3 Sensory Biology of Sea Turtles

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3.1 INTRODUCTION

The study of sensory biology in sea turtles is still in its infancy. Even the basic morphology of the eye, ear, and nose of sea turtles has been described in detail in only one or two species. The same may be said for electrophysiological and behavioral studies of sea turtles' sensory systems. The ontogenetic and interspecific difference in the sensory biology of sea turtles has been little studied and the sensory biology of the leatherback (*Dermochelys coriacea*), a species whose ecology is greatly different from the cheloniids, is virtually unknown. The present chapter will focus on the current state of knowledge of the sensory biology of vision, hearing, and olfaction in sea turtles.

## 3.2 VISION

3.2.1 Morphology and Anatomy of the Eye

3.2.1.1 Main Structures of the Eye

The anatomy of the sea turtle eye appears to be typical of that found in all vertebrates (Granda, 1979; Walls, 1942). The eyeball is filled with two ocular fluids, aqueous and vitreous humors, and is organized into three layers: (1) the outermost layer, consisting of the sclera and cornea; (2) the middle layer, which includes the choroid, ciliary body, and iris; and (3) the inner layer, or the retina. The sclera is inelastic and is responsible for the eyeball's static shape, whereas the aqueous humor keeps this fibrous layer distended. The anterior portion of the sclera, the cornea, is transparent and responsible for much of the refraction of light in air, yet is virtually transparent in water. The choroid of the middle layer is highly pigmented and vascularized; the pigmentation deflects stray light from entering the eye and prevents internal reflections. The inner layer of the eyeball, the retina, contains the visual cells (rod and cone photoreceptor cells) and ganglion cells, and is continuous with the optic nerve (Walls, 1942; Copenhaver, 1964; Granda, 1979; Ali and Klyne, 1985; Bartol, 1999).

The lens of the green sea turtle (*Chelonia mydas*) is nearly spherical and rigid (Ehrenfeld and Koch, 1967; Granda, 1979; Walls, 1942), and appears to be quite different from that of freshwater turtles, which have developed an advanced means of accommodation through the manipulation of an extremely pliable lens. For sea turtles, however, ciliary processes do not reach the lens and the *ringwulst* is weakly developed, and thus active accommodation does not appear to be possible (Ehrenfeld and Koch, 1967). However, this type of spherical lens is ideal for underwater vision. In the absence of corneal refraction while underwater, the refractive index of the cornea is nearly identical to that of seawater, and the lens is the only structure responsible for the refraction of incoming light. The spherical lens has a high refractive index, which compensates for the lack of corneal refraction (Sivak, 1985; Fernald, 1990).

3.2.1.2 Cells of the Retina

The vertical organization of the retina has been examined in the juvenile loggerhead sea turtle (*Caretta caretta;* Bartol and Musick, 2001) (Figure 3.1). The layers of the
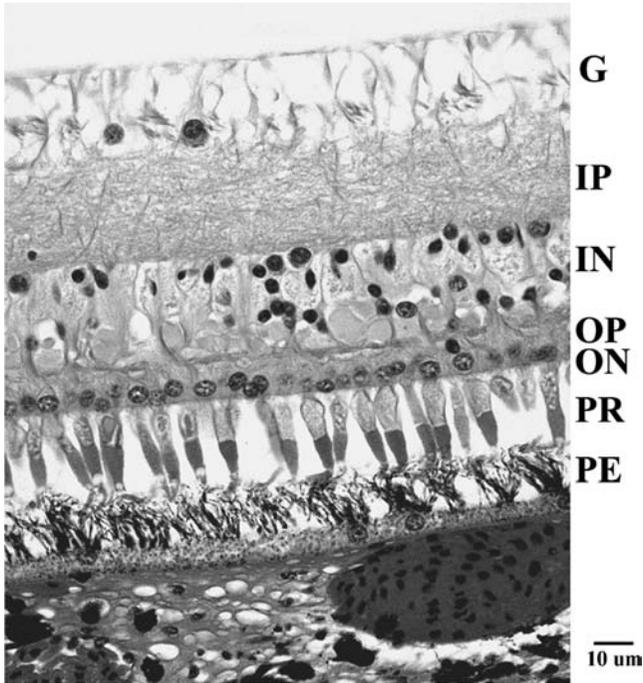
FIGURE 3.1 Light micrograph of the retina of a juvenile loggerhead sea turtle (*C. caretta*). Abbreviations: G = ganglion layer; IP = inner plexiform layer; IN = inner nuclear layer; OP = outer plexiform layer; ON = outer nuclear layer; PR = photoreceptor layer; PE = pigment epithelium. Scale bar equals 10 µm. (From Bartol, S.M. and Musick, J.A., Morphology and topographical organization of the retina of juvenile loggerhead sea turtles (*Caretta caretta*), *Copeia*, 3, 718, 2001. With permission.)

retina are consistent with the generalized vertebrate plan and consist of seven layers (from the center of the eye out to the edge): ganglion layer, inner plexiform layer, inner nuclear layer, outer plexiform layer, outer nuclear layer, photoreceptor layer, and the pigment epithelium. Bartol and Musick (2001) focused mainly on the photoreceptor layer, which contains the stimulus receptors, and found that it is duplex in nature, consisting of both rod and cone photoreceptors. These two types of photoreceptor cells are similar in diameter and height, yet the rod does not have an oil droplet above the ellipsoid element, and the outer segment of the rod photoreceptor is longer and more cylindrical than that of the cone photoreceptor. Homogeneity of photoreceptor cell types is unusual; typically rods are much longer and narrower than cones in vertebrate retinas. However, this same homogeneity of cells can be found in the retina of the common snapping turtle (*Chelydra serpentina*; Walls, 1942).

In the loggerhead, Bartol and Musick (2001) found that the pigment epithelium, the outermost layer of the retina, is firmly connected to the choroid, and contains heavy pigment-laden processes that intertwine with the outer segments

of the photoreceptor cells. The outer nuclear layer houses the photoreceptor cell nuclei and is generally only one cell wide. The outer plexiform layer is homogenous, but in Bartol and Musick's preparations, the synaptic connections between the nuclear layers could not be identified. The inner nuclear layer is composed of the nuclei of bipolar, amacrine, and horizontal cells, although these cells were not differentiated in this study. The inner plexiform layer is similar to the outer plexiform layer and is composed of synaptic connections between the inner nuclear layer and ganglion layer. Finally, the innermost layer, the ganglion cell layer, is relatively thick (23% of the overall width of the retina) and is composed solely of the ganglion cells and their axons (Bartol and Musick, 2001).

3.2.2 Sensitivity to Color

3.2.2.1 Photopigments and Oil Droplets

The spectral sensitivity of sea turtles has been investigated using morphological, electrophysiological, and behavioral methods. Liebman and Granda (1971) examined the visual pigments associated with photoreceptor cells of the red-eared freshwater turtle (*Pseudemys scripta elegans*) and green turtle (*C. mydas*). Microspectrophotometric measurements were performed on preparations of these cells to determine the absorption spectra of these light-absorbing visual pigments. Both species have a duplex retina containing both rod and cone photoreceptor cells. For the green turtle, the rod photosensitive pigments absorbed light maximally at 500–505 nm. This retinal pigment was indistinguishable from the rhodopsin identified in frog preparations. Three photopigments were found associated with cone photoreceptors for *C. mydas*. The most common pigment, identified as iodopsin, absorbed light maximally at 562 nm. The two other cone visual pigments identified absorbed light maximally at 440 and 502 nm (Figure 3.2). Note that one cone photoreceptor visual pigment was identical to that of the rod visual pigment. The authors hypothesized that the cone that absorbs at 502 nm is actually the accessory cone of a double cone pair. The double cones of *C. mydas* have been found to have a principal receptor (full-sized cone with oil droplet) and a secondary receptor (the non-oil droplet member) (Walls, 1942; Liebman and Granda, 1971). Liebman and Granda (1971) suggest that the accessory cone actually contains the rhodopsin pigment of the rod photoreceptor. The freshwater turtle (*P. scripta elegans*) examined in this study contained visual pigments that absorb longer wavelengths than those found in *C. mydas*; rods absorbed maximally at 518 nm and cones contained photopigments that absorbed 450, 518, and 620 nm maximally (Figure 3.2). The authors concluded that the light-absorbing visual pigments in both the freshwater and marine turtle were suitable for the environments in which the animals reside (seawater transmits shorter wavelengths than freshwater) (Liebman and Granda, 1971; Granda, 1979).

3.2.2.2 Electrophysiology

The spectral sensitivity of *C. mydas* has also been investigated through the collection of electroretinograms (ERGs) from dark-adapted eyes (Granda and O'Shea, 1972).
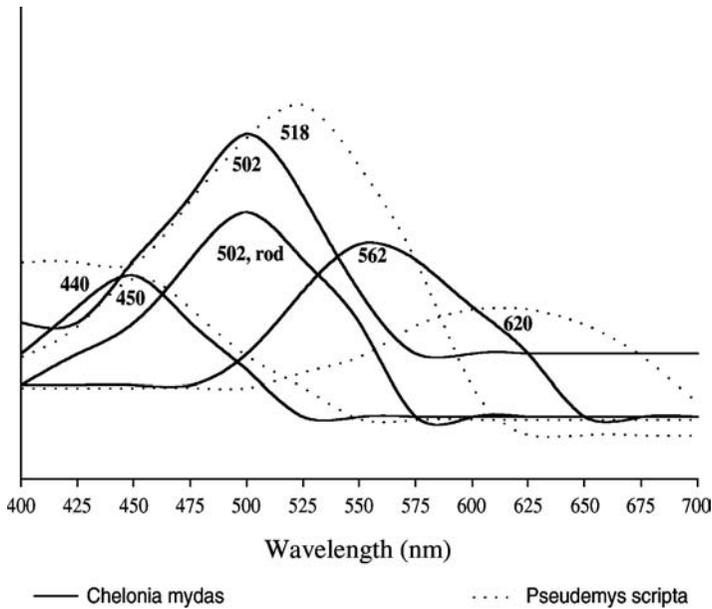
FIGURE 3.2 Visual pigment measurements, using microspectrophotometric techniques, of rod and cone photoreceptors for both *C. mydas* (solid lines) and *P. scripta* (dotted lines). (Data redrawn from Liebman, P.A. and Granda, A.M., Microspectrophotometric measurements of visual pigments in two species of turtle, *Vision Res.*, 11, 105, 1971.)

An ERG is a recording of rapid action potentials between the cornea and retina when the eye is stimulated, and is a robust measurement of early retinal stages in the visual pathway (preganglion cell responses) (Davson, 1972; Riggs and Wooten, 1972; Ali and Klyne, 1985). Granda and O'Shea (1972) found the spectral sensitivity for *C. mydas* to peak at 520 nm, with secondary peaks at 450–460 and 600 nm. The spectral sensitivities recorded using these methods were longer (except for the shortest wavelength) than those found through light microspectrophotometric measurements (440, 502, and 562 nm; Leibman and Granda, 1971), and the discrepancy of wavelength measurements is attributed to the interaction of the visual pigments and the cone oil droplets (Granda and O'Shea, 1972). For cone photoreceptors, light must first pass through oil droplets before it reaches and excites the photopigments. In *C. mydas*, the cone oil droplets are saturated oil globules that can be clear, yellow, or orange. The orange and yellow droplets are optically dense and can act as filters, shifting the wavelength that excites the photopigments (Granda and O'Shea, 1972; Granda and Dvorak, 1977; Peterson, 1992). Specific colored oil droplets appear to be paired with a specific photopigment: the clear oil droplet appears to be associated with the 440 nm photopigment (no shift in absorbed spectral sensitivity), the yellow oil droplet with the 502 nm photopigment (shifting the absorbed spectral sensitivity to 520 nm), and the orange oil droplet with the 562 nm photopigment (shifting the absorbed spectral sensitivity to 600 nm) (Granda and O'Shea, 1972; Peterson, 1992).

3.2.2.3 Behavior

Behavior studies on sea turtles performed in the aqueous setting are limited because of the difficulties associated with training turtles to respond to specific stimuli. Fehring (1972), however, used the sea turtle's ability to detect colors to develop a hue discrimination behavioral study. Broadband hues were used (deep blue, magenta, and red-orange) to determine whether loggerhead sea turtles (*C. caretta*) could be trained to use hue in search for food. The research study was not designed to test for an inherent hue preference, but rather was designed to test whether the turtles could be trained to pick one hue over another. Each animal was given a choice of two hues and, through training, was taught that only one of these hues would provide a food reward. Fehring found that these animals were easily trained, with relatively few errors, and thus concluded that sea turtles are able to use their ability to distinguish colors to find food (1972).

3.2.3 VISUAL ACUITY

3.2.3.1 Topographical Organization of the Retina

Retinal morphology and topography research can describe the potential resolving power of an eye under differing illumination conditions. Within the retina itself, two factors can affect the ability of an animal to resolve items under varying light conditions: convergence of photoreceptor cells onto ganglion cells, and the topographical organization of photoreceptor cells along the surface of the retina (Walls, 1942; Davson, 1972; Ali and Klyne, 1985). Within the photoreceptor layer, the sea turtle has two types of cells: rods and cones. For most vertebrates, and sea turtles are no exception, the general function of the rod photoreceptor is to maximize sensitivity of the eye to dim stimuli, whereas the general function of the cone photoreceptor is to resolve details of a visual object (Copenhaver, 1964; Davson, 1972; Stell, 1972). Convergence of photoreceptor cells upon ganglion cells, otherwise termed summation, can prove to be both beneficial and disadvantageous. When the stimulus is weak (under dim light conditions), more than one rod photoreceptor cell converging onto a single ganglion cell will subsequently increase the strength of the neural signal, allowing the stimulus to be recognized. However, when summation occurs between cone photoreceptor cells and ganglion cells, the information relayed to the optic tectum is not characteristic of one cone, but rather a summation of many, resulting in reduced spatial resolution (Walls, 1942; Davson, 1972).

Topographical distribution of cone photoreceptor cells also can be an indication of the resolution ability of an animal. The retinas of many vertebrates have regions of higher cell densities, often called an area centralis or visual streak, which provides a region of increased visual acuity. The area centralis can vary in shape and location along the retina among species, and this variation is often indicative of behavior and life history attributes of the animal (Walls, 1942; Brown, 1969; Heuter, 1991).

Both summation and regional density of photoreceptor cells have been examined in both hatchling and juvenile sea turtles (Oliver et al., 2000; Bartol and Musick, 2001). Oliver et al. (2000) examined the ganglion cell densities of three species of sea turtle hatchlings: greens (*C. mydas*), loggerheads (*C. caretta*), and leatherbacks (*D. coriacea*). From plots of contour maps of ganglion cells, visual streaks were found for all three species; however, the streaks varied in shape. *Caretta mydas* was found to have a narrow and long streak, with a much higher cell concentration within the streak as opposed to areas outside the streak. Of the three turtles, *C. mydas* had the most characteristically horizontal streak. *Caretta caretta* had a wider streak dorsoventrally, with lower density counts than the green sea turtle. The retina of *D. coriacea* contained a distinct rounded area temporalis (a site of high cell counts) as well as a horizontal streak. Cell counts were the highest for the retina within this area temporalis. The authors attribute the differences among species to the environment that these hatchlings occupy. For example, as hatchlings, *C. mydas* may be found in clear water, feeding during the day as omnivores beneath the flat ocean surface, whereas *C. caretta* is typically found within sargassum mats, feeding in an environment with a less defined horizon. This behavior of feeding beneath a defined, flat surface helps explain why green sea turtles have a stronger horizontal streak than other sea turtles. *Dermochelys coriacea* hatchlings feed on gelatinous prey in the open ocean, an environment where an area temporalis would be more advantageous than a horizontal streak (Oliver et al., 2000).

Bartol and Musick (2001) examined the vertical organization of the main features of the retina as well as the spatial variation of the photoreceptor cells of large juvenile loggerhead sea turtles (*C. caretta*). On the basis of the properties of the neural layers, the vertical organization of the retina indicated a low degree of summation. In animals with a low summation level, the inner nuclear layer (composed of bipolar cells, horizontal cells, and amacrine cells) and the ganglion layer are thick relative to the rest of the retina, indicating a high number of neurons corresponding to each photoreceptor cell (Walls, 1942). In juvenile loggerheads, these two layers (out of the seven overall layers) comprised approximately 37% of the total retina (Bartol and Musick, 2001; see Figure 3.1). Bartol and Musick (2001) also examined the topography of the retina by plotting the counts of cone and rod photoreceptor cells and ganglion cells (Figure 3.3). Both cone photoreceptors and ganglion cells progressed from high to low density in a stair-step fashion from the back to the front of the eye. Rod photoreceptors, however, were more likely to maintain a constant density throughout the back half of the eye, rapidly decreasing in number near the cornea. Dorsal–ventral differences were also observed when the cell counts were plotted on a three-dimensional sphere. A horizontal streak of ganglion cells and cone photoreceptor cells in the dorsal hemisphere of the eye indicated a region of decreased summation and thus increased acuity. Rods, however, were found in lower numbers and ubiquitously throughout the two hemispheres, resulting in a constant sensitivity to low light situations. This regionalization of cells was hypothesized to aid the juvenile loggerhead in finding benthic slow-moving prey in their shallow water habitat (Bartol and Musick, 2001).
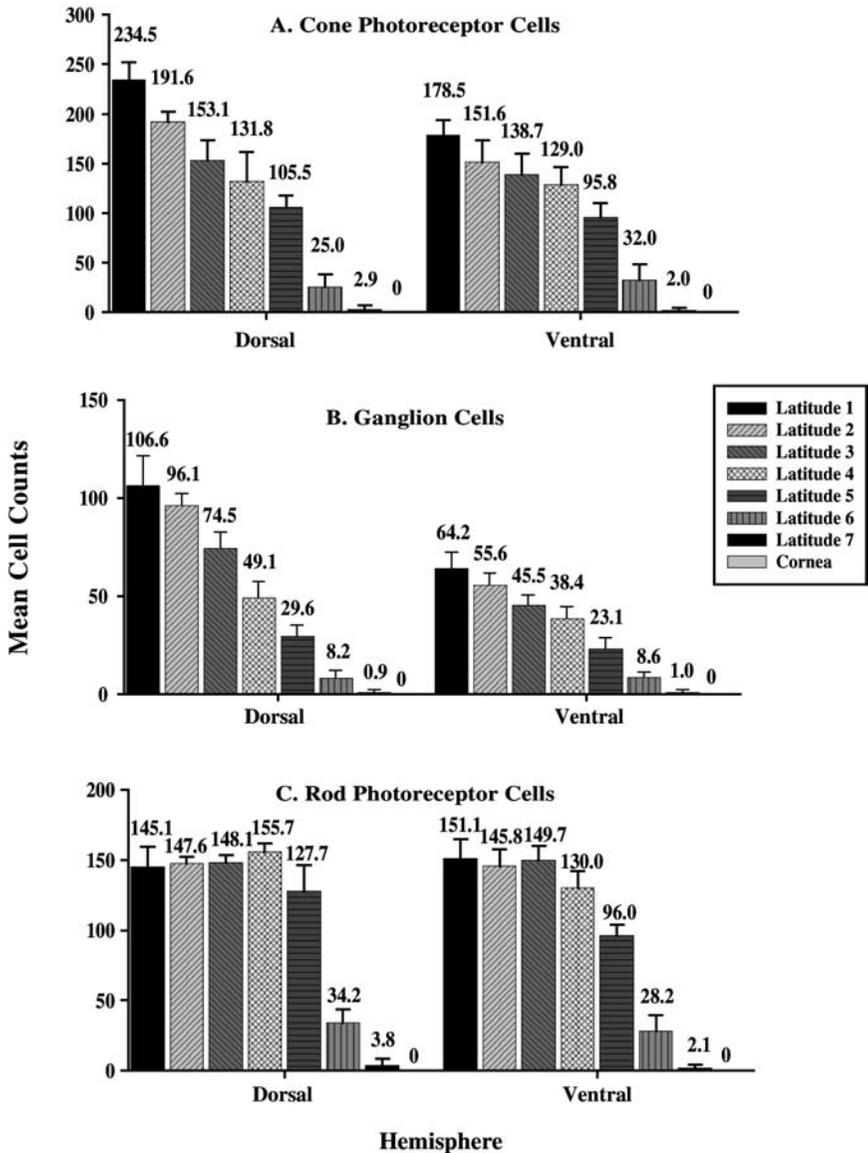
FIGURE 3.3 Mean cell counts, collected from the retinas of juvenile loggerhead sea turtles (*C. caretta*), for the eight latitudes of the eye in both the ventral and dorsal hemispheres. All error bars denote + 1 SD. (A) Cone photoreceptor cells. (B) Ganglion cells. (C) Rod photoreceptor cells. (From Bartol, S.M. and Musick, J.A., Morphology and topographical organization of the retina of juvenile loggerhead sea turtles (*Caretta caretta*), *Copeia*, 3, 718, 2001. With permission.)

3.2.3.2 Electrophysiology

Electrophysiological techniques have also been employed to investigate the visual acuity thresholds of sea turtles (Bartol et al., 2002). Electrical responses recorded from the visual system provide an objective measure of a variety of visual phenomena, including the dependence of a response on the character of the stimulus (Riggs and Wooten, 1972; Bullock et al., 1991). In the Bartol et al. (2002) study, the technique of visual evoked potentials (VEPs) was used. VEPs are compound field potentials of any neural tissue in the visual pathway and can be obtained from a subject animal by the use of surface electrodes placed on the head directly above the optic nerve and corresponding optic tectum. In this study, the researchers used a modified goggle filled with seawater over the stimulated eye. This apparatus allowed for the testing of underwater acuity. The stimuli were black and white striped patterns of decreasing size, yet always of equal brightness. One peak in the VEP recordings was found by the researchers to be present in all suprathreshold recordings, showing a dependence of peak amplitude on stimulus stripe size (Figure 3.4). From this peak, Bartol et al. (2002) were able to identify an acuity threshold level of 0.187 (visual angle = 5.34 min of arc) when data from all six turtles were pooled. This level of acuity would permit loggerheads to discern prey, such as horseshoe and blue crabs, as well as large predators, and is comparable to many species of marine fishes. Interestingly, these researchers were unable to collect any discernible VEP response when the turtles were tested with their eyes in air (i.e., without the water-filled goggle), suggesting that the sea turtle eye operates much differently in the two media (Bartol et al., 2002) (Figure 3.4).

3.2.3.3 Behavior

Psychophysical methods were used to investigate the visual acuity of juvenile loggerhead sea turtles (*C. caretta*) in the aquatic medium (Bartol, 1999). An operant conditioning method was developed to train juvenile loggerheads in a tank environment to identify a striped stimulus. The tank was set up with two response keys: one was located below a striped panel and the other below a gray panel. Turtles were trained by receiving a food reward only when the response key was chosen below the striped panel. Once training of these turtles was achieved, the stimulus was reduced in size until the turtle could no longer respond correctly. These turtles were found to be highly appropriate subject animals for an in-tank behavior study, and retained their training over time. From these trials, Bartol (1999) found the behavioral acuity threshold for juvenile loggerheads to be approximately 0.078 (visual angle of 12.89 min of arc), comparable to that found in the electrophysiology study (Bartol et al., 2001) and similar to the visual acuity of other benthic shallow-water marine species.

3.2.4 Visual Behavior on Land

The visual behavior of hatchling and nesting female sea turtles as they orient toward water while on land also has been studied. Vision has been identified in numerous articles as the primary sense used in sea-finding behavior of both hatchlings and
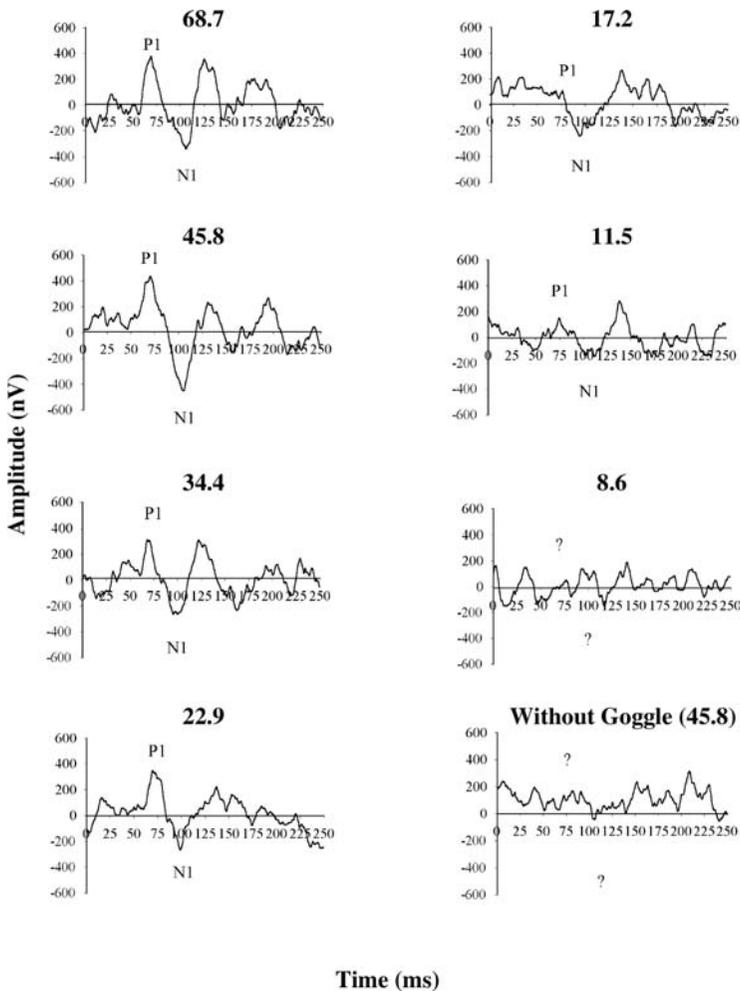
FIGURE 3.4 Visual evoked potential recordings for a session with one loggerhead sea turtle (*C. caretta*) using seven stimuli sizes ranging from 68.7 to 8.6 min of arc, visual angle and the recording for a trial without the goggle (in-air experiment) for 45.8 min of arc, visual angle. Notice that the amplitude difference between P1 and N1 decreases with a decrease in stripe size, until it can no longer be identified. Furthermore, for trials without the goggle, neither peak is identifiable, nor could the amplitude differences be measured. Each wave is an average of 500 responses; time zero is the start of stimulation. (Based on Bartol, S.M., Musick, J.A., and Ochs, A.L., Visual acuity thresholds of juvenile loggerhead sea turtles (*Caretta caretta*): an electrophysiological approach, *J. Comp. Physiol. A.*, 187, 953, 2002. With permission.)

adults. The type of visual stimuli used by sea turtles (whether shapes, colors, or brightness cues) has been the subject of many research articles (Ehrenfeld and Carr, 1967; Ehrenfeld, 1968; Mrosovsky and Shettleworth, 1968; Witherington and Bjorndal, 1991; Salmon and Wyneken, 1990; 1994). In some of the earliest studies,

blindfolds were placed on the turtles to determine whether they could orient without visual input. Bilaterally blindfolded turtles were unable to find the sea at all (Daniel and Smith, 1947; Carr and Ogren, 1960; van Rhijn, 1979), and unilaterally blind-folded sea turtles circled toward the uncovered eye, suggesting that the sea turtle finds the sea using tropotactic behavior (comparing intensities in both eyes and moving accordingly) (Ehrenfeld, 1968; Mrosovsky and Shettleworth, 1968; Mros-ovsky, 1972; Mrosovsky et al., 1979). These hatchling sea turtles are attracted to, and move toward, the brightest direction.

Shape identification, or the ability of a sea turtle to visualize objects on the beach, has also been investigated in the context of sea-finding behavior. The reaction by hatchlings to a horizon obstructed by objects found on or surrounding the beach has been documented in many studies (Parker, 1922; Limpus, 1971; Salmon et al., 1992). Salmon and Wyneken (1994) found that sea-finding for sea turtles depends on three rules when orienting toward the sea: (1) sea turtles move toward brighter regions, (2) sea turtles move away from high beach silhouettes (such as foliage or sand dunes), and (3) when these two cues are inconsistent, sea turtles move in relation to elevation (beach silhouettes), not brightness. Ehrenfeld and Carr (1967) tested the extent to which green sea turtles (*C. mydas*) visualize objects on the beach when making decisions about which direction to crawl. Adult turtles were fitted with an eye-covering apparatus that was designed to hold wax paper filters. The wax paper filter acted to soften sharp images by scattering light. The results showed that if the turtles were allowed to acclimate to the wax paper filter for 10 min, then their sea-finding ability was not hampered by a diffuse vision. The result of this research implies that *C. mydas* adults are not using sharp visual acuity to find water, but rather diffuse beach silhouettes.

Brightness level, a known stimulus to which sea turtles respond, is often a result of the wavelength characteristics of that stimulus. Therefore, wavelength preferences of turtles on the beach have also been investigated as a tool for finding the sea after hatching or a nesting event. Ehrenfeld and Carr (1967) found that adult female green sea turtles (*C. mydas*) wearing colored filters (red, green, and blue) were still able to find water better than those turtles that were blindfolded. However, some colors worked better than others. For example, sea turtles wearing a green filter performed as well as the control group (nonblindfolded turtles). However, turtles wearing the red filter showed a sharp decrease in performance, indicating a possible upper limit to spectral sensitivity.

Mrosovsky and Shettleworth (1968) found that green hatchling sea turtles had a preference for short wavelengths, even if the intensity of the longer wavelengths was stronger. Mrosovsky (1972) found that red wavelengths had very little effect on green sea turtles except when very bright, but turtles were attracted to blue light even at low energy levels. These studies indicate that green turtles have a preference for shorter wavelength light. Witherington and Bjorndal (1991) tested loggerhead (*C. caretta*) and green (*C. mydas*) sea turtle hatchlings for color preference in air using a V-maze, two-choice design. When placed in the maze, both species chose 360 (near-ultraviolet), 400 (violet), and 500 (blue-green) nm wavelengths over a constant light source, but did not choose 600 (yellow-orange) or 700 (red) nm wavelengths. Loggerheads actually moved away

from 560 (green-yellow), 580 (yellow), and 600 (yellow-orange) nm wavelengths when the choice was color vs. a darkened window, but green sea turtles did not. These results indicate that loggerhead sea turtles are capable of seeing at least from 360 to 700 nm, whereas green sea turtles see wavelengths from 360 to 500 nm. Furthermore, loggerheads appear to be xanthophobic (averse to yellow-orange light) (Witherington and Bjorndal, 1991).

3.2.5 CONCLUDING REMARKS

Researchers are just beginning to develop a complete picture of the visual niche of sea turtles. The mechanisms by which sea turtles, as both hatchlings and adult females, return to the sea after hatching or nesting on land involve visual cues to find the ocean, though these cues seem to be restricted to diffuse images, and brightness levels and/or contrasts. This information has been invaluable in both defining the ecology of sea turtles on land and providing guidelines for the protection of these animals from anthropogenic light sources. The role of visual stimuli underwater for sea turtles also has been recently elucidated. From morphological studies, the roles of visual photoreceptor cells are being defined for both color vision and visual acuity. Retinal morphology studies may reveal the maximum capability of a visual system; certain cells and structures must be present for the retina of a typical vertebrate eye to process visual stimulation. Consequently, predictions have been made from identifying cell characteristics, describing pathways from one cell layer to the next, and mapping regions within the retina of high- and low-density cell counts. Electrophysiological studies on both color vision and visual acuity have supported the morphological work. Sea turtles have color vision, primarily in the shorter wavelengths (450–620 nm), and have the visual acuity to discern relatively small objects within the marine environment. Behavior studies further support these conclusions.

3.3 HEARING

3.3.1 MORPHOLOGY AND ANATOMY OF THE EAR

3.3.1.1 Main Structures of the Middle and Inner Ear

Sea turtles do not have an external ear; in fact, the tympanum is simply a continuation of the facial tissue. The tympanum is posterior to the midline of the skull and is distinguishable only by palpation of the area. Beneath the tympanum is a thick layer of subtympanal fat, a feature that distinguishes sea turtles from both terrestrial and semiaquatic turtles. The middle ear cavity lies posterior to the tympanum; the eustachian tube connects the middle ear with the throat near the posteroventral edge of the middle ear cavity (Lenhardt et al., 1985; Wever, 1978) (Figure 3.5).

The ossicular mechanism of the sea turtle ear consists of two elements, the columella and the extracolumella. The extracolumella is a cartilaginous, mushroom-shaped disk under the tympanic membrane, which is attached by its posterior end firmly to the columella. The columella, a long rod with the majority of the mass concentrated at each end, travels through a bone channel, and expands within the
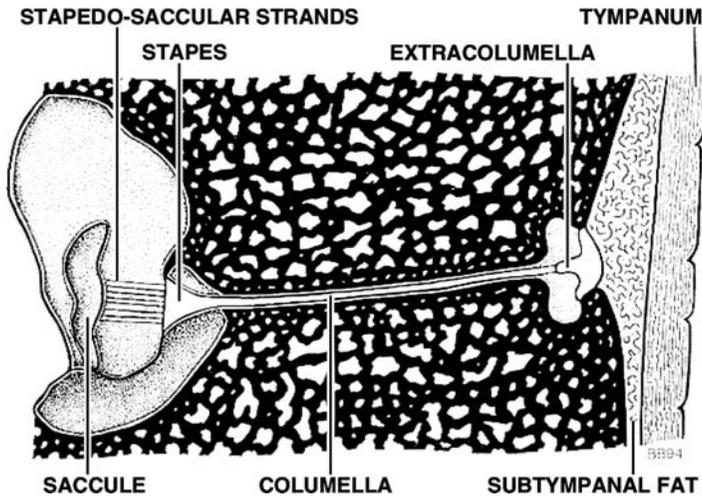
FIGURE 3.5 Schematic of middle ear anatomy of the juvenile loggerhead sea turtle. (From Moein, S.E., Auditory evoked potentials of the loggerhead sea turtle (*C. caretta*), master's thesis, College of William and Mary, Virginia Institute of Marine Science, Gloucester, VA, 1994. With permission.)

oval window to form a funnel-shaped stapes. The columella is free to move only longitudinally within this channel, so when the tympanum is depressed directly above the middle of the extracolumella, the columella moves readily in and out of the oval window, without any flexion of the columella. The stapes and oval window are connected to the saccular wall by fibrous strands, a unique feature of turtles. It is thought that these stapedo-saccular strands relay vibrational energy of the stapes to the saccule (Wever and Vernon, 1956; Lenhardt et al., 1985) (Figure 3.5).

We have not found any research on the inner ear of the sea turtle, but we can speculate from research performed on other species of turtles. The cochlea of turtles is thought to employ a reentrant fluid circuit for pressure relief (unlike most lizards, birds, and mammals, which release fluid pressure by means of protruding the round window membrane) (Turner, 1978; Wever, 1978). When the inward movements of the stapes displace the fluids of the inner ear, these fluids circle around the cochlear pathway, past the round window, back to the lateral side of the stapes (the direction of the fluid is reversed with an outward movement of the stapes). A limitation of this circular fluid motion is the added volume, from the displaced fluid, found at the site of the stapes that must be moved by alternating sound pressure. This fluid circuit may help describe the frequency range for turtles. Under these conditions of mass loading, the amount of sound pressure needed to move the columella increases with an increase in frequency, resulting in turtles' being insensitive to high frequencies. Loading does not present a problem at low frequencies, and sea turtles are thought to hear primarily in the low frequency range (Wever and Vernon, 1956; Turner, 1978; Wever, 1978).

The auditory ending, or sensory organ, within the inner ear of the reptilian cochlea is the basilar papilla (also known as the basilar membrane). The basilar

membrane is a thin partition in the circular fluid pathway, which contains two basic cell types: hair cells and supporting cells. In most reptiles, and presumably in sea turtles as well, the tectorial membrane overlies the hair cells of the basilar papilla (Wever, 1978; Lewis et al., 1985).

3.3.1.2 Water Conduction vs. Bone Conduction Hearing

The functional morphology of the sea turtle ear is still under some debate. Lenhardt et al. (1985) postulated that the sea turtle ear is a poor aerial receptor. For the terrestrial vertebrate ear, the middle ear acts as an impedance transformer between the media by which the sound is propagated (air) and the media by which the receptor cells reside (fluid). Generally, this impedance mismatch can be overcome by having a high ratio of the area of the tympanic membrane to that of the oval window, and by employing a columella lever ratio. Lenhardt et al. (1985) found both of these ratios to be low in the loggerhead sea turtle compared to its terrestrial counterparts. They suggested, instead, that the shape of the columella and its interactions with the cochlea and saccule are not optimized for hearing in air, but rather are adapted for sound conduction through two media, bone and water. If the turtle uses bone conduction to process sound, sound flows through the bones and soft tissue to stimulate the inner ear. The tympanum would act as a release mechanism rather than a sound receptor. However, if the turtle uses water conduction to process sound, the tympanum and subtympanal fat could act as low-impedance channels for underwater sound, resulting in columellar displacement to stimulate the inner ear. Recent imaging data strongly suggest that the fats adjacent to the tympanal plates in at least three turtle species are highly specialized for underwater sound conduction (Ketten et al., 1999).

3.3.2 Electrophysiology

Electrophysiological studies on hearing have been conducted on juvenile green turtles (*C. mydas*) (Ridgeway et al., 1969) and on juvenile loggerheads (*C. caretta*) (Bartol, 1999). Ridgeway et al. (1969) used both aerial and vibrational stimuli to obtain auditory cochlear potentials. The active electrode was placed, using surgical techniques, in the perilymph spaces of the labyrinth. Sounds were presented either with a loudspeaker or with a mechanical vibrator. Absolute thresholds were not measured; instead, cochlear response curves of 0.1 μV potential were plotted for frequencies ranging from 50 to 2000 Hz. Green sea turtles detect a limited frequency range (200–700 Hz), with best sensitivity at the low tone region of about 400 Hz. Although this investigation examined two separate modes of sound reception (air conduction and bone conduction), sensitivity curves were relatively similar (Figure 3.6). These results suggest that the inner ear is the main structure for determining frequency sensitivity (Ridgeway et al., 1969).

Bartol et al. (1999) used a second technique for obtaining electrophysiological responses to sound stimuli from sea turtles, the collection of auditory brainstem responses (ABRs). ABRs are sequences of events originating in the brain stem and are generated by separate parts of the auditory pathway in the first 10 msec after
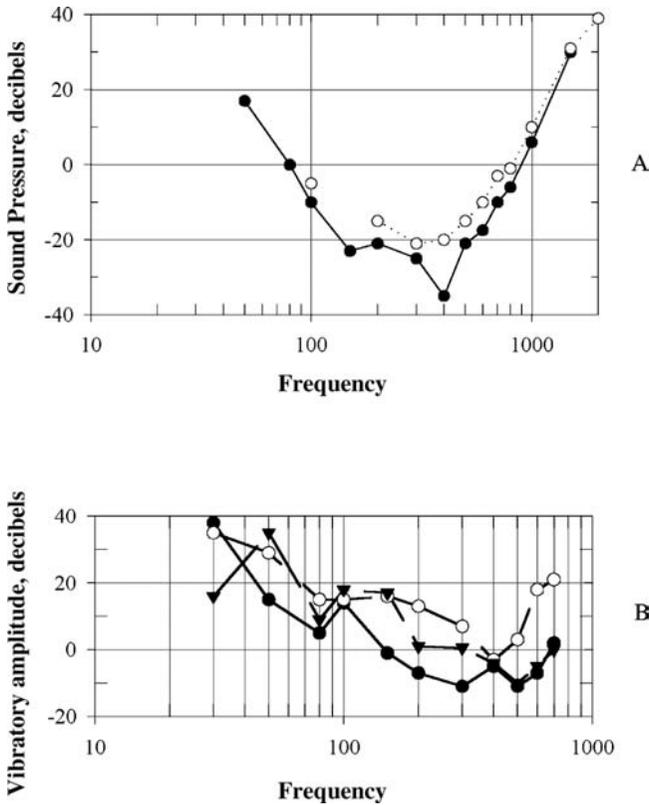
FIGURE 3.6 Hearing sensitivity curves obtained from green sea turtles (*C. mydas*). (A) Data collected from aerial sound stimuli. The sound pressure is shown in decibels relative to 1 dyne/cm² required to produce a cochlear potential of 0.1 µV. (B) Data collected from vibratory stimuli. The vibratory amplitude is shown in decibels relative to 1 mµ, required to produce a cochlear potential of 0.1 µV. (From Ridgeway, S.H. et al., Hearing in the giant sea turtle, *Chelonia mydas*, *Proc. Natl. Acad. Sci.*, 64, 884, 1969. With permission.)

stimulation. ABRs reflect the synchronous discharge of large populations of neurons within the auditory pathway, and therefore are useful monitors of the functioning of the throughput of the auditory system. Historically, ABRs have been used as a method for testing for audition and acoustic threshold in noncommunicative species. The technique is noninvasive, is rapid, and requires no overt training of the subjects. These recordings have been found to be consistent within species and similar across vertebrate classes in general form and origin, regardless of auditory apparatus (Corwin et al., 1982). Furthermore, the technique can be performed on awake subject animals (Bullock, 1991; Corwin et al., 1982). Bartol et al. (1999) recorded auditory evoked potentials from juvenile loggerheads using subdermal platinum electrodes implanted on awake animals. Vibratory stimuli, of known frequency, were delivered directly to the dermal plates over the sea turtle's tympanum. Signal averaging techniques were used to isolate the auditory evoked potentials from unrelated neural

and muscular activity. Thresholds were recorded for both tonal and click stimuli. Best sensitivity was found in the low-frequency region of 250–1000 Hz. The decline in sensitivity was rapid after 1000 Hz, and the most sensitive threshold tested was at 250 Hz (the lowest frequency tested), with a mean threshold of ~26.3 dB re 1 *g* root mean square (rms) + 2.3 dB standard deviation (SD).

3.3.3 Behavior

Two research studies have examined the response of juvenile loggerheads to sound in their natural environment (Moein et al., 1995; O'Hara and Wilcox, 1990). In both cases, these studies were initiated to assist in the development of an acoustic repelling device for sea turtles. O'Hara and Wilcox (1990) attempted to create a sound barrier for loggerhead turtles at the end of a canal of Florida Power & Light using seismic air guns. The test results indicated that at 140 kg/cm^2 the air guns were effective as a deterrent for a distance of about 30 m. The sound output of this system was characterized as approximately 220 dB re 1 µPa at 1 m in the 25–1000 Hz frequency range. However, this study did not account for the reflection of sound by the canal walls. Consequently, the stimulus frequency and intensity levels are ambiguous (O'Hara and Wilcox, 1990).

Moein et al. (1995) investigated the use of pneumatic energy sources (air guns) to repel juvenile loggerhead sea turtles from hopper dredges. A net enclosure (approximately 18 m × 61 m × 3.6 m) was erected in the York River, VA, to contain the turtles, and an air gun was stationed at each end of the net. A float attached to the posterior of the carapace was used to note the position of the turtle as the air guns fired. Sound frequencies of the air guns ranged from 100 to 1000 Hz (Zawila, 1995). Three decibel levels (175, 177, and 179 dB re 1 µPa at 1 m) were used every 5 sec for 5 min. Avoidance of the air guns was observed upon first exposure for the juvenile loggerheads. However, these animals also appeared to habituate to the sound stimuli. After three separate exposures to the air guns, the turtles no longer avoided the stimuli (Moein et al., 1995).

3.3.4 Concluding Remarks

These studies highlight the need for more research on the auditory capabilities of sea turtles. It is believed that physiological and behavioral adaptations may have evolved for sea turtles based on their selection of aquatic niches with each ontogenetic stage. For these three stages of life, the sensory environment also changes. Shallow-water habitats of the juvenile and adult stages are a much "noisier" world than the open ocean environment of the hatchling stage. Ambient noise in the inshore environment is heavily weighted to low-frequency sound (Hawkins and Myrberg, 1983). In highly developed areas (coastal waters) low-frequency noises associated with shipping lanes, recreational boat traffic, and biological organisms are prominent. Differences in functional morphology and behavioral hearing capabilities among species and life history stages have not been documented for sea turtles in the literature. In fact, only juvenile loggerhead and green sea turtles have undergone any auditory investigations. Both the middle

and inner ear regions of sea turtles need to be reexamined using the latest laboratory techniques. Furthermore, behavioral responses by multiple life history stages of sea turtles to sound stimuli, in the form of behavioral audiograms, need to be pursued in future research studies.

3.4 CHEMORECEPTION

3.4.1 ANATOMY OF THE NASAL STRUCTURES

The structure of the sea turtle nose is relatively simple: it opens to the outside world through external nares and into the palate through the internal nares on the posterior end. The external nares are connected to the nasal cavity by a tubelike vestibulum, and the nasal cavity is connected to the palate by a long nasopharyngeal duct (Scott, 1979). The nasal cavity is divided into two regions: the intermediate region and the olfactory region (Figure 3.7). The intermediate region lies ventrally and is attached to both the vestibulum and the nasopharyngeal duct. The intermediate region is large, occupies $^3/_4$ of the nasal cavity, and has two pockets of sensory epithelium called the Jacobson's organs. The functional significance of the Jacobson's organ is unknown, and although it appears to be capable of chemoreception, it has been assumed that this region is nonolfactory in the anatomy literature. In the sea turtle, these Jacobson's organs receive information in the same manner as olfactory epithelium. However, the information from this sensory epithelium is sent to the accessory olfactory bulb and the trigeminal nerve system. Posterodorsally in the nasal cavity lies the olfactory region, which is small compared to the intermediate region. The olfactory region is lined with a second type of sensory epithelium, Bowman's glands, which send information directly to the main part of the olfactory bulb. The olfactory nerve arises from these two types of sensory epithelium of the nose and forms two groups of trunks that lead to distinct portions of the olfactory bulb and accessory bulb. In the sea turtle, both the olfactory and accessory bulbs are notably large for a vertebrate (Parsons, 1959; 1971; Scott, 1979).

Tucker (1971) discussed the nonolfactory response within the nasal cavity and argued that the intermediate region received chemical stimulation in a similar manner to the olfactory region. However, because the intermediate region is ventrally located within the nasal cavity, it is almost continually bathed with water. The olfactory region, on the other hand, could contain an air bubble because of its dorsal location and thus remain dry as the turtle draws water into the nasal cavity. Tucker (1971) also made the assumption that an air-breathing animal cannot smell underwater. Thus, only the region called the olfactory region, and not the intermediate region, could be responsible for olfactory, chemosensory reception. The intermediate region was assumed to be involved with nonolfactory chemoreception (Parsons, 1971; Tucker, 1971). These assumptions, based on anatomical descriptions, have been debunked by several behavioral studies, and in fact sea turtles have been shown to "smell" underwater (see Section 3.4.2.2). In addition, recent research on fishes (Walker et al., 1997) has found that the receptor organs for geomagnetic orientation are located in the olfactory epithelium and are innervated by the trigeminal system. Sea turtles have been shown to have an elegant geomagnetic sense (Lohmann and Lohmann, 1994; Lohmann et al., 1997). Could the Jacobson's organ be the location of geomagnetic receptors in sea turtles?
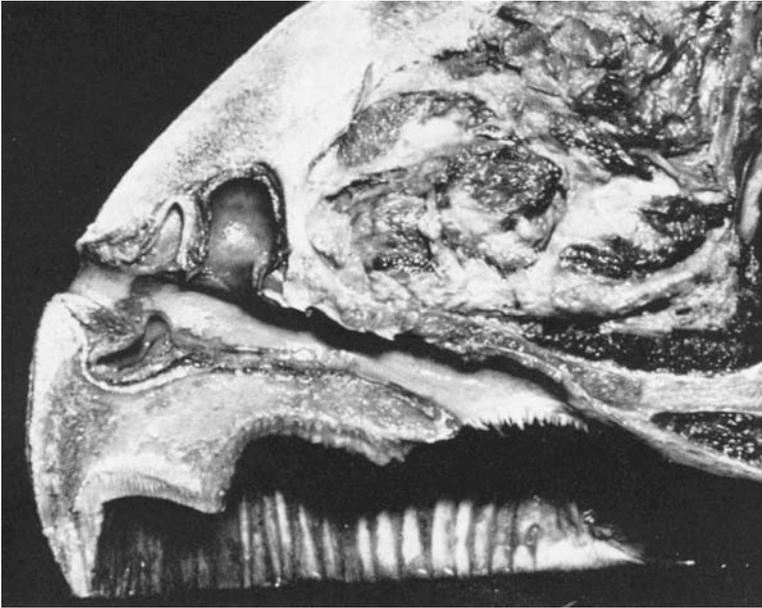
FIGURE 3.7 Right nasal cavity of green sea turtle (*C. mydas*). (From Parsons, T.S., Anatomy of nasal structures from a comparative viewpoint, in *Handbook of Sensory Physiology Vol. IV/I*, Beidler, L.M., Ed., Springer-Verlag, Berlin, 1971. With permission.)

3.4.2 BEHAVIOR

3.4.2.1 General Behavioral Observations

In a study that generally documented the sea turtle's natural behavior, Walker (1959) reported that sea turtles open their nostrils and move their mouths slowly open and closed while underwater. Walker postulated that this throat-pumping behavior moves water over the nostrils for olfaction, as had been suggested for many freshwater turtles (McCutcheon, 1943; Root, 1949). Throat-pumping has not been observed when sea turtles are resting or when they are breathing at the surface. This repetitive blowing of water out of the external nares while underwater occurs only while the animal is awake and active, and is postulated to be a mechanism for moving water over the chemoreceptor organs (Manton, 1979).

3.4.2.2 Odor Discrimination

Two operant conditioning studies examining underwater chemosensory behavior in green sea turtles (*C. mydas*) have been performed (Manton et al., 1972a; 1972b). Both studies used similar procedures. A tank was set up with two response keys suspended underwater; a light was mounted over each key (Figure 3.8). The turtles were able to swim freely within the tank environment. Turtles were first trained (using a food reward as reinforcement) to press either the right or the left key in
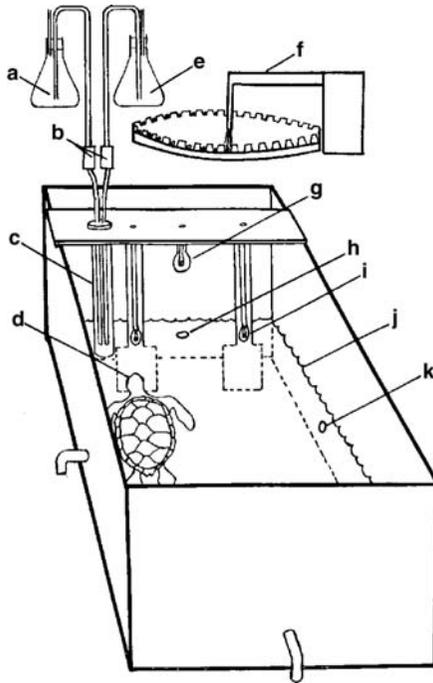
FIGURE 3.8 Diagram of experimental tank used to examine chemoreceptory ability of green sea turtles (*C. mydas*). (From Manton, M.L., Karr, A., and Ehrenfeld, D.W., Chemoreception in the migratory sea turtle, *Chelonia mydas*, *Biol. Bull.*, 143, 184, 1972. With permission.)

response to a light stimulus. Once the turtles were trained, the light signal was progressively reduced, and replaced with a chemical signal. For all remaining tests, the turtles first pressed the left key. If a chemical was released into the water, the turtles could then press the right key to receive a food reward. If no chemical was released into the water, and the turtles subsequently pressed the right key, this was marked as an incorrect response. All trials were completed with the turtles completely submerged underwater. This behavioral technique proved to be very successful, and once trained, the turtles completed the sequence rapidly. Habituation was never encountered (Manton et al., 1972a; 1972b).

The first of these two studies tested for underwater chemoreception (Manton et al., 1972a). The chemicals used for this study were organic compounds selected based on the chemosensory literature, and included such volatile compounds as phenethylalcohol and acetate, as well as two nonvolatile amino acids, serine and glycine. The control in this experiment was tank water. Except for the amino acids (which were not detected), the turtles responded to the chemicals with a mean correct detection of 89%, a much higher probability than for the control. When the chemical was released into the water, the turtles always directed their nostrils downward and performed the characteristic throat-pumping action (Manton et al., 1972a).

Although this study provides convincing evidence that sea turtles are capable of chemoreception, it does not distinguish between chemoreception by olfaction and

taste. The same group of researchers also tested for olfaction by temporarily inducing anosmia (loss of the sense of smell) in their subject animals (Manton et al., 1972b). By exposing the internal nares to ZnSO4, while ensuring that the oral cavity did not come into contact with the chemical, they were able to temporarily render the olfactory sense inoperative. After treatment with ZnSO4, the turtles were unable to distinguish the chemical from the control, indicating that these animals were using olfaction and not taste for chemoreception. Chemosensory acuity was also estimated from the data. These turtles were found to be able to detect chemicals at a relatively low level; the threshold occurred at concentrations of approximately 5×10^{-6} to 5×10^{-5} M (Manton et al., 1972b).

3.4.3 CHEMICAL IMPRINTING HYPOTHESIS

Chemoreception has long been proffered as the basis for orientation and long-distance migration by sea turtles (Koch et al., 1969; Manton, 1979; Owens et al., 1982). Though there appears to be very little evidence that sea turtles use chemoreception to navigate long distances, some research has been performed on the role that chemical cues play in the identification of a natal beach by adult nesting female sea turtles. Grassman et al. (1984) explored the theory that these animals can retain olfactory information gathered from the nesting beach and surrounding waters as hatchlings (that is, they become imprinted) and store this information for many years until they return as nesting females. They used Kemp's ridley (*Lepidochelys kempii*) hatchlings collected from Rancho Nuevo, Mexico, during oviposition and moved the eggs to Padre Island National Seashore in Texas. The eggs were incubated in Padre Island sand until hatching; hatchlings were allowed to perform their natural crawl across the sand and enter the surf zone. These animals were recaptured, and raised in tanks. At 4 months old, these same turtles were tested in a multipartitioned arena. When placed in this arena, the turtles could choose among a section containing a solution of Padre Island sand and water; a section containing a solution of Galveston, TX, sand and water; and two sections containing untreated solutions. Turtles spent significantly more time in the Padre Island compartment than either the Galveston or untreated sections. Although the turtles entered the Galveston compartment frequently, they did not stay in the compartment any longer than when the turtles had entered the untreated sections. The authors interpreted this behavior as a preference for the Padre Island treatment (Grassman et al., 1984).

A second experiment investigated the behavioral responses of sea turtles exposed to two chemicals, morpholine and 2-phenylethanol (Grassman and Owen, 1987). These chemicals were chosen because they are not naturally occurring, yet from the previous operant conditioning studies (Manton et al., 1972b), the researchers knew that green turtles could detect low concentrations of similar organic chemicals. Eggs were collected; the artificial nest environment was moistened with either one of the two chemicals or with untreated water. When the sea turtles hatched, they were placed in holding tanks that were also treated with the same chemical as the nest for 3 months. The turtles were segregated into four treatments: (1) both the nest and the water were treated with a chemical, (2) only the nest was treated, (3) only the water was treated, and (4) both the nest and water were untreated. After 2 additional

months of no exposure, the animals were placed in the same multipartitioned arena as in the previous study (Grassman et al., 1984). The only group of turtles that spent significantly more time in the chemically treated compartment, as opposed to the untreated compartment, was the group that was exposed to the chemicals both in the nest and in the water. These results suggested that not only the environment of the nest, but also the chemosensory environment of the water are important in the imprinting process (Grassman and Owens, 1987).

3.4.4 CONCLUDING REMARKS

Many of the inferences made from anatomical studies were based on the assumption that an air-breathing vertebrate could not detect chemicals underwater using olfaction. Behavioral studies have proved that this is not the case for sea turtles. The anatomy of the sea turtle olfactory system should be revisited with the behavioral data in mind.

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