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Sensory Physiology and Behavior of Elasmobranchs

Jayne M. Gardiner, Robert E. Hueter, Karen P. Maruska, Joseph A. Sisneros, Brandon M. Casper, David A. Mann, and Leo S. Demski

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12.1 Introduction

Sharks are practically legendary for their sensory capabilities, with some of this reputation deserved and some 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 approach 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 (e.g., direction of a sound or odor, resolution of a visual image) and type (e.g., frequency of sound, odorant chemical, wavelength of light). 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; with about 1000 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. This perception was pervasive 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 transform 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 benthic vs. pelagic habits. Eye size in elasmobranchs is generally small in relation to body size but relatively larger in juveniles (Lisney et al., 2007) and in some notable species, such as the bigeye thresher shark, *Alopias superciliosus*. In general, sharks have larger eyes than batoids, but eye size differences also correlate with habitat type, activity level, and prey type. Oceanic species have relatively larger eyes than

coastal and benthic species, and more active swimmers that feed on active, mobile prey have relatively larger eyes than more sluggish species that feed on sedentary prey (Lisney and Collin, 2007). As with osteichthyan fishes (Warrant and Locket, 2004), relative eye size in mesopelagic deep-sea sharks is often large to allow for enhanced light gathering.

In all elasmobranchs, the two eyes oppose each other, which can allow for a nearly 360° visual field in at least one plane of vision (Figure 12.1). In the case of swimming sharks using a laterally sinusoidal swimming pattern, the dynamic visual field can be extended beyond 360°. Limited eye movements are observed in some species, primarily to compensate for swimming movements and to stabilize the visual field (Harris, 1965). Binocular overlap is generally small, except in the hammerhead sharks (Sphyrnidae) and some batoids, but their enhanced frontal vision comes at the expense of larger posterior blind areas (Litherland et al., 2009a; McComb and Kajiura, 2008; McComb et al., 2009) (Figure 12.1). 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 sharks, 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) (Figure 12.2). This membrane functions to protect the eye from damaging abrasion and may be extended when the shark feeds or comes into contact with an 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 12.3) is comprised of a thick cartilaginous sclera and a gently curving, transparent cornea, the fine structure of which includes sutural fibers that resist corneal 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) (Figure 12.4). 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 (Figure 12.4E,F) 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, *Negaprion 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 (*Carcharhinus obscurus*), and the tiger shark (*Galeocerdo cuvier*), but interestingly not in another carcharhinid and shallow-water shark, the lemon shark (*Negaprion 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 selecting for the presence or absence of these lens filters. Nelson et al. (2003) described a related UV-filtering mechanism in the corneas of scalloped

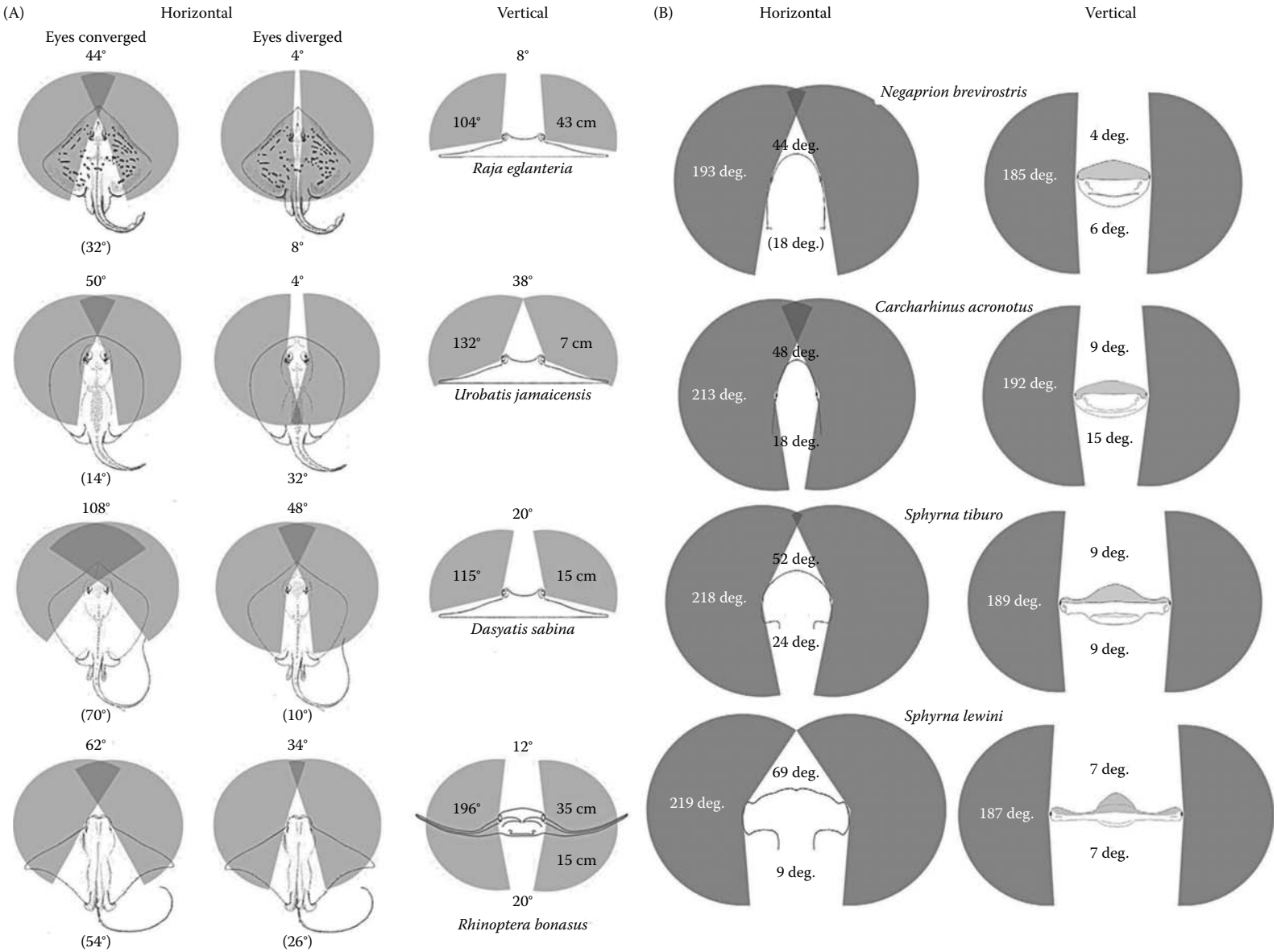

FIGURE 12.1
Visual fields of elasmobranchs. (A) Dynamic horizontal visual fields (when the eyes are fully converged and diverged) and static vertical visual fields of four batoid species. (Adapted from McComb, D.M. and Kajiura, S.M., *J. Exp. Biol.*, 211, 482–490, 2008.) (B) Maximum dynamic horizontal visual fields (when the eyes are fully converged and diverged and with maximum lateral head yaw) and static vertical fields of four shark species. Values within the shaded areas represent the monocular fields. Values outside of the shaded areas represent degrees of binocular overlap (anterior and posterior) or blind areas, if in parentheses. (Adapted from McComb, D.M. et al., *J. Exp. Biol.*, 212, 4010–4018, 2009.)

FIGURE 12.2
Lemon shark, *Negaprion brevirostris*, with its nictitating membrane partially retracted. (From Gruber, S.H. and Cohen, J.L., in *Sensory Biology of Sharks, Skates, and Rays*, Hodgson, E.S. and Mathewson, R.F., Eds., U.S. Office of Naval Research, Arlington, VA, 1978, pp. 11–105. Photograph by E. Fisher and used with permission.)

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 (farsighted) in the resting state of the eye (Hueter, 1980; Hueter and Gruber, 1982; Sivak, 1978b; Spielman and Gruber, 1983). This condition is problematic in that objects at optical infinity would be out of focus and the closer an object approaches an eye, the more out of focus it becomes.

Hueter et al. (2001), however, discovered that unrestrained, free-swimming lemon sharks, *Negaprion 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 observed in many elasmobranchs under restraint could be an induced, unnatural artifact resulting from handling stress. Eliminating this artifact, it is possible that most elasmobranchs would be emmetropic (neither farsighted nor nearsighted) in the resting state and have accommodative ability. This complication aside, there is some indication that benthic elasmobranchs, such as the nurse shark, *Ginglymostoma cirratum*, and the bluntnose stingray, *Dasyatis say*, 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.

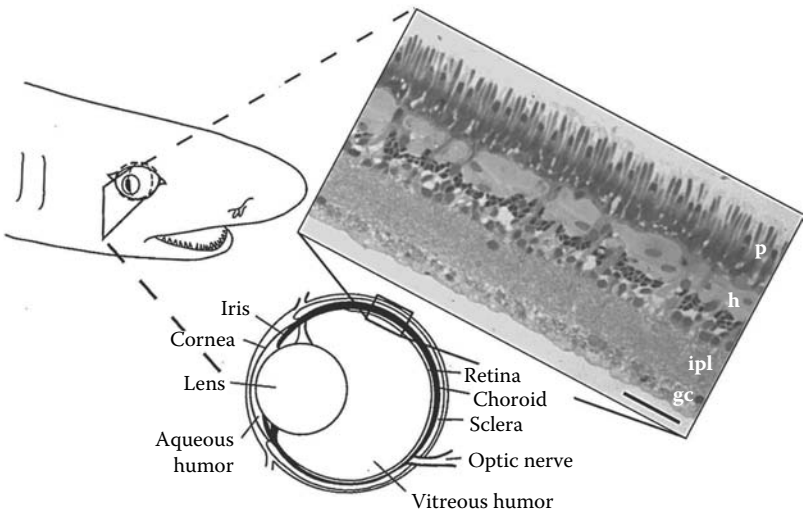

FIGURE 12.3
Cross-section through an elasmobranch eye showing ocular and retinal anatomy. (Adapted from Hueter, R.E. and Gilbert, P.W., in *Discovering Sharks*, Gruber, S.H., Ed., American Littoral Society, Highlands, NJ, 1990, pp. 48–55.) Inset: Light micrograph of the retina of the giant shovelnose ray, *Rhinobatos typus*, showing the photoreceptive layer (longer receptors are rods, shorter receptors are cones). *Abbreviations:* gc, ganglion cell layer; h, horizontal cell layer; ipl, inner plexiform layer; p, photoreceptor layer. Scale bar: 100 µm. (Adapted from Hart, N.S. et al., *J. Exp. Biol.*, 207, 4587–4594, 2004.)

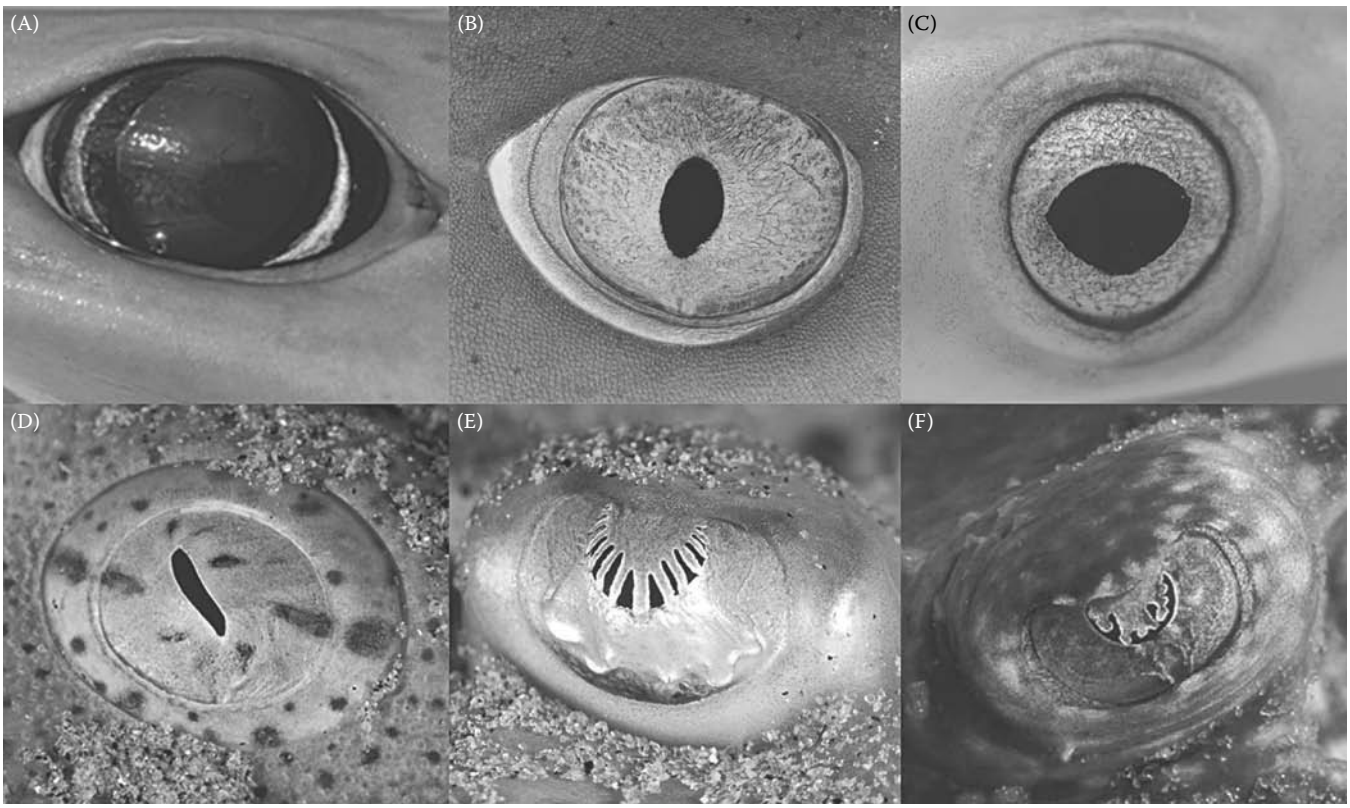

FIGURE 12.4
(See color insert.) Diversity of pupil shapes among elasmobranchs. (A) Circular pupil in a gulper shark, *Centrophorus* sp. (Photograph by José Castro and used with permission.) (B) Vertical slit in the whitetip reef shark, *Triaenodon obesus.* (Photograph by Christian Loader and used with permission.) (C) Horizontal slit in the bonnethead, *Sphyrna tiburo.* (Photograph by D.M. McComb and S.M. Kajiura and used with permission.) (D) Oblique slit in the Pacific angel shark, *Squatina californica.* (Photograph by Alison Vitsky and used with permission.) (E) Crescent-shaped pupil with papillary apertures in the shovelnose guitarfish, *Rhinobatos productus.* (Photograph by Alison Vitsky and used with permission.) (F) The yellow stingray, *Urobatis jamaicensis.* (Adapted from McComb, D.M. and Kajiura, S.M., *J. Exp. Biol.*, 211, 482–490, 2008.)

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 the retina to the 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 (Denton and Nicol, 1964; Gilbert, 1963). This layer functions 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 boost 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 within tapetal melanophores to block the passage of light under photopic conditions (Heath, 1991; Nicol, 1964) (Figure 12.5). 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. Nonocclusible 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 elasmobranch visual function came with the realization that nearly all elasmobranchs have duplex retinas containing both rod and cone photoreceptors (Gruber and Cohen, 1978) (Figure 12.6), beginning with the discovery by Gruber et al. (1963) of cones in the retina of the

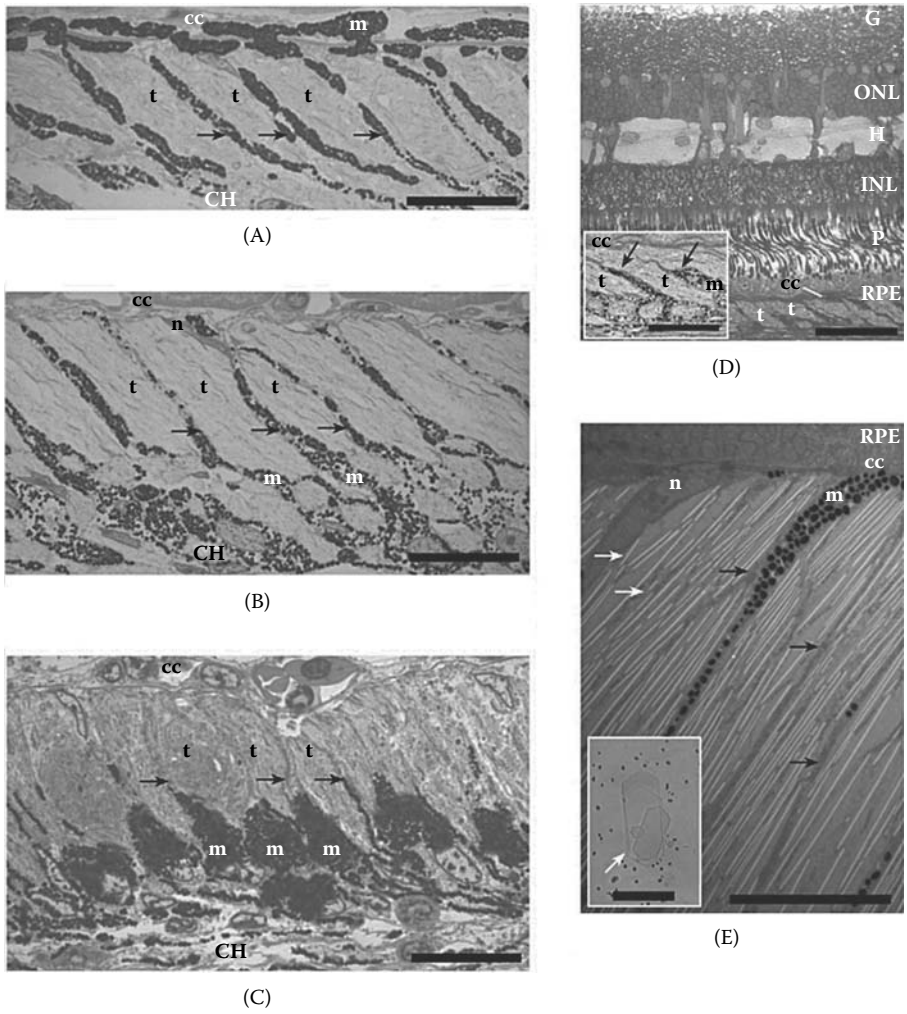

FIGURE 12.5
Morphological variation in the structure of the tapetum lucidum. (A–C) Light micrographs of the occlusible tapetum lucidum of the sandbar shark, *Carcharhinus plumbeus*, showing the occlusion of the tapetal cells by pigment migration in a light-adapted tapetum (A), a partially dark-adapted tapetum (B), and a fully dark-adapted tapetum (C). Note the dispersal of melanosomes along the melanocyte cell processes to occlude the tapetal cells in the light-adapted state and the aggregations of the melanosomes toward the choroid in the dark-adapted state. Scale bar: 20 µm. (D) Transverse section of the retina of the shortspine spurdog, *Squalus mitsukurii*. Inset highlights the tapetal cells. Scale bar: 50 µm; inset scale bar: 20 µm. (E) High-power electronmicrograph illustrating the arrangement of the reflective crystals within a *C. plumbeus* tapetal cell. Inset: light micrograph of crystal plates. Scale bars: 10 µm. Black arrows: melanocyte processes; white arrows: reflective crystals. *Abbreviations:* cc, choriocapillaris; CH, choroid; G, ganglion cell layer; H, horizontal cells; INL, inner nuclear layer; m, melanocyte containing melanosomes; n, nucleus of tapetal cell; ONL, outer nuclear layer; P, photoreceptor layer; rc, reflective crystals; RPE, retinal pigment epithelium; t, tapetal cell. (From Litherland, L. et al., *J. Exp. Biol.*, 212, 3583–3594, 2009. With permission.)

lemon shark, *Negaprion brevirostris*. 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. 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 (Dowling and Ripps, 1991; Ripps and Dowling, 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 rhodopsins, which provides maximum sensitivity for clearer, shallow ocean waters associated with

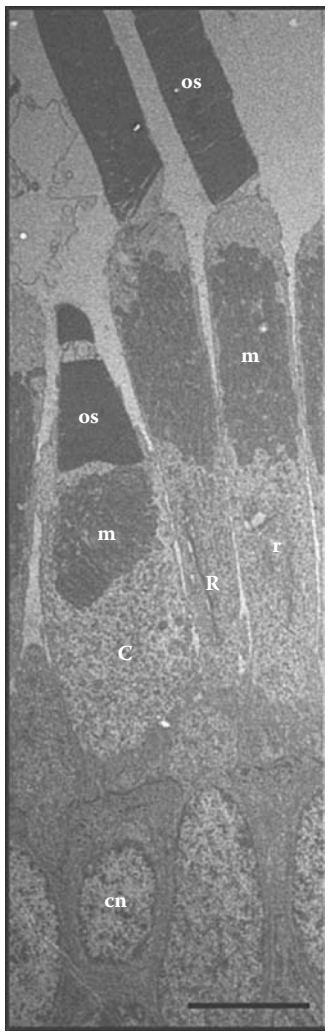

FIGURE 12.6
Photoreceptor ultrastructure in the giant shovelnose ray, *Rhinobatos typus*, showing the typical morphology of rods (R) and cones (C). *Abbreviations:* cn, cone nucleus; m, mitochondria; os, outer segment. Scale bar: 5 µm. (Adapted from Hart, N.S. et al., *J. Exp. Biol.*, 207, 4587–4594, 2004.)

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. Cohen et al. (1990), however, found a porphyropsin with maximum sensitivity (λ_{max}) of 522 nm (yellow–green) in the juvenile lemon shark, *Negaprion brevirostris*, whereas adult lemon sharks have a rhodopsin with λ_{max} = 501 nm (blue–green). In this species, the visual pigment apparently changes from a porphyropsin adapted for maximum sensitivity in inshore, shallow waters to a rhodopsin better suited for clearer, bluer oceanic waters (Figure 12.7). This visual adaptation matches a habitat shift from shallow to oceanic waters that occurs between juvenile and adult stages of this shark (Cohen et al., 1990).

A duplex (rod–cone) retina does not necessarily provide for color vision in all cases. Color discrimination normally requires at least two types of cones, each containing different visual pigments with different spectral sensitivities. Microspectrophotometry has revealed that the giant shovelnose ray, *Rhinobatos typus* (Hart et al., 2004), the eastern shovelnose ray, *Aptychotrema rostrata* (Hart et al., 2004), and the blue-spotted maskray, *Dasyatis kuhlii* (Theiss et al., 2007), possess three different cone pigments with different spectral sensitivities, suggesting that these animals are capable of color vision. By contrast, only one cone pigment per species was found in 17 species of sharks examined, suggesting that these animals may have monochromatic vision, similar to some marine mammals (Hart et al., 2011). Possessing only a single cone pigment does not, however, completely eliminate the capacity for color vision. If the rod and cone pigments have different spectral sensitivities and the retina and brain are capable of comparing signals between them, dichromatic color vision is possible. This may be the case in the blacknose shark, *Carcharhinus acronotus*, the scalloped hammerhead, *Sphyrna lewini*, and the bonnethead, *Sphyrna tiburo*, as electroretinography has revealed two absorbance peaks (blue and green) in their photoreceptors (McComb et al., 2010).

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) (Figure 12.3), which transmit impulses ultimately to visual centers in the CNS. Elasmobranch retinas are rod dominated, ranging from the skates with all-rod retinas (Dowling and Ripps, 1991) to species with apparently few cones such as *Mustelus* (Sillman et al., 1996; Stell and Witkovsky, 1973) to lamnid and carcharhinid sharks with as many as one cone for every 4 to 13 rods (Gruber and Cohen, 1978; Gruber et al., 1963). 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) of elasmobranch species. That sharks, skates, and rays have rod-dominated retinas does not in itself allow us to conclude that 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.

On the other hand, the spatial topography of retinal cells can reveal much about the quality of vision in these animals. Although elasmobranchs do not have all-cone foveas, they do have retinal areas (areae) of higher cone

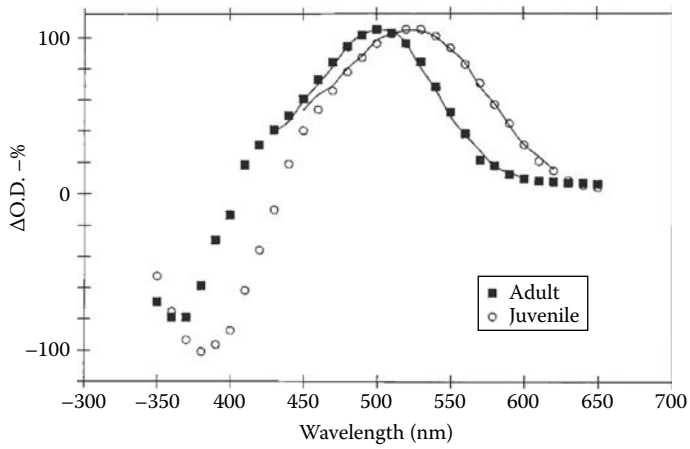

FIGURE 12.7
Normalized difference spectra for visual pigment absorption characteristics of adult vs. juvenile lemon sharks (*Negaprion brevirostris*). Peak absorption for the juvenile pigment is 522 nm, whereas the adult peak is 501 nm, demonstrating a shift in this species from a more yellow–red-sensitive porphyropsin in the juvenile to a more blue–green-sensitive rhodopsin in the adult. (From Cohen, J.L. et al., *Vision Res*., 30, 1949–1953, 1990. With permission.)

or ganglion cell density, indicating regional specializations for higher visual acuity (Collin, 1999; Hueter, 1991). Higher cone concentrations have been found in the "central" retina of the nurse shark, *Ginglymostoma cirratum* (Hamasaki and Gruber, 1965), whitespotted 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 smoothhound, *Mustelus mustelus*.

Retinal whole-mount techniques have been used to map the topographic distributions of retinal cells in 33 elasmobranch species representing 17 families of sharks, skates, and rays and one family of chimaera (Bozzano, 2004; Bozzano and Collin, 2000; Collin, 1988, 1999; Hueter, 1991; Lisney and Collin, 2008; Litherland and Collin, 2008; Litherland et al., 2009a; Logiudice and Laird, 1994; Peterson and Rowe, 1980; Theiss et al., 2007). Most species have horizontal visual streaks with one or more areas of increased photoreceptor and ganglion cell density (areae centrales) (Figure 12.8A,B). The position and extent of the horizontal streak appear to vary with habitat and ecology. Benthic species such as batoids (Bozzano and Collin, 2000; Collin, 1988; Litherland and Collin, 2008; Logiudice and Laird, 1994; Theiss et al., 2007), chimaeras (Collin, 1999; Lisney and Collin, 2008), catsharks (Bozzano and Collin, 2000; Lisney and Collin, 2008), bamboo and carpet sharks (Bozzano and Collin, 2000; Lisney and Collin, 2008; Litherland and Collin, 2008), lantern sharks (Bozzano and Collin, 2000), horn sharks (Collin, 1999; Peterson and Rowe, 1980), and sleeper sharks (Bozzano, 2004) generally have dorsally located horizontal streaks, providing increased sampling of the ventral visual field. This is thought to reflect the importance of the horizon at the substrate–water

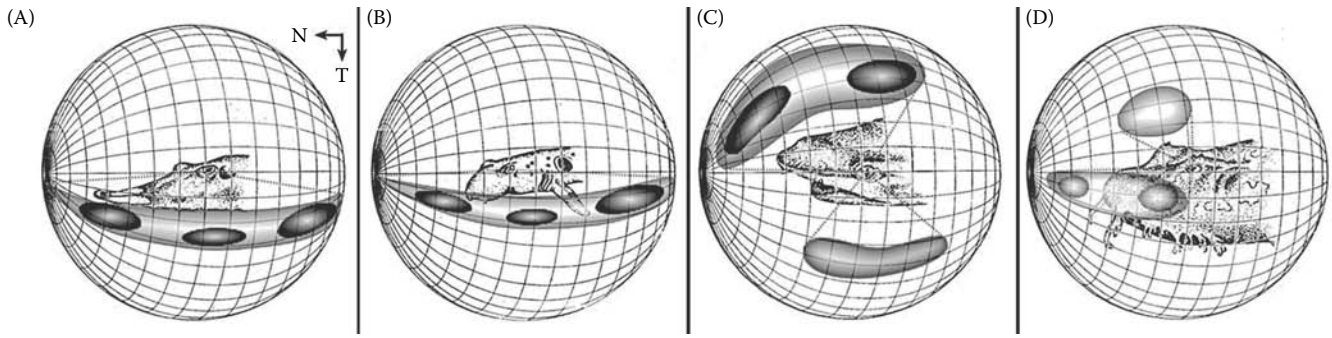

FIGURE 12.8
Diagrammatic representation of regions of the visual field subserved by regions of higher retinal cell density, depicting horizontal streaks (lightly shaded bands) with multiple areae (darkly shaded ovals) in the eastern shovelnose ray, *Aptychotrema rostrata* (A) and the epaulette shark, *Hemiscyllium ocellatum* (B); concentric retinal areae in the whitetip reef shark, *Triaenodon obesus* (C) and the ornate wobbegong, *Orectolobus ornatus* (D). *Abbreviations:* N, nasal; T, temporal. (Adapted from Litherland, L. and Collin, S.P., *Visual Neurosci*., 25, 549–561, 2008.)

interface in animals that feed off the benthos or bury themselves in the sand (Bozzano and Collin, 2000). Centrally located horizontal streaks have been found in benthopelagic species such as lemon sharks, *Negaprion brevirostris* (Hueter, 1991), blacktip reef sharks, *Carcharhinus melanopterus* (Collin, 1999), and blackmouth dogfish, *Galeus melastomus* (Bozzano and Collin, 2000), providing increased sampling of the lateral visual field. Ventral horizontal streaks found in tiger sharks, *Galeocerdo cuvier* (Bozzano and Collin, 2000), and bigeye thresher sharks, *Alopias superciliosus* (Lisney and Collin, 2008), provide increased sampling of the dorsal visual field. This may represent an adaptation for detecting prey from below. Tiger sharks prey on birds, sea turtles, and marine mammals, which are commonly found on or near the sea surface (Lowe et al., 1996), and common thresher sharks, *Alopias vulpinus*, a sister species to the bigeye thresher, have been demonstrated to attack prey from below, using the elongated dorsal lobe of their caudal fin to stun their prey (Aalbers et al., 2010).

In contrast, concentric retinal areae (Figure 12.8C,D) are more applicable for visualizing a limited spot in the visual field or for operating in complex, three-dimensional visual environments, such as reefs. Areae have been found in phylogenetically and ecologically diverse species of sharks, including blue sharks (*Prionace glauca*), sand tiger sharks (*Carcharias taurus*), hammerheads (*Sphyrna* spp.), bull sharks (*Carcharhinus leucas*), gray reef sharks (*Carcharhinus amblyrhynchos*) (Lisney and Collin, 2008), sandbar sharks (*Carcharhinus plumbeus*) (Litherland et al., 2009a), and whitetip reef sharks (*Triaenodon obesus*) (Litherland and Collin, 2008). These species range from pelagic, open ocean environments to reef, coastal, and even riverine habitats, yet all have areae of one kind or another. Cookie-cutter sharks, *Isistius brasiliensis*, and white sharks, *Carcharodon carcharias*, are both ambush predators in open water, while ornate wobbegongs, *Orectolobus ornatus*, are benthic ambush predators, and all three have retinal areae, not streaks (Bozzano and Collin, 2000; Litherland, 2001; Litherland and Collin, 2008). It appears, therefore, that habitat is not the only factor selecting for the presence or absence of retinal areae in sharks. Locomotory style could influence the adaptiveness of visual streaks vs. areae—for example, by favoring streaks in species that are constantly moving forward (Hueter, 1991). The possible ecological and behavioral correlates with elasmobranch retinal topography have been discussed by Bozzano and Collin (2000) and Lisney and Collin (2008).

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, 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 known to subserve the other senses as well, particularly for multimodal integration (Bodznick, 1991). In the lemon shark, *Negaprion 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 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 little skate, *Leucoraja erinacea* (formerly *Raja erinacea*). The retinal topography of this skate is unknown, but a related species (*Raja 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, *Negaprion brevirostris*, to locate a square white target for food reward (Clark, 1959). Later, Clark (1963) trained lemon sharks to discriminate visually 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 (*Ginglymostoma cirratum*) sharks, again without quantified visual parameters but providing evidence that sharks can learn visual tasks about as quickly as teleosts (cichlids) and mammals (mice).

Rigorous psychophysical methods including operant and classical conditioning 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 that (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 hour, 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. This work confirmed that the lemon shark possesses superior scotopic vision in extremely dim light and also is potentially capable of color vision under photopic conditions.

The ultimate behavioral 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. In a study of the Pacific angel shark, *Squatina californica*, by Fouts and Nelson (1999), 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. Gardiner and Atema (2007) demonstrated that smooth dogfish, *Mustelus canis*, can perform rheotaxis behaviors using vision when the lateral line system had been chemically ablated. Gardiner et al. (2011) also used sensory knockout techniques to determine that vision is used to line up strikes on live prey in blacktip sharks, *Carcharhinus limbatus*, and bonnetheads, *Sphyrna tiburo*. 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 orient visually 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. The explorations of the ear and hearing in elasmobranchs are also important as they reveal a basal stage in the evolution of vertebrate audition within a group of fishes that have evolved little over hundreds of millions of years. 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 (Corwin, 1981, 1989; Myrberg, 2001; Popper and Fay, 1977; Wisby et al., 1964). 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 (Maisey, 2001; Retzius 1881) (Figure 12.9). 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

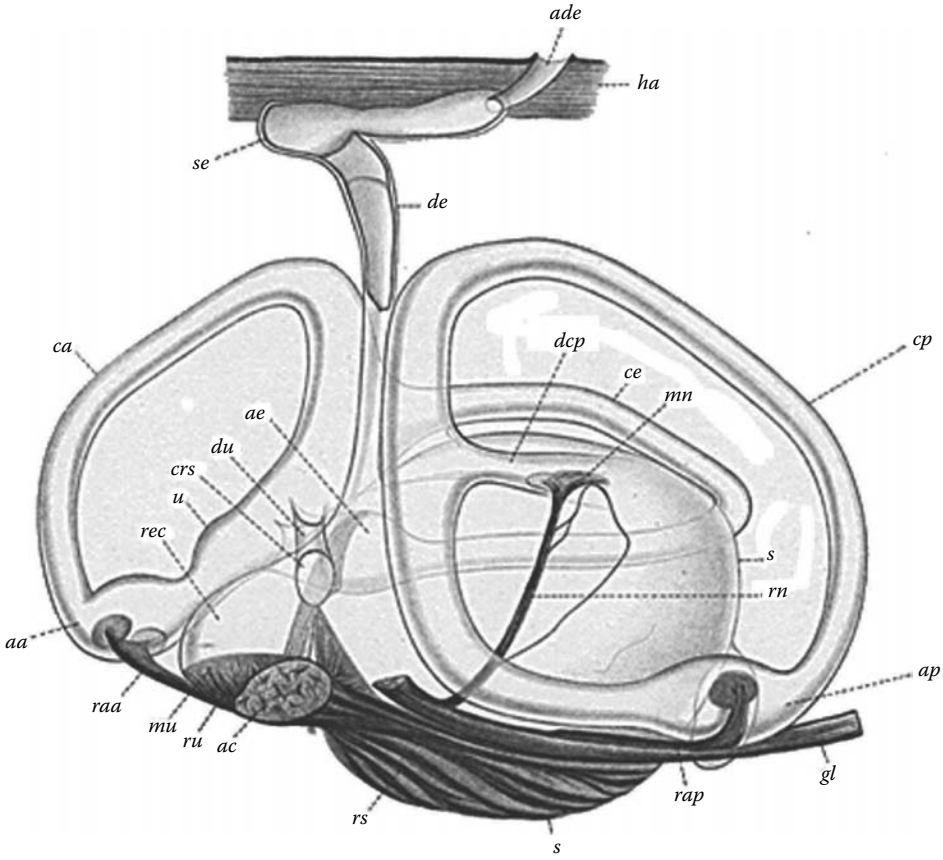

FIGURE 12.9
Anatomy of the ear of the thornback ray, *Raja clavata*. *Abbreviations:* aa, ampulla of anterior canal; ac, acoustic nerve; ade, opening of endolymphatic duct; ae, ampulla of horizontal canal; ap, ampulla of posterior canal; ca, anterior semicircular canal; ce, horizontal semicircular canal; cp, posterior semicircular canal; crs, saccular recess; dcp, posterior canal duct; de, endolymphatic duct; du, utricular duct; ha, chondrocranium; l, lagena; mn, macula neglecta; mu, utricule macula; pl, lagena macula; raa, ramus anterior ampulla; rap, ramus posterior ampulla; rec, utricular recess; rn, ramus neglectus; rs, ramus sacculus; ru, ramus utriculus; s, saccule; se, endolymphatic sac; u, utricule. (Adapted from Retzius, G., *Das Gehörorgan der Wirbelthiere*, Vol. 1, Samson and Wallin, Stockholm, 1881.)

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 (Figure 12.10). 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). Elasmobranchs also have an endolymphatic duct that connects to the saccule and leads to a small opening on the dorsal surface of the shark (Figure 12.10). 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). A more recent analysis of the entire auditory structure of 17 different species of

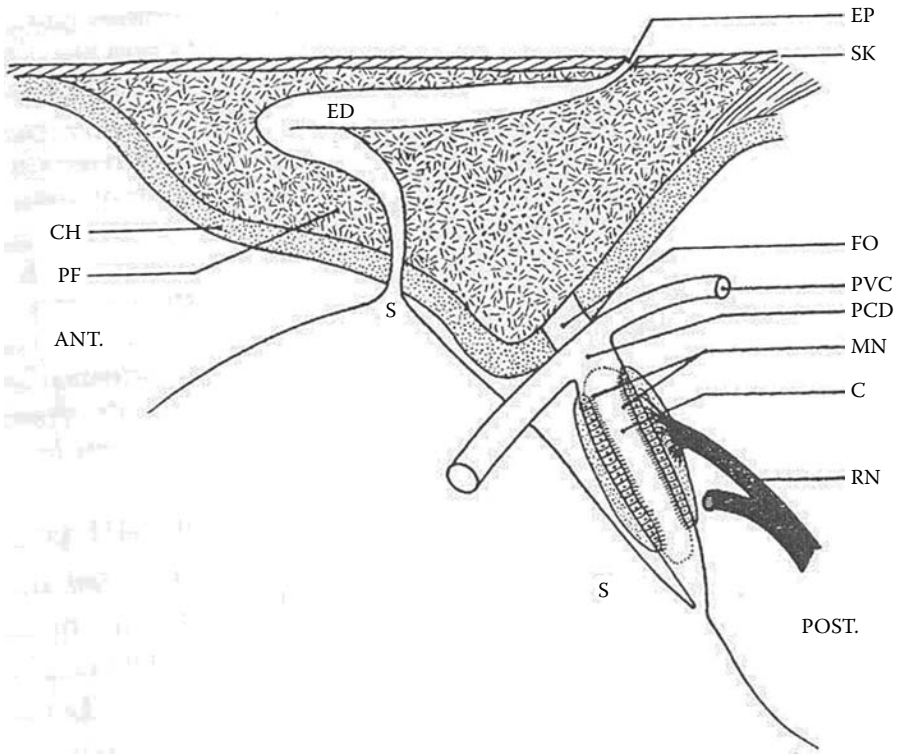

FIGURE 12.10
Cross-section of the elasmobranch ear focusing on the location of the parietal fossa and macula neglecta relative to the saccular chamber. *Abbreviations:* C, cupula; CH, chondrocranium; ED, endolymphatic duct; EP, endolymphatic pore; FO, fenestra ovalis; MN, macula neglecta; PCD, posterior canal duct; PF, parietal fossa; PVC, posterior vertical canal; RN, ramus neglectus nerve; S, saccule; SK, skin covering fossa. (From Fay, R.R. et al., *Comp. Biochem. Physiol. A Physiol.*, 47, 1235–1240, 1974. With permission.)

sharks and rays suggests that variations within the ear may be a combination of phylogeny as well as behavior and ecology (Evangelista et al., 2010); 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 (Barber et al., 1985; Corwin, 1983). 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 (Barry, 1987; Corwin and Northcutt, 1982). Much work remains to be done regarding both the anatomy and neurophysiology of the CNS as it relates to audition.

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 animals. To date, there are only six published audiograms in elasmobranchs (summarized in Figure 12.11). 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, including all elasmobranchs, detect the *particle motion* component of sound (can be described in terms of acceleration, velocity, and displacement). Fishes with swimbladders, especially those with connections between the swimbladder and ear, such as 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 motion 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

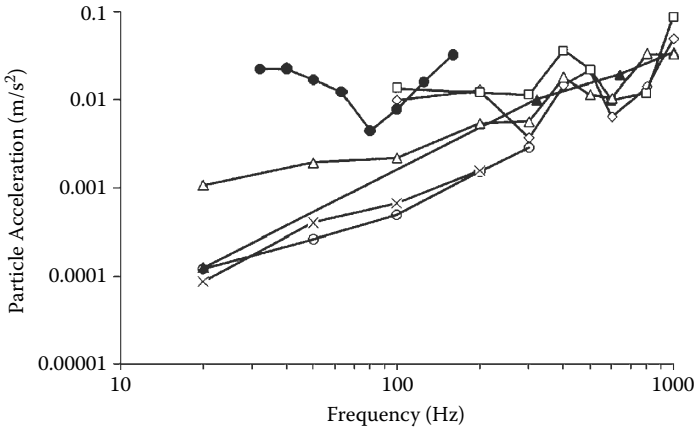

FIGURE 12.11
Particle acceleration audiograms of elasmobranchs in response to monopole (underwater speaker) and dipole (vibrating bead) sound stimuli. Open diamond, *Ginglymostoma cirratum*; open square, *Urobatis jamaicensis*; open triangle, *Rhizoprionodon terraenovae*; x, *Chiloscyllium griseum* (dipole); open circle, *Heterodontus francisci* (dipole); filled triangle, *Negaprion brevirostris*; filled circle, *Heterodontus francisci*. The open shapes and x's are elasmobranch audiograms obtained using auditory evoked potential (AEP) methods, and the filled shapes are audiograms obtained using classical conditioning methods. (From Casper, B.M. and Mann, D.A., *J. Exp. Biol.*, 210, 75–81, 2007; Casper, B.M. and Mann, D.A., *J. Fish Biol.*, 75, 2768–2776, 2009. With permission.)

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). It was not clear whether higher frequency thresholds (640 Hz in Banner, 1967; 100 to 160 Hz in Kelly and Nelson, 1975) in these species are dominated by either pressure or particle displacement sensitivity. This could be because of measurement errors or because the sharks are detecting some other measurement of the sound field, such as the pressure gradient. Particle motion thresholds have also been measured in the nurse shark (*Ginglymostoma cirratum*), yellow stingray (*Urobatis jamaicensis*), and the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) by measuring auditory evoked potentials elicited from the brain in response to acoustic stimuli (Casper and Mann, 2006, 2009).

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 (Banner, 1967; Casper and Mann, 2006, 2009; Casper et al., 2003; Kelly and Nelson, 1975; Kritzler and Wood, 1961; Nelson, 1967).

Several papers show the importance of the macula neglecta in detecting sound 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) and Casper and Mann (2007a) 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 small-spotted catshark, *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 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 can 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 (Myrberg et al., 1969, 1972; Nelson and Gruber, 1963). 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 hypotheses about shark hearing abilities. An implanted data logger has been used to record the acoustic environment of a free-swimming shark (Meyer et al., 2008), but it was not used for measuring behavioral responses to sounds as has been accomplished with marine mammals (Johnson and Tyack, 2003).

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. The otolithic organs in other fishes 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 why 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 Kalmijn, 1988b; van den Berg and Schuijf, 1983). 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). Directional sensitivity was also measured in two species of bamboo sharks, with results suggesting that these sharks were able to detect sounds equally well from all directions (Casper and Mann, 2007b). Clearly, we need to collect more data with regard to 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 (for reviews, see Bleckmann, 2008; Coombs and Montgomery, 1999). In contrast to the amount of information available on lateral line morphology, physiology, 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 and support cells covered by a gelatinous cupula (Figure 12.12A). Ultrastructural studies have revealed that the support cells of the neuromast have apical microvilli that are taller than those observed in other vertebrate lateral line organs, but the function of this morphological difference is not yet known (Peach and Marshall, 2009). Elasmobranch fishes have several different types of mechanosensory end organs that are classified by morphology and location: superficial neuromasts (also called 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; Kroese and Schellart, 1992; Maruska and Tricas, 2004; Münz, 1989).

Superficial neuromasts (SNs) are distributed on the skin surface either in grooves positioned on raised papillae (skates, rays, and some sharks) or between modified placoid scales/denticles (sharks) with their cupulae directly exposed to the environment (Peach and Marshall, 2000, 2009; Tester and Nelson, 1967) (Figure 12.12B). There is considerable diversity in the morphology and position of SNs among elasmobranch taxa (e.g., SNs covered by overlapping denticles, in grooves bordered by denticles, or in grooves without associated denticles), and these morphological features may have functional implications related to water flow, filtering properties, and directionality, but this remains to be tested (Maruska, 2001; Peach, 2003; Peach and Marshall, 2000, 2009). 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 (dorsolateral neuromasts), a pair anterior to the endolymphatic pores, and a small group lateral to the eyes associated with the spiracle (spiracular neuromasts),

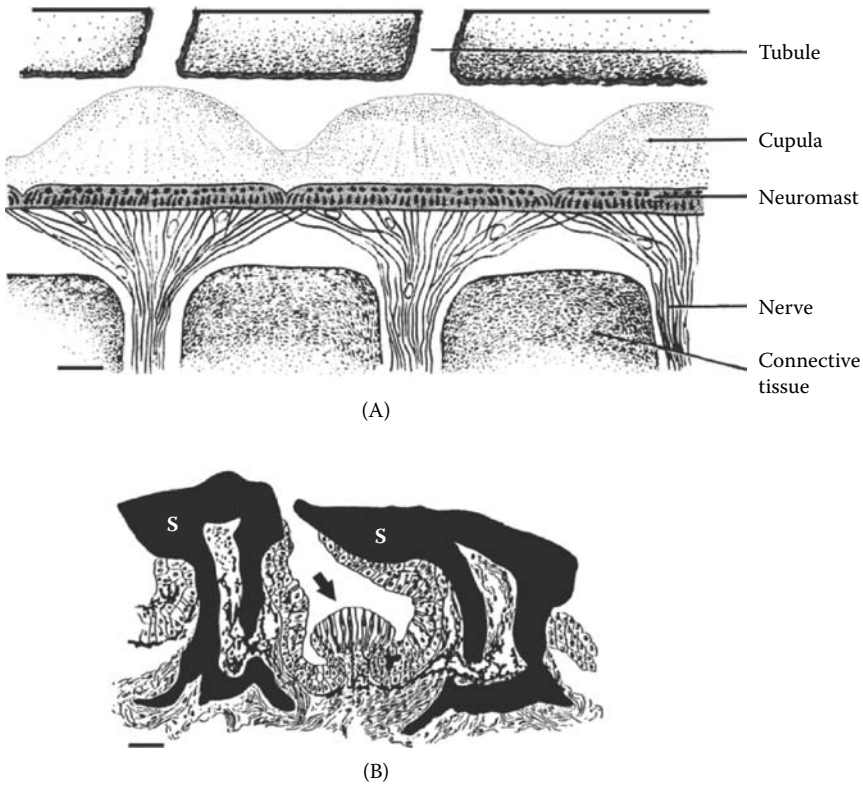

FIGURE 12.12
Morphology of the lateral line canal system and superficial neuromasts in elasmobranchs. (A) Diagrammatic longitudinal section of a pored canal from a juvenile gray reef shark, *Carcharhinus amblyrhynchos*. Innervated canal neuromasts are arranged in a nearly continuous sensory epithelium 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. (Adapted from Tester, A.L. and Kendall, J.I., *Pac. Sci*., 23, 1–16, 1969.) (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. (Adapted from Budker, P., in *Traité de Zoologie. Anatomie, Systémique, Biologie*. Tome XIII. *Agnathes et Poissons*, Grassé, P.P., Ed., Masson et Cie, Paris, 1958, pp. 1033–1062.)

which may have been lost in myliobatiform rays (Ewart and Mitchell 1892; Maruska, 2001; Maruska and Tricas, 1998; Peach and Rouse, 2004) (Figure 12.13A). The number of SNs in batoids examined thus far ranges from ~25 per side in some skates (*Raja* spp.) to >100 in some rhinobatids (Maruska, 2001; Peach and Rouse, 2004).

In sharks, SNs are positioned on the dorsolateral and lateral portions of the body and caudal fin (dorsolateral neuromasts), posterior to the mouth (mandibular row), between the pectoral fins (umbilical row; disappears during ontogeny in some species), and as a pair anterior to each endolymphatic pore (Budker, 1958; Peach and Marshall, 2000; Tester and Nelson, 1967) (Figure 12.13B,C,D). However, the distribution pattern varies among taxa with one or more of the neuromast groups absent in some species. The number of SNs ranges from less than 50 per side in the horn shark (*Heterodontus* spp.) to 80 per side in the spiny dogfish, *Squalus acanthias*, to more than 600 per side in the scalloped hammerhead, *Sphyrna lewini* (Tester and Nelson, 1967, 1969) (Figure 12.13C,D). A phylogenetic analysis of the distribution and abundance of SNs also showed that (1) the distinctive overlapping denticles covering the SNs in many sharks are a derived feature, (2) plesiomorphic elasmobranchs have SNs in open slits with widely spaced accessory denticles, (3) SN number on the ventral surface of rays has been reduced during evolution, and (4) spiracular SNs have changed position or were lost on several occasions in elasmobranch evolution (Peach and Rouse, 2004). In general, elasmobranchs with the fewest SNs include many benthic/demersal rays and sharks, while those with the most abundant SNs are pelagic sharks. Exceptions to this rule, however, such as high SN abundance in some demersal batoids and low SN abundance in some pelagic rays, indicate there is likely no straightforward relationship between SN abundance and pelagic lifestyle in elasmobranchs (Peach and Rouse, 2004).

The position of the SN 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 likely encode the velocity of water motion and

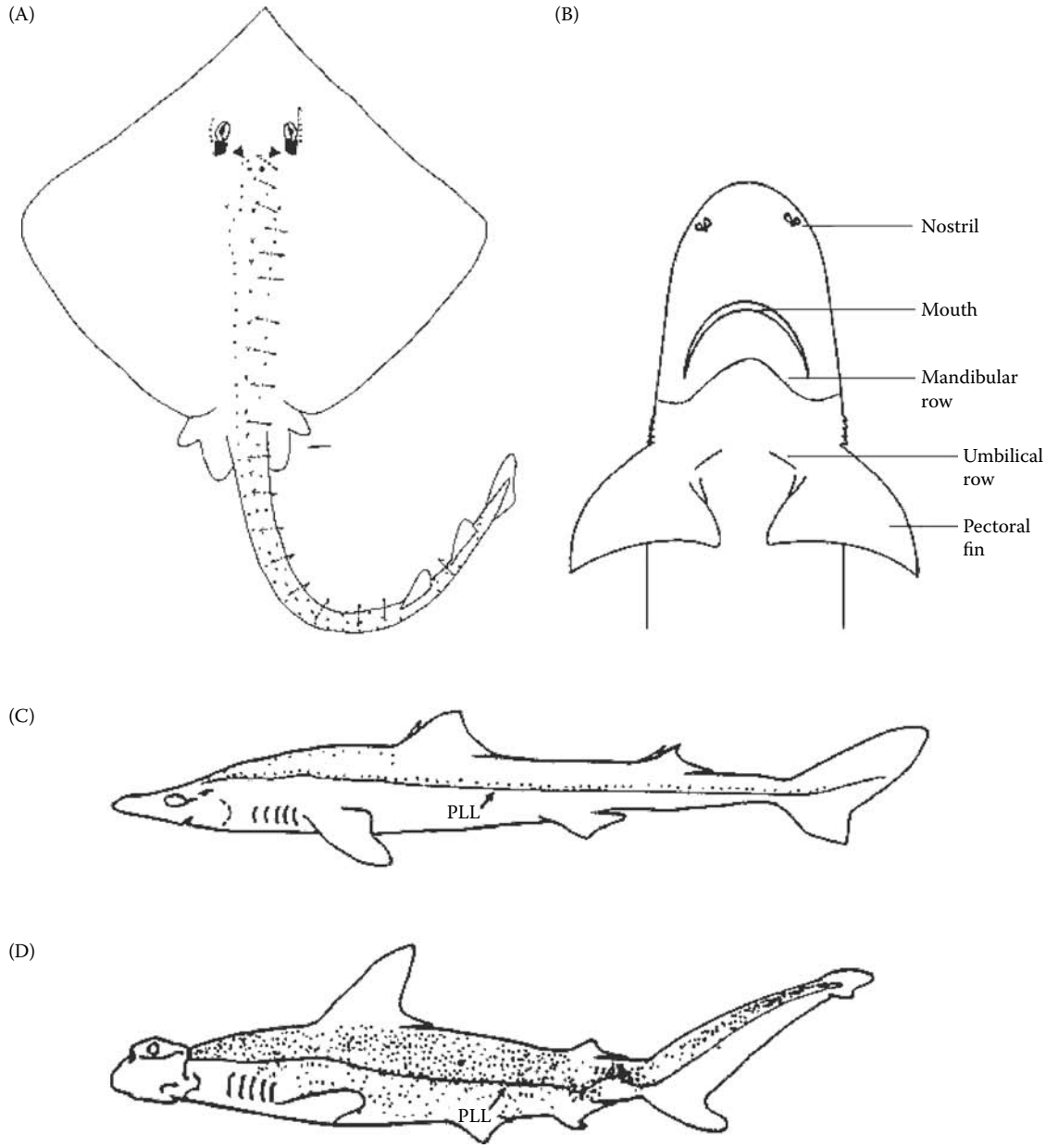

FIGURE 12.13
Distribution of superficial neuromasts (pit organs) in elasmobranchs. Each dot represents a single superficial neuromast. (A) Superficial neuromasts on the clearnose skate, *Raja eglanteria*, are located in bilateral rows along the dorsal midline to the end of the tail, a pair anterior to 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. (Adapted from Maruska, K.P., *Environ. Biol. Fish.*, 60, 47–75, 2001.) (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. (Parts B, C, and D adapted from Tester, A.L. and Nelson, G.J., in *Sharks, Skates, and Rays*, Gilbert, P.W. et al., Eds., The Johns Hopkins University Press, Baltimore, MD, 1967, pp. 503–531.)

may function to detect water movements generated by predators, conspecifics, or currents similar to that demonstrated for bony fishes (Blaxter and Fuiman, 1989; Kroese and Schellart, 1992; Montgomery et al., 1997), but physiological studies on the response properties of SNs in elasmobranchs are lacking.

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 (Boord and Campbell, 1977; Chu and Wen,

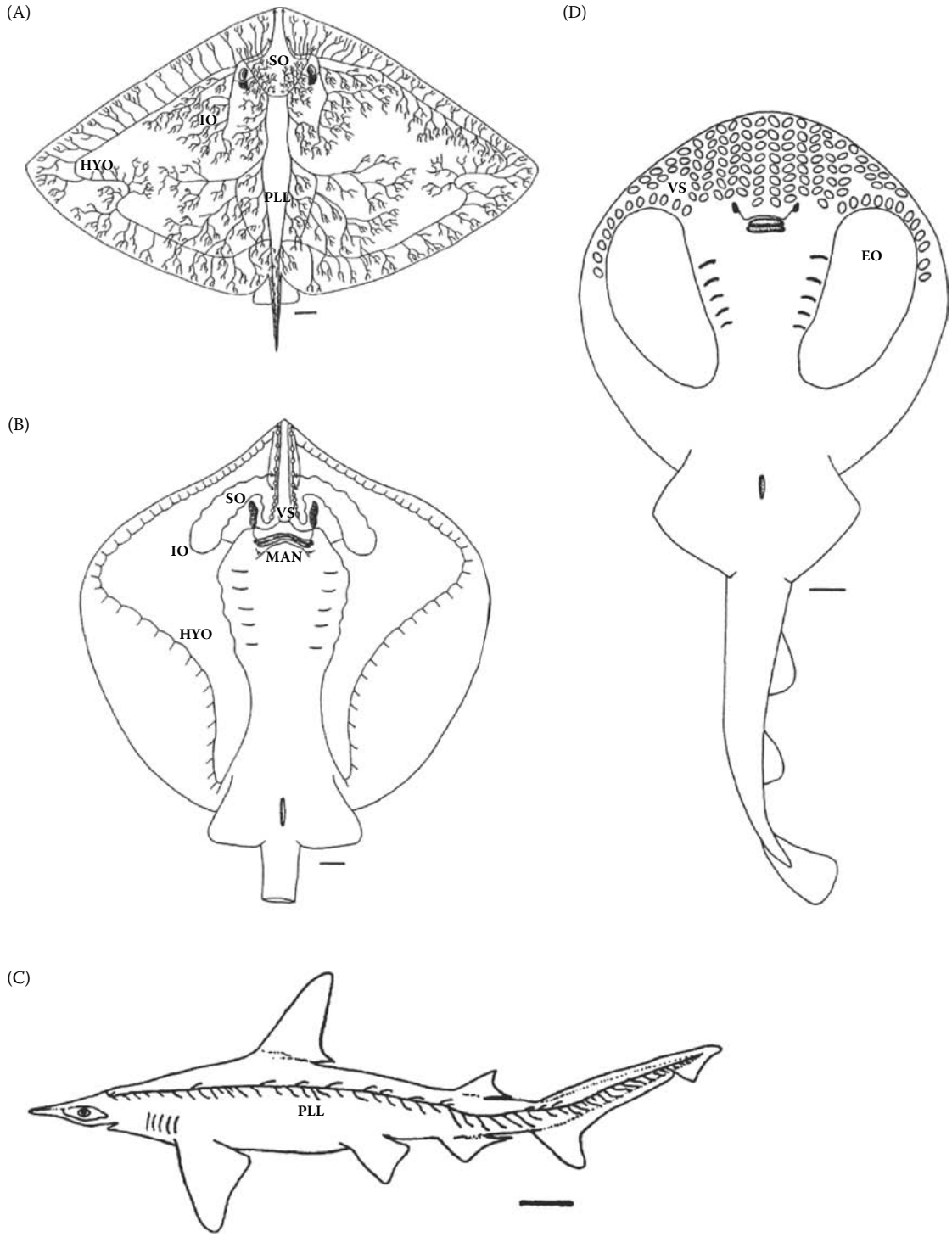

FIGURE 12.14
Distribution of lateral line canals and vesicles of Savi in elasmobranchs. The end of each line represents a pore opening on the skin surface. (A) Distribution of lateral line canals on the dorsal surface of the butterfly ray, *Gymnura micrura*. Canals are interconnected with extensive tubule branching that covers the majority of the disk surface. Scale bar: 1 cm. (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. Scale bar: 1 cm. (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. Scale bar: 0.5 cm. (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). Scale bar: 1 cm. *Abbreviations:* HYO, hyomandibular canal; IO, infraorbital canal; MAN, mandibular canal; PLL, posterior lateral line canal; SO, supraorbital canal; VS, vesicles of Savi. (Adapted from Maruska, K.P., *Environ. Biol. Fish.*, 60, 47–75, 2001.)

1979; Maruska, 2001; Roberts, 1978; Tester and Kendall, 1969) (Figure 12.14). 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 12.14A). 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 12.14C). These lateral line canals all 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 12.12A). This differs from bony fishes that have a single discrete neuromast positioned between adjacent pores, but the extent of this morphological organization among different canal subtypes or among species, as well as its functional significance, is still 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; Jordan, 2008; Maruska, 2001) (Figure 12.14A). In general, 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, as demonstrated in bony fishes (Coombs and Montgomery, 1999; Hassan, 1989; Kroese and Schellart, 1992; Montgomery et al., 1995). Neurophysiological recordings from primary afferent neurons that innervate pored canal neuromasts in the stingray, *Dasyatis sabina*, also demonstrate that, similar to bony fishes, pored canals show response properties consistent with acceleration detectors (Maruska and Tricas, 2004).

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; Jordan, 2008; Maruska, 2001; Maruska and Tricas, 1998; Wueringer and Tibbetts, 2008). 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 (Jordan, 2008; Maruska, 2001; Maruska and Tricas, 1998) (Figure 12.14B). 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; Maruska and Tricas, 2004). The number and distribution of pored vs. nonpored canals differ widely among species and may be explained by phylogeny and/or correlated with ecology and behavior. Jordan et al. (2009a), for example, showed that morphological variation in lateral line canals of several stingray species (*Urobatis halleri*, *Myliobatis californica*, *Pteroplatytrygon violacea*) was related to functional differences in detection capabilities and also corresponded well to their individual feeding ecologies.

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 and is stimulated by flexion of the cranial–hyomandibular joint; although its biological role is unclear, morphological and physiological studies indicate it functions as a joint proprioceptor (Barry and Bennett, 1989; Barry et al., 1988a,b). 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 (Barry and Bennett, 1989; Chu and Wen, 1979; Maruska, 2001; Savi 1844) (Figure 12.14B,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 (Barry and Bennett, 1989; Maruska, 2001; Nickel and Fuchs, 1974; Norris, 1932).

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 the spontaneous primary afferent firing rate. Thus, water motion stimuli effectively modulate

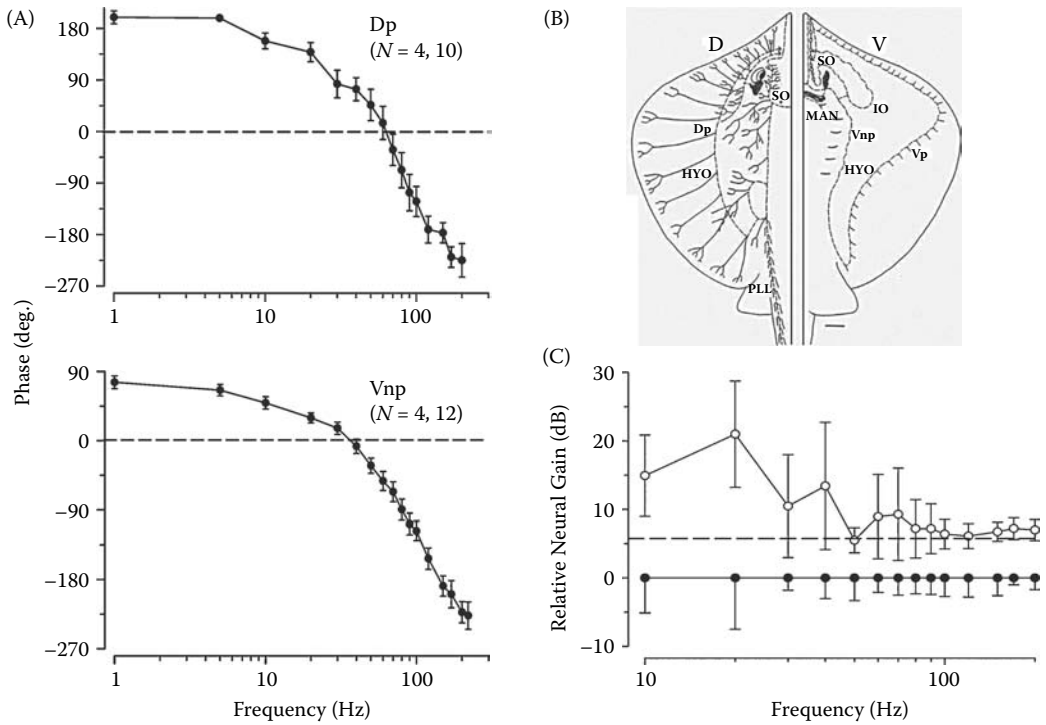

FIGURE 12.15
Response properties of primary afferent neurons that innervate canal neuromasts in the Atlantic stingray, *Dasyatis sabina*. (A) Phase plots for frequency responses of primary afferent neurons from dorsal pored (Dp) and ventral nonpored (Vnp) hyomandibular canals show a low-frequency phase lead of ~180° (acceleration-sensitive) for Dp canals and ~90° (velocity-sensitive) for Vnp canals. Phase of the peak neural response is expressed in degrees (mean ± SEM) relative to the peak displacement of a vibrating sphere. (*N* = number of animals, number of neurons). (B) Lateral line canal system on the dorsal (D) and ventral (V) surface of the stingray shows the distribution of Dp and ventral pored (Vp) and Vnp canals. *Abbreviations:* HYO, hyomandibular canal; IO, infraorbital canal; MAN, mandibular canal; PLL, posterior lateral line canal; SO, supraorbital canal. Scale bar: 1 cm. (C) Increase in relative neural gain to tactile stimulation (open circles) over hydrodynamic flow (closed circles) for primary afferents from Vnp canals. The average neural response is 6 to 20 dB greater (or 2 to 10 times more sensitive) to tactile stimuli compared to hydrodynamic stimuli above the canal, especially at low frequencies. (Adapted from Maruska, K.P. and Tricas, T.C., *J. Exp. Biol.*, 207, 3463–3476, 2004.)

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, location, and identity of the stimulus source (Bleckmann et al., 1989; Denton and Gray, 1988; Kalmijn, 1989). In general, neuromasts are sensitive to low-frequency stimuli (≤200 Hz), and neurophysiology studies indicate that the lateral line system is sensitive to velocities in the μm s^{-1} range and accelerations in the mm s^{-2} range (Bleckmann et al., 1989; Coombs and Janssen, 1990; Maruska and Tricas, 2004; Münz, 1985). Recordings from primary afferent neurons in the stingray *Dasyatis sabina* also show that pored canals exhibit response characteristics consistent with acceleration detectors (best frequencies of 20 to 30 Hz) whereas ventral nonpored canals better encode the velocity of canal fluid induced by skin movements (best frequencies of ≤10 Hz) at a 20-fold or greater sensitivity than that of the cutaneous tactile receptor system (Maruska and Tricas, 2004) (Figure 12.15).

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 (Bleckmann et al., 1987; Bodznick and Northcutt, 1980; Koester, 1983; 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 12.16). Further neurophysiological studies show bimodal and multimodal neurons

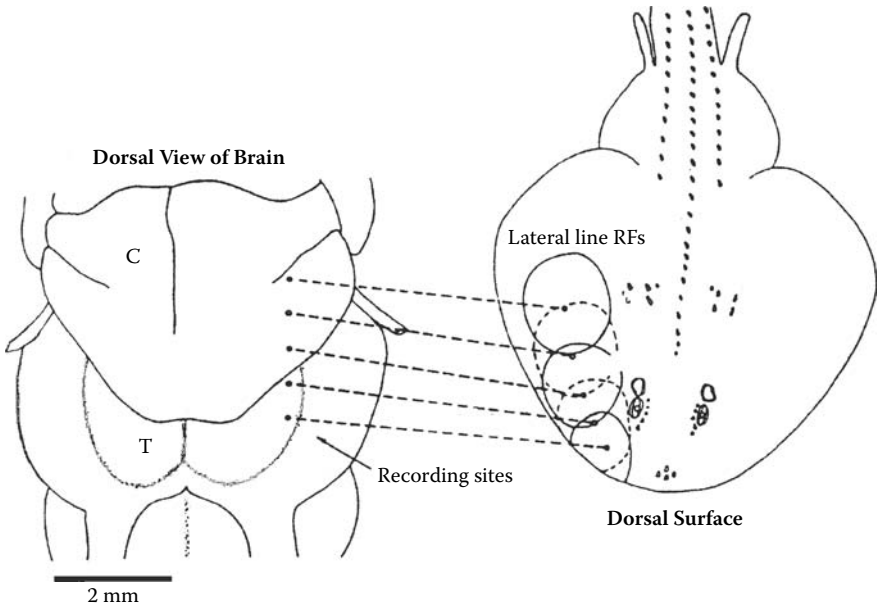

FIGURE 12.16
Mechanosensory lateral line receptive fields (RFs) on the body are somatotopically organized in a point-to-point rostrocaudal map in the midbrain of the thornback ray, *Platyrhinoidis triseriata*. Receptive fields on the anterior, mid-, and posterior body are mapped onto the contralateral rostral, mid-, and caudal dorsomedial nucleus of the midbrain. *Abbreviations:* C, cerebellum; T, tectum. (Adapted from Bleckmann, H. et al., *J. Comp. Physiol. A*, 161, 67–84, 1987.)

within midbrain and forebrain centers that respond to hydrodynamic flow as well as to auditory, 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 and Function

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. Similarly, Jordan et al. (2009a) compared behavioral responses of several ray species to water jets that mimicked signals produced by potential prey and demonstrated that a greater proportion of pored canals, high degree of canal branching, and high pore numbers corresponded with an increased behavioral response to water flow. Furthermore, based on the peripheral morphology of the lateral line system and feeding behavior of the Atlantic stingray, *Dasyatis 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. Early neurophysiology experiments also demonstrated that touching the skin near the nonpored canals caused a transient stimulation of the neuromasts (Sand, 1937), and more recent recordings showed that the ventral nonpored canals in the stingray *D. sabina* are 2 to 10 times more sensitive to direct skin depression velocity than to hydrodynamic dipole stimulation near the skin, which supports the hypothesized mechanotactile function (see Figure 12.15) (Maruska and Tricas, 2004). Although prey detection is mediated by the integration of multiple sensory inputs (i.e., electroreception, olfaction, vision), the mechanosensory lateral line likely also 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 portusjacksoni*, with their dorsolateral superficial neuromasts (pit organs) ablated showed 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). A recent study in the smooth dogfish, *Mustelus canis*, also demonstrated that in addition to olfaction an intact lateral line system is required for efficient and precise tracking of odor-flavored wakes used for eddy chemotaxis (e.g., simultaneous analysis of chemical and hydrodynamic dispersal fields) (Gardiner and Atema, 2007). In the smooth dogfish, as well as other species that are primarily crepuscular or nocturnal hunters, reliance on lateral line information is likely essential.

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, neuromast morphology) 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 or are possibly explained by phylogeny. The ability of the lateral line system to separate signal from noise is also critical, and future studies should examine the behavioral and physiological strategies used by elasmobranch fishes to enhance signal detection in a noisy environment (Montgomery et al., 2009). Finally, direct behavioral studies are sorely needed to clarify the many putative functions of the mechanosensory system in elasmobranch fishes, other than prey detection and rheotaxis, 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; see also 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 less than 5 nV/cm (Jordan et al., 2009b; Kajiura, 2003; Kalmijn, 1982, 1997). 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 (Dotterweich, 1932; Parker, 1909), but were then later shown to be also temperature sensitive (Hensel, 1955; Sand, 1937). A mechanoreceptive function was again proposed later (Loewenstein, 1960; Murray, 1957, 1960b) 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 (1960a) and Dijkgraaf and Kalmijn (1962) were the first to demonstrate the electrosensitivity of the ampullae of Lorenzini. More recently, the temperature sensitivity of ampullae was reconfirmed by Brown (2003; but for a complete review of this topic, see Brown, 2010), 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., 1982a), is hypothesized to function in geomagnetic navigation (Kalmijn, 1974, 1988a, 2000; Paulin, 1995), and is known to be important for the detection of the bioelectric fields produced by prey (Blonder and Alevizon, 1988; Jordan et al., 2009b; Kajiura, 2003; Kajiura and Fitzgerald, 2009; Kalmijn, 1971, 1982; Tricas, 1982), 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 12.17A) (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

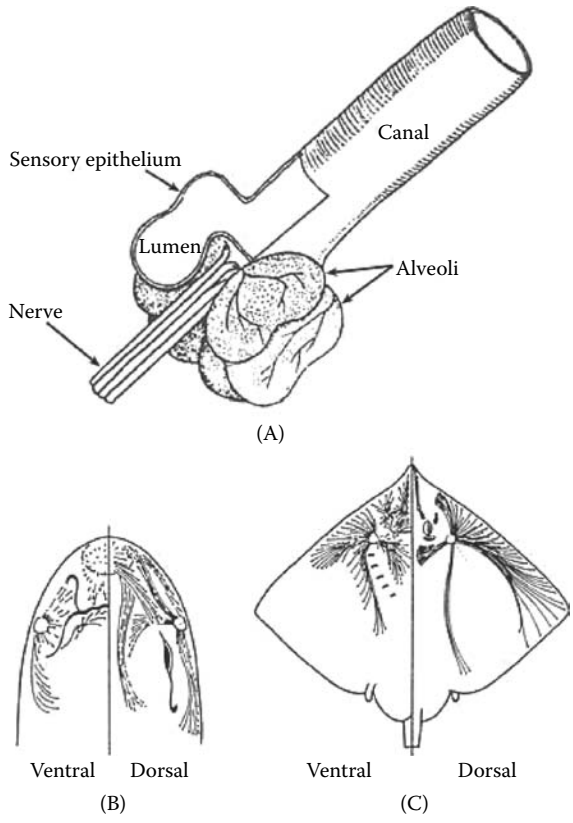

FIGURE 12.17
Ampullary electroreceptor organ of elasmobranchs. (A) The ampulla of Lorenzini consists of a small ampulla chamber composed of multiple alveoli that share a common lumen and a subdermal ampullary canal that projects to a pore on the surface of the skin. The sensory epithelium forms a high-resistance 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. (Adapted from Waltman, B., *Acta Physiol. Scand*., 66(Suppl. 264), 1–60, 1966.) (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 small-spotted catshark, *Scyliorhinus canicula*. (Adapted from Dijkgraaf, S. and Kalmijn, A.J., *Z. Vergl. Physiol*., 47, 438–456, 1963.) (C) Horizontal distribution of the ampullae of Lorenzini in the skate, *Raja clavata*. (Adapted from Murray, R.W., *J. Exp. Biol*., 37, 417–424, 1960.)

receptors to create a high-resistance electrical barrier between the basal and apical surfaces of the sensory epithelium, which form the ampulla wall (Sejnowski and Yodlowski, 1982; Waltman, 1966). 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 low-resistance uniform hydrogel (25 to 31 Ω-cm) composed of sulfated glycoprotein molecules with an ionic composition similar to that of seawater (Brown et al., 2005; Doyle, 1963; Waltman, 1966). The shark hydrogel has a lower admittance than seawater or synthetic (collagen) hydrogels, and it promotes a charge-induced voltage gradient along the interior length of the canal rather than acting as previously thought as a core conductor providing direct electrical contact to the external seawater environment (Brown et al., 2004).

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 12.17B) and the head and pectoral fins of skates and rays (Figure 12.17C). 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 canal which projects to the 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, 1988a; 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, 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; Bodznick and Schmidt, 1984; Koester, 1983). 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 the 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 (Northcutt, 1978; Platt et al., 1974). 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 (Bodznick and Northcutt, 1984; Bullock, 1979; Schweitzer and Lowe, 1984). Some electrosensory information is also conveyed to the cerebellum (Fiebig, 1988; Tong and Bullock, 1982).

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. The average resting or "spontaneous" discharge rates of electrosensory afferents in batoid elasmobranchs range from 8.6 impulses/s at 7°C in the little skate, *Leucoraja 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, *Raja eglanteria* (Sisneros et al., 1998), and 52.1 impulses/s at 21 to 23°C in the Atlantic stingray, *Dasyatis sabina* (Sisneros and Tricas, 2002b). 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 neonates to adults in both *R. eglanteria* and *D. sabina* (Sisneros and Tricas, 2002b; Sisneros et al., 1998). 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 (Ratnam and Nelson, 2000; Sisneros and Tricas, 2002b; Stein, 1967).

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, whereas 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 (Montgomery, 1984; Murray, 1965; Tricas and New, 1998). Electrosensory afferents are most responsive to electric fields oriented parallel to the vector between the 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; New, 1990; Peters and Evers, 1985; Sisneros and Tricas, 2000; Sisneros et al., 1998; Tricas and New, 1998; Tricas et al., 1995). Sensitivity (gain) of the electrosensory afferents to a sinusoidal uniform electric field is 0.9 spikes/s per μV/cm for the little skate, *Leucoraja erinacea* (Montgomery and Bodznick, 1993), 4 spikes/s per μV/cm for the thornback guitarfish, *Platyrhinoidis triseriata* (Montgomery, 1984), 7.4 spikes/s per μV/cm average for the Atlantic stingray, *Dasyatis sabina* (Sisneros and Tricas, 2000, 2002b), 17.7 spikes/s per μV/cm average for the clearnose skate, *Raja eglanteria* (Sisneros et al., 1998), and 24 spikes/s per μV/cm average for the round stingray, *Urolophus halleri* (Tricas and New, 1998).

12.5.2.2 Central Physiology

Although neurophysiological studies of the elasmobranch central electrosensory system have been limited, several features of electrosensory processing in the hindbrain and midbrain, and to a lesser extent in the thalamus and forebrain, have been well characterized. 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). Average resting discharge rates of AENs range from 0 to 5 spikes/s in the little skate, *Leucoraja erinacea* (Bodznick and Schmidt, 1984; New, 1990) to 10 spikes/s in the thornback guitarfish, *Platyrhinoidis 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/s per μV/cm for *L. 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, 1999; 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 *Platyrhinoidis 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 in this study, 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 *P. triseriata* (Schweitzer, 1986) and 4 to 8 ampullary pores in the thorny skate, *Raja 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 *Leucoraja erinacea* (Bodznick and Northcutt, 1984) and in *Platyrhinoidis 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 small-spotted catshark, *Scyliorhinus canicula*, and the thornback ray, *Raja clavata*, executed well-aimed feeding responses to small, visually inconspicuous buried flounder (Figure 12.18A) 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 12.18B). When the agar-screened prey was covered by a thin plastic film that insulated the prey electrically, the flounder remained undetected (Figure 12.18C). 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 12.18D). 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

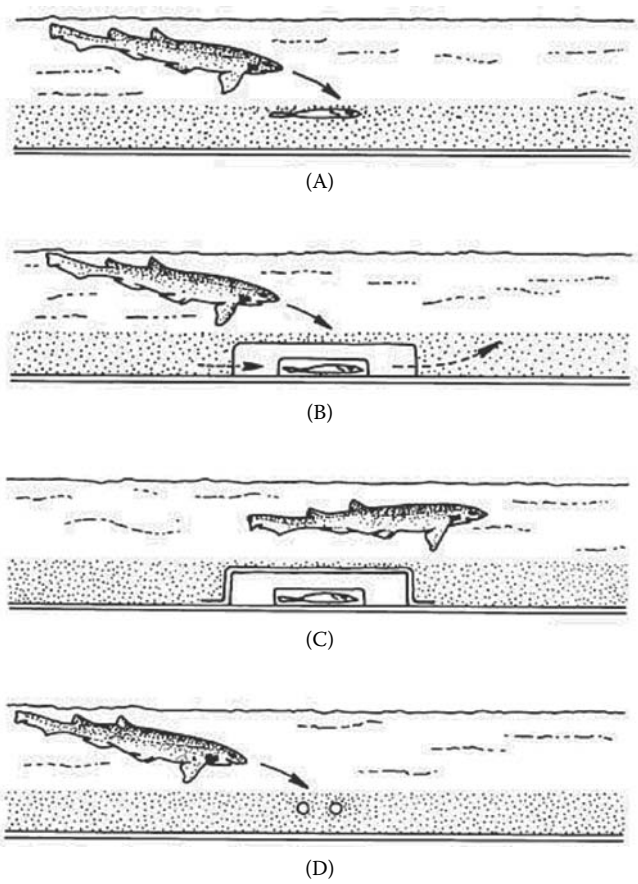

FIGURE 12.18
Use of the elasmobranch electric sense for the detection of electric fields produced by prey organisms. Behavioral responses of the small-spotted catshark, *Scyliorhinus canicula*, to a small flounder buried in the sand (A), a flounder buried in a seawater agar-screened chamber permeable 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. (Adapted from Kalmijn, A.J., *J. Exp. Biol.*, 55, 371–383, 1971.)

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. Subsequently, other elasmobranch species were shown to demonstrate well-aimed feeding responses at electrically simulated prey; these elasmobranch species include the Atlantic stingray (*Dasyatis sabina*) (Blonder and Alevizon, 1988), sandbar shark (*Carcharhinus plumbeus*), scalloped hammerhead (*Sphyrna lewini*), and neonate bonnethead (*Sphyrna tiburo*) (Kajiura, 2003; Kajiura and Fitzgerald, 2009; Kajiura and Holland, 2002), as well as more recently three batoid species: round stingray (*Urobatis halleri*), pelagic stingray (*Pteroplatytrygon violacea*), and bat ray (*Myliobatis californica*) (Jordan et al., 2009b).

McGowan and Kajiura (2009) recently showed that the euryhaline Atlantic stingray, *Dasyatis sabina*, responded similarly to prey-simulating stimuli when tested across a broad range of salinities from freshwater (0 ppt) to full-strength seawater (35 ppt), but there was a reduction in the electrosensitivity and detection range of stingrays in freshwater environments that is most likely due to the water's electrical resistivity and the physiological function of the stingray's ampullary canals. Other work by Kajiura and Holland (2002) 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. Work on the clearnose skate, *Raja eglanteria*, demonstrates that the electric sense of egg-encapsulated embryonic skates is well suited to detect potential egg predators (Sisneros et al., 1998), which include other elasmobranchs, teleost fishes, marine mammals, and

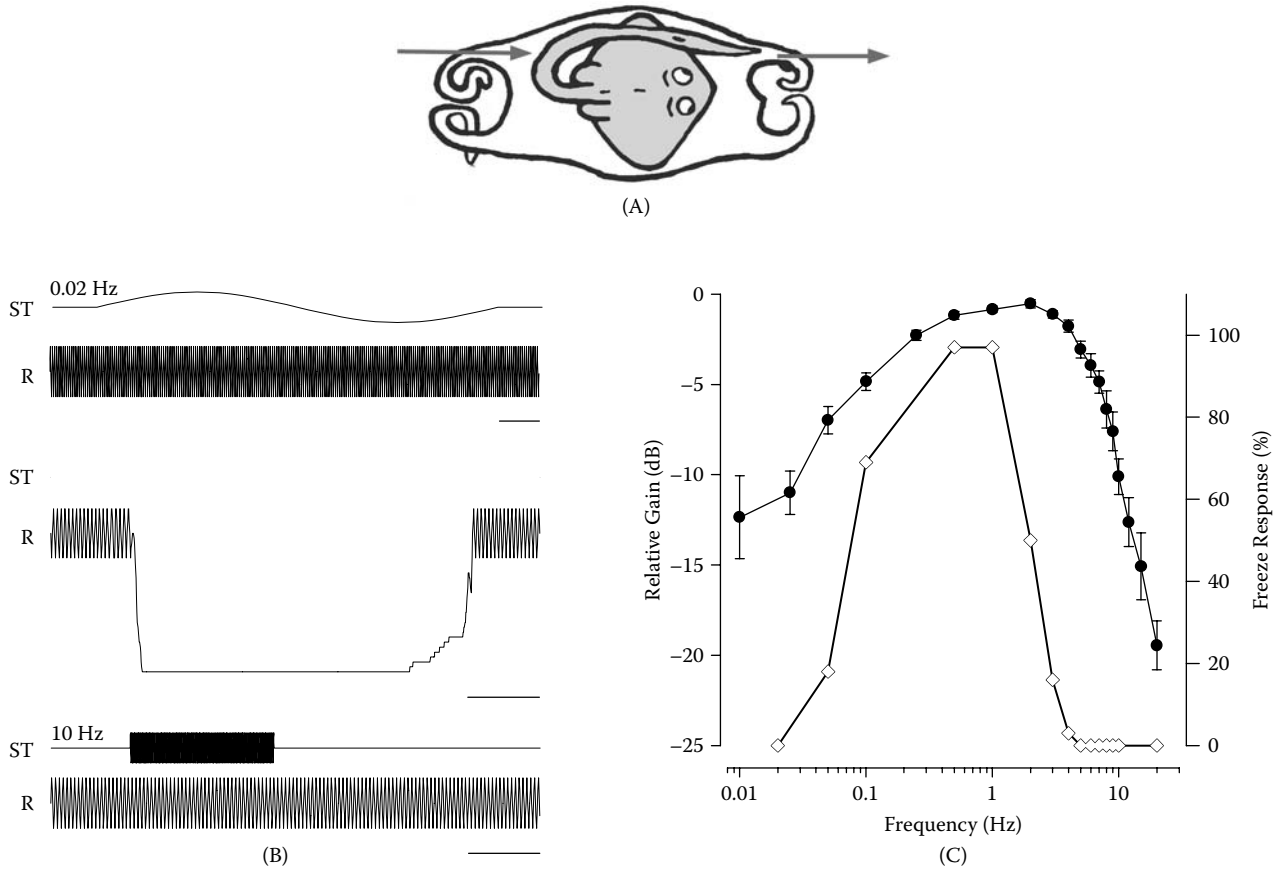

FIGURE 12.19
Behavioral response of embryonic clearnose skates, *Raja eglanteria*, to weak electric stimuli. (A) Ventilation behavior of embryonic skates. Diagram depicts a late-term embryonic skate circulating seawater within the egg case by undulating its tail in one corner of the egg near ventilation 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 μV 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. (Adapted from Sisneros, J.A. et al., *J. Comp. Physiol. A*, 183, 87–99, 1998.)

molluscan gastropods (for a 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 12.19A). 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 12.19B,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. (1982a) showed via behavioral experiments that the small-spotted catshark, *Scyliorhinus 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., 1982b). Thus, in theory, elasmobranch fishes may be 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 12.20). A different hypothesis 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 to 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.

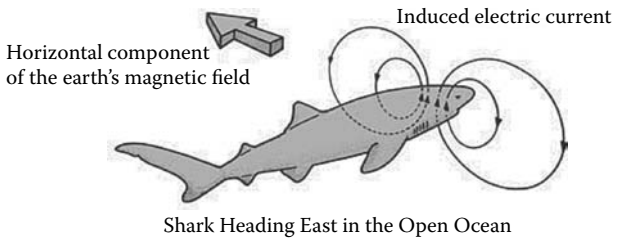

FIGURE 12.20
Use of the elasmobranch electric sense in the active mode of navigation. Diagram depicts the induction of electric current induced in the head and body of the animal as the shark swims through the horizontal component of the Earth's geomagnetic field. (Adapted from Kalmijn, A.J., in *Sensory Biology of Aquatic Animals*, Atema, J. et al., Eds., Springer-Verlag, New York, 1988, pp. 151–186.)

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, *Urolophus 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 hammerheads, *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.

Many other animals also use the Earth's magnetic field for navigation and homing. For these animals, many hypotheses have been proposed that link magnetoreception to either the visual system or magnetite particles found in the head or body (Gould et al., 1978; Leask, 1977; Phillips and Borland, 1992; Walcott et al., 1979; Walker et al., 1997). Walker et al. (1997) were the first researchers 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) 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 (Sisneros and Tricas, 2002a; Tricas et al., 1995). Male and female round stingrays, *Urolophus halleri*, use the electric sense to detect and locate the bioelectric fields of buried conspecifics during the mating season (Figure 12.21A). Stingrays produce a standing DC bioelectric field that is partially modulated by the ventilatory movements of the mouth, spiracles, and gill slits (Figure 12.21B) (Kalmijn, 1984; 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 (Sisneros and Tricas, 2002a; Tricas et al., 1995). The round

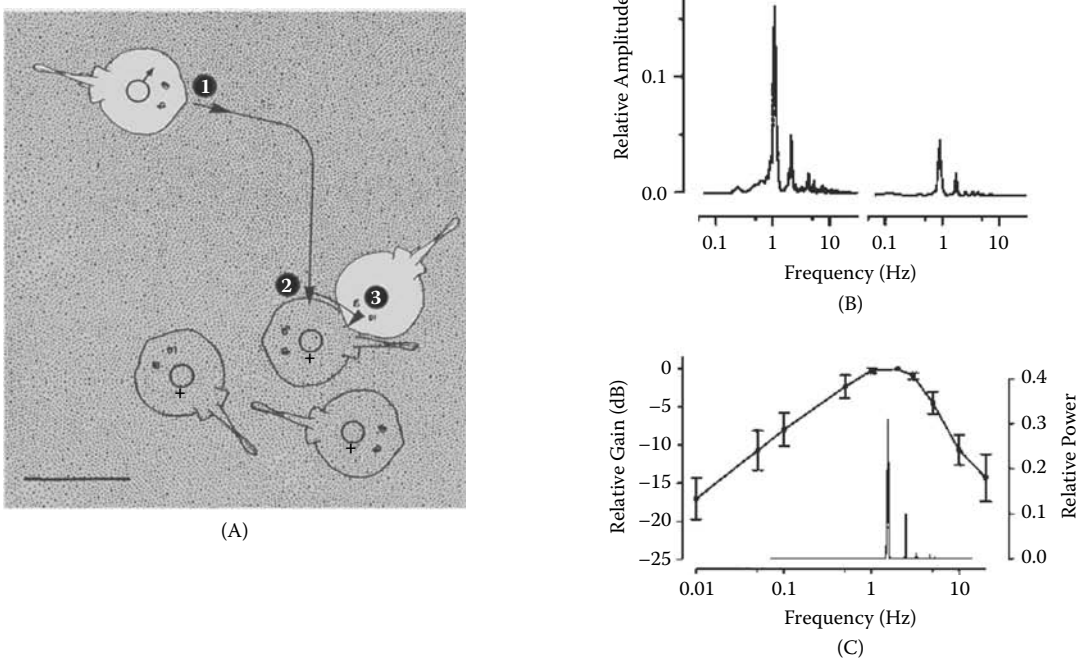

FIGURE 12.21
Detection of conspecific mates, bioelectric stimuli, and the frequency response of the peripheral electrosensory system in the round stingray, *Urolophus halleri*. (A) Orientation response by a male round stingray to cryptically buried conspecific females during the mating season. Males localize, orient toward, and inspect buried females 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 begin 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). (Adapted from Tricas, T.C. et al., *Neurosci. Lett*., 202, 29–131, 1995.)

stingray's peak frequency sensitivity of the peripheral electrosensory system matches the modulated frequency components of the bioelectric fields produced by conspecific stingrays (Figure 12.21C). 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. In addition to the detection of conspecific bioelectric fields, the electric sense is also used by skates to detect the weak electric organ discharges (EODs) produced by conspecifics during social and reproductive behaviors (New, 1994; Sisneros et al., 1998). All marine skates of the family Rajidae produce intermittently pulsed, weak electric discharges from spindle-shaped electric organs found bilaterally in the tail (Figure 12.22). The EODs of skates are relatively low in amplitude and species specific in duration, and they are thought to serve an important communication function during social and reproductive interactions (Bratton and Ayers, 1987; Mikhailenko, 1971; Mortenson and Whitaker, 1973). Peak frequency sensitivity of the peripheral electrosensory system in the clearnose skate, *Raja eglanteria*, matches the pulse rate of EODs produced by conspecific skates during social and mating behaviors (Sisneros et al., 1998). A similar match between peak frequency sensitivity of the peripheral electrosensory and EOD pulse rate also occurs in the little skate, *Leucoraja erinacea* (Bratton and Ayers, 1987; New, 1990). Thus, the match between the electrosensory-encoding and EOD properties in these skates likely facilitates electric communication during social and reproductive behaviors.

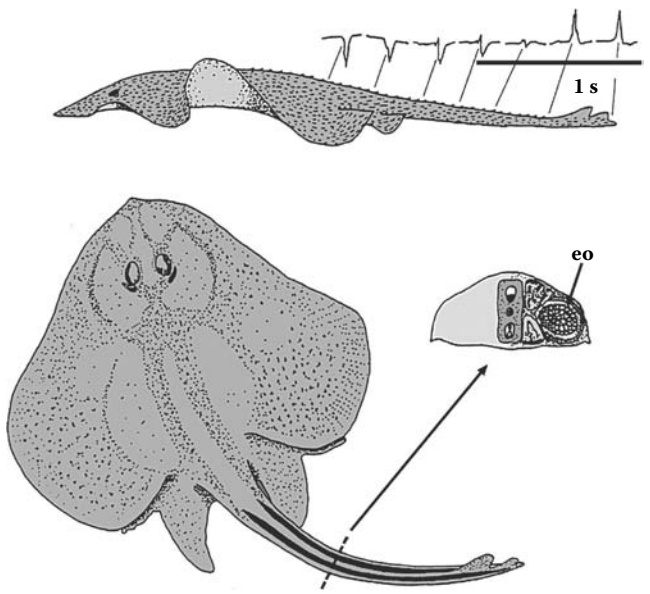

FIGURE 12.22
Diagram of the little skate, *Leucoraja erinacea*, showing the position of the electric organ (eo; black) in the tail and the corresponding monophasic, head-negative electric organ discharge waveform recorded 1 cm from the skin in the tail regions indicated. Note that the cross-section of the tail shows the position of the electric organ and lateral displacement of muscle bundles around the electric organ. (Adapted from Bratton, B.O. and Ayers, J.L., *Environ. Biol. Fish.*, 20, 241–254, 1987.)

12.6 Olfaction and Other Chemical Senses

Elasmobranchs, sharks in particular, are renowned for their olfactory capabilities. Often described as "swimming noses," sharks are the subject of several pervasive myths, such as possessing the ability to detect a single drop of blood in an Olympic-sized swimming pool. These popular perceptions have been fueled by anecdotal observations and early experimental studies that identified olfaction as an important, if not the primary, means by which sharks find food (Parker, 1909, 1914; Parker and Sheldon, 1913; Sheldon, 1909, 1911). In addition, shark olfaction has been thought to be important due to the relatively large size of their olfactory structures, compared to those of other vertebrates (reviewed in Northcutt, 1978). Interest in preventing shark attacks 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, 1978a). 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 two elasmobranch olfactory organs are ellipsoid saclike structures, situated in laterally placed cartilaginous capsules on the ventral aspect of the head, in front of the mouth. They are open to the environment via nostrils (nares), which are typically divided by skin-covered flaps into a more lateral incurrent nostril (naris) and a more medial excurrent nostril (Tester, 1963a; Theisen et al., 1986; Zeiske et al., 1986, 1987). In most species, the olfactory organs are entirely separate from the mouth, but in a few species they are in close association with the mouth or even connected to it via a deep groove, called the *nasoral groove*, which extends posteriorly from the excurrent naris, forming a virtual tube between the naris and the mouth (e.g., Orectolobidae, Heterodontidae) (Bell, 1993; Tester, 1963a). The external nasal morphology varies greatly among species, though some broad trends have been found based on lifestyle. Benthic and sedentary species tend to have large nasal openings, while benthopelagic and faster-swimming species tend to have smaller, slit-like openings or large nasal flaps (Schluessel et al., 2008). An anterior depression or groove may be present, helping to channel water into the incurrent opening, and the excurrent opening may be associated with a shallow posterior depression (Tester, 1963a; Zeiske et al., 1986, 1987). In hammerhead sharks (Sphyrinidae), these prenarial grooves are particularly well developed (Gilbert, 1967). In addition to the deep, narrow (prenarial) grooves, which extend along the anterior edge of each side of the head, linking to the incurrent nares (major nasal grooves), a second set of smaller grooves (minor nasal grooves) run parallel and anterior to each incurrent nostril on the dorsal side of the head, further assisting with channeling water into the incurrent naris (Abel et al., 2010) (Figure 12.23).

The olfactory sac is nearly completely filled by an olfactory rosette consisting of two rows of stacked wing-shaped plates, called *lamellae*, which originate from a central ridge (raphe) and attach to the wall of the olfactory cavity (Kajiura et al., 2005; Meredith and Kajiura,

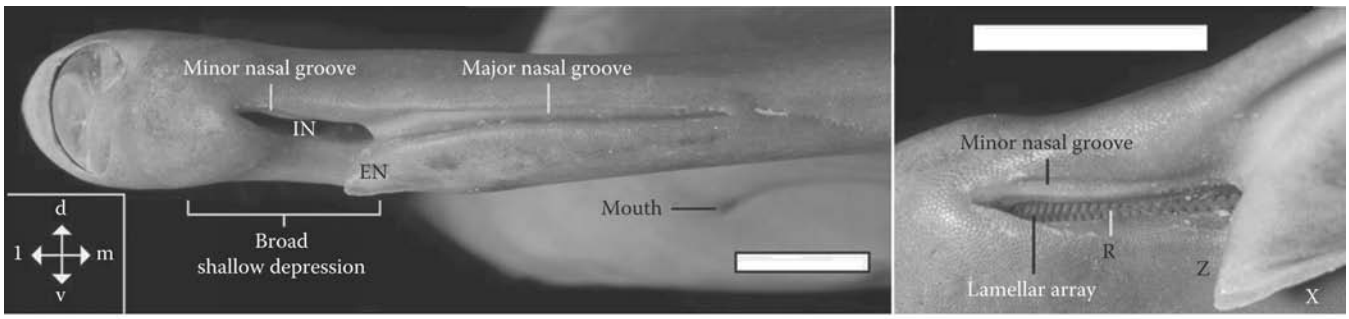

FIGURE 12.23
Nasal grooves in the golden hammerhead, *Sphyrna tudes*. (A) anterior and (B) anteroventral views of the right nasal region, with the lamellae visible through the incurrent nostril. *Abbreviations:* d, dorsal; l, lateral; m, medial; v, ventral; EN, excurrent nostril region; IN, incurrent nostril; R, raphe; X and Z, ventral and lateral edges of the excurrent nostril, respectively. Scale bars: 1 cm. (Adapted from Abel, R.L. et al., *Comp. Biochem. Physiol. A Comp. Physiol.*, 155(4), 464–475, 2010.)

2010; Tester, 1963a; Theisen et al., 1986; Zeiske et al., 1986, 1987) (Figure 12.24A,B). The lamellae are largest in the middle, decreasing in size toward both the medial and lateral ends (Meredith and Kajiura, 2010; Theisen et al., 198, 2009). Each lamella is covered with secondary folds (secondary lamellae), which greatly increase the surface area of the olfactory epithelium. The olfactory epithelium is divided into sensory and nonsensory areas. The nonsensory, squamous epithelium is composed of cells that bear microvilli only and numerous goblet cells (Schluessel et al., 2008; Theisen et al., 1986, 2009; Zeiske et al., 1986, 1987). It is generally found on the margins of the lamellae, although in some species it extends along the ridges of the secondary folds, and in other species a patchy, irregular distribution of sensory and nonsensory areas is found (Schluessel et al., 2008; Theiss et al., 2009) (Figure 12.24C,D). The much larger, centrally located sensory epithelium is composed of pseudostratified, columnar epithelium. It contains receptor cells, supporting cells (which bear numerous cilia), and basal cells, along with occasional goblet cells. It 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 (olfactory knob) from which extends a tuft of microvilli (Reese and Brightman, 1970; Schluessel et al., 2008; Theisen et al., 1986, 2009; Zeiske et al., 1986, 1987) (Figure 12.24E). 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 (smallspotted catshark, *Scyliorhinus canicula*) from the ciliated receptors of amphibians, rodents, and some bony fishes (Francheschini 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 olfactory morphology of numerous elasmobranch species has been examined. Olfactory rosette size, lamellar number, and sensory surface area vary by species (Kajiura et al., 2005; Meredith and Kajiura, 2010; Schluessel et al., 2008; Theiss et al., 2009); these differences can be correlated with habitat type but not phylogeny or prey type (Schluessel et al., 2008). Benthopelagic sharks and rays possess higher numbers of lamellae, larger olfactory surface areas, and larger rosettes than benthic species (Meredith and Kajiura, 2010; Schluessel et al., 2008). The ontogeny of the olfactory system has been examined in only a handful of species, but it appears to be well developed at birth, undergoing only minor changes as the animal grows. The morphology of the nares and olfactory rosettes and the ultrastructure of the epithelium of juveniles closely resemble those of adults (Schluessel et al., 2010). The olfactory bulbs undergo growth, increasing with body size, although not proportionally (Schluessel et al., 2010), such that the olfactory bulbs represent a larger proportion of the brain volume in adults as compared with juveniles (Lisney et al., 2007). The olfactory rosettes undergo similar growth; whereas lamellar surface area increases with body size, lamellar number does not, except in the spotted eagle ray, *Aetobatus narinari* (Meredith and Kajiura, 2010; Schluessel et al., 2010).

Interspecific differences in olfactory morphological data have often been used to assess olfactory capability, with increased sensitivity inferred from increased size (Kajiura et al., 2005; Lisney et al., 2007; Schluessel et al., 2008, 2010; Theisen et al., 1986, 2009; Zeiske et al., 1986, 1987), but electrophysiological data refute this. The

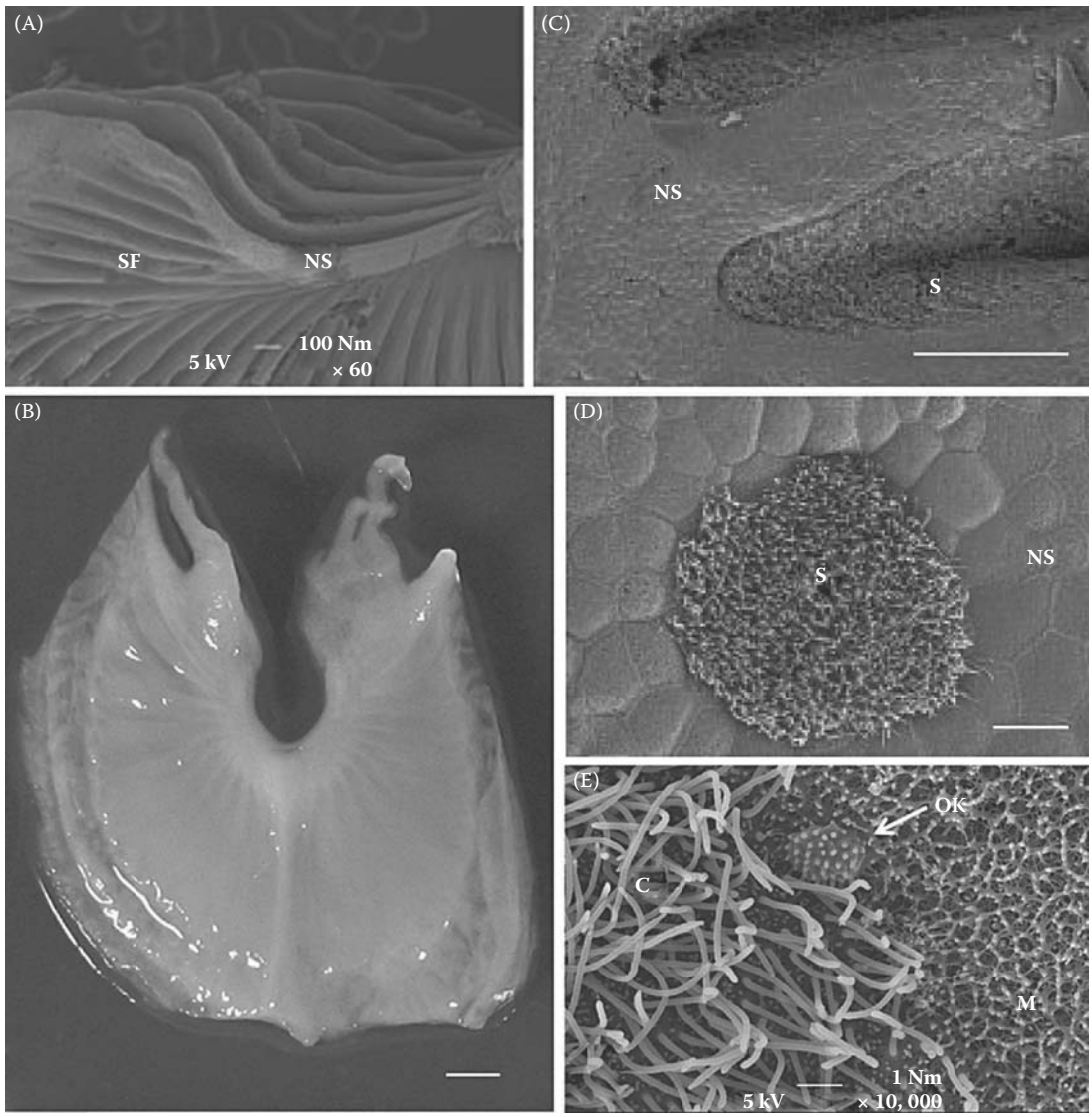

FIGURE 12.24
The olfactory rosette. (A) Low-power SEM image of stacks of lamellae in the bull shark, *Carcharhinus leucas*. (B) Whole lamella from the western wobbegong, *Orectolobus hutchinsi* (scale bar: 1 mm). (C) High-power SEM showing extension of the nonsensory epithelium along the secondary folds in the spotted eagle ray, *Aetobatus narinari* (scale bar: 100 µm). (D) High-power SEM showing division between the sensory (ciliated region) and nonsensory (nonciliated region with microvilli) in the blue-spotted maskray, *Dasyatis kuhlii* (scale bar: 100 µm). (E) High-power SEM showing an olfactory knob present on the lamellae of *O. hutchinsi*. *Abbreviations:* C, cilia; M, microvilli; NS, non-sensory epithelium; OK, olfactory knob; S, sensory epithelium; SF, secondary folds. (Parts A, C, and D adapted from Schluessel, V. et al., *J. Morphol*., 269, 1365–1386, 2008. Photographs in Parts B and E by Susan M. Theiss and used with permission.)

underwater electroolfactogram (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 eight elasmobranchs: the nurse shark, *Ginglymostoma cirratum* (Hodgson and Mathewson, 1978b); the Atlantic stingray, *Dasyatis sabina* (Meredith and Kajiura, 2010; Silver, 1979; Silver et al., 1976); the lemon shark, *Negaprion brevirostris* (Meredith and Kajiura, 2010; Zeiske et al., 1986); the thornback ray, *Raja clavata* (Nikonov et al., 1990); the scalloped hammerhead, *Sphyrna lewini* (Tricas et al., 2009); the clearnose skate, *Raja eglanteria*; the yellow stingray, *Urobatis jamaicensis*; and the bonnethead, *Sphyrna tiburo* (Meredith and Kajiura, 2010). 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 these species, and extracts of squid muscle were also used in the lemon shark study (Zeiske et al., 1986). The thresholds for individual amino acids varied by species, but, in general, neutral amino acids are more stimulatory, while valine, proline, and isoleucine

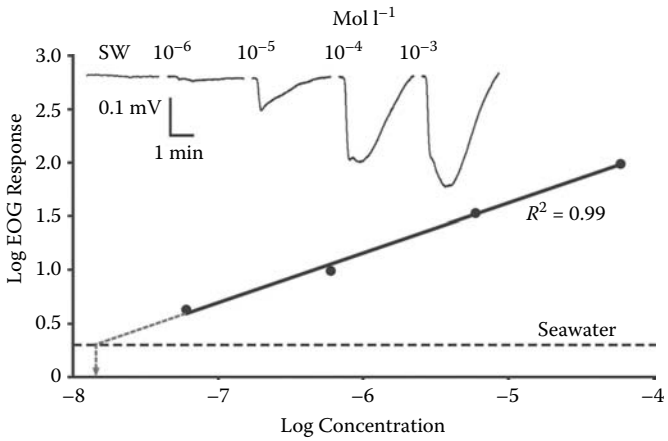

FIGURE 12.25
Representative electroolfactogram (EOG) concentration–response curve for a bonnethead, *Sphyrna tiburo*. The magnitude of the log EOG response (a percentage of the 10^{-3} mol/L alanine standard) is linearly related to the log amino acid stimulus concentration (10^{x} mol/L). The horizontal dashed black line indicates the averaged response to the seawater (SW) control. The olfactory threshold is calculated as the point where the regression line for the best-fit line of the response intersects the averaged response to the SW control. The inset shows representative EOG responses to the SW control and to increasing log concentrations of L-alanine. Based on absorbance calculations of diluted dye, all stimuli were diluted to 6% of their injected concentration at the entrance to the incurrent naris. The estimated diluted stimulus concentrations are plotted at arrival to the olfactory organ. (From Meredith, T.M. and Kajiura, S.M., *J. Exp. Biol.*, 213, 3449–3456, 2010. With permission.)

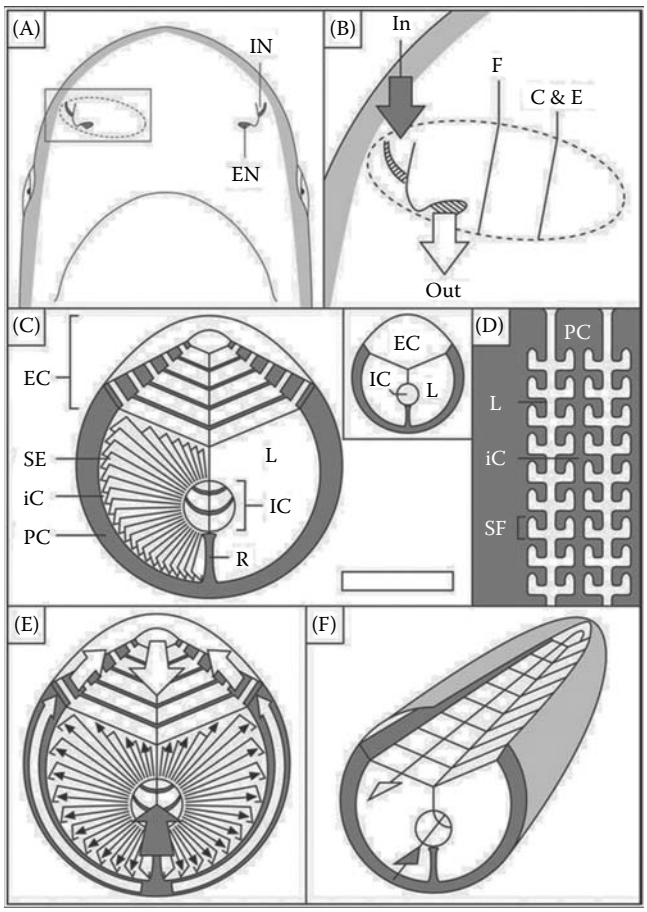

FIGURE 12.26
Schematics of the functional morphology of the nasal region of an active elasmobranch. (A) Ventral surface of the head of a lemon shark, *Negaprion brevirostris* (based on Zeiske et al., 1986). The dotted line is the approximate location of the olfactory chamber. (B) Boxed region in part A. Lines labeled C, E, and F indicate positions of the front face of sections in panels (C), (E), and (F), respectively. (C) Sagittal section through the olfactory chamber, toward the medial end of the chamber (based on Zeiske et al., 1986), with secondary lamellae shown on the left lamella only. Scale bar: 5 mm. Inset: Outlines of incurrent and excurrent channels created by lamellae and the roof of the olfactory chamber. (D) Transverse section through two lamellae, toward the side wall of the olfactory chamber, showing the convoluted nature of the interlamellar channel. (E) Flow through the olfactory chamber, same view as part C. (F) Cut-away view to one side of the olfactory chamber, showing principal flow (arrowed line) through incurrent and excurrent channels (interlamellar gaps and secondary lamellae omitted for clarity). Gray arrows, incurrent flow; white arrows, excurrent flow; dark arrows, flow in interlamellar channels. *Abbreviations:* EC, excurrent channel; EN, excurrent nostril; iC, interlamellar channel; IC, incurrent channel; IN, incurrent nostril; L, lamella; PC, peripheral channel; R, raphe; SF, secondary fold. (From Abel, R.L. et al., *Comp. Biochem. Physiol. A Comp. Physiol.*, 155(4), 464–475, 2010. With permission.)

(also neutral, but with branched side-chains or secondary amine groups) are the least stimulatory. These results are similar for elasmobranchs and teleost fishes (Hara, 1994; Meredith and Kajiura, 2010). The EOG magnitude increased exponentially with the log of the stimulus concentration (Figure 12.25), and calculated thresholds ranged between 10^{-6} and 10^{-11} *M*. These levels are similar to those reported for bony fishes (teleosts) (Hara, 1994), as well as the levels of free amino acids in seawater (Kuznetsova et al., 2004; Pocklington, 1971). Despite differences in lamellar number and surface area, olfactory thresholds do not differ significantly among elasmobranch species. Because behavioral evidence is lacking, the functional significance of interspecific differences in olfactory morphology and physiology are unknown.

The dynamics of nasal water circulation (nasal ventilation) have been analyzed in a series of detailed studies on several sharks. Briefly, water enters the incurrent nostril, passes along the incurrent channel, and is drawn through the interlamellar channels, out into peripheral channels on the outer edges of the lamellae, and then into the excurrent channel; it then passes back out to the environment via the excurrent nostril (Abel et al., 2010; Theisen et al., 1986; Zeiske et al., 1986, 1987) (Figure 12.26). In actively swimming elasmobranchs, this water flow is likely generated by differences in pressure between the incurrent and excurrent nostrils that are primarily caused by the forward motion of the animal (Theisen et al., 1986; Zeiske et al., 1986, 1987). In benthic

and more sedentary species, nasal ventilation may be aided by a buccopharygeal pump: As water is pumped into the mouth to ventilate the gills, it is also drawn through the "virtual tube" between the olfactory organ and the mouth, which results in the flow of water into the incurrent nostril and through the olfactory rosette. These structures thus act as a functional internal naris (Bell, 1993) (Figure 12.27). Whether the multiciliated non-sensory cells act to propel water is unknown, but no nasal currents were observed in stationary lemon sharks, *Negaprion brevirostris* (Zeiske et al., 1986).

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 12.28). 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 bonnetheads, *Sphyrna tiburo* (Dryer and Graziadei, 1993, 1994a, 1996) and electrophysiology of the OB of the small-spotted catshark, *Scyliorhinus canicula* (Bruckmoser and Dieringer, 1973), and the little skate, *Leucoraja 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 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 size of the OB relative to total brain mass or volume have been calculated in several elasmobranch species and used to suggest differences in ecology, particularly in reliance on smell in a variety of behaviors, particularly feeding and social behavior (Demski and Northcutt, 1996; Lisney and Collin, 2006; Lisney et al., 2007; Northcutt, 1978). It is unclear at this time, however, how much of the variation can be attributed to phylogeny as opposed to interspecific differences in behavior and ecology. Without supporting behavioral and ecological evidence, it is impossible to determine how observed differences in the size of any of the sensory structures relate to differences in performance.

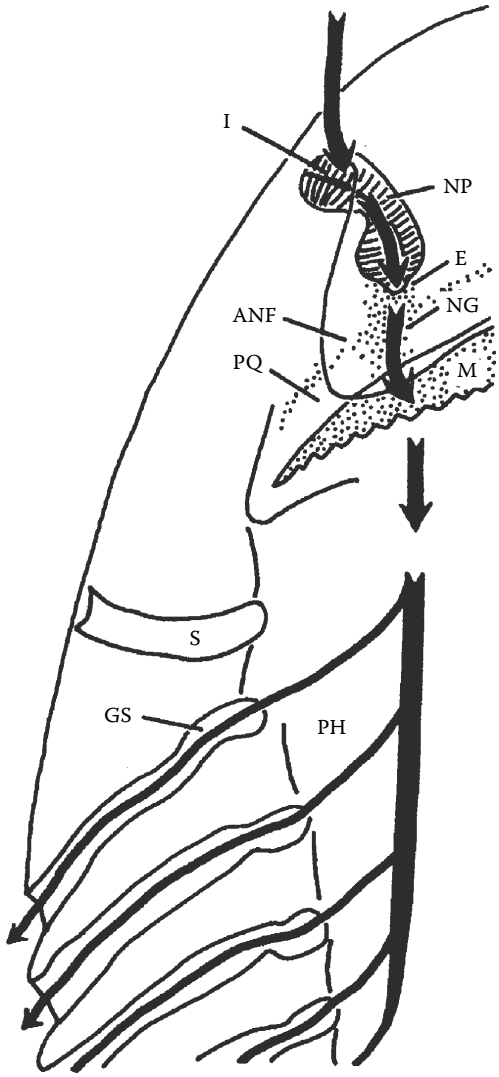

FIGURE 12.27
Proposed path of water drawn through the olfactory chamber by the buccopharyngeal pump in a sedentary elasmobranch (ventral view; anterior is up). Water (arrows) enters through the incurrent opening (I), flows through the nasal pouch (olfactory chamber; NP), and exits the excurrent opening (E) into the nasoral groove (NG), which is covered by the anteromedial nasal flap (ANF). Water continues through the nasoral groove across the palatoquadrate (PQ) and into the mouth (M). Finally, water exits the pharynx (PH) through the gill slits (GS). The first two complete gills slits and spiracle (S) are shown. (From Bell, M.A., *Copeia*, 1993, 144–158, 1993. With permission.)

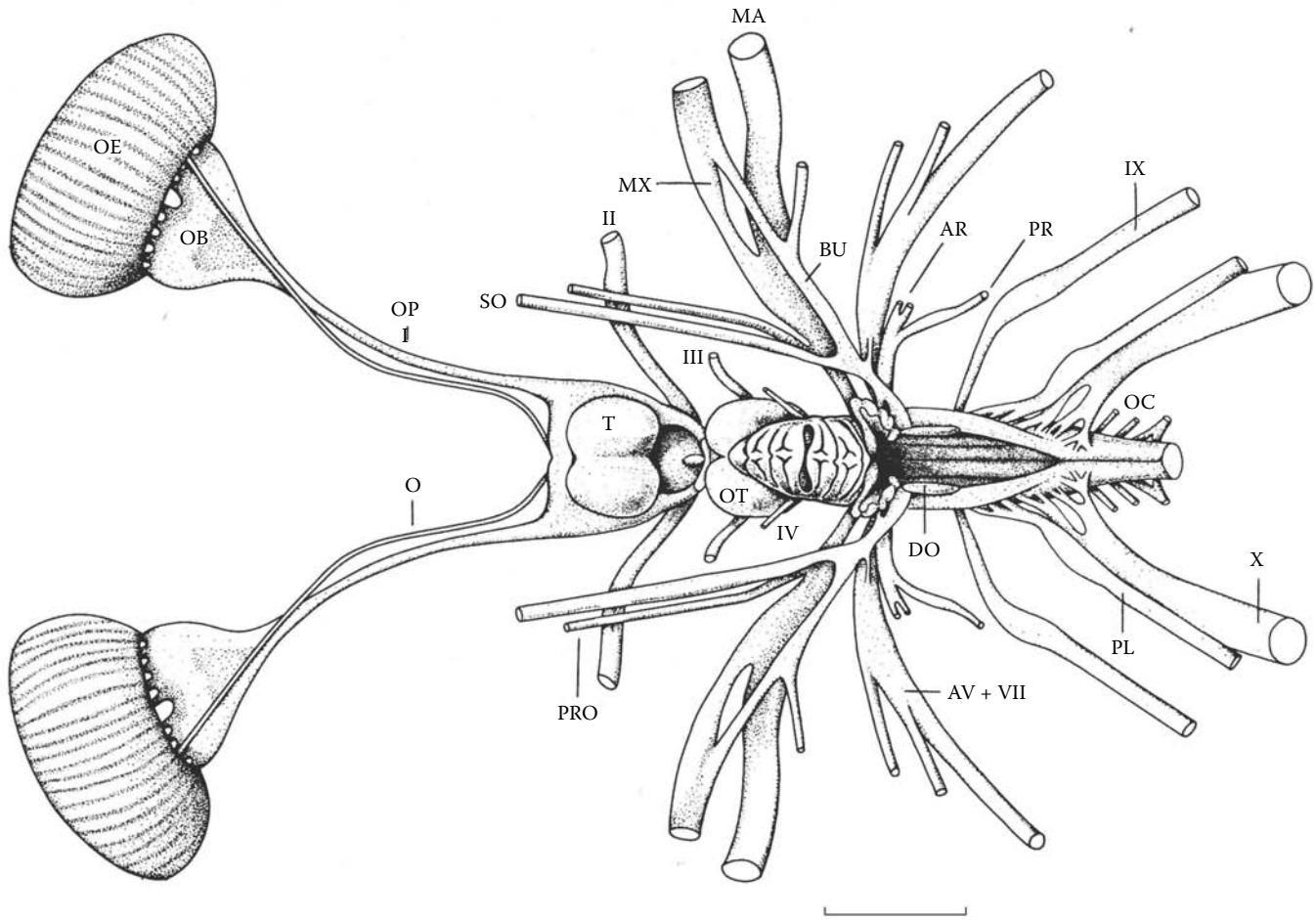

FIGURE 12.28
Dorsal view of the brain and olfactory system of the white shark, *Carcharodon carcharias*. The large partially divided olfactory bulb (OB) is closely applied to peripheral olfactory sac or epithelium (OE). Receptor cells in the epithelium project axons into the olfactory bulb (as the olfactory 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). *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; SO, 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. Scale bar: 3 cm. (From Demski, L.S. and Northcutt, R.G., in *Great White Sharks: The Biology of Carcharodon carcharias*, Klimley A.P. and Ainley, D.G., Eds., Academic Press, San Diego, CA, 1996, pp. 121–130. With permission.)

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 (Dryer and Graziadei, 1994b; Ebbesson, 1972, 1980; Ebbesson and Heimer, 1970; Ebbesson and Northcutt, 1976; Northcutt, 1978; Smeets, 1983, 1998; Smeets et al., 1983). 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, *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 (Bleckmann et al., 1987; Cohen et al., 1973; Ebbesson and Schroeder, 1971; Graeber, 1978, 1980; Graeber et al., 1973, 1978; Luiten, 1981a,b; Platt et al., 1974; Schroeder and Ebbesson, 1974; Smeets and Northcutt, 1987). This current view indicates that the elasmobranch telencephalon is similar in general organization and function to that of other vertebrates (Demski and Northcutt, 1996; Northcutt, 1978, 1989).

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 (1914) 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 or regions for multisensory or sensorimotor integration.

It should be noted that in bony fishes the OBs project to the hypothalamus of the diencephalon (Bass, 1981; Finger, 1975; 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 or bloodborne factors associated with the dietary conditions.

12.6.2 Olfactory-Mediated Behaviors

12.6.2.1 Olfactory Control of Feeding

Critical early studies on captive animals demonstrated that many elasmobranchs rely on olfactory cues to locate food (Bateson 1890; Parker, 1909, 1914; Parker and Sheldon, 1913; Sheldon, 1909, 1911). Smooth dogfish, *Mustelus canis*, in large outdoor pens could locate food without visual cues, but animals with both nares blocked showed no interest in visible prey (Sheldon, 1911). Olfactory involvement in elasmobranch feeding includes several phases that can roughly be categorized as: (1) arousal, (2) directed approach (tracking) and attack, and (3) continued search, if the prey or bait is not located or is lost. These components vary depending on circumstance and species. Arousal is often indicated by a sudden change from normal swimming (cruising) behavior, such as sudden tight circling by, for example, bonnetheads, *Sphyrna tiburo* (Johnsen and Teeter, 1985); by a sharp turn; or by a sudden drop or spiral to the bottom, such as for smooth dogfish, *M. canis* (Parker, 1914), or blacktip reef sharks, *Carcharhinus melanopterus* (Tester, 1963a,b). Elasmobranchs were previously thought to accomplish this initial odor orientation by performing bilateral comparisons between the two nares, turning toward the highest concentration, termed *tropotaxis* (Hodgson and Mathewson, 1971; Johnsen and Teeter, 1985). This notion dates back to the early studies of Parker (1914). Control (unblocked) smooth dogfish, *M. canis*, located food using an equal frequency of turns to either side; blocking one naris resulted in a predominance of turning behavior to the unblocked side. In the aquatic environment, however, water flow is inevitable, be it from currents, the tail beats of prey, or the tail beats of the predator (self-generated noise). Flowing water causes turbulent mixing, resulting in an odor plume that is highly chaotic and intermittent, with

a high degree of variance in concentration (reviewed in Webster, 2007). A spatial concentration gradient can only be obtained by averaging over several minutes, far slower than the tracking speed of most animals, including elasmobranchs. Using animals fitted with headstages driven by computer-synchronized pumps, Gardiner and Atema (2010) demonstrated that, for instantaneous bilateral comparisons, *M. canis* responds to differences in the timing of arrival of odor at the two nares, not concentration. Even when the animals receive a weak odor pulse ahead of a strong one, the animals turn toward the naris that first receives an odor cue. This likely aids the animals in initially orienting to odor patches, steering them into the plume. Further work is needed to determine if concentration information is used over time, by comparing concentrations detected across several subsequent odor patch encounters (i.e., through klinotaxis) during odor tracking.

During tracking, many elasmobranchs approach odors from downstream, including white sharks, *Carcharodon carcharias* (Strong et al., 1992, 1996); gray reef sharks, *Carcharhinus amblyrhynchos*; blacktip reef sharks, *Carcharhinus melanopterus*; whitetip reef sharks, *Triaenodon obesus* (Hobson, 1963); and smooth dogfish, *Mustelus canis* (Gardiner and Atema, 2007). Tight circles and figure-eight patterns are common (Gardiner and Atema, 2007; Parker, 1914; Tester, 1963a,b), and animals cover a greater area in the presence of food odors than when these odors are absent (searching behavior, such as in nurse-hounds, *Scyliorhinus stellaris*, and smoothhounds, *Mustelus mustelus*) (Kleerekoper, 1978, 1982). Hodgson and Mathewson suggested two different tracking tactics based on their work with lemon sharks, *Negaprion brevirostris*, and nurse sharks, *Ginglymostoma cirratum*, in large outdoor pens (Hodgson and Mathewson, 1971; Mathewson and Hodgson, 1972). When presented with an attractive odor stimulus, such as glutamic acid and trimethylamine oxide (TMAO), lemon sharks swam upstream into the strongest current, regardless of where the odor source was actually located. In contrast, nurse sharks began moving up the odor corridor and were always able to localize the source. The authors concluded that in lemon sharks the reaction to an odor stimulus is dominated by a rheotactic (orientation to the mean current) bias or release mechanism, a behavior referred to as *odor-stimulated rheotaxis*, whereas in nurse sharks a chemical stimulus triggers true concentration gradient searching (sequential comparisons of concentrations at different points), termed *klinotaxis* (Hodgson and Mathewson, 1971; Mathewson and Hodgson, 1972). Kleerekoper et al. (1975), however, found that nurse sharks in stagnant water could not locate the source of odor release. Gardiner and Atema (2007) demonstrated that the smooth dogfish, *M. canis*, requires information from the lateral line system to locate the source of turbulent food odors (squid rinse). This species can navigate upstream through an odor field to the general area of a turbulent odor source using either vision (visual flow field) or the lateral line system (hydrodynamic flow field), performing odor-stimulated rheotaxis, but the lateral line is necessary to precisely locate the source of coincident odor and flow (i.e., the source). This suggests that these animals are tracking the fine-scale structure of the plume—a turbulent wake flavored with food or prey odor, shed by a moving prey item in still water, or a still piece of food in flowing water (termed *eddy chemotaxis*) (Atema, 1996). In the event that the target is not located, continued search can involve repeated bouts of swimming back downstream and then retracing the plume (e.g., smooth dogfish, *M. canis*) (Gardiner and Atema, 2007) or continuous circling, sometimes for hours (e.g., white sharks, *C. carcharias*) (Strong et al., 1996, 1992).

Most studies of feeding behavior have used live prey (Sheldon, 1911), pieces of bait (Hobson, 1963; Parker, 1914), or food rinses or extracts (Gardiner and Atema, 2007, 2010; Johnsen and Teeter, 1985; Kleerekoper et al., 1975; Tester, 1963a). Tester (1963b) 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. 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" (Tester, 1963b) and could accurately pinpoint a source of water flowing from tanks of stressed fish (Hobson, 1963), suggesting that sharks can use odors to discriminate between stressed and unstressed prey fish. Hodgson and Mathewson (Hodgson and Mathewson, 1971; Mathewson and Hodgson, 1972) successfully elicited feeding behavior from nurse sharks, *Ginglymostoma cirratum*, and lemon sharks, *Negaprion brevirostris*, using a mixture of chemical attractants (glutamic acid and TMAO) at concentrations of 0.1 *M* and released into the water in the pen. Thus, the actual concentration of chemicals at the olfactory epithelium is unknown in behavioral experiments. Meanwhile, electrophysiological studies (see Sections 12.6.1.1 and 12.6.1.2) have examined brain and olfactory receptor responses to precisely measured concentrations of single amino acids. Only one study has matched behavior and electrophysiology. Hodgson et al. (1967) performed experiments on free-swimming lemon sharks in which EEG responses were correlated with changes in swimming behavior when

the animals were exposed to 10^{-4} *M* glycine, betaine, trimethylamine, and TMAO. The stimuli were released into flowing water in the test tank, however, so the exact concentration at the olfactory receptors remains unknown. There is, therefore, a disconnect between electrophysiological and behavioral studies, an area that certainly warrants further investigation.

12.6.2.2 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. Although 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, *Sphyrna tiburo* (Myrberg and Gruber, 1974); nurse shark, *Ginglymostoma cirratum* (Carrier et al., 1994; Klimley, 1980); spotted eagle ray, *Aetobatus 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.

12.6.2.3 Olfaction and Predator Avoidance

Lemon sharks, *Negaprion brevirostris*, and American crocodiles, *Crocodylus acutus*, overlap in their distributions, and where such is the case the crocodiles may 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, and 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.

12.6.3 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 (Sheldon, 1909; see also 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 (Figure 12.29A). Older descriptive anatomical studies of several sharks indicate that the taste organs are supplied by branches of the facial (VII), glossopharyngeal (IX), and vagus (X) nerves (Aronson, 1963; Daniel, 1928; Herrick, 1924; Norris and Hughes, 1920), as is the case with other vertebrates (reviewed in Northcutt, 2004).

Whitear and Moate (1994a) carried out a detailed ultrastructural analysis of the taste buds of the small-spotted catshark, *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.

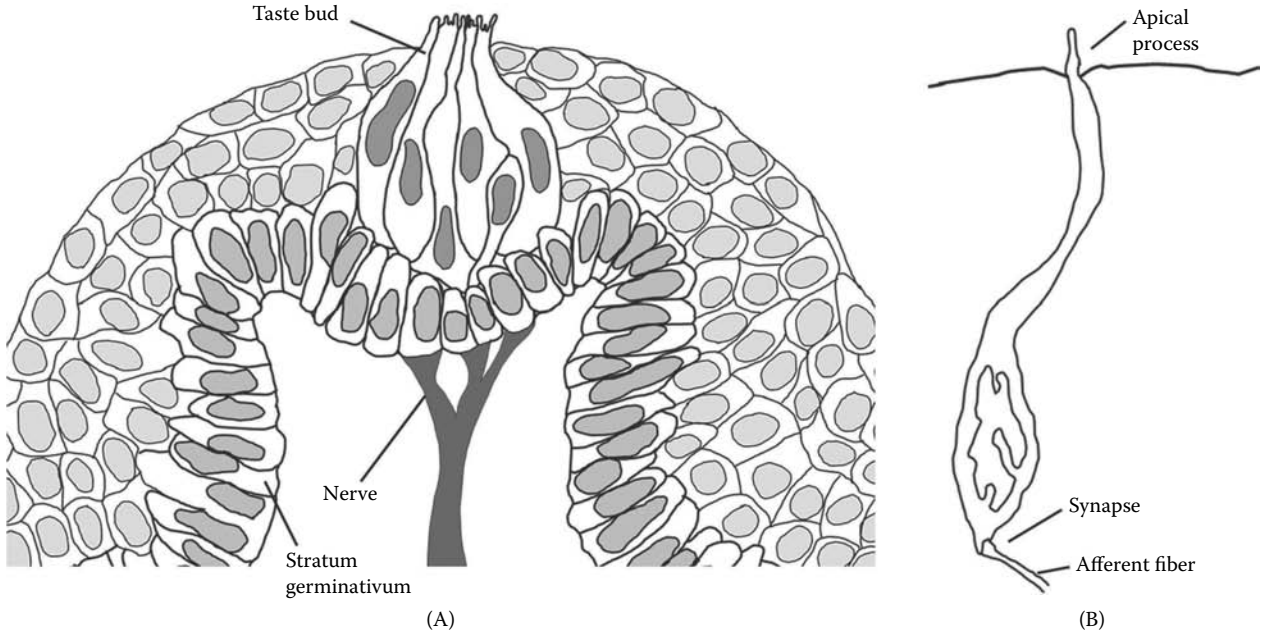

FIGURE 12.29
Line drawings of (A) an elasmobranch taste bud (Cook and Neal, 1921; Whitear and Moate, 1994a) and (B) solitary chemosensory cell (Whitear and Moate, 1994b). (From Gardiner, J.M., *Multisensory Integration in Shark Feeding Behavior*, University of South Florida, Tampa, 2011. With permission.)

12.6.4 Solitary Chemosensory Cells

Solitary chemosensory cells (SCCs) are found in a number of lower vertebrate taxa. These spindle-shaped, epidermal sensory cells are found protruding between the squamous cells of the superficial layer of the epidermis, with a single apical process that bears one or a few microvilli (fish, amphibians) or many microvilli (oligovillous cells in lampreys), and are innervated by spinal or cranial (VII, facial) nerves (reviewed in Kotrschal, 1995) (Figure 12.29B). Their structure resembles that of taste buds, suggesting a chemosensory function, verified through electrophysiological experiments on teleost fish (Peters et al., 1987; Silver and Finger, 1984) and lampreys (Baatrup and Doving, 1985) which demonstrated that they are sensitive to skin washes and bile from other fish, but not amino acids. It has been hypothesized that in rocklings SCCs allow for bulk water sampling, mainly for detecting the presence of predators upstream (Kotrschal et al., 1996), while in sea robins they may be used to find food (Silver and Finger, 1984). SCCs have been examined in only a handful of species; thus, their biological function remains poorly understood, particularly in elasmobranchs, and to date no term for the sense that they mediate has been developed. In elasmobranchs, SCCs have only been confirmed in one species, the thornback ray, *Raja clavata* (Whitear and Moate, 1994b), where they are found in the oral cavity. It has recently been suggested, however, that they may be present on the dorsolateral surface of the skin, near the pit organs, in Port Jackson sharks, *Heterodontus portusjacksoni*, and in whitetip reef sharks, *Triaenodon obesus* (Peach, 2005). Further work is needed to determine the distribution and function of SCCs in elasmobranchs.

12.6.5 Common Chemical Sense

The common chemical sense, the ability to detect irritating substances, is considered separate from olfaction and gustation. Free nerve endings, which in fish occur in the oral and nasal cavities, as well as all over the skin, serve as receptors (Tester, 1963a). 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, including spinal nerves and cranial nerves V (trigeminal), VII (facial), IX (glossopharyngeal), and vagus (X). The sense conveyed by these chemosensitive components has been renamed *chemesthesis* to reflect this relationship (Bryant and Silver, 2000).

Studies in *Mustelus canis* demonstrated that sharks respond behaviorally to injections of certain chemicals (irritants) into the nostrils, 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 (1909) considered

that this chemosensitivity was mediated by free nerve endings; however, this has not been verified with histological studies. Presumably, the function of this system in elasmobranchs, as in other vertebrates, is protection from damaging chemicals. The adverse reactions certain sharks demonstrate to natural toxins, such as that produced by the skin of the Moses sole, *Pardachirus marmoratus* (Clark, 1974), may be mediated by this category of unmyelinated somatosensory ending.

12.7 Multimodal Integration

Our understanding of the sensory biology of elasmobranchs and most other vertebrates is largely due to isolated studies of the individual senses rather than multiple senses working together. This has led to important advances in our comprehension of one sensory system or another but not their complementary and alternating roles. Integration of 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.

12.7.1 Multimodal Integration in the Brain

Early studies (reviewed in Aronson, 1963) concluded there was little multisensory integration in the elasmobranch brain, and those conclusions influenced the naming of the brain regions; for example, the tectum of the mesencephalon was called the *optic tectum*, as it was presumed to be dominated by vision, and the telencephalon was called the *olfactory lobe*, as it was presumed to be dominated by olfactory inputs (Ariëns Kappers et al., 1936). However, electrophysiology has revealed areas of the telencephalon that show responses to multiple sensory stimuli. The pallium, or roof, of the telencephalon can be divided into lateral, medial, and dorsal portions. The lateral pallium has been found to be dominated by olfaction (Hoffman and Northcutt, 2008; Smeets, 1983), while the dorsal (or general) pallium and medial pallium appear to be multisensory. The dorsal pallium is the site of recordings in response to visual (optic nerve) and trigeminal nerve stimuli, which may represent cutaneous mechanoreceptors or electroreceptors, in the nurse shark, *Ginglymostoma cirratum* (Cohen et al., 1973; Ebbesson, 1980). The medial (or hippocampal) pallium has been found to respond to visual, electrosensory, and lateral line stimuli in the little skate, *Leucoraja erinacea* (Bodznick and Northcutt, 1984), visual and cutaneous (somatosensory or electrosensory) stimuli in other batoids (Veselkin and Kovacevic, 1973), and visual, olfactory, and electrosensory stimuli in spiny dogfish, *Squalus acanthias* (Bodznick, 1991; Nikaronov, 1983; Nikaronov and Lukyanov, 1980). Units responsive to visual, auditory, and electrosensory stimuli have been recorded from the brains of several galeomorphs, possibly from the pars centralis or medial pallium (Bullock and Corwin, 1979). Additionally, retrograde dye labeling in thornback rays, *Platyrhinoidis triseriata*, has revealed olfactory areas in the dorsomedial pallium (Hoffman and Northcutt, 2008). Interestingly, the medial portion of the telencephalon is larger in batoids and squalomorphs, while the dorsal pallium is better developed in galeomorphs and myliobatoids (Northcutt, 1978).

The tectum of the mesencephalon is heavily visual, although the highest center of visual processing is the telencephalon (see above), and nurse sharks can still perform some visual discrimination tasks after the tectum has been removed (Graeber et al., 1973). Most of the retinal efferents project to the tectum of the mesencephalon, particularly the superficial tectal laminae, where they form a topographic map (reviewed in Bodznick, 1991; Hueter, 1991). The deeper layers, however, are multimodal. The electrosensory and mechanosensory medullar nuclei project to a nucleus in the roof of the midbrain, called the *lateral mesencephalic nucleus* (Boord and Northcutt, 1982, 1988). Recordings from the tectum have been made in response to electrosensory, common cutaneous, and auditory stimuli in several species of rays and sharks (Platt et al., 1974), and single multimodal (visual, electrosensory, tactile/lateral line) neurons have been found in the tectum of the little skate, *Leucoraja erinacea* (Bodznick, 1991). Hoffman and Northcutt's (2008) retrograde dye labeling study on thornback rays, *Platyrhinoidis triseriata*, suggested that olfactory, electrosensory, and mechanosensory (lateral line) information converges in the lateral mesencephalic nucleus. Although this has yet to be confirmed with electrophysiology, all of these senses are important for locating prey buried in the substrate.

12.7.2 Multimodal Integration in Behavior

A biological target (prey item, predator, or potential mate) might simultaneously emit several signals: odor; a hydrodynamic disturbance (sound), such as from gill movements or tail beats (reviewed in Bleckmann, 1994); or a weak electrical field (Kalmijn, 1972) (summarized in Figure 12.30). Based on the threshold of the elasmobranch electrosensory system (reviewed above under Section 12.5) for electric fields produced by aquatic animals (Kalmijn, 1972), the limit of detection for most bioelectric stimuli translates to a distance of less than a meter from the source. The detection limits of the visual system of most aquatic animals are not well known but

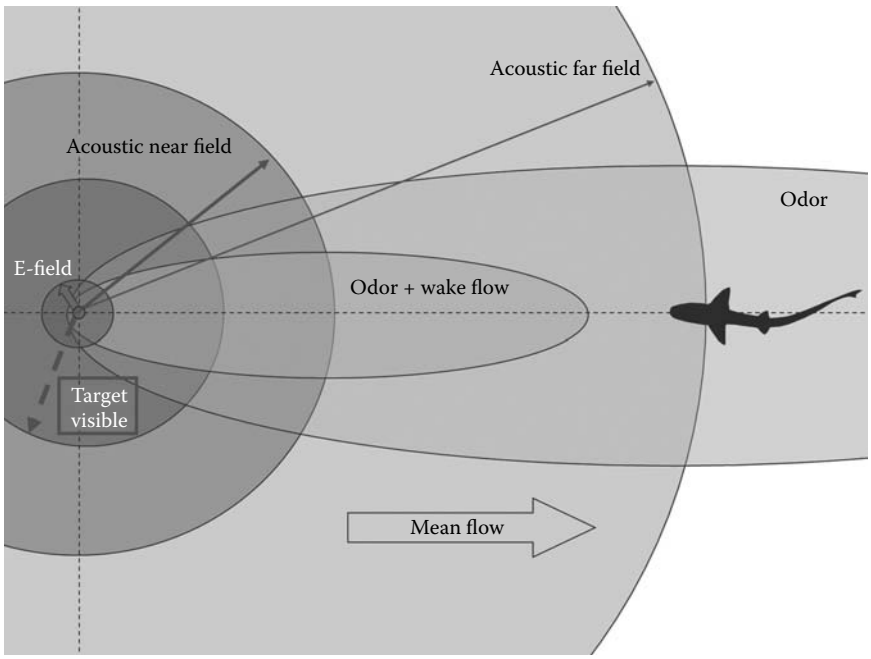

FIGURE 12.30
Summary of the hypothetical stimulus fields emitted by a biological target (small dark-gray circle) in an unbounded, laminar flow environment. In the natural world, any number of environmental, physical, or biological variables could attenuate any of these sensory inputs to the elasmobranch. In very clear, well-lit waters, the visual stimulus could range much farther than depicted, and the acoustic regime is frequency dependent, such that low-frequency sounds will extend over a greater range, possibly even as far as olfaction, and the near-/far-field boundary will be found at a greater distance from the source. (From Gardiner, J.M., *Multisensory Integration in Shark Feeding Behavior*, University of South Florida, Tampa, 2011. With permission.)

depend on the amount of available light, the amount of scatter (Duntley, 1963; Mazur and Beauchamp, 2003), and the background contrast in intensity, polarization, and pattern of reflected light (Johnsen, 2005; Johnsen and Sosik, 2004). In clear, well-lit waters the visual detection range rarely exceeds tens of meters. Sound can be divided into the near acoustic field, primarily particle motion detected in teleosts by the otoliths as particle acceleration (Kalmijn, 1988b; Schellart and Popper, 1992), and the far field, primarily pressure transmitted in teleosts by the swimbladder to the inner ear (Popper and Fay, 1999). For a dipole sound source, the near field dominates at a distance from the source of less than one sixth of the wavelength of the sound ($\lambda/2\pi$); for a sound of 100 Hz, a frequency in the hearing range of many fishes, this translates to approximately 2.5 m (Kalmijn, 1988b). The maximum range of detection of the lateral line has been shown to be one to two body lengths from the source (Coombs et al., 2001).

Odor, on the other hand, may be carried a great distance from the source by the mean flow. In flowing water, odors are dispersed by two mechanisms: advection and turbulent mixing (reviewed in Webster, 2007). Advection refers to the transportation of a filament or patch of odor by the mean or bulk flow. Turbulent flow generates swirling packets, referred to as *eddies*, that break up into a series of successively smaller eddies through a process known as the *Kolmogorov cascade* (reviewed in Weissburg, 2000). The hydrodynamic motion of these eddies can be detected by the lateral line system. Intermolecular viscous forces dissipate the energy until they reach the smallest eddy size that still contains turbulent energy, known as the *Kolmogorov length scale*, on the order of millimeters. Beyond this scale, in the odor far field, only very patchy odor information is available, carried by the bulk flow (Figure 12.30). Thus, locating a biological target involves: (1) initially detecting and orienting to a patchy odor field, (2) tracking the odor plume, and (3) localizing and orienting to the target. In the case of food, this progression culminates with striking at and capturing the prey.

The sequence in 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. How animals use sensory information depends not only on what sensory stimuli are available, as determined by the animal's proximity to the prey, the physics of the stimulus fields (Figure 12.30), and the thresholds of detection for each species, but also on which stimulus or stimuli the animal chooses to focus upon when information from multiple senses is available simultaneously.

For a given task, the senses may have complementary or alternating roles; for example, smooth dogfish, *Mustelus canis*, requires simultaneous input from the olfactory system and the lateral line to precisely locate the source of a turbulent odor plume, through a process known as *eddy chemotaxis* (Gardiner and Atema, 2007). On the other hand, navigating large-scale flow, such as a current, can be accomplished using either cues from the lateral line system (hydrodynamic flow field) or vision (visual flow field) (Gardiner and Atema, 2007). As an animal approaches a biological target, the sensory environment becomes increasingly complex and the animal might either integrate new information encountered in an additive fashion (e.g., using olfaction and the lateral line for eddy chemotaxis, above) or demonstrate *sensory switching*. Sharks that have been tracking odor plumes switch their focus from an olfactory signal to an electrical signal once it is within the range of detection, with a sudden sharp turn toward, and bite on, the source of the electric field (Jordan et al., 2009b; Kajiura, 2003; Kajiura and Fitzgerald, 2009; Kajiura and Holland, 2002; Kalmijn, 1982). Few studies, however, have examined more than one or two senses at a time.

Recently, Gardiner (2011) conducted a study on three species of sharks, examining their ability to capture live, tethered prey items after selective blocks of the visual, olfactory, lateral line, and electrosensory systems. Nurse sharks, *Ginglymostoma cirratum*, rely heavily on olfaction to feed. This species is capable of orienting to the prey using non-olfactory cues but will not ingest the food unless an attractive odor is present. This suggests that this species relies entirely on olfactory cues to confirm the identity of a target as food. Bonnetheads, *Sphyrna tiburo*, generally rely on an attractive odor to initiate tracking behaviors but will strike at prey based on visual cues. The electrosensory system, however, is essential for a successful strike. Animals with the electrosensory system blocked are capable of precisely lining up a strike, based on visual cues, but the jaws do not begin to move without the appropriate electrical cues, and thus the prey is not ingested. Blinded animals display an inability to line up a strike, suggesting that orientation to the prey is visually mediated. Blacktip sharks, *Carcharhinus limbatus*, also rely on olfactory cues to perform tracking behaviors. They demonstrate sensory switching, focusing on visual cues to line up a rapid, ram strike. If the olfactory system is blocked, they will strike visually if their swimming motions bring them within visual range of the prey. They can successfully orient to prey using non-visual cues, but the process is much slower and typically involves a number of misses before a successful capture. If olfaction and vision are simultaneously blocked, feeding behaviors cease altogether. This suggests that appropriate olfactory or visual cues are essential in these species for an item to be identified as food, whereas non-visual cues are used to direct the strikes and time the jaw movements. This is in contrast to short-tailed stingrays, *Dasyatis brevicaudata*, which will strike at weak water jets that mimic the hydrodynamic signature of buried bivalve prey in the absence of odor cues (Montgomery and Skipworth, 1997).

12.8 Summary and Conclusions

Are sharks and their relatives sensory marvels or not? There is no doubt that the combination of well-developed visual, acoustical, mechanical, electrical, and chemical sensing systems in elasmobranchs 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 use 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.

Our understanding of these sensory processes progressed rapidly in the latter half of the 1900s. A lull in this research toward the end of the century has been replaced with a renewed interest in the field, which has been gaining increasing momentum over the last decade. Exciting new technologies have opened the door for fine-scale investigations into the behavior and ecology of these animals, both in captivity and in the wild (see Chapter 9). How sharks, skates, and rays integrate complex multimodal environmental information through their various senses and which cues they choose to focus on to form an adaptive response are among the most interesting questions left in elasmobranch sensory biology. Investigations into multimodal integration have begun, but this remains a ripe area for further research.

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