic (neither far-sighted nor near-sighted) in the resting state and have accommodative ability. This complication aside, there is some indication that benthic elasmobranchs, such as the nurse shark *G. cirratum* and the bluntnose stingray, *Dasyatis sayi*, may have greater accommodative range than more active, mobile elasmobranchs (Sivak, 1978b). This may be attributable to the stability of the visual field

in sedentary species, providing advantages for a more refined focusing mechanism, but more research into the interrelationship between vision and locomotion in elasmobranchs is needed.

At the back of the elasmobranch eye behind the retina and in front of the sclera lies the choroid, the only vascularized tissue within the adult elasmobranch eye. The elasmobranch retina itself is not vascularized and typically contains no obvious landmarks other than the optic disk (corresponding to a small blind spot in the visual field), which contains no photoreceptors and marks the exit of retinal ganglion cell fibers via the optic nerve from retina to CNS. The choroid in nearly all elasmobranchs contains a specialized reflective layer known as the tapetum lucidum, which consists of a series of parallel, platelike cells containing guanine crystals (Gilbert, 1963; Denton and Nicol, 1964). The function of this layer is to reflect back those photons that have passed through the retina and not been absorbed by the photoreceptor layer, allowing a second chance for detection of photons and thereby boosting sensitivity of the eye in dim light. The alignment of the tapetal cells provides for specular reflection; that is, photons are reflected back along the same path and are not scattered within the eye, which would blur the image.

Many elasmobranchs, furthermore, possess an occlusible tapetum, in which the reflective layer can be occluded by dark pigment granules that migrate under light-adapted conditions within tapetal melanophores to block the passage of photons (Nicol, 1964; Heath, 1991). Although there are exceptions, occlusible tapeta tend to be found in more surface-dwelling, arrhythmic species with both diurnal and nocturnal activity, which selects for visual adaptation to widely varying light levels. Non-occlusible tapeta in which the reflective layer is permanently exposed are found in sharks that inhabit the deep sea, where light levels are consistently dim (Nicol, 1964).

12.2.2 Retina and CNS

The largest impact on our understanding of visual capabilities in elasmobranchs came with the eventual finding that practically all elasmobranchs have duplex retinas containing both rod and cone photoreceptors (Gruber and Cohen, 1978), beginning with the unequivocal evidence of cones in the lemon shark (*N. brevirostris*) retina presented by Gruber et al. (1963). Cones subserve photopic and color vision and are responsible for higher visual acuity; rods subserve scotopic vision and are involved in setting the limits of visual sensitivity in the eye. Prior to 1963, elasmobranchs were thought to possess all-rod retinas, and thus were thought to have poor visual acuity and no capability for color vision, which we now know is untrue. The only elasmobranchs that appear to have no cone photoreceptors are skates (*Raja* spp.), but even their rods appear to have conelike functions under certain photic conditions (Ripps and Dowling, 1991; Dowling and Ripps, 1991).

Both rods and cones contain visual pigments that absorb photons and begin the process of vision. These pigments consist of a protein called opsin and a chromophore prosthetic group related to either vitamin A_1 or A_2, the former type called rhodopsins or chrysopsins and the latter called porphyropsins (Cohen, 1991). Rhodopsins are maximally sensitive to blue-green light, chrysopsins to deep-blue light, and porphyropsins to yellow-red light. Most elasmobranchs have been found to possess rhodopsin, which provides maximum sensitivity for clearer, shallow ocean waters associated with epipelagic environments (Cohen, 1991). Chrysopsin has been found in deep-sea squaliform sharks such as *Centrophorus*, *Centroscymnus,* and *Deania* (Denton and Shaw, 1963), which inhabit regions where the little available light is deep blue. Porphyropsin, which is common in freshwater teleosts and is more suited for turbid, yellowish photic conditions, is rare in elasmobranchs, even freshwater species.

However, Cohen et al. (1990) found a porphyropsin with maximum sensitivity (λ_{max}) of 522 nm (yellow-green) in the juvenile lemon shark, *N. brevirostris*, whereas adult lemon sharks have a rhodopsin with λ_{max} = 501 nm (blue-green). In this species, the visual pigment apparently changes over from a porphyropsin adapted for maximum sensitivity in inshore, shallow waters to a rhodopsin better suited for clearer, bluer oceanic waters (Figure 12.2). This visual adaptation matches a habitat shift from shallow to oceanic waters that occurs between juvenile and adult stages of the lemon shark (Cohen et al., 1990).

The density and spatial distribution of photoreceptors in the retina fundamentally affect visual acuity and sensitivity, as do the retinal interneurons (bipolar, amacrine, horizontal, ganglion cells), which transmit impulses ultimately to visual centers in the CNS. Elasmobranch retinas are rod-dominated,

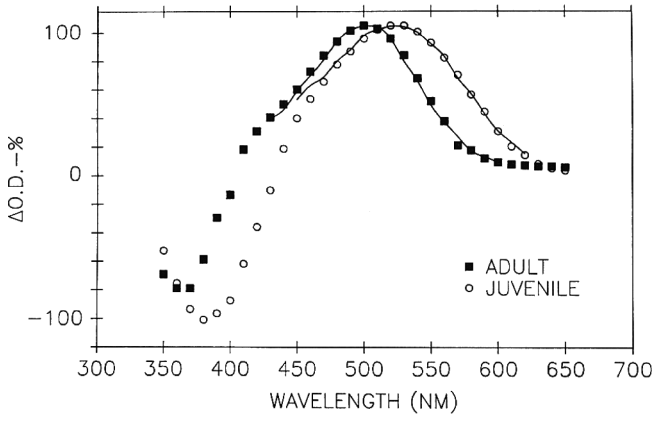

FIGURE 12.2 Normalized difference spectra for visual pigment absorption characteristics of adult vs. juvenile lemon sharks (*Negaprion brevirostris*). Peak absorption for the juvenile pigment is 522 nm whereas the adult peak is 501 nm, demonstrating a shift in this species from a more yellow-red-sensitive porphyropsin in the juvenile to a more blue-green-sensitive rhodopsin in the adult. (From Cohen, J.L. et al. 1990. *Vision Res.* 30:1949–1953. With permission.)

ranging from the skates with all-rod retinas (Dowling and Ripps, 1991), to species with apparently few cones such as *Mustelus* (Stell and Witkovsky, 1973; Sillman et al., 1996), to lamnid and carcharhinid sharks with perhaps as many as one cone for every 4 to 13 rods (Gruber et al., 1963; Gruber and Cohen, 1978). Some authors have suggested a correlation between greater rod-to-cone ratios and more scotopic habits (such as nocturnal behavior) or habitats (visually murky environments or deep-sea) in elasmobranch species. That sharks, skates, and rays have rod-dominated retinas does not inherently mean their vision is adapted primarily for low-light conditions, sensitivity to movement, and crude visual acuity; the human retina also has many more rods than cones, and our diurnal vision and acuity are among the best in the animal kingdom.

The spatial topography of retinal cells can, however, reveal much about the quality of vision in these animals. Although elasmobranchs do not have all-cone foveas, they do have retinal areas of higher cone and/or ganglion cell density, which indicate regional specializations for higher visual acuity (Hueter, 1991; Collin, 1999). Higher cone concentrations have been found in the "central" retina of the nurse shark, *Ginglymostoma cirratum* (Hamasaki and Gruber, 1965), white-spotted bamboo shark, *Chiloscyllium plagiosum* (Yew et al., 1984), and white shark, *Carcharodon carcharias* (Gruber and Cohen, 1985). Franz (1931) was the first to report horizontal streaks of higher ganglion cell density in the small-spotted catshark, *Scyliorhinus canicula,* and smooth hound, *Mustelus mustelus*.

More recently, Peterson and Rowe (1980), Hueter (1991), and Bozzano and Collin (2000) have used retinal whole-mount techniques to map the topographic distributions of retinal cells in nine elasmobranch species representing six families of sharks and skates. All of these species were found to have horizontal visual streaks of higher cell density, except for the cookie-cutter shark, *Isistius brasiliensis*, which has a specialized concentric area in the temporal retina (Bozzano and Collin, 2000). The horizontal visual streak is an adaptation for more or less two-dimensional terrain environments such as the sea bottom or sea surface, two environments commonly inhabited by many elasmobranch species, and species with prominent horizontal streaks include the horn shark, *Heterodontus francisci* (Peterson and Rowe, 1980), lemon shark, *N. brevirostris* (Hueter, 1991), small-spotted catshark, *Scyliorhinus canicula* (Bozzano and Collin, 2000), and tiger shark, *Galeocerdo cuvier* (Bozzano and Collin, 2000). The first three of these are benthically oriented species; the tiger shark feeds on prey such as birds, sea turtles, and marine mammals commonly found on or near the sea surface (Lowe et al., 1996).

Concentric retinal areas are more applicable for imaging a limited spot in the visual field or for operating in complex, three-dimensional visual environments, such as reefs. Interestingly, both the cookie-cutter shark and white shark are ambush predators in open water, and both appear to have retinal areas, not streaks. However, retinal topography in the white shark needs to be assessed more thoroughly

before conclusions about this species' spatial vision can be made. In addition to habitat, locomotory style may influence the adaptiveness of visual streaks vs. areas (Hueter, 1991). A thoughtful discussion of the possible ecological and behavioral correlates with elasmobranch retinal topography has been presented by Bozzano and Collin (2000).

The elasmobranch retina projects via ganglion cell fibers in the optic nerve primarily to the mesencephalic optic tectum, but most species also possess at least ten other retinofugal targets in the brain in addition to the optic tectum, similar to the pattern in other vertebrates (Graeber and Ebbesson, 1972; Northcutt, 1979, 1991). These targets include the large elasmobranch telencephalon, once believed to be primarily an olfactory center but now thought to subserve the other senses as well, particularly for multimodal integration (Bodznick, 1991). In the lemon shark, *N. brevirostris*, the visual streak found in the cone and ganglion cell layers of the retina is preserved in the retinotectal projection to the surface of the optic tectum, where three times more tectal surface is dedicated proportionally to vision inside the streak than in the periphery of the visual field (Hueter, 1991).

A similar result was reported by Bodznick (1991) in the optic tectum of the skate *Raja erinacea*. The retinal topography of this skate is unknown but a related species (*R. bigelowi*) has a prominent visual streak (Bozzano and Collin, 2000). Bodznick (1991) furthermore found that a spatial map of electroreceptive input, aligned with the visual map, also overrepresented the animal's sensory horizon in the tectum. These findings give tantalizing insights into the coordination of multimodal sensory function in the elasmobranch brain, but much more work needs to be done in this area.

12.2.3 Visual Performance

Controlled experiments to test visual performance in sharks began in 1959 when Clark trained adult lemon sharks, *N. brevirostris,* to locate a square white target for food reward (Clark, 1959). Later, Clark (1963) trained lemon sharks to visually discriminate between a square vs. diamond and a white vs. black-and-white striped square. Parameters such as visual angle, contrast, and luminance of targets were not quantified, but the demonstration that sharks could learn certain visually mediated tasks was noteworthy at the time. Wright and Jackson (1964) and Aronson et al. (1967) added to Clark's findings with further conditioning experiments on lemon, bull (*Carcharhinus leucas*), and nurse sharks (*Ginglymostoma cirratum*), again without quantified visual parameters, but providing evidence that sharks can learn visual tasks about as quickly as teleosts (cichlids) and mammals (mice).

Rigorous methods of psychophysics, including both operant and classical conditioning techniques, were applied to the study of juvenile lemon shark vision by Gruber (reviewed in Gruber and Cohen, 1978). In a series of elegant behavioral experiments conducted over nearly two decades, Gruber elucidated many aspects of lemon shark visual performance, including brightness discrimination, dark adaptation, critical flicker fusion (CFF), and spectral (color) sensitivity. Among the many findings from this line of research were (1) lemon sharks can be trained to discriminate the brighter of two visual targets down to a 0.3 log unit difference (as opposed to a 0.2 log unit threshold in human subjects); (2) lemon sharks slowly dark-adapt to scotopic conditions over the course of about 1 h, eventually becoming more than 1 million times (6 log units) more sensitive to light than under photopic conditions (and more sensitive than dark-adapted human subjects); (3) a kink in the CFF vs. light intensity curve for the lemon shark demonstrates the rod–cone break characteristic of a duplex retina; and (4) a shift in the lemon shark's light-adapted vs. dark-adapted spectral sensitivity, also confirmed electrophysiologically by Cohen et al. (1977), provides further evidence of duplex visual function in this shark. The upshot of this work was the confirmation that sharks are capable of vision in extremely dim light and that they also are capable of color vision.

The ultimate test of whether elasmobranchs use color vision in the wild to discriminate visual targets has yet to be reported. Sharks can be attracted to bright colors, including the brilliant orange of life vests — a source of concern to the U.S. Navy, which funded many shark sensory studies in the 1960s and 1970s to understand shark behavior — but it is unclear whether the animals are visually cueing on color, brightness, or contrast. Similarly, the functional visual acuity of sharks in the wild is poorly known. Hueter (1991) calculated that the juvenile lemon shark has a theoretical resolving power of 4.5′ of arc, based on the closest separation of cones in the retina and the eye's optics. This acuity is about one ninth

that of the human eye, which can resolve down to about 30″ of arc, but the prediction remains to be behaviorally tested.

The importance of vision in the daily lives of elasmobranchs certainly finds support in the complexity of their anatomical and physiological visual adaptations, many of which appear to be correlated with species behavior and ecology. Field reports of sharks appearing to use vision during the final approach to prey items are common, but controlled tests are not. One exception was a study of the Pacific angel shark, *Squatina californica,* by Fouts and Nelson (1999), in which chemical, mechanical, and electrical cues were eliminated to determine that visual stimuli released an ambush attack by these benthic sharks on nearby prey items. Based on their observations, the authors hypothesized that the angel shark visual system probably is specialized for anterodorsally directed vision. A study of retinal topography in this species would help to confirm this hypothesis. Strong (1996) tested behavioral preferences of white sharks, *Carcharodon carcharias,* approaching differently shaped visual targets. The sharks were attracted to the testing area with olfactory stimuli but they appeared to use vision as they approached the objects, which were ≥15-cm-diameter surface-borne targets to which the sharks appeared to visually orient from depths of ≥17 m. At that depth, a 15-cm target would subtend a visual angle of about 0.5°, or 30′ of arc, which is more than six times as large as the theoretical minimum separable angle of the juvenile lemon shark eye. This visual task should not be a problem for a white shark with a relatively large, cone-rich eye (Gruber and Cohen, 1985).

12.3 Hearing

Hearing in sharks is of great interest because sound in the ocean presents a directional signal that is capable of propagating over large distances. Sharks are not known to make sounds, so their hearing abilities have likely been shaped by the ambient noise (both physical and biological) in their environment. Hearing in sharks and rays has been reviewed by numerous authors (see Wisby et al., 1964; Popper and Fay, 1977; Corwin, 1981, 1989; Myrberg, 2001). These reviews provide both an excellent overview of shark hearing research and a historical perspective on the scientific approaches to studying shark hearing. The purpose of this section is to describe what is known about shark hearing with an emphasis on what remains to be learned.

12.3.1 Anatomy

12.3.1.1 Inner Ear — The inner ear of sharks, skates, and rays consists of a pair of membranous labyrinths with three semicircular canals and four sensory maculae each (Retzius, 1881; Maisey, 2001) (Figure 12.3). The semicircular canals are similar to those in other vertebrates, and are used to sense angular acceleration. They are not known to be involved in sound perception.

The saccule, lagena, and utricle are three sensory areas that are thought to be involved in both balance and sound perception. They consist of a patch of sensory hair cells on an epithelium overlain by an otoconial mass. The otoconia, made of calcium carbonate granules embedded in a mucopolysaccharide matrix, act as an inertial mass (Tester et al., 1972). As in fishes, these otolith organs are thought to be responsive to accelerations produced by a sound field, which accelerate the shark and the sensory macula relative to the otoconial mass. Some elasmobranchs, such as the spiny dogfish, *Squalus acanthias*, have been found to incorporate exogenous sand grains as a way to increase the endogenous otoconial mass (Lychakov et al., 2000).

12.3.1.2 Macula Neglecta — Sharks are unique among fishes in having a tympanic connection, the fenestra ovalis, to the posterior semicircular canal that enhances audition (Howes, 1883). The fenestra ovalis is located in the base of the parietal fossa, which makes a depression in the posterior portion of the skull. The fenestrae lead to the posterior canal ducts of the semicircular canals, each of which contains a sensory macula, the macula neglecta, that is not overlain by otoconia (Tester et al., 1972).

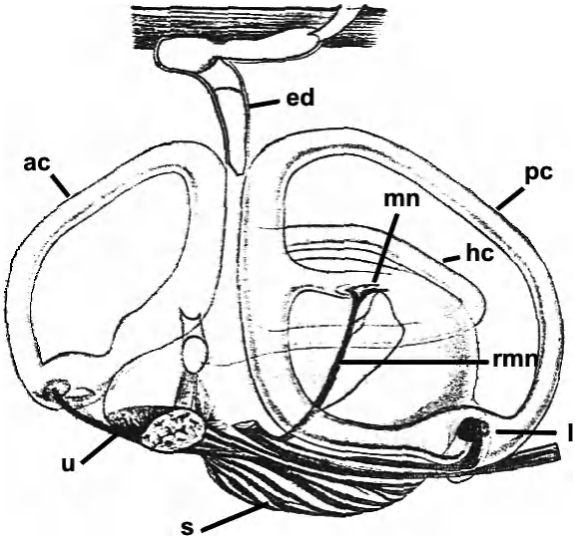

FIGURE 12.3 Anatomy of the ear of the thornback ray, *Raja clavata*. ed, endolymphatic duct; ac, anterior semicircular canal; pc, posterior semicircular canal; hc, horizontal semicircular canal; s, saccule; u, utricle; l, lagena; mn, macula neglecta; rmn, ramus of VIIIth nerve innervating macula neglecta. (Modified from Retzius, 1881.)

Elasmobranchs also have an endolymphatic duct that connects to the saccule and leads to a small opening on the dorsal surface of the shark. This connection has been hypothesized to act as a site of release of displacement waves (Tester et al., 1972), as any flow induced over the fenestrae ovalis would propagate down the posterior canal duct and into the sacculus.

Because of the specialization of the posterior canal in sharks, most hearing research has focused on the macula neglecta. The macula neglecta consists of one patch of sensory hair cells in rays, and two patches of sensory hair cells in carcharhinid sharks (Corwin, 1977, 1978). The macula neglecta lacks otoconia, but does have a crista like other hair cells in the semicircular canals. In rays, the hair cells show a variety of orientations. In carcharhinids, the hair cells are oriented in opposite directions in each sensory patch, and the orientation patterns are positioned so that fluid flows in the posterior canal would stimulate the hair cells. Variation of the structure of the macula neglecta has been hypothesized to be linked to the foraging behavior of different elasmobranchs (Corwin, 1978). However, until the function of the macula neglecta is determined, this hypothesis will be difficult to test.

The macula neglecta in rays has been shown to add hair cells continually as the fish grows (Corwin, 1983; Barber et al., 1985). Sex differences have also been found: females have been found to have more hair cells than males. The increase in hair cell number has been shown to increase vibrational sensitivity in neurons innervating the macula neglecta.

12.3.1.3 Central Pathways — As in other vertebrates, the ear of elasmobranchs is innervated by the VIIIth cranial (octaval) nerve. Studies of afferent connections and the physiology of the octaval nerve from individual end organs (saccule, lagena, utricle, and macula neglecta) show projections ipsilaterally to five primary octaval nuclei: magnocellular, descending, posterior, anterior, and periventricular. (Corwin and Northcutt, 1982; Barry, 1987). Much work remains to be done regarding both the anatomy and neurophysiology of the CNS.

12.3.2 Physiology

12.3.2.1 Audiograms — Audiograms are measures of hearing sensitivity to sounds of different frequencies. Audiograms are the most basic information that is collected about hearing systems in

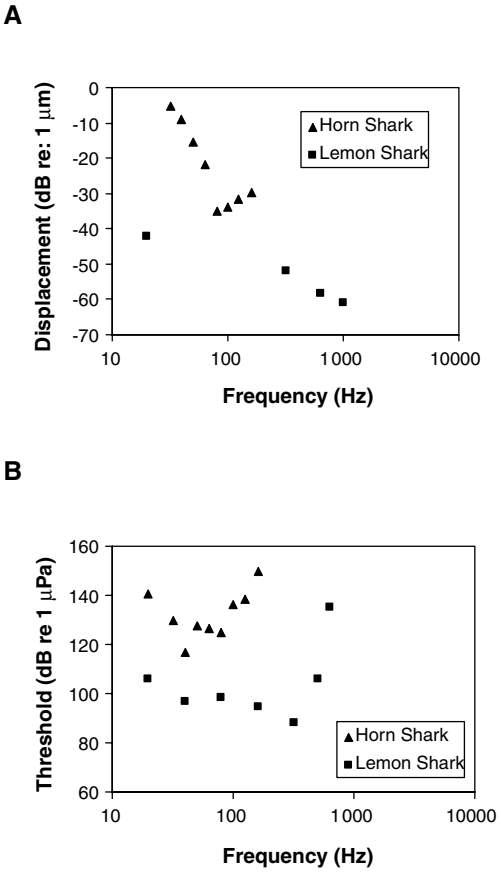

FIGURE 12.4 Elasmobranch audiograms: (A) Displacement audiograms, (B) pressure audiograms. (Redrawn from data presented in Fay, 1988; horn shark from Kelly and Nelson, 1975; lemon shark from Banner, 1967.)

animals. To date, there are only five published audiograms in elasmobranchs (summarized in Figure 12.4). Given the diversity of the group, more audiograms are warranted.

The greatest issue in measuring audiograms is what component of sound is relevant to acoustic detection in sharks. Fishes without swimbladders, such as flounders, detect the *particle displacement* component of sound. Fishes with swimbladders, especially those with connections between the swimbladder and ear like the goldfish, also detect the *pressure* component of sound. In these fishes, the swimbladder acts as a pressure-to-displacement transducer.

One way to determine the importance of particle displacement vs. pressure is to measure hearing sensitivity at different distances from a sound projector. The ratio of pressure to particle displacement changes as the distance from the sound changes. Measurements in the lemon shark, *Negaprion brevirostris*, and in the horn shark, *Heterodontus francisci*, show that sharks are sensitive to particle displacement rather than sound pressure at least at low frequencies (Banner, 1967; Kelly and Nelson, 1975). In both of these papers it was not clear that higher-frequency thresholds (640 Hz in Banner; 100 to 160 Hz in Kelly and Nelson) were dominated by either pressure or particle displacement sensitivity. This could be because of measurement errors in the setups or because the sharks are detecting some other measurement of the sound field, such as the pressure gradient.

Despite these issues, laboratory studies indicate that shark hearing is not as sensitive as that of some other fishes, especially those with hearing adaptations coupling a swimbladder to the inner ear. All the sharks tested show mainly low-frequency sensitivity, and there is no evidence that they are more sensitive at low frequencies than other fishes (Kritzler and Wood, 1961; Banner, 1967; Nelson, 1967; Kelly and Nelson, 1975; Casper et al., 2003).

Several papers show the importance of the macula neglecta in detecting sound and/or vibration (Lowenstein and Roberts, 1951). Fay et al. (1974) measured the response of the macula neglecta to vibrational stimuli applied to the parietal fossa. This showed that the parietal fossa is indeed in some way linked to hearing in the macula neglecta. Bullock and Corwin (1979) obtained similar results in finding that auditory evoked potentials were highest when a sound source was placed over the parietal fossa.

12.3.2.2 Pressure Sensitivity — Isolated preparations of dogfish, *Scyliorhinus canicula,* hair cells from the horizontal semicircular canals have recently been shown to respond to changes in ambient pressure (Fraser and Shelmerdine, 2002). Increased ambient pressure led to increased spike rates in response to an oscillation at 1 Hz. This result shows that sharks have a sensor that could be used to sense depth and atmospheric pressure, and recent studies by Heupel et al. (2003) demonstrate that blacktip sharks, *Carcharhinus limbatus,* behaviorally respond to decreases in atmospheric pressure associated with tropical storms. The physiological findings need to be pursued in other parts of the ear to determine whether responses to sound are modulated by pressure as well, and if shark hair cells could detect sound pressures directly. The ambient pressures tested were on the order of 200 dB re 1 μPa, which would be extremely loud for a sound.

12.3.3 Behavior

12.3.3.1 Attraction of Sharks with Sound — Several studies have shown that sharks can be attracted with low-frequency sounds in the field (Nelson and Gruber, 1963; Myrberg et al., 1969, 1972). In some of these tests, the received sound pressure levels were likely well below thresholds obtained from laboratory studies of shark hearing. This apparent disconnect between field and laboratory studies needs to be addressed. There are problems with each type of study. In the laboratory, sound fields are very complicated near-field stimuli that are rarely quantified. In the field, it is often difficult to know the distribution of sharks prior to playback and difficult to control for other stimuli, such as visual stimuli. The fact that sharks show a behavioral response to sound presentation should present a good system for testing theories about shark hearing abilities. New technology for tracking sharks should provide a means to monitor a shark's response to sound presentation in field situations.

12.3.3.2 Other Aspects of Hearing — There is more to hearing than just detection of sound. The ability to localize a sound source is just as an important as being able to hear the sound. The otolithic organs in other fishes have been shown to respond directionally to sound presentations due to the polarizations of the sensory hair cells (Lu and Popper, 2001). This is likely to be the case with sharks as well. One reason that the debate over the ability of sharks to detect sound pressure has been intense is that theoretical arguments have been made that sharks must be able to detect sound pressure to resolve a 180° ambiguity about the location of a source (see van den Berg and Schuijf, 1983; Kalmijn, 1988a). The acoustic attraction experiments show that sharks have the ability to localize a sound source, and laboratory experiments show that the lemon shark can localize a sound source to about 10° (Nelson, 1967).

There clearly needs to be more data collected about hearing sensitivity, masking by noise, frequency discrimination, intensity discrimination, and temporal sensitivity. Regardless of the actual mechanism of sound detection, data collected on these attributes of sound will be important for understanding the acoustic world of sharks.

12.4 Mechanosenses

The ability to detect water movements at multiple scales is essential in the lives of fishes. The detection of large tidal currents provides information important for orientation and navigation, and small-scale flows can reveal the location of prey, predators, and conspecifics during social behaviors. The mechanosensory lateral line system is stimulated by differential movement between the body and surrounding water, and is used by fishes to detect both dipole sources (e.g., prey) and uniform flow fields (e.g.,

currents). This sensory system functions to mediate behaviors such as rheotaxis (orientation to water currents), predator avoidance, hydrodynamic imaging to localize objects, prey detection, and social communication including schooling and mating (see Coombs and Montgomery, 1999, for review). In contrast to the amount of information available on lateral line morphology and function in bony fishes, relatively little is known about mechanosensory systems in elasmobranchs.

12.4.1 Peripheral Organization

The functional unit of all lateral line end organs is the mechanosensory neuromast, which is a group of sensory hair cells surrounded by support cells and covered by a gelatinous cupula (Figure 12.5A). Elasmobranch fishes have several different types of mechanosensory end organs that are classified by morphology and location: superficial neuromasts (pit organs or free neuromasts), pored and nonpored canals, spiracular organs, and vesicles of Savi. The variety of surrounding morphological structures and spatial distribution of these sensory neuromasts determine functional parameters such as response properties, receptive field area, distance range of the system, and which component of water motion (velocity or acceleration) is encoded (Denton and Gray, 1983, 1988; Münz, 1989; Kroese and Schellart, 1992).

Superficial neuromasts are distributed on the skin surface either in grooves positioned on raised papillae (skates, rays, and some sharks) or between modified placoid scales (sharks) with their cupulae directly exposed to the environment (Tester and Nelson, 1969; Peach and Marshall, 2000) (Figure 12.5B). Superficial neuromasts in the few batoids examined thus far are located in bilateral rows along the dorsal midline from the spiracle to the tip of the tail, a pair anterior to the endolymphatic pores, and a small group lateral to the eyes (Ewart and Mitchell, 1892; Maruska and Tricas, 1998; Maruska, 2001) (Figure 12.6A). In sharks, superficial neuromasts are positioned on the dorsolateral and lateral portions of the body and caudal fin (dorsolateral neuromasts), posterior to the mouth (mandibular row), between the

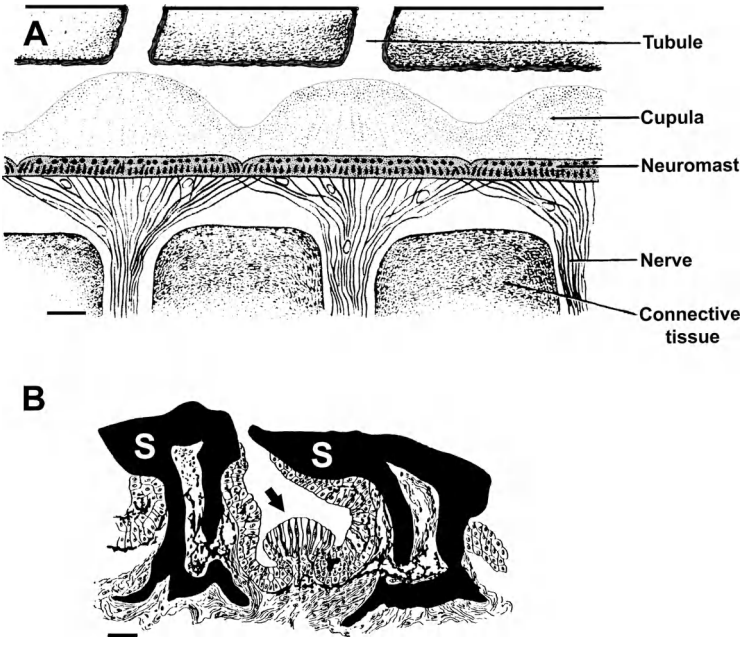

FIGURE 12.5 Morphology of the lateral line canal system and superficial neuromasts in elasmobranchs. (A) Diagrammatic longitudinal section of a pored canal from a juvenile grey reef shark, *Carcharhinus amblyrhynchos.* Innervated canal neuromasts are arranged in a nearly continuous sensory epithelium and covered by gelatinous cupulae. Pored canals are connected to the environment via tubules that terminate in openings on the skin surface. Scale bar = 150 µm. (Modified from Tester, A.L. and Kendall, J.I. *Pac. Sci*. 1969. With permission.) (B) Schematic transverse section of a single superficial neuromast (pit organ) in the nurse shark, *Ginglymostoma cirratum*. The sensory neuromast (arrow) is positioned between modified scales (S). Scale bar = 50 µm. Cupula is not shown. (Modified from Budker, 1958.)

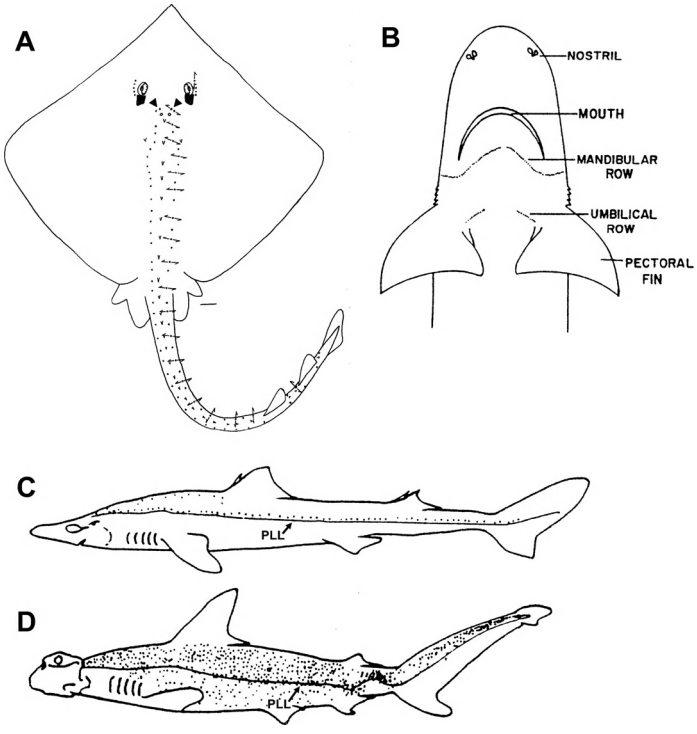

FIGURE 12.6 Distribution of superficial neuromasts (pit organs) in elasmobranchs. Each dot represents a single superficial neuromast. (A) Superficial neuromasts on the clearnose skate, *Raja eglanteria,* are located in bilateral rows along the dorsal midline to the end of the tail, a pair anterior to each endolymphatic pore (arrowheads), and a small group positioned lateral to each eye. Arrows indicate the groove orientation on every other neuromast. Scale bar = 1 cm. (B) Ventral surface of the lemon shark, *Negaprion brevirostris* (67 cm total length), shows the mandibular and umbilical rows of superficial neuromasts found on many shark species. (C) Superficial neuromasts on the spiny dogfish, *Squalus acanthias* (79 cm total length), are relatively few in number and positioned along the dorsal aspect of the posterior lateral line canal (PLL). (D) Superficial neuromasts on the scalloped hammerhead, *Sphyrna lewini* (61 cm total length), are more numerous (>600 per side) and located both dorsal and ventral to the posterior lateral line canal. (A, Modified from Maruska, K.P. 2001. *Environ. Biol. Fish.* 60, 47–75. With permission. B through D, Modified from Tester, A.L. and G.J. Nelson. 1969. In *Sharks, Skates, and Rays*. P.W. Gilbert, R.F. Mathewson, and D.P. Rall, Eds., Johns Hopkins University Press, Baltimore, 503–531. With permission.)

pectoral fins (umbilical row), and a pair anterior to each endolymphatic pore (Budker, 1958; Tester and Nelson, 1969; Peach and Marshall, 2000) (Figure 12.6B to D). However, the distribution pattern varies among taxa with one or more of the neuromast groups absent in some species. The number of superficial neuromasts ranges from less than 80 per side in the spiny dogfish, *Squalus acanthias*, to more than 600 per side in the scalloped hammerhead, *Sphyrna lewini* (Tester and Nelson, 1969) (Figure 12.6C and D). The position of the sensory epithelium within grooves or between scales differs from bony fishes and may enhance water flow parallel to the cupula to provide greater directional sensitivity. Superficial neuromasts encode the velocity of water motion and likely function to detect water movements generated by predators, conspecifics, or currents (Blaxter and Fuiman, 1989; Kroese and Schellart, 1992; Montgomery et al., 1997).

The most visible part of the mechanosensory system is the network of subepidermal fluid-filled canals distributed throughout the body. The main lateral line canals located on the head of elasmobranchs include the supraorbital, infraorbital, hyomandibular, and mandibular canals (Tester and Kendall, 1969; Boord and Campbell, 1977; Roberts, 1978; Chu and Wen, 1979; Maruska, 2001) (Figure 12.7). These canals show varying degrees of complex bifurcations on the head in sharks, or branching patterns that extend laterally onto the pectoral fins in skates and rays (Figure 12.7A). The principal canal on the remainder of the body is the posterior lateral line canal, which extends caudally from the endolymphatic pores on the dorsal surface of the head to the tip of the tail (Figure 12.7C). These lateral line canals all

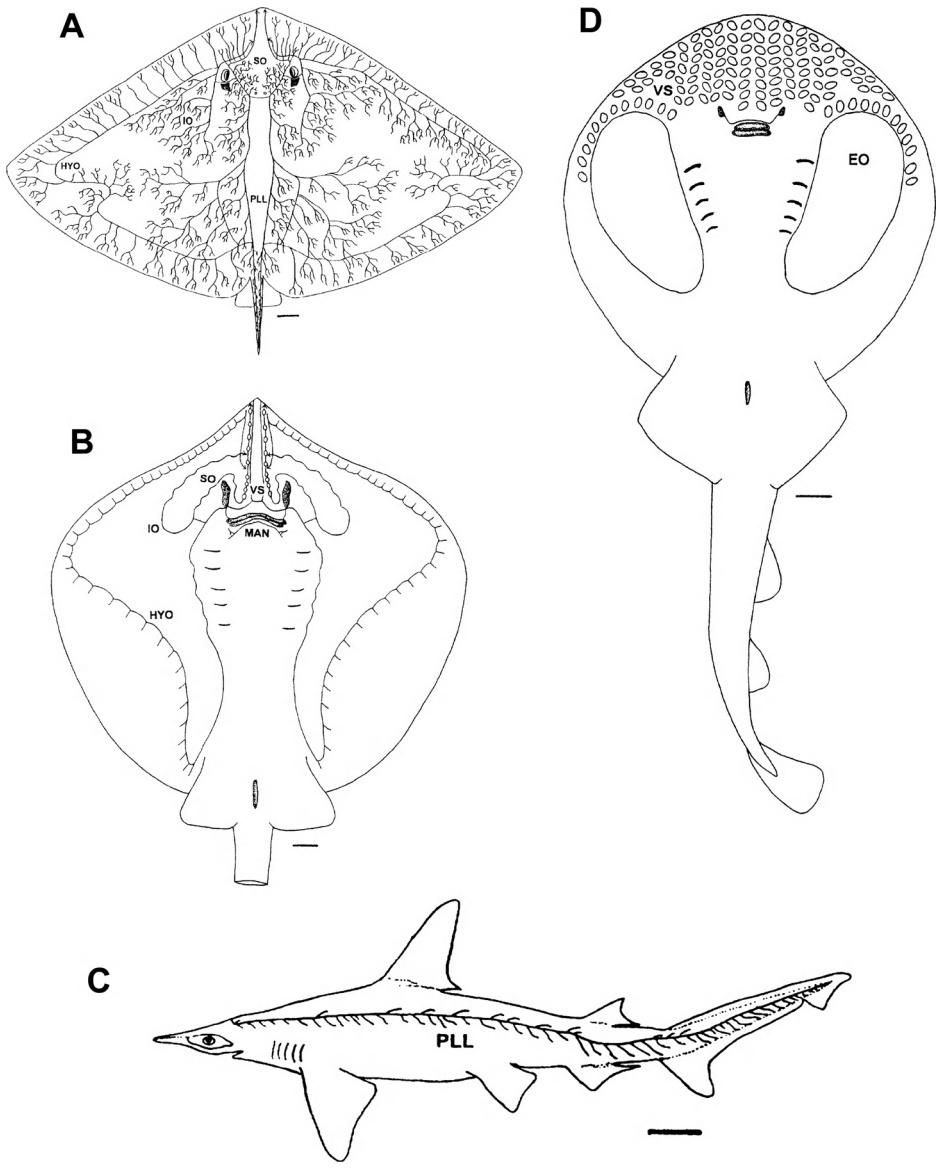

FIGURE 12.7 Distribution of lateral line canals and vesicles of Savi in elasmobranchs. The end of each line represents a pore opening on the skin surface. (A) Distribution of lateral line canals on the dorsal surface of the butterfly ray, *Gymnura micrura.* Canals are interconnected with extensive tubule branching that covers the majority of the disk surface. (B) Ventral lateral line system of the Atlantic stingray, *Dasyatis sabina,* contains pored canals along the disk margin, nonpored canals along the midline and around the mouth, and vesicles of Savi (ovals) on the rostral midline. (C) Lateral view of the posterior lateral line canal on the bonnethead shark, *Sphyrna tiburo*, which extends from the endolymphatic pores on the head to the upper lobe of the caudal fin. (D) Vesicles of Savi (ovals) on the ventral surface of the lesser electric ray, *Narcine brasiliensis,* are located in rows on the rostrum and along the anterior edge of the electric organ (EO). HYO = hyomandibular canal, IO = infraorbital canal, MAN = mandibular canal, PLL = posterior lateral line canal, SO = supraorbital canal, VS = vesicles of Savi. Scale bar = 1 cm in A, B, and D and 0.5 cm in C. (Modified from Maruska, K.P. 2001. *Environ. Biol. Fish.* 60, 47–75. With permission.)

contain between tens and thousands of neuromasts organized into an almost continuous sensory epithelium that results in multiple neuromasts between pores (Ewart and Mitchell, 1892; Johnson, 1917) (Figure 12.5A). This differs from bony fishes that have a single discrete neuromast positioned between adjacent pores, but the functional significance of this organization is unclear.

Elasmobranchs contain two different morphological classes of lateral line canals: pored and nonpored. Pored canals are in contact with the surrounding water via neuromast-free tubules that terminate in pores on the skin surface. These canals are abundant on the dorsal head of sharks and dorsal surface of batoids, where they often form complex branching patterns that increase the mechanosensory receptive field on the disk (Chu and Wen, 1979; Maruska, 2001) (Figure 12.7A). Pored canals encode water accelerations and are best positioned to detect water movements generated by prey, predators, conspecifics during social interactions or schooling, and distortions in the animal's own flow field to localize objects while swimming (Hassan, 1989; Kroese and Schellart, 1992; Montgomery et al., 1995; Coombs and Montgomery, 1999).

The presence of an extensive plexus of nonpored canals represents one of the most significant differences between teleost and elasmobranch lateral line systems. Nonpored canals are isolated from the environment and thus will not respond to pressure differences established across the skin surface. These canals are most common on the ventral surface of skates and rays, but are also found on the head of many shark species (Chu and Wen, 1979; Maruska and Tricas, 1998; Maruska, 2001). In the batoids, these nonpored canals have wide diameters, are located beneath compliant skin layers, and are concentrated along the midline, around the mouth, and on the rostrum (Maruska and Tricas, 1998; Maruska, 2001) (Figure 12.7B). These morphological characteristics indicate that nonpored canals may function as tactile receptors that encode the velocity of skin movements caused by contact with prey, the substrate, or conspecifics during social interactions (Maruska, 2001). The number and distribution of pored vs. nonpored canals differ widely among species and may be correlated with ecology and behavior, or explained by phylogeny.

Specialized mechanoreceptors in elasmobranchs are the spiracular organs and vesicles of Savi, both of which are isolated from the surrounding water. Spiracular organs are bilaterally associated with the first (spiracular) gill cleft and consist of a tube or pouch lined with sensory neuromasts and covered by a cupula (Barry and Bennett, 1989). This organ is found in both sharks and batoids, is stimulated by flexion of the cranial-hyomandibular joint, and although its biological role is unclear, morphological and physiological studies indicate it functions as a joint proprioceptor (Barry et al., 1988a,b; Barry and Bennett, 1989). Vesicles of Savi consist of neuromasts enclosed in sub-epidermal pouches, are most abundant on the ventral surface of the rostrum, and are thus far only found in some torpedinid, narcinid, and dasyatid batoids (Savi, 1844; Chu and Wen, 1979; Barry and Bennett, 1989; Maruska, 2001) (Figure 12.7B and D). Vesicular morphology differs slightly among these taxa and, although these mechanoreceptors are hypothesized to represent an obsolescent canal condition or serve as specialized touch or substrate-borne vibration receptors, their proper biological function also remains unclear (Norris, 1932; Nickel and Fuchs, 1974; Barry and Bennett, 1989; Maruska, 2001).

12.4.2 Adequate Stimulus and Processing

The necessary stimulus for the lateral line system is differential movement between the body surface and surrounding water. Because the flow amplitude of a dipole stimulus falls off rapidly with distance from the source (rate of $1/r^3$), the lateral line can only be stimulated within the inner regions of the so-called near-field (e.g., within one to two body lengths of a dipole source) (Denton and Gray, 1983; Kalmijn, 1989). Movement of the overlying cupula by viscous forces is coupled to stereocilia and kinocilia motions such that displacement of stereocilia toward the single kinocilium causes depolarization of the hair cell and an increase in the spontaneous discharge rate of the primary afferent neuron. Displacement in the opposite direction causes hyperpolarization of the hair cell and an inhibition or decrease in primary afferent firing. Thus, water motion stimuli effectively modulate the spontaneous primary afferent neuron discharges sent to the mechanosensory processing centers in the hindbrain. This modulation of neural activity from spatially distributed end organs throughout the body provides the animal with information about the frequency, intensity, and location of the stimulus source (Denton and

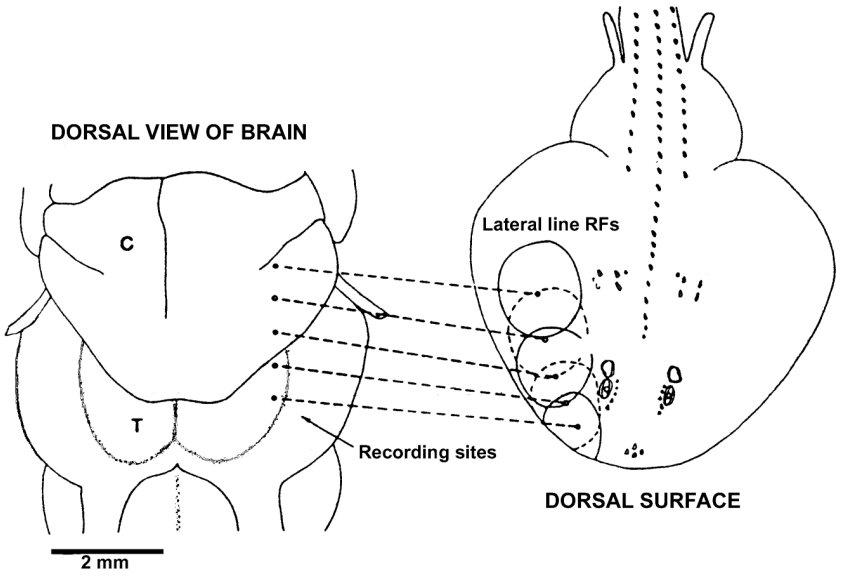

FIGURE 12.8 Mechanosensory lateral line receptive fields (RFs) on the body are somatotopically organized in a point-to-point rostrocaudal map in the midbrain of the thornback ray, *Platyrhinoidis triseriata*. Receptive fields on the anterior, mid, and posterior body are mapped onto the contralateral rostral, mid, and caudal dorsomedial nucleus of the midbrain. C = cerebellum, T = tectum. (Modified from Bleckmann, H. et al. 1987. *J. Comp. Physiol. A* 161:67–84. With permission.)

Gray, 1988; Kalmijn, 1989; Bleckmann et al., 1989). In general, neuromasts are sensitive to low-frequency stimuli (≤200 Hz), and neurophysiology studies indicate the lateral line system is sensitive to velocities in the μm s^{-1} range and accelerations in the mm s^{-2} range (Münz, 1985; Bleckmann et al., 1989; Coombs and Janssen, 1990).

Lateral line neuromasts are innervated by a distinct set of nerves separate from the traditional 11 to 12 cranial nerves described in most vertebrates (Northcutt, 1989a). The cephalic region of elasmobranchs is innervated by the ventral root of the anterior lateral line nerve complex and the body and tail by the posterior lateral line nerve complex (Koester, 1983). Both complexes contain efferents as well as afferent axons that enter the brain and terminate somatotopically within octavolateralis nuclei of the hindbrain (Bodznick and Northcutt, 1980; Koester, 1983; Bleckmann et al., 1987; Puzdrowski and Leonard, 1993). Ascending lateral line pathways continue to the lateral mesencephalic nucleus and tectum in the midbrain and to the thalamic and pallial nuclei in the forebrain (Bleckmann et al., 1987; Boord and Montgomery, 1989). Bleckmann et al. (1987) also demonstrated that mechanosensory receptive fields are somatotopically organized in a point-to-point rostrocaudal body map within the midbrain of the thornback ray (Figure 12.8). Further neurophysiological studies show bimodal and multimodal neurons within midbrain and forebrain centers that respond to hydrodynamic flow as well as to auditory, or visual, or electrosensory stimuli (Bleckmann and Bullock, 1989; Bleckmann et al., 1989). Thus, these processing regions can integrate information from several sensory systems to help mediate appropriate behavioral responses to complex biological stimuli.

12.4.3 Behavior

Among bony fishes, the lateral line system is known to function in schooling behavior, social communication, hydrodynamic imaging, predator avoidance, rheotaxis, and prey detection. However, behavioral experiments to demonstrate these lateral line–mediated behaviors in elasmobranch species are available only for prey detection and rheotaxis.

The best-known behavioral use of the lateral line system is in prey detection. The concentration of mechanoreceptors on the cephalic region of sharks and ventral surface of batoids, as well as the low-frequency, close range of the system, indicates an important role in the detection, localization, and

capture of prey. Swimming and feeding movements of invertebrates and vortex trails behind swimming fish can produce water movements within the frequency and sensitivity range of the lateral line system (Montgomery et al., 1995). Montgomery and Skipworth (1997) showed that the ventral lateral line canal system of the short-tailed stingray, *Dasyatis brevicaudata*, could detect small transient water flows similar to those produced by the bivalves found in their diet. Furthermore, based on the peripheral morphology of the lateral line system and feeding behavior of the Atlantic stingray, *D. sabina,* Maruska and Tricas (1998) hypothesized that the nonpored canals on the ventral surface of the ray function as specialized tactile receptors that encode the velocity of skin movements caused by contact with small benthic prey. Neurophysiology experiments also demonstrate that touching the skin near the nonpored canals causes a transient stimulation of the neuromasts (Sand, 1937), which supports the hypothesized mechanotactile function. While prey detection is mediated by the integration of multiple sensory inputs (i.e., electroreception, olfaction, vision), the mechanosensory lateral line likely plays an important role in feeding behavior across elasmobranch taxa.

Recent evidence in sharks demonstrates that superficial neuromasts provide sensory information for rheotaxis, similar to that found in teleosts (Montgomery et al., 1997). Resting Port Jackson sharks, *Heterodontus portjacksoni,* with their dorsolateral superficial neuromasts (pit organs) ablated show a reduced ability to orient upstream in a flume when compared to intact individuals (Peach, 2001). Positive rheotaxis in sharks, skates, and rays may be important for species-specific behaviors and is hypothesized to facilitate water flow over the gills, to help maintain position on the substratum, to help orient to tidal currents, and to facilitate prey detection by enabling the animal to remain within an odor plume (see Peach, 2001).

The structure and function of the elasmobranch mechanosensory system are ripe for future study. For example, the variety of morphological specializations (e.g., nonpored canals, vesicles of Savi) found in elasmobranchs requires quantitative examinations of response properties among receptor types. Comparisons of specific mechanoreceptor distributions on the body are needed across elasmobranch taxa to test hypotheses on whether species-specific distributions have some ecological significance and represent specializations driven by evolutionary selective pressures. In addition, direct behavioral studies are sorely needed to clarify the many putative functions of the mechanosensory system in elasmobranch fishes such as schooling, object localization, predator avoidance, and social communication.

12.5 Electrosenses

All elasmobranch fishes possess an elaborate ampullary electroreceptor system that is exquisitely sensitive to low-frequency electric stimuli (see review by Bodznick and Boord, 1986; also see Montgomery, 1984; New, 1990; Tricas and New, 1998). The ampullary electroreceptor system consists of subdermal groups of electroreceptive units known as the ampullae of Lorenzini, which can detect weak extrinsic electric stimuli at intensities as low as 5 nV/cm (Kalmijn, 1982). The ampullae of Lorenzini were first recognized and described long ago by Stenonis (1664) and Lorenzini (1678), but their physiological and behavioral functions remained unknown for almost another three centuries. Initially, the ampullae of Lorenzini were thought to be mechanoreceptors (Parker, 1909; Dotterweich, 1932), but were then later shown to be also temperature sensitive (Sand, 1938; Hensel, 1955). A mechanoreceptive function was again proposed later (Murray, 1957, 1960a; Loewenstein, 1960) along with a proposed function as detectors for changes in salinity (Loewenstein and Ishiko, 1962) before current ideas about their use in electroreception were generally accepted. Murray (1960b) followed by Dijkgraaf and Kalmijn (1962) were the first to demonstrate the electrosensitivity of the ampullae of Lorenzini. Recently, the temperature sensitivity of ampullae was reconfirmed by Brown (2003), who demonstrated that the extracellular gel from the ampullae develops significant voltages in response to very small temperature gradients. Thus, temperature can be translated into electrical information by elasmobranchs without the need of cold-sensitive ion channels as used by mammals (Reid and Flonta, 2001, Viana et al., 2002). The extremely sensitive ampullary electroreceptor system of elasmobranchs is now known to mediate orientation to local inanimate electric fields (Kalmijn, 1974, 1982; Pals et al., 1982b), theorized to function in geomagnetic navigation (Kalmijn, 1974, 1988b, 2000; Paulin, 1995), and is known to be important for the

detection of the bioelectric fields produced by prey (Kalmijn, 1971, 1982; Tricas, 1982; Blonder and Alevizon, 1988), potential predators (Sisneros et al., 1998), and conspecifics during social interactions (Tricas et al., 1995).

12.5.1 Anatomy

12.5.1.1 Ampullae of Lorenzini — Single ampullae of Lorenzini consist of a small chamber (the ampulla) and a subdermal canal about 1 mm wide that projects to the surface of the skin (Figure 12.9A) (Waltman, 1966). Small bulbous pouches known as alveoli form the ampulla chamber. Within each alveolus, hundreds of sensory hair-cell receptors and pyramidal support cells line the alveoli wall with only the apical surface of the sensory receptors and support cells exposed to the internal lumen of the ampulla chamber. Tight junctions unite the support cells and sensory receptors to create a high-resistance electrical barrier between the basal and apical surfaces of the sensory epithelium, which form the ampulla wall (Waltman, 1966; Sejnowski and Yodlowski, 1982). The basal surface of the sensory receptor cell is innervated by 5 to 12 primary afferents of the VIIIth cranial nerve with no efferents present (Kantner et al., 1962). The wall of the canal consists of a double layer of connective tissue fibers and squamous epithelial cells that are tightly joined together to form a high electrical resistance (6 MΩ-cm) between the outer and inner surface of the canal wall. In contrast, the canal and ampulla are filled with a high-potassium, low-resistance gel (25 to 31 Ω-cm) composed of mucopolysaccharides (Doyle, 1963) that form an electrical core conductor with a resistance equaling that of seawater, such that the ampullary chamber becomes isopotential with a charge at the skin pore (Murray and Potts, 1961; Waltman, 1966).

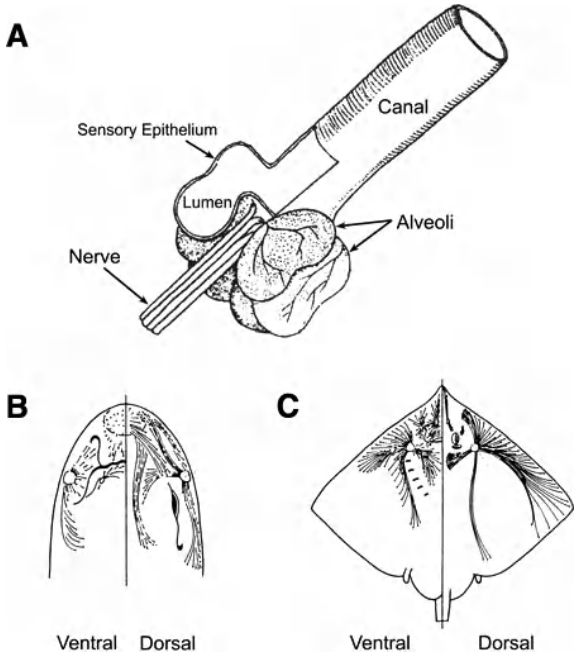

FIGURE 12.9 Ampullary electroreceptor organ of elasmobranchs. (A) The ampulla of Lorenzini consists of a small ampulla chamber composed of multiple alveoli that share a common lumen and a subdermal ampullary canal that projects to a pore on the surface of the skin. The sensory epithelium forms a high resistance ampulla wall composed of a single layer of sensory receptor cells and support cells. The basal surface of the sensory receptor cells is innervated by primary afferents of the VIIIth cranial nerve. (Modified from Waltman, B. 1966. *Acta Physiol. Scand.* 66(Suppl. 264):1–60. With permission.) (B) Diagrammatic representation of the horizontal distribution of the subdermal ampullary clusters and their radial canals that terminate at surface pores on the ventral and dorsal surfaces of the cat shark, *Scyliorhinus canicula.* (Modified from Dijkgraaf, S. and A.J. Kalmijn. 1963. *Z. Vergl. Physiol.* With permission.) (C) Horizontal distribution of the ampullae of Lorenzini in the skate, *Raja clavata.* (Modified from Murray, R.W. 1960. *J. Exp. Biol*. 37:417–424. With permission.)

In marine elasmobranchs, many individual ampullae are grouped into discrete, bilateral cephalic clusters from which project the subdermal canals that radiate in many directions and terminate at individual skin pores on the head of sharks (Figure 12.9B) and the head and pectoral fins of skates and rays (Figure 12.9C). The ampullary clusters, which usually vary in number (three to six per side of animal) and location depending on species, are innervated by different branches of the anterior lateral line nerve (VIII) (Norris, 1929). The special arrangement of the contiguously grouped ampullae within the cluster creates a common internal potential near the basal region of the sensory receptors within each cluster. The sensory receptor cells within individual ampullae detect potential differences between the animal's common internal potential at the ampullary cluster and seawater at the surface pore of the skin, which is isopotential with the subdermal canal and internal lumen of the ampulla (Bennett, 1971). In effect, electroreceptors measure the voltage drop of the electric field gradient along the length of the ampullary canal. Thus, ampullae with long canals sample across a greater distance within a uniform field, provide a larger potential difference for the sensory receptors, and thus have a greater sensitivity than do ampullae with short canals (Broun et al., 1979; Sisneros and Tricas, 2000). The morphological arrangement of the ampullary canals and clusters permits detection of both small local fields produced by small prey organisms and also the uniform electric fields of inanimate origins for possible use in orientation and navigation (Kalmijn, 1974; Tricas, 2001).

In contrast to marine species, freshwater elasmobranchs have a very different morphology and organization of the ampullary electroreceptors that are thought to reflect sensory adaptations to the highly resistive environment of freshwater (Kalmijn, 1974, 1982, 1988b; Raschi and Mackanos, 1989). One such adaptation is a thicker epidermis that functions to increase transcutaneous electrical resistance. In addition, the size of the ampullary electroreceptors in freshwater elasmobranchs is greatly reduced, and thus the ampullae are referred to as microampullae or miniampullae. Furthermore, the ampullary electroreceptors are distributed individually, rather than in clusters, over the head and pectoral fins and have very short subdermal canals (~0.3 to 2.1 mm long) that extend to the surface pores on the skin.

12.5.1.2 Central Pathways — The ampullae of Lorenzini are innervated by primary afferent neurons that convey sensory information to the brain via the dorsal root projections of the anterior lateral line (VIII). The electrosensory primary afferents from ipsilateral ampullae terminate in a somatotopic order within the central zone of the dorsal octavolateralis nucleus (DON), the first-order hindbrain electrosensory nucleus (Bodznick and Northcutt, 1980; Koester, 1983; Bodznick and Schmidt, 1984). The large electrosensory multipolar principal cells in the DON known as ascending efferent neurons (AENs) receive afferent input from the dorsal granular ridge and both the peripheral and central zones of the DON. AENs ascend to the midbrain via a lateral line lemniscus and terminate in somatotopic order in a part of the contralateral midbrain known as lateral mesencephalic nucleus (LMN) and in deep layers of the tectum (Bodznick and Boord, 1986). The LMN is one of the three elasmobranch midbrain nuclei that compose the lateral mesencephalic nuclear complex (Boord and Northcutt, 1982), which is a midbrain region considered to be homologous to the torus semicircularis in electrosensory teleost fishes (Platt et al., 1974; Northcutt, 1978). Electrosensory information processed in the LMN is sent to the posterior lateral nucleus of the thalamus, where it is then relayed to the medial pallium of the forebrain (Bullock, 1979; Bodznick and Northcutt, 1984; Schweitzer and Lowe, 1984). Some electrosensory information is also conveyed to the cerebellum (Tong and Bullock, 1982; Fiebig, 1988).

12.5.2 Physiology

12.5.2.1 Peripheral Physiology — Electrosensory primary afferent neurons that innervate the ampullae of Lorenzini exhibit a regular pattern of discharge activity in the absence of electrical stimulation. Average resting discharge rates of electrosensory afferents in batoid elasmobranchs range from 8.6 impulses/s at 7°C in the little skate, *Raja erinacea* (New, 1990), to 18.0 impulses/s at 16 to 18°C in the thornback guitarfish, *Platyrhinoidis triseriata* (Montgomery, 1984), 34.2 impulses/s at 18°C in the round stingray, *Urolophus halleri* (Tricas and New, 1998), 44.9 impulses/s at 20°C in the clearnose skate, *R. eglanteria* (Sisneros et al., 1998), and 52.1 impulses/s at 21 to 23°C in the Atlantic stingray,

Dasyatis sabina (Sisneros and Tricas, 2002a). These differences in resting discharge rates among batoids are most likely due to the influence of temperature, which in the case of higher temperatures can decrease the thresholds required for membrane depolarization of the sensory receptors and spike initiation of the electrosensory primary afferents (Carpenter, 1981; Montgomery and MacDonald, 1990). Resting discharge rates and discharge regularity of the electrosensory afferents are influenced by the animal's age. Both the rate and discharge regularity of electrosensory afferents increase during development from the neonate to the adult elasmobranch (Sisneros et al., 1998; Sisneros and Tricas, 2002a). The resting discharge rate and pattern of the electrosensory afferents are important determinants of the sensitivity and low-frequency information encoding of the electric sense (Stein, 1967; Ratnam and Nelson, 2000; Sisneros and Tricas, 2002a).

The resting discharge patterns of the electrosensory primary afferent neurons in all elasmobranch fishes are modulated by extrinsic electric fields as a function of stimulus polarity and intensity. Presentation of a cathodal (negative) stimulus at the ampullary pore increases the neural discharge activity of electrosensory afferents while an anodal (positive) stimulus decreases discharge activity (Murray, 1962, 1965). Stimulation of the electroreceptors with a sinusoidal electric field modulates the neural discharges of electrosensory afferents as a linear function of the stimulus intensity over the dynamic range of the peripheral electrosensory system, which is from 20 nV/cm to 25 μV/cm (Murray, 1965; Montgomery, 1984; Tricas and New, 1998). Electrosensory afferents are most responsive to electric fields oriented parallel to the vector between ampullary canal opening on the skin surface and the respective ampulla. Within the intensity range of natural biologically relevant electric fields, electroreceptors are broadly tuned to low-frequency electric stimuli and respond maximally to sinusoidal stimuli from approximately 0.1 to 15 Hz (Andrianov et al., 1984; Montgomery, 1984; Peters and Evers, 1985; New, 1990; Tricas et al., 1995; Tricas and New, 1998; Sisneros et al., 1998; Sisneros and Tricas, 2000). Sensitivity of the electrosensory afferents to a sinusoidal uniform electric field is 0.9 spikes/s per μV/cm for the little skate, *R. erinacea* (Montgomery and Bodznick, 1993), 4 spikes/s per μV/cm for thornback guitarfish, *P. triseriata* (Montgomery, 1984), 7.4 spikes/s per μV/cm average for the Atlantic stingray, *D. sabina* (Sisneros and Tricas, 2000, 2002a), 17.7 spikes/s per μV/cm average for the clearnose skate, *R. eglanteria* (Sisneros et al., 1998), and 24 spikes/s per μV/cm average for the round stingray, *U. halleri* (Tricas and New, 1998).

12.5.2.2 Central Physiology — Although neurophysiological studies of the central electrosensory system in elasmobranchs are not very extensive, several features of electrosensory processing in the hindbrain and midbrain, and to a lesser extent in the thalamus and forebrain, are known. The principal cells of the DON known as AENs exhibit lower resting discharge rates and are more phasic in response than primary afferent neurons found in the peripheral electrosensory system (Bodznick and Schmidt, 1984; New, 1990). The resting discharge rates of AENs range from 0 to 5 spikes/s in the little skate, *R. erinacea* (Bodznick and Schmidt, 1984; New, 1990), to an average of 10 spikes/s in the thornback guitarfish, *P. triseriata* (Montgomery, 1984). However, AENs are similar to electrosensory primary afferents in that they are excited by cathodal stimuli and inhibited by anodal stimuli (New, 1990). Sensitivity to sinusoidal uniform electric fields is higher for second-order AENs than the primary afferent neurons. The sensitivity of AENs ranges from 2.2 spikes/sc per μV/cm for *R. erinacea* (Conley and Bodznick, 1994) to 32 spikes/s per μV/cm for *P. triseriata* (Montgomery, 1984). The increased gain of AENs is most likely due to the convergent input of multiple electrosensory primary afferents onto AENs, which have excitatory receptive fields that comprise two to five adjacent ampullary electroreceptor pores (Bodznick and Schmidt, 1984). AENs are also similar to electrosensory primary afferents in their frequency response with a maximum response in the range 0.5 to 10 Hz, followed by a sharp cutoff frequency between 10 and 15 Hz (Andrianov et al., 1984; Montgomery, 1984; New, 1990; Tricas and New, 1998).

One important function of the second-order AENs is to filter out unwanted noise or reafference created by the animal's own movements, which could interfere with the detection of biologically relevant signals (Montgomery and Bodznick, 1994). Electrosensory AENs show a greatly reduced response to sensory reafference that is essentially similar or common mode across all electrosensory primary afferents. An adaptive filter model was proposed by Montgomery and Bodznick (1994) to account for the ability of

electrosensory AENs to suppress common mode reafference. The suppression of common mode signals by AENs is mediated by the balanced excitatory and inhibitory components of their spatial receptive fields (Bodznick and Montgomery, 1992; Bodznick et al., 1992; Montgomery and Bodznick, 1993).

The response properties of the central electrosensory system have also been studied in the midbrain of elasmobranchs. The midbrain electrosensory neurons of *P. triseriata* are usually "silent" and exhibit no resting discharge activity (Schweitzer, 1986). Midbrain unit thresholds range from less than 0.3 μV/cm, the lowest intensity tested, to 5 μV/cm in *P. triseriata* (Schweitzer, 1986) to even lower thresholds of 0.015 μV/cm measured with evoked potentials in the blacktip reef shark, *Carcharhinus melanopterus* (Bullock, 1979). Midbrain neurons respond maximally to frequency stimuli from 0.2 Hz (lowest frequency tested) to 4 Hz in *P. triseriata*, 10 to 15 Hz in the freshwater stingray, *Potamotrygon* sp., and at higher frequencies from 20 to 30 Hz in the blacktip reef shark, *C. melanopterus* (Bullock, 1979; Schweitzer, 1986). Such discrepancies in frequency sensitivity may be due to differences in methodology or to variation among species. Electrosensory neurons in the LMN of the midbrain may have small, well-defined minimum excitatory receptive fields that include 2 to 20 ampullary pores in *Platyrhinoidis triseriata* (Schweitzer, 1986) and 4 to 8 ampullary pores in the thorny skate, *R. radiata* (Andrianov et al., 1984). Electroreceptive fields are somatotopically mapped in the midbrain such that the anterior, middle, and posterior body surfaces are represented in the rostral, middle, and caudal levels of the contralateral midbrain. Like electrosensory primary afferents and AENs, the electrosensory midbrain neurons are also sensitive to the orientation of uniform electric fields with maximal response corresponding to the vector parallel to the length of the ampullary canal.

Neurophysiological recordings of electrosensory processing areas in the thalamus and forebrain have been limited at best. Multiunit and evoked potential recordings have localized electrosensory activity in the lateral posterior nucleus of the thalamus in *R. erinacea* (Bodznick and Northcutt, 1984) and in *P. triseriata* (Schweitzer, 1983). Bodznick and Northcutt (1984) also recorded electrosensory evoked potentials and multiple-unit activity throughout the central one third of the skate forebrain in a pallial area that corresponds to the medial pallium.

12.5.3 Behavior

12.5.3.1 Prey and Predator Detection — The first demonstrated use of the elasmobranch electric sense was for the detection of the bioelectric fields produced by prey organisms (Kalmijn, 1971). In laboratory behavioral experiments, Kalmijn (1971) demonstrated that both the catshark, *Scyliorhinus canicula*, and the skate, *Raja clavata*, executed well-aimed feeding responses to small, visually inconspicuous buried flounder (Figure 12.10A) and to flounder buried in a seawater agar-screened chamber that permitted the emission of the prey's bioelectric field but not its odor (Figure 12.10B). When the agar-screened prey was covered by a thin plastic film that insulated the prey electrically, the flounder remained undetected (Figure 12.10C). Feeding responses indistinguishable from those mediated by natural prey were observed again directed toward dipole electrodes that simulated bioelectric prey fields when buried under the sand or agar (Figure 12.10D). In later field experiments, Kalmijn (1982) also demonstrated that free-ranging sharks such as the smooth dogfish, *Mustelus canis*, and the blue shark, *Prionace glauca*, were attracted to an area by odor but preferentially attacked an active dipole source that simulated the prey's bioelectric field rather than the odor source of the prey. In addition, Tricas (1982) showed that the swell shark, *Cephaloscyllium ventriosum*, uses its electric sense to capture prey during nocturnal predation on small reef fish. More recent work with the Atlantic stingray (Blonder and Alevizon, 1988), sandbar shark, and scalloped hammerhead shark (Kajiura and Holland, 2002) also demonstrates well-aimed feeding responses at electrically simulated prey. Kajiura and Holland (2002) recently demonstrated that the "hammer" head morphology of sphyrnid sharks does not appear to confer a greater electroreceptive sensitivity to prey-simulating dipole electric fields than the "standard" head shark morphology, but it may provide a greater lateral search area to increase the probability of prey encounter and enhance maneuverability for prey capture.

Another important function of the elasmobranch electric sense is for use in predator detection and avoidance. Recent work on the clearnose skate, *R. eglanteria*, demonstrates that the electric sense of egg-encapsulated embryonic skates is well suited to detect potential egg predators (Sisneros et al., 1998),

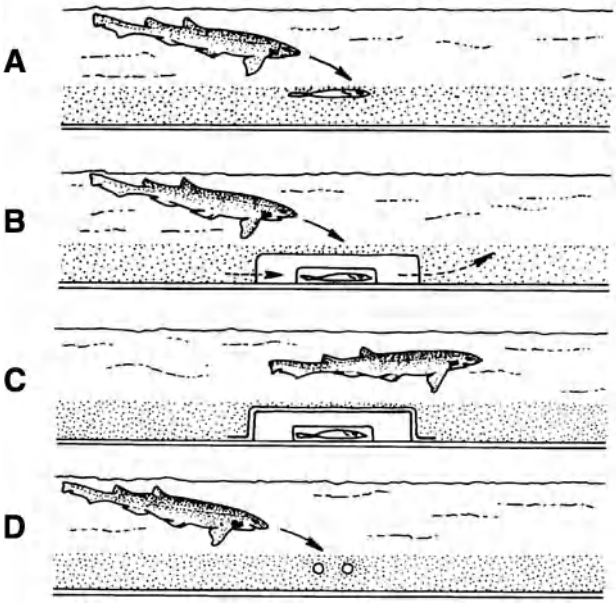

FIGURE 12.10 Use of the elasmobranch electric sense for the detection of electric fields produced by prey organisms. Behavioral responses of the catshark, *Scyliorhinus canicula*, to a small flounder buried in the sand (A), a flounder buried in a seawater agar-screened chamber permeable to bioelectric fields (B), a flounder in an agar chamber covered by a plastic film that insulates the prey electrically (C), and electrodes simulating the bioelectric fields produced by a flounder (D). Solid arrows indicate path of attack by the catshark; broken arrows indicate flow of seawater. (Modified from Kalmijn, A.J. 1971. *J. Exp. Biol*. 55:371–383. With permission.)

which include other elasmobranchs, teleost fishes, marine mammals, and molluscan gastropods (for review see Cox and Koob, 1993). Late-term embryonic skates circulate seawater within the egg case by undulating their tail in one corner of the egg near ventilation pores found in the horn of the egg case (Figure 12.11A). This action draws fresh seawater through pores on the opposite end of the egg case and creates a localized vortex near the exit pore by the tail, which can provide potential predators with olfactory, electrosensory, and mechanosensory cues needed for the detection and localization of the egg-encapsulated embryo. The peak frequency sensitivity of the peripheral electrosensory system in embryonic clearnose skates matches the frequency of phasic electric stimuli produced by large fish predators during ventilatory activity (0.5 to 2 Hz) and also corresponds to the same frequency of phasic electric stimuli that interrupts the respiratory movements of skate embryos and elicits an antipredator freeze behavior (Figure 12.11B and C) (Sisneros et al., 1998). This freeze response exhibited by embryonic skates stops the ventilatory streaming of seawater from the egg case and decreases the likelihood of sensory detection by predators. Phasic electric stimuli of 0.1 to 1 Hz are also known to interrupt the ventilatory activity of newly posthatched catsharks, *Scyliorhinus canicula* (Peters and Evers, 1985), and thus may represent an adaptive response in skates and other elasmobranchs to enhance survival during their early life history.

12.5.3.2 Orientation and Navigation — The electric sense of elasmobranchs is known to mediate orientation to local inanimate electric fields and in theory is sensitive enough to function in geomagnetic navigation. Pals et al. (1982b) showed via behavioral experiments that the catshark, *S. canicula*, could use electric DC fields for orientation in a captive environment. Furthermore, Kalmijn (1982) demonstrated that the round stingray, *Urolophus halleri*, can orient within a uniform electric DC field, discriminate the direction of the DC field based on its polarity, and detect voltage gradients as low as 5 nV/cm. The electric fields used in the behavioral experiments by Kalmijn (1982) were similar to those caused by both ocean and tidal currents, which can have peak amplitudes that range from 500 nV/cm (Kalmijn, 1984) to 8 μV/m (Pals et al., 1982a). Thus, in theory, elasmobranch fishes may be

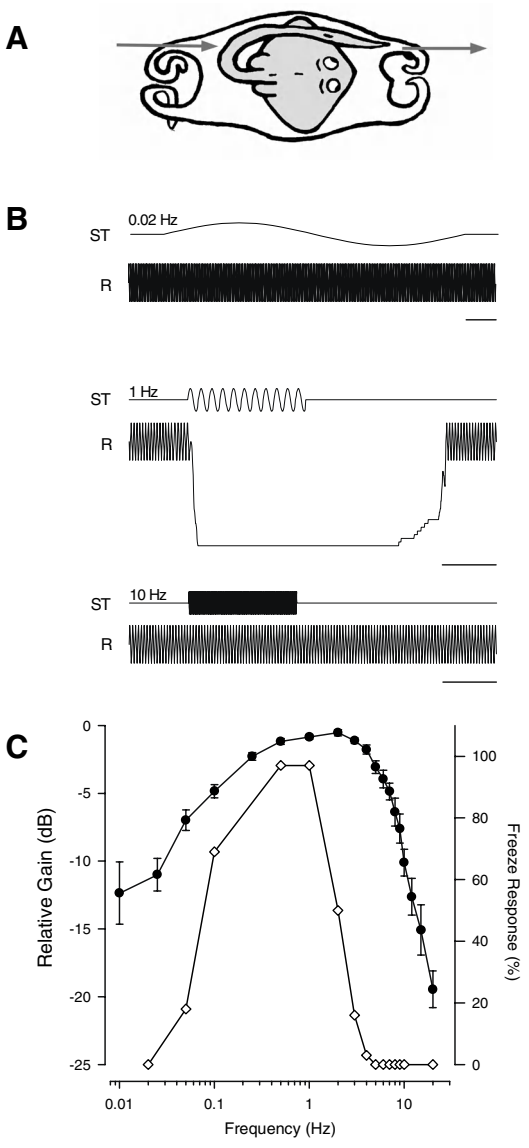

FIGURE 12.11 Behavioral response of embryonic clearnose skates, *Raja eglanteria*, to weak electric stimuli. (A) Ventilation behavior of embryonic skates. Diagram depicts a late-term embryonic skate circulating seawater within the egg case by undulating its tail in one corner of the egg near ventilation pores found in the horn of the egg case. The tail-beating action of the skate draws fresh seawater through pores on the opposite end of the case and creates a localized vortex near the exit pore by the tail. Arrow indicates flow of seawater. (B) Behavioral responses of skate embryos to sinusoidal uniform electric fields at stimulus (ST) frequencies of 0.02, 1, and 10 Hz. Stimuli were applied at an intensity of 0.56 $\mu V\ cm^{-1}$ across the longitudinal axis of the skate. The response (R) is expressed as a change in the peak-to-peak (PTP) tail displacement of the skate within the egg case. Prestimulus tail displacement for each record was 10 mm PTP. At 1 Hz, note the large tail displacement that occurs during coiling of the tail around the body after the onset of the electrical ST and a period of no tail movement during and after stimulation. Time bars = 5 s. (C) Freeze response of embryonic skates to weak electric stimuli. Behavioral responses (open diamonds) are shown as a percentage of total ST presentation to 0.02 to 20 Hz. Note that the peak frequency sensitivity of electrosensory primary afferent neurons (solid dots) for embryonic skates is at 1 to 2 Hz and is aligned with the freeze response peak of 0.5 to 1 Hz. (Modified from Sisneros, J.A. et al. 1998. *J. Comp. Physiol*. 183A:87–99. With permission.)

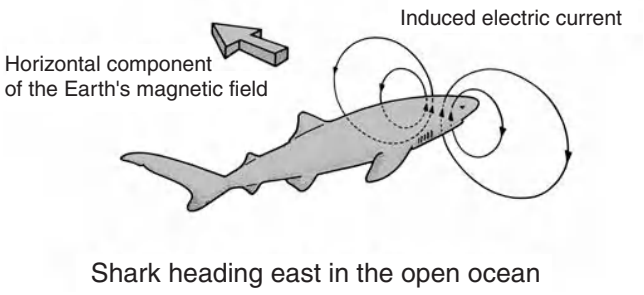

FIGURE 12.12 Use of the elasmobranch electric sense in the active mode of navigation. Diagram depicts the induction of electric current induced in the head and body of the animal as the shark swims through the horizontal component of the Earth's geomagnetic field. (Modified from Kalmijn, A.J. 1988. In *Sensory Biology of Aquatic Animals*. J. Atema et al., Eds., Springer-Verlag, New York, 151–186. With permission.)

able to estimate their passive drift within the flow of tidal or ocean currents from the electric fields produced by the interaction of the water current moving through the Earth's magnetic field.

According to Kalmijn (1981, 1984), elasmobranchs can theoretically use the electric sense for two modes of navigation. In the passive mode, the elasmobranch simply measures the voltage gradients in the external environment. These electric fields are produced by the flow of ocean water through the Earth's magnetic field. In the active mode, the elasmobranch measures the voltage gradients that are induced through the animal's body due to its own swimming movements through the geomagnetic field (Figure 12.12). A different theory of active electronavigation proposed by Paulin (1995) maintains that directional information is acquired from the modulation of electrosensory inputs caused by head turning during swimming movements. Sufficient electrosensory information is obtained during head turns that allow the elasmobranch to extract directional cues from electroreceptor voltages induced in the animal as it swims in different directions. Thus, the comparison of electrosensory and vestibular inputs could then be used by the elasmobranch to determine a compass heading.

Evidence already exists to support the case that elasmobranchs use magnetic field information for orientation and navigation. Kalmijn (1982) showed that in the absence of an imposed electric field round stingrays, *U. halleri*, could be conditioned by food reward to locate and enter an enclosure in the magnetic east and to avoid a similar enclosure in the magnetic west. Kalmijn (1982) also showed that the stingrays could discriminate the direction and polarity of the magnetic field. More recently, Klimley (1993) showed that scalloped hammerhead sharks, *Sphyrna lewini*, seasonally aggregate near seamounts in the Gulf of California and follow daily routes to and from the seamounts, routes that correlate with the pattern of magnetic anomalies on the ocean floor. This suggests that under natural conditions elasmobranchs may use the geomagnetic field for navigation.

In contrast to the elasmobranch fishes, many other animals also use the Earth's magnetic field for navigation and homing. For these animals, many theories have been proposed that link magnetoreception to either the visual system or magnetite particles found in the head or body (Leask, 1977; Gould et al., 1978; Walcott et al., 1979; Phillips and Borland, 1992; Walker et al., 1997). Recently, Walker et al. (1997) were the first to discover, in any vertebrate, neurophysiologically identified magnetite-based magnetoreceptors, in the nasal region of the long-distance migrating rainbow trout, *Oncorhynchus mykiss*. Based on their behavioral, anatomical, and neurophysiological experiments, Walker et al. (1997) have provided the best evidence to date of a structure and function for a magnetite-based vertebrate magnetic sense. The identification of the key components of the magnetic sense in the rainbow trout will no doubt lead to new perspectives in the study of long-distance orientation and navigation in a variety of vertebrate groups.

12.5.3.3 Conspecific Detection — Work on non-electric stingrays demonstrates that the elasmobranch electric sense is used for conspecific detection and localization during social and reproductive behaviors (Tricas et al., 1995; Sisneros and Tricas, 2002b). Male and female round stingrays, *U. halleri*,

use the electric sense to detect and locate the bioelectric fields of buried conspecifics during the mating season (Figure 12.13A). Stingrays produce a standing DC bioelectric field that is partially modulated by the ventilatory movements of the mouth, spiracles, and gill slits (Figure 12.13B) (Kalmijn, 1974; Tricas et al., 1995). Male rays use the electric sense to detect and locate females for mating, and females use their electric sense to locate and join other buried, less-receptive females for refuge (Tricas et al., 1995; Sisneros and Tricas, 2002b). The round stingray's peak frequency sensitivity of the peripheral electrosensory system matches the modulated frequency components of the bioelectric fields produced by conspecific stingrays (Figure 12.13C). Thus, the stingray's electric sense is "tuned" to social bioelectric stimuli and is used in a sex-dependent context for conspecific localization during the mating season.

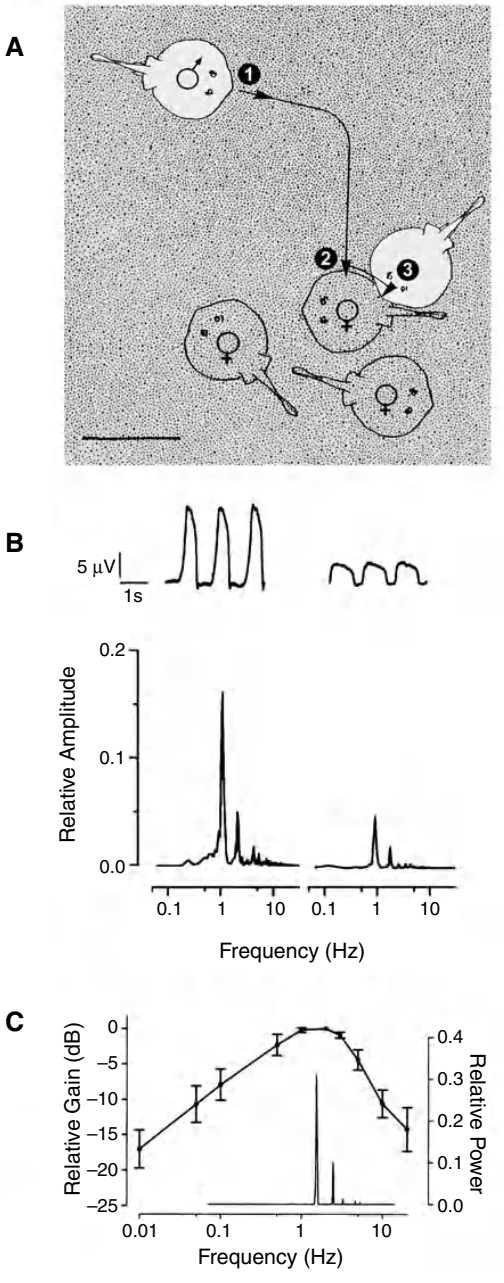

FIGURE 12.13 Detection of conspecific mates, bioelectric stimuli, and the frequency response of the peripheral electrosensory system in the round stingray, *Urolophus halleri*. (A) Orientation response by a male round stingray to cryptically buried conspecific females during the mating season. Males localize, orient toward, and inspect buried females buried in the sandy substrate. Search path of the male ray (1) changes abruptly after the detection of the female's bioelectric field. Males inspect buried females near the margins of her body disk (2) and pelvic fins (3). Active courtship and copulation begins after the male excavates the buried female and grasps the female's body disk with his mouth. Scale bar = 25 cm. (B) Bioelectric potentials recorded from a female stingray on the ventral surface near the gill slits (top, left record) and dorsal surface above the spiracle (top, right record). Recorded potentials are similar for both male (not shown) and female rays. Scales apply to both top records. Bottom graphs are Fourier transforms that show strong frequency components near 1 to 2 Hz that result from ventilatory movements. (C) Match between the peak frequency sensitivity of electrosensory primary afferent neurons and the frequency spectrum of the modulated bioelectric waveforms produced by round stingrays. The response dynamics of the electrosensory primary afferents in *U. halleri* show greatest frequency sensitivity at approximately 1 to 2 Hz with a 3 dB drop at approximately 0.5 and 4 Hz. Data are plotted as the relative gain of mean discharge peak (±1 SD). (Modified from Tricas, T.C. et al. 1995. *Neurosci. Lett.* 202:29–131. With permission.)

12.6 Olfaction and Other Chemosenses

Experimental studies in the first decades of the last century clearly identified olfaction as an important if not the primary means that sharks find food. The results provided well-founded starting points for later investigations. Interest in preventing shark attack on military personnel in World War II sparked a second generation of investigations on shark feeding and its olfactory control. This work continued into the mid-1970s (Hodgson and Mathewson, 1978b). More recent studies on olfaction in elasmobranchs have detailed aspects of the anatomy and physiology of olfactory systems, identified mechanisms of olfactory control of feeding, and suggested that female sex pheromones attract males and that predators may be detected by smell. Limited information on gustation and the common chemical sense or chemesthesis in elasmobranchs suggests similarities to their counterparts in other vertebrates.

12.6.1 Anatomy and Physiology of the Olfactory System

Information on the anatomical pathways for smell in elasmobranchs derives mostly from considerable work in comparative vertebrate neuroanatomy in the second half of the 20th century (Smeets, 1998). Physiological studies on elasmobranch olfaction, while limited, are consistent with the anatomical and behavioral data.

12.6.1.1 Peripheral Organ and Epithelium — The olfactory organs of elasmobranchs are situated in laterally placed cartilaginous capsules on the ventral aspect of the head well in front of the mouth. The ellipsoid saclike structures are typically divided by skin-covered flaps into a more lateral incurrent nostril (nares) and a more medial excurrent nostril (Tester, 1963a). A depression or groove helps to channel water into the incurrent opening where it traverses a rosette-like formation of plates or lamellae each with secondary folds that support the epithelium containing the primary olfactory receptors and supporting cells and tissues (Figure 12.14). The dynamics of the circulation path for the water movement have been analyzed in a series of detailed studies on several sharks (Theisen et al., 1986; Zeiske et al., 1986, 1987).

The epithelium is similar to that found in olfactory systems of most vertebrates with the major exception that the elasmobranch bipolar receptor cells are not ciliated but rather have a dendritic knob from which extends a tuft of microvilli (Reese and Brightman, 1970; Theisen et al., 1986; Zeiske et al., 1986, 1987). Similar microvillous receptors have been found along with the "typical" ciliated type in certain bony fishes. Cell surface lectin-binding patterns also differentiate the elasmobranch microvillous receptors (spotted dogfish, *Scyliorhinus canicula*) from the ciliated receptors of amphibians, rodents, and some bony fishes (Franceschini and Ciani, 1993). Studies on the clearnose skate, *Raja eglanteria*, identify two types of nonciliated olfactory receptor neurons (Takami et al., 1994). Type 1 is typical of those found in the other fishes (as above); the type 2 cell, so far unique to elasmobranchs, is distinguished from the type 1 by its thicker dendritic knob and microvilli that are shorter, thicker, and more regularly arranged. The functional meaning of the morphological differences in receptor types has yet to be determined.

The underwater electro-olfactogram (EOG) is a tool for recording the extracellular DC field potentials or analog of the summed electrical activity of the olfactory epithelium in response to chemical stimulation (Silver et al., 1976). EOG responses have been studied in two elasmobranchs, the Atlantic stingray, *Dasyatis sabina* (Silver et al., 1976; Silver, 1979) and the lemon shark, *Negaprion brevirostris* (Zeiske et al., 1986). Several amino acids, known to be effective stimuli for evoking EOGs in bony fishes and behavioral responses in both bony fishes and elasmobranchs, were tested in both species while extracts of squid muscle were also used in the lemon shark study. As expected, the squid extract evoked a significant response in the lemon shark. In both species, L isomers of the amino acids were highly stimulatory and for the most part their relative effectiveness was similar to that found in the teleosts. The EOG magnitude increased exponentially with the log of the stimulus concentration. Calculated thresholds ranged between 10^{-6} and 10^{-8} *M*. These levels are similar to those reported for bony fishes (teleosts) and for electroencephalographic (EEG) studies in nurse and lemon sharks (see above and

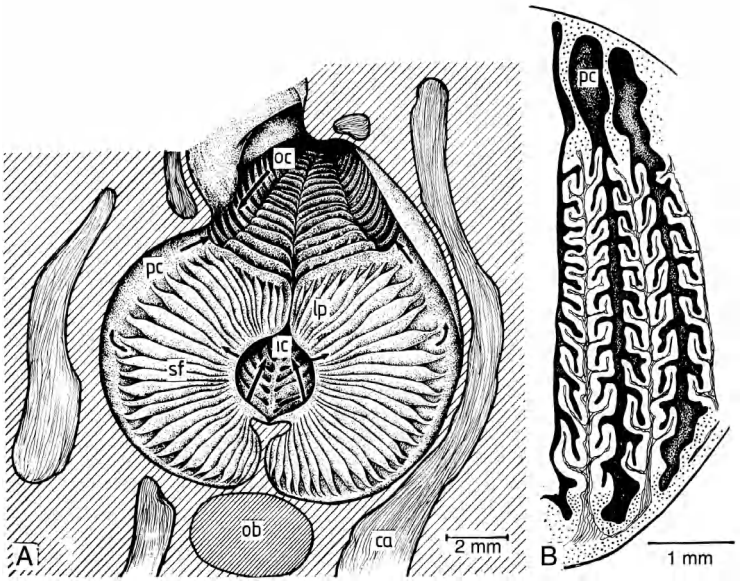

FIGURE 12.14 (A) Internal view of the hind part of the olfactory organ of a lemon shark (*Negaprion brevirostris*) as observed in an anterior-posterior direction with respect to the longitudinal axis of the organ. The olfactory cavity is divided into inlet and outlet chambers by lamellar protrusions of successive olfactory lamellae. Arrows indicate the calculated seawater flow direction. Ca, cartilage; ic, inlet chamber; lp, lamellar protrusion; ob, olfactory bulb; oc, outlet chamber; pc, peripheral channel; sf, secondary folds. (B) Lateral cross section through successive olfactory lamellae. Densely stippled areas represent the gap system between lamellae. The unstippled/white structures depict olfactory lamellae with secondary folds (the area covered by the sensory epithelium); fine lines indicate exiting olfactory nerve fibers (axons). Dark/shaded regions outline the peripheral channel (pc). (From Zeiske, E. et al. 1986. In *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*. T. Uyeno et al., Eds., Ichthyological Society of Japan, Tokyo, 381–391. With permission.)

Hodgson and Mathewson, 1978b). The similarity of detection abilities in the elasmobranchs and teleosts is surprising considering the far greater size of the olfactory organs in the former.

12.6.1.2 Olfactory Bulb — The first level of synaptic processing of olfactory information takes place in the olfactory bulb (OB), a part of the brain that receives the output from the olfactory receptors via their axons, which form the olfactory nerve. The olfactory bulbs of elasmobranchs are large structures that are closely applied to the olfactory epithelium or sac (Figure 12.15). The cytoarchitecture of the OB is conservative, and similar in elasmobranchs to other vertebrates (Andres, 1970; Smeets, 1998). Its concentric layers (from superficial to deep) include the olfactory nerve fibers; a layer of complex synaptic arrangements or glomeruli; a layer of large mitral cells, neurons functioning as the chief integrative units of the OB and, via their axons, the output pathway of the OB, the medial and lateral olfactory tracts; and a layer containing many small local circuit neurons, the granular cells. The olfactory tracts or peduncles travel to the cerebral hemispheres or telencephalon proper to make contact with secondary olfactory areas.

Only fairly recently has information on the ultrastructure and electrophysiology of the OB of elasmobranchs become available. Studies on the topography of inputs and synaptic organization of the OB of bonnethead sharks, *Sphyrna tiburo* (Dryer and Graziadei, 1993, 1994a, 1996) and electrophysiology of the OB of the dogfish, *Scyliorhinus canicula* (Bruckmoser and Dieringer, 1973), and the little skate *Raja erinacea* (Cinelli and Salzberg, 1990), have greatly advanced the understanding of the structure in elasmobranchs and permit some useful comparisons to the OB of other better studied "model" species. Unlike other vertebrates, the OB of elasmobranchs is compartmentalized in a series of swellings or independent sub-bulbs each exclusively receiving input from the adjacent olfactory epithelium. The mitral cells in fishes (teleosts and elasmobranchs) lack the basal dendrites characteristic of mitral cells

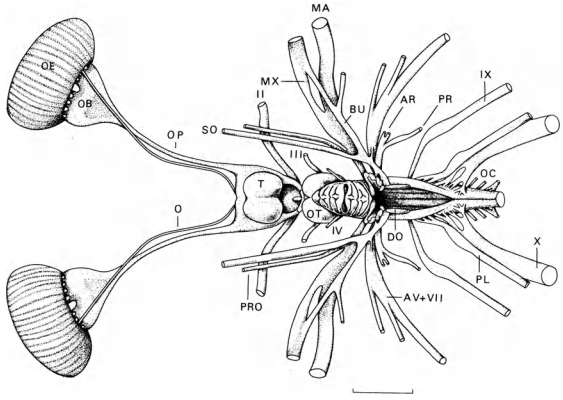

FIGURE 12.15 Dorsal view of the brain and olfactory system of the white shark, *Carcharodon carcharias*. The large partially divided olfactory bulb (OB) is closely applied to peripheral olfactory sac or epithelium (OE). Receptor cells in the epithelium project axons into the olfactory bulb (as the olfactory nerve) to make connections in complex synaptic arrangements. The mitral cells of the olfactory bulb distribute their axons to the secondary olfactory areas of the telencephalic hemisphere (T) via the elongated olfactory tracts or peduncles (OP). The terminal nerve or cranial nerve zero (O), which also extends from the olfactory epithelium to the hemisphere, may have chemosensory-related function(s) (see Demski and Schwanzel-Fukuda, 1987). Other abbreviations: AR, anterior ramus of the octaval nerve; AV, anteroventral lateral-line nerve; BU, buccal ramus of the anterodorsal lateral line nerve; DO, dorsal octavolateralis nucleus; MA, mandibular ramus of the trigeminal nerve; MX, maxillary ramus of the trigeminal nerve; OC, occipital nerves; OT, optic tectum; PL, posterior lateral line nerve; PR, posterior ramus of the octaval nerve; PRO, profundal nerve; SC, superficial ophthalmic ramus of the anterodorsal lateral line nerve; II, optic nerve; III, oculomotor nerve; IV, trochlear nerve; VII, facial nerve; IX, glossopharyngeal nerve; X, vagus nerve. Bar, 3 cm. (From Demski, L.S. and R.G. Northcutt. 1996. In *Great White Sharks: The Biology of Carcharodon carcharias*. A.P. Klimley and D.G. Ainley, Eds., Academic Press, San Diego, 121–130. With permission.)

of tetrapods, a finding that suggests differences in information processing, especially lateral inhibition (for details see Andres, 1970; Dryer and Graziadei, 1993, 1994a, 1996).

Species differences in the mass of the OB relative to total brain mass, as calculated in nine shark species (see Northcutt, 1978; Demski and Northcutt, 1996), suggest differences in reliance on smell in feeding and/or social behavior. The relative mass of the OB in the white shark, *Carcharodon carcharias* (Figure 12.15), at 18% is the highest followed by that of the smooth and spotted dogfishes (*Mustelus* and *Scyliorhinus*) at 14%. Intermediate in this regard are spiny dogfish, *Squalus acanthias*, deepwater dogfish, *Etmopterus* spp., and hammerhead sharks, *Sphyrna* spp., at 6, 7, and 9%, respectively. The lowest ratios are 3% for requiem sharks, *Carcharhinus* spp., blue sharks, *Prionace glauca*, and shortfin mako sharks, *Isurus oxyrinchus*. These figures must be interpreted cautiously as the percentages for the OB would be significantly higher in some sharks (e.g., *Carcharhinus* spp. and *Sphyrna* spp.) if their greatly enlarged telencephalic hemispheres are discounted.

The high ratio in the white shark is somewhat surprising, particularly compared with that of the closely related mako. The difference may reflect observations that, while both types consume fish, only the adult white sharks heavily prey on marine mammals including pinnipeds, the colonies of which introduce considerable odoriferous material into the water (Tricas and McCosker, 1984; Long et al., 1996; Strong et al., 1992; see also below).

12.6.1.3 Higher Level Systems — Projections from the OB to the telencephalic hemisphere have been mapped using contemporary neuroanatomical techniques in a variety of species (Ebbesson and Heimer, 1970; Ebbesson, 1972; 1980; Ebbesson and Northcutt, 1976; Northcutt, 1978; Smeets, 1983, 1998; Smeets et al., 1983; Dryer and Graziadei, 1994b). The results are in general agreement that the primary olfactory tract projection is to the lateral region of the ipsilateral hemisphere. Less well developed contralateral projections are reported in some species but not others. Spatial mapping of the projection of the medial and lateral olfactory tracts has been documented in the bonnethead shark, *Sphyrna tiburo* (Dryer and Graziadei, 1994b).

The findings refute earlier claims (see Aronson, 1963) that the entire hemisphere was dominated by the olfactory inputs and consequently that the enlarged hemispheres of sharks and rays could be attributed to their highly developed sense of smell. Other neuroanatomical, physiological, and behavioral studies have demonstrated that, other than the modest area of olfactory tract projection, most of the remainder of the hemisphere either receives specific inputs from other senses, including vision, hearing, mechanosenses, and electrosenses, or is multisensory in function (Ebbesson and Schroeder, 1971; Cohen et al., 1973; Graeber et al., 1973, 1978; Platt et al., 1974; Schroeder and Ebbesson, 1974; Graeber, 1978, 1980; Luiten, 1981a,b; Bleckmann et al., 1987; Smeets and Northcutt, 1987). This current view indicates that the elasmobranch telencephalon is similar in general organization and function to that of other vertebrates (see reviews by: Northcutt, 1978, 1989b; Demski and Northcutt, 1996).

There are few studies concerning the function of the olfactory areas in the elasmobranch hemisphere. Bruckmoser and Dieringer (1973) recorded evoked potentials from the surface of the hemisphere in response to electrical stimulation of the olfactory epithelium and OB in *Scyliorhinus canicula* and from electrical stimulation of the olfactory tracts in the torpedo ray, *Torpedo ocellata*. Short latency responses indicative of direct projections of the OB were observed only in the lateral olfactory area as defined by the anatomical studies.

Electrical stimulation of the lateral olfactory area in a free-swimming nurse shark (*Ginglymostoma cirratum*) evoked feeding-related responses of inconsistent mouthing or eating food (cut fish soaked to remove most of its juices) and a slow side-to-side head movement, which dragged the rostral sensory barbels across the substrate (Demski, 1977). The specific type of head movement was observed in unoperated sharks when colorless fish extracts were delivered to their home tank. Stimulation in the area also triggered circling toward the side of the electrode (ipsilateral). The latter result is consistent with Parker's observation that sharks with a unilateral occlusion of the nostril circle toward the side of the open nostril. Thus, the physiological and behavioral studies available are consistent with the anatomical projections and suggest that the olfactory area of the lateral hemisphere is involved in the arousal of feeding by olfactory stimulation.

Bruckmoser and Dieringer (1973) recorded potentials of longer latency (20 to 800 ms) including regular EEG-synchronous afterpotentials in other areas of the hemispheres. This secondary activity was more labile than the primary responses and differed in the two species. It is most likely indicative of areas involved in higher-level processing of the olfactory information and/or regions for multisensory or sensorimotor integration.

It should be noted that in bony fishes, the OBs project to the hypothalamus of the diencephalon (Finger, 1975; Bass, 1981; Murakami et al., 1983; Prasada Rao and Finger, 1984), an area from which feeding activity has been evoked by electrical stimulation (Demski, 1983) and potentials triggered by olfactory tract stimulation (Demski, 1981). Although a direct olfactory bulb projection to the hypothalamus has not been reported for elasmobranchs, projections from the lateral olfactory area of the hemisphere to the hypothalamus are suggested (Ebbesson, 1972; Smeets, 1998). Electrical stimulation of the hypothalamus in nurse sharks has evoked "feeding" as evidenced by relatively continuous swimming, consistent mouthing or eating food, and the barbel-dragging, side-to-side head movement (Demski, 1977). Based on the comparative data, a similar hypothalamic feeding area has been proposed for teleosts and sharks (Demski, 1982). Also in this regard, Tester (1963b) observed that thresholds for olfactory-triggered feeding in blacktip reef sharks, *Carcharhinus melanopterus*, are lowered by starvation (see below). Such increased sensitivity may have resulted from hypothalamic modulation of the olfactory system in response to changes in visceral sensory activity and/or blood-borne factors associated with the dietary conditions.

12.6.2 Olfactory Control of Feeding

12.6.2.1 Studies of Sharks in Large Enclosures and Open Water — The critical early studies on olfactory mediation of feeding in sharks were done by Sheldon and Parker (Sheldon, 1911, Parker and Sheldon, 1913; Parker, 1914) working with captive smooth dogfish, *Mustelus canis,* in large outdoor pens at Woods Hole, MA. The behavior patterns of normal animals with one or both nares blocked with cotton wool were described by Parker (1914). Normal animals and those with only one nostril blocked readily located a packet of crabmeat wrapped in cheesecloth to exclude visual

identification. Fish with both nostrils blocked totally ignored the bait. Normals essentially turned equally to either side and often made figure-8 movements while experimental sharks turned almost exclusively to the unblocked side, as if this was the direction of the odor corridor.

Olfactory involvement in elasmobranch feeding includes several phases, which can be roughly categorized as arousal; directed approach and attack; and if the prey or bait is not located or is lost, usually continued search. These components vary depending on circumstance and species. Notable studies on elasmobranch feeding and olfaction on several species of carcharhiniform sharks were carried out by Tester and his student Hobson (Tester, 1963a,b; Hobson, 1963). Tester's description of feeding in blind blacktip reef sharks, *Carcharhinus melanopterus,* is especially revealing. The blind sharks fed avidly on food that settled to the bottom of their tank, thusly: "The sharks would detect the odor while swimming in mid-water and would spiral down, converging on the food by swimming in a figure-8 pattern to the bottom." Tester commented on the similarity of the response to that reported by Parker (above) for *M. canis*. Indeed, the pattern may be typical of, at least, the carcharhiniform sharks.

Tester recorded responses of several shark species to a variety of extracts of fish and invertebrates as well as human urine, blood, and sweat. Essentially all food substance extracts were "attractive." Regarding responses to human materials, sharks demonstrated "attraction" to blood, "sensing" but otherwise indifference to urine, and although highly variable, "repulsion" to sweat. Blind reef blacktip sharks were more sensitive to odors than those with normal sight. In addition, starvation in these animals generally resulted in greater responses to food extracts. Sharks were "attracted" to introduction of water from containers with prey fish that were not stressed but the sharks soon adapted to the stimuli; in contrast, the sharks showed concerted "hunting reactions" to the test water when the prey fish were "frightened and excited by threatening them with a stick." The results strongly suggest that sharks can use odors to discriminate between stressed and unstressed prey fish.

Hobson's field studies complemented the laboratory tests reported above. Observations were made underwater with SCUBA and from the surface using a glass-bottomed boat. Three species were studied in the lagoon at Eniwetok: gray reef sharks; blacktip reef sharks; and whitetip reef sharks, *Triaenodon obesus*. He reported that the sharks used an olfactory corridor and local water currents to locate bait (a tethered but otherwise "uninjured" prey fish, or extract of grouper meat). The sharks could also accurately pinpoint a source of water flowing from tanks holding stressed but otherwise uninjured prey fish. The results were consistent with Tester's laboratory study.

Studies on two Atlantic species yielded similar results. Working at the Lerner Marine Laboratory in Bimini, Bahamas, Hodgson and Mathewson tested the responses of nurse sharks (*Ginglymostoma cirratum*) and lemon sharks (*Negaprion brevirostris*) to release of known chemical feeding attractants (glutamic acid and trimethylamine oxide, TMAO) in large outdoor pens (Hodgson and Mathewson, 1971, 1978b; Mathewson and Hodgson, 1972). The authors concluded that the two sharks use different strategies to localize the source of the odor. The nurse shark employs a true gradient search behavior (a klinotaxis or temporally based gradient sampling, i.e., sequential comparisons of concentrations from different points) as it scans across the olfactory corridor, whereas the lemon shark becomes aroused on contact with the stimuli and then turns in the direction of the greatest current and heads upstream. The pattern conforms to a rheotactic bias or release mechanism as suggested to account for odor tracking behavior of other sharks (Kleerekoper, 1969). Under most natural circumstances the lemon shark would find the source by moving upstream to its location. Indeed, from the studies cited above and others referred to by them, most advances by sharks on prey or artificial stimuli are from downstream locations. Field tests carried out in open water at Bimini indicated that several shark species use a rheotaxis-release mechanism in tracking a TMAO-glycine mixture.

Working at Dangerous Reef in South Australian waters, Strong and colleagues (1992, 1996) investigated olfactory orientation in tagged white sharks, *Carcharodon carcharias*. Female white sharks responded to baits of tuna and horsemeat by typically circling downstream of the olfactory corridor ("searching") for periods of up to 12 h. After several hours of circling, some sharks traveled among the nearby inshore islands ("island patrolling"). The authors indicated that considerable odoriferous material from nearby pinniped colonies is released into the sea and that white sharks cruise around these islands in search of such odors. The observations confirm for another shark species the use of downstream approach as a major strategy for at least general location of prey. Perhaps more important is the long-

lasting effect of the stimulation and the complex behavior patterns it triggers. The movements among the islands could not be guided directly by odor trails but rather must represent innate and/or learned responses, which take control after the arousal by odors and the search for prey in the vicinity is not successful. Such behavior is most likely controlled by the highest integrative centers of the telencephalic hemispheres of the brain.

12.6.2.2 Laboratory Studies — Kleerekoper (1978, 1982) analyzed the motor behavior of *Scyliorhinus stellaris* and *M. mustelus* in response to chemical stimulation in a circular arena. The preliminary studies revealed that the olfactory stimulus caused a decrease in the mean angle of turns made by the swimming sharks such that the area covered was greater during chemical tests vs. control stimulations. The behaviors, likened to "searching," occurred even in the absence of directional cues and thus can be considered arousal responses that trigger a stereotyped response leading in most cases to increased opportunity of locating the source of the odors.

Kleerekoper and colleagues (Kleerekoper et al., 1975; Kleerekoper, 1978, 1982) also studied the responses of nurse sharks to extracts of shrimp in a large enclosure ($5 \times 5 \times 0.5$ m). They concluded (Kleerekoper et al., 1975) that a precise localization of a chemical stimulus is dependent on both the flow of the medium and the stimulus gradient within it. In nonmoving water only generalized location of the release site is possible, whereas flowing water provides the nurse shark with a direction vector that is used to pinpoint the source of the stimulus. Thus, different mechanisms of location appear to be used in flow vs. stagnant conditions.

Johnsen and Teeter (1985) studied the reactions of bonnethead sharks, *Sphyrna tiburo*, to extracts of blue crabs injected either into the water of the study arena (a 1.8 m circular tank) or directly into the nares of one or both sides via tubes mounted to the shark's head. The animals were monitored under conditions of current and no current (Figure 12.16). The responses to direct and external presentation of the extract were essentially the same. In slack water the sharks reacted to the odor by suddenly stopping their typical circling around the outer limit of the tank and began moving in tight circles in the vicinity of the stimulation site. In contrast, when a current was present, the sharks, which typically swim against the current, reacted to the stimulation by reversing direction. The behavior was repeated "as sharks appeared to follow the stimulus bolus around the edge of the tank. The paths of the fish then had the appearance of connected loops." It is noteworthy that the responses to the direct stimulation of the nares continued past the point where calculations indicate that the stimuli would have been diluted below threshold levels. Such being the case, the responses are likely part of a neural program that is initiated by the odor but not dependent on it for continuation. The circling and looping would appear to be an effective means of guiding the animal back to the odor trail.

EEG studies in sharks carried out by Gilbert and colleagues (Gilbert et al., 1964; Hodgson et al., 1967; Hodgson and Mathewson, 1978b) at the Lerner Marine Laboratory were complementary to the field studies of the 1960s. The researchers studied electrical activity changes in the brains of nurse,

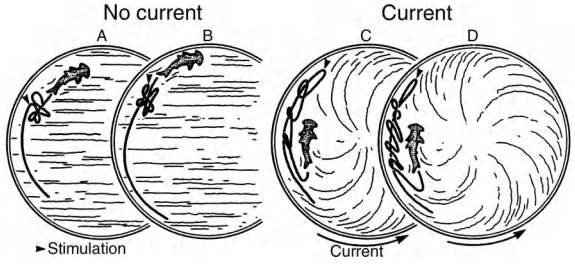

FIGURE 12.16 Responses of captive bonnethead sharks, *Sphyrna tiburo*, to chemical stimuli delivered either into the open water of a circular test tank or via a head mount directly into the shark's nares. Tests were conducted under two conditions of water current. A = Response to 10-ml sample of crab homogenate introduced in still water; B = Response to 0.5-ml sample delivered via head mount; C = Response to 10-ml sample delivered into 15 cm/s water current; D = Response to 0.5-ml sample delivered via the head mount in presence of 15 cm/s water current. (From Johnsen, P.B. and J.H. Teeter. 1985. *Mar. Behav. Physiol.* 11:283–291. With permission.)

bonnethead, and lemon sharks in response to stimulation with extracts of natural foods like crab and tuna as well as amino acids and amines known to stimulate feeding in fishes. Recording sites were located on the surface of the OBs, the telencephalic hemispheres, optic lobes or tectum, the cerebellum and medulla, and deep in the hemispheres. Sites in the tectum and cerebellum were unresponsive to chemical stimulation, whereas sites in the anterior telencephalon (an area later determined to be the primary olfactory center; see above) showed increases in both frequency and amplitude to most of the chemicals tested. Activity in the OB of a free-swimming lemon shark was greatly increased in response to a stimulus of 10^{-4} *M* glycine. These results and some additional preliminary findings of chemically evoked forebrain activity in anesthetized lemon sharks (Agalides, 1967) confirm the arousal function of food odors and artificial stimulants, and essentially mark the beginning of studies on elasmobranch brain systems that control both olfactory processing and feeding behavior.

12.6.3 Sex Pheromones in Mating

The evidence for use of olfactory cues in social-sexual behavior of elasmobranchs is indirect; nevertheless, it is consistent across several groups of sharks and batoids. The most compelling suggestion of olfactory sex attraction was reported by Johnson and Nelson (1978), who recounted an incident of "close following" behavior of blacktip reef sharks, *Carcharhinus melanopterus*, at Rangiroa Atoll in French Polynesia. One shark tracked down another, which was initially out of its view, and then followed it closely with its snout directed toward the leader's vent. The latter swam close to the substrate in an atypical slow, sinuous manner with its head inclined downward and its tail uplifted. The authors concluded that only an olfactory cue could have guided the second shark to the position of the other. While sex was not determined in this incidence, other observations indicated that unusual swimming and following behaviors appeared to be sex specific to the females and males, respectively.

There are scattered observations of males of other elasmobranch species following closely behind females, usually with their nose directed to the female's vent, sometimes pushing on it. This has been reported for the bonnethead shark, *Sphyrna tiburo* (Myrberg and Gruber, 1974), nurse shark, *Ginglymostoma cirratum* (Klimley, 1980; Carrier et al., 1994), spotted eagle ray, *Aetobatis narinari* (Tricas, 1980), clearnose skate, *Raja eglanteria* (Luer and Gilbert, 1985), and sand tiger shark, *Carcharias taurus* (Gordon, 1993); see also review by Demski (1991). Other indications of the sex-related nature of the encounters include the presence of scars on the females or swelling of the pelvic fins and cloacal area suggestive of recent mating; male attempts to mount the female; and in captive female sand tiger sharks, "cupping and flaring" of the pelvic fins in response to the close presence of the male. Thus, although there are no direct experimental findings to document female sex-attraction pheromones, behavioral observations in natural and captive environments strongly suggest their existence.

12.6.4 Olfaction and Predator Avoidance

Lemon sharks, *N. brevirostris,* and American crocodiles, *Crocodylus acutus*, overlap in their distributions, and where such is the case, the crocodiles will prey on the sharks. Rasmussen and Schmidt (1992) demonstrated that water samples taken from ponds holding *C. acutus* and delivered to the nares of juvenile lemon sharks consistently aroused the sharks from a state of tonic mobility (induced by inversion and restraint), an established bioassay for chemical awareness. Water from ponds containing alligators, *Alligator mississippiensis*, which have no substantial natural contact with lemon sharks, had no such effect. The authors identified three organic compounds produced by the crocodiles (2-ethyl-3-methyl maleimide; 2-ethyl-3-methyl succinimide; 2-ethylidene-3-methyl succinimide) that accounted for the positive results. Synthetic versions of the chemicals were also effective. The results strongly suggest that lemon sharks and perhaps other elasmobranchs use olfactory cues to avoid potential predators.

12.6.5 Gustation

Anatomical studies in elasmobranchs have identified receptors that closely resemble taste organs in other vertebrates. A few behavioral observations suggest gustation is important for the acceptance of food in

sharks (see Sheldon, 1909, and review by Tester, 1963a). Cook and Neal (1921) mapped the distribution of taste buds in the oral-pharyngeal cavity of the spiny dogfish, *Squalus acanthias*. While located over the entire region, the receptor organs appear most numerous on the roof of the cavity. In microscopic section, the taste buds are characterized as small papillae covered with a multilayer epithelium that has a central cluster of elongate sensory receptor cells. Nerve fibers are associated with the base of the receptors. Older descriptive anatomical studies of several sharks indicate that the taste organs are supplied by branches of the facial, glossopharyngeal, and vagus nerves (Norris and Hughes, 1920; Herrick, 1924; Daniel, 1928; Aronson, 1963), as is the case with other vertebrates.

Whitear and Moate (1994) carried out a detailed ultrastructural analysis of the taste buds of the dogfish, *Scyliorhinus canicula*. The apical regions of the receptors with their protruding microvilli form pores, which are clearly visible in their scanning electron micrographs. Nerve fibers were associated with the receptors as well as possible free nerve endings. Part of a taste bud was reconstructed from serial transmission electron micrographs. In general, the organization of the peripheral gustatory system of sharks appears comparable with that of other vertebrates. Unfortunately, detailed physiological and behavioral studies are not available to further support this observation. It seems reasonable to assume that the gustatory apparatus in sharks functions primarily in the final determination of food vs. nonfood.

12.6.6 Common Chemical Sense

Studies in *Mustelus canis* demonstrated that sharks respond behaviorally to injections into the nostrils of certain chemicals (irritants) even with the olfactory tracts severed. In these cases, detection was through components of the maxillary branch of the trigeminal nerve (Sheldon, 1909). The animals reacted similarly to applications on the body surface. The latter responses were triggered via spinal nerves. Sheldon considered that this chemosensitivity was mediated by free nerve endings.

Studies in other vertebrates indicate that the nerves involved in such reactions are part of the somatosensory system and appear to represent a subset of temperature- and pain-sensitive fibers. The sense conveyed by these chemosensitive components has been renamed “chemesthesis” to reflect this relationship (Bryant and Silver, 2000). The function of this system in elasmobranchs, as in other vertebrates, appears to be protection from damaging chemicals. It seems likely that the adverse reactions certain sharks demonstrate to natural toxins, such as that produced by the skin of the Moses sole, *Pardachirus marmoratus* (Clark, 1974), is likely mediated by this category of unmyelinated somatosensory ending.

12.7 Conclusions

Are elasmobranchs sensory marvels, or not? There is no doubt that the combination of well-developed visual, acoustical, mechanical, electrical, and chemical sensing systems in sharks, skates, and rays distinguishes the group and makes them well-adapted for life in the sea. The sensory ecology of these fishes is complex. Depending on species and ambient conditions, elasmobranchs may utilize one or more of their senses to monitor their environment, detect and locate prey and mates, avoid predators, and find their way in the ocean.

The range at which each of the sensory modalities operates depends on the qualities of the particular sensory system, the strength of the stimulus, and the physical characteristics of the environment that affect transmission of the signal. For example, the range of effective vision in sharks is not a fixed distance but depends on the sensitivity and acuity of the shark’s eye, the optical characteristics of the target, the ambient light levels, and the absorption and scattering of light by the surrounding seawater. Similarly, olfactory range depends on the sensitivity of the shark’s nose for a given chemical scent, the concentration of odorant at the source, and water characteristics affecting the odorant’s transmission, such as currents. In typical situations, it is clear that the senses of olfaction and hearing can orient an elasmobranch to a stimulus source from far distances, mechanosenses and vision typically can begin to operate at intermediate distances from the stimulus, and electrosenses and gustation operate very near to the stimulus. The sequence with which each of the sensory modalities comes into play depends on a

multitude of factors, however, and there is no single sensory hierarchy that operates under all circumstances for all elasmobranch species.

Integration of this multimodal sensory information in the elasmobranch CNS ultimately leads to a behavioral response at the level of the whole animal. How sharks, skates, and rays integrate the complex input of environmental information through their various senses to form an adaptive response is among the most interesting questions in elasmobranch sensory biology, and a ripe area for further research.

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