

HEARING IN THE GIANT SEA TURTLE, *CHELONIA MYDAS**

BY SAM H. RIDGWAY, ERNEST GLEN WEVER, JAMES G. McCORMICK,
JERRY PALIN, AND JOHN H. ANDERSON

AUDITORY RESEARCH LABORATORIES, PRINCETON UNIVERSITY, AND MARINE BIOSCIENCE FACILITY,
NAVAL UNDERSEA RESEARCH AND DEVELOPMENT CENTER, POINT MUGU, CALIFORNIA

Communicated August 27, 1969

Abstracts.—Measurements were made of the cochlear potentials in three specimens of the giant sea turtle, *Chelonia mydas*, in response to both aerial and mechanical stimulation of the ear. The results show maximum sensitivity in the region of 300 to 400 Hz, with a rather rapid decline in sensitivity for lower and especially for higher tones. The upper limit for the observation of cochlear potentials without injury is 2000 Hz, and a practical limit of usefulness of this ear is probably about 1000 Hz.

The presence of hearing in turtles is now well established through both behavioral and electrophysiological observations. However, these observations have been limited to the small and readily available species, and nothing definite is known about the giant marine forms. An early attempt by Foá and Peroni to record auditory potentials in large specimens of *Thalassochelys caretta* gave no useful results.¹

Measurements of auditory sensitivity in terms of the cochlear potentials were carried out by Wever and Vernon in 1956 on four of the small common species: *Chrysemys p. picta*, *Clemmys insculpta*, *Pseudemys scripta*, and *Terrapene c. carolina*, all belonging to the family Emydidae.²⁻⁴ More recently, the hearing of one of these species, *Pseudemys scripta*, was tested by a behavioral method by Patterson.⁵

The patterns of auditory sensitivity obtained for all these animals, and by both methods on *P. scripta*, were closely similar.⁶ In every instance a fairly high level of sensitivity was observed for low tones, with the best responsiveness in the region of 200 to 700 Hz. For tones below 100 Hz the sensitivity was found to decline slowly in the two species in which tests were made in this region, and for tones above 700 Hz the sensitivity of all species was found to fall off with great rapidity, so that beyond 3000 Hz no tests could be made without injury to the ear.

The present experiments were carried out on the giant sea turtle, *Chelonia mydas*. The specimens were obtained from commercial sources in Hawaii, and thus no doubt represent the Pacific subspecies. Measurements of sensitivity to sounds were made by the cochlear potential method in 3 animals, whose weights were 50, 68, and 75 pounds. Several additional animals were used for anatomical and surgical studies. All the potential measurements were made on the left ear.

Procedure.—The animals were held in a saltwater pool until needed for the experiments. While in the pool, they were observed to remain on the bottom at a depth of 8 ft most of the time, and they came to the surface periodically to breathe. The smaller specimens usually surfaced at intervals of ten minutes

or so, and the larger specimens at longer intervals of up to 30 minutes. At the surface the animals usually took two to five breaths in fairly rapid succession, thus thoroughly flushing out the lungs.

After some preliminary experimentation we adopted a gas method of anesthesia that used a Bird respirator that had been modified for dolphins. It included an apneustic plateau device which made it possible to fill the lungs with an oxygen-anesthetic mixture of a desired concentration and hold the lungs inflated until the time for the next breath. For the turtles the machine was operated manually at intervals of five to ten minutes, and with the anesthetic gas concentration adjusted as required to hold the animal at a surgical level of anesthesia. Halothane was the anesthetic agent.

Earlier experiments on small turtles had shown that locations of an active electrode at various points in the perilymph spaces of the labyrinth give suitable recordings of the cochlear potentials, with variations among positions amounting to only 4 or 5 db. In the present experiments, therefore, we used the method that had been found the most convenient and reliable, which was an approach to one of the semicircular canals where it comes nearest to the dorsolateral surface of the skull. A needle passed through a bone suture in this region enters the perilymph space of the canal. For this placement an opening was first made in the outer case of the head in the left dorsolateral region to expose the temporalis and other muscles. These muscles were removed in part, but mainly pushed away to expose the cranial surface. After the suture between paroccipital and supraoccipital bones was located, a needle could easily be inserted. The use of a plain needle was found to be satisfactory as long as the cavity around the needle shank was kept free of fluids, but this required frequent sponging. After the first experiment, we inserted a hypodermic needle and then passed through its tube a Teflon-insulated silver wire with only its tip exposed. Shorting effects due to the accumulation of fluid in the field were thereby eliminated. Two other electrodes consisted of stainless steel needles inserted into inactive tissues at the borders of the incision. An amplifier with balanced input produced a gain of 1000 times and led to a wave analyzer that was used as a selective voltmeter.

Sounds were presented in two principal ways, from a loudspeaker and from a mechanical vibrator. The loudspeaker led to a tube that passed through the wall of the shielded, soundproofed chamber in which the animal was kept, and then this tube was connected to a terminal piece that expanded suddenly to a diameter of 2.5 cm. This expanded end was brought close to the side of the head and the narrow gap between it and the skin surface was sealed with a ring of cotton fibers soaked in petroleum jelly. Connected to the terminal piece was a probe tube whose end was in the air space close to the skin surface and that led to a condenser microphone. The probe-microphone system was calibrated to show for various tones the sound pressures existing in the space adjacent to the skin surface.

For mechanical stimulation, a Goodmans vibrator was used to actuate a rod with a blunt tip 4 mm in diameter. An accelerometer was located between vibrator and rod, and was calibrated by means of an optical device (a Fotonic sensor, type KD-45 made by Mechanical Technology, Inc., that uses fiber optics

principles). From the accelerometer readings, we obtained the rms amplitude of the vibratory motion.

The vibrator rod was applied to the side of the head in a region that gentle palpation showed to be most yielding. This region was identified as lying over the lateral head of the extracolumella, and preliminary exploration showed that here the best sensitivity was obtained, and as the vibrator was moved away in any direction the sensitivity fell, at first gradually and then rapidly, as the distances reached 2 or 3 cm.

Anatomical Relations.—The conditions of stimulation both by aerial and by vibratory methods can be better understood from a consideration of Figure 1, in which the anatomy of the ear of *Chelonia* is represented. There is no tympanic membrane, but the function of such a membrane is served by the superficial tissues at the side of the head. The skin layer consists of a heavy fibrous plate with a thin scale-like surface. Beneath the skin is a layer of tissue consisting of

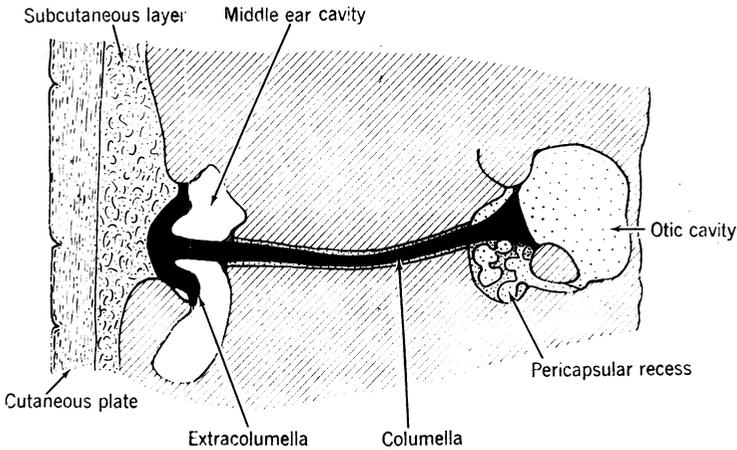


FIG. 1.—The auditory mechanism in *Chelonia mydas*. The left ear is shown in a dorsal view. Scale: $\times 2$.

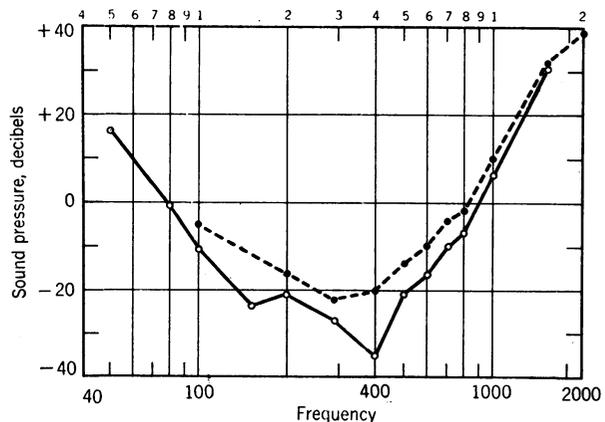
fatty material embedded in a delicate fibrous network. This tissue fills the space between the cutaneous plate and the deeper bone surface, and becomes particularly thick as it enters a depression in the bone. The osseous columella lies within a narrow bony channel and emerges from this channel at its outer end as it makes connection with the shaft of the cartilaginous extracolumella. The extracolumella has a mushroom shape. Its shaft—the stem of the mushroom—passes through the middle ear cavity, and the head protrudes into the lateral depression in the bone surface. This head is loosely attached to the surrounding bone except at its posterior end where the attachment is firm. When its middle portion is depressed, the whole surface rocks about the posterior attachment. The subcutaneous layer is loosely attached to its enclosing cutaneous and bony surfaces except around the peripheral edges of the head of the columella, where the fibrous network is firmly attached. The columella expands rapidly at its medial end to form a stapedia footplate, which lies in the oval

window of the otic capsule. This expanded portion of the columella is contained in a special chamber, called the pericapsular recess. This recess shows some variations from the one found in smaller turtles, such as *Pseudemys scripta*. There it is a simple fluid-filled chamber that encloses the stapes and runs first posteriorly and then curves medially to form a channel from the back of the stapes to the perilymph of the cochlea, and with its fluid separated from the perilymph by a pericapsular membrane. In *Chelonia mydas*, the recess posterior to the stapes contains a loose spongy tissue with large communicating spaces and does not itself make the connection with the otic cavity. This connection is made by a narrow tube that lies deep in the otic cavity and enters the recess at its deeper portion. The figure does not show this deep location and also does not represent the cochlea. No doubt the basilar membrane lies across the path between the medial surface of the stapes footplate and this connecting tube, for this is the arrangement observed in the smaller turtles. These features could not be made out clearly in gross examination, and also the pericapsular membrane was not identified (though it has been suggested in the figure). These details will have to be studied in serial sections, now being prepared.

The cutaneous plate serves as the sound receiving surface, and its vibratory movements are communicated to the underlying fatty material that acts much like a fluid in transmitting the pressures inward to the head of the extracolumella. This head can move in and out of the air cavity of the middle ear, and its movements are transmitted to the shaft of the columella. This shaft is a thin rod of bone, but it is closely contained in a bony tube and surrounded by a thin fibrous layer, so that it is free to move longitudinally but is prevented from undergoing any appreciable amount of transverse flexion. This is an important feature, for such flexion would produce a loss of intensity and a distortion of the transmitted waves. The footplate of the vibrating stapes is able to produce displacements of the fluid of the otic cavity because of the presence of the recurrent pathway through the pericapsular recess to the back surfaces of the stapes.

Results.—The results of stimulation with aerial sounds for two animals are shown in Figure 2. The curves represent the sound pressures, in decibels relative to a zero level of 1 dyne/cm², required to produce a cochlear potential of 0.1

FIG. 2.—Sensitivity curves for aerial sounds, obtained in two specimens of *Chelonia mydas*. The sound pressure is shown, in decibels relative to 1 dyne/cm² required to produce a cochlear potential of 0.1 μ v.



μv . As we have found to be desirable for these measurements in the simpler ears that are subject to distortion and overloading at relatively low levels, the observations were made at as low a level as was convenient, which ordinarily was two or three times the noise level. Often this level was $0.1 \mu v$, but for the lower tones for which the noise background is greater, the level was raised as necessary. For convenience, the sound pressures have been calculated for a constant output of $0.1 \mu v$. This calculation assumes linearity of the intensity functions, which is a valid assumption at these low levels.

The two animals shown in Figure 2 gave closely similar sensitivity curves, though in only one were the measurements carried below 100 Hz. The maximum sensitivity is at 300 Hz for one animal and at 400 Hz for the other, and the decline for lower and higher tones is fairly rapid. For the high tones the rate of decline in sensitivity is about 35 db per octave.

Results for mechanical vibration are shown for three animals in Figure 3. The tests were not carried above 700 Hz because the large amplitudes required for such high tones presented a danger of injury to the ear. It is certain that the sensitivity falls with great rapidity in the high-tone region, and the slope, as far as we could determine it, is of the same order of magnitude as found for the aerial tones.

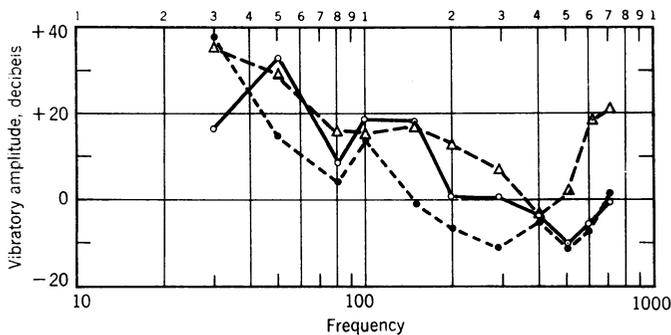


FIG. 3.—Sensitivity for vibratory stimulation. Shown is the rms amplitude, in decibels relative to $1 m\mu$, required to produce a cochlear potential of $0.1 \mu v$.

The three ears show some variations, but their general trend is similar: as the frequency rises, the sensitivity improves, attains a region of maximum, and then declines. The maximums vary for the three animals from 300 to 500 Hz, and here we see a close resemblance to the aerial curves.

A comparison of results obtained in these two ways is complicated because of the very different impedances involved. In aerial stimulation we are concerned first with the relative acoustic impedances of the air and the tissues, and then with the mechanical impedances of the columellar system and the inner ear structures, which in some degree are reflected to the surface tissues. These impedances

determine the ratio between reflected and transmitted waves, and they vary greatly with frequency.

With vibratory stimulation as carried out here and with an accelerometer used to show the amplitude of motion, the peripheral impedances are of no consequence; the vibrator simply imposes its movements upon the peripheral structures to the degree indicated. The extent to which these motions are transmitted through the columella to the footplate and the cochlear structures is a matter of importance. Thus the final patterns of displacement set up on the basilar membrane almost certainly vary as a function of frequency, even when the peripheral amplitudes are kept constant. The sensitivity curves as shown reflect these varying patterns.

The close similarity between the sensitivity curves obtained by aerial and vibratory forms of stimulation suggest that the responsive characteristics of the inner ear—the basilar membrane and its hair cells—are the main determining factors.

Discussion.—A comparison of the aerial sensitivity curves for *Chelonia mydas* and for the four species of small turtles studied previously shows a remarkable degree of similarity. This comparison is somewhat limited by the fact that in the earlier studies the sensitivity only once was measured below 100 Hz. Most of the functions for the small species are rather flat from 100 to the region of 500 to 700 Hz, then rise rapidly—at a rate of about 38 db per octave—as the frequency increases, and finally in the region beyond 3000 Hz it becomes difficult or impossible to determine the sensitivity without serious injury to the ear. In the one instance in which testing extended below 100 Hz (in *Terrapene carolina*), the sensitivity also declined rapidly as the frequency was reduced below the optimum region, which was between 100 and 500 Hz.

Chelonia mydas follows this pattern also, but with two differences: the region of best sensitivity is much narrower, and on the whole it is lower in frequency. Most of the curves for the small turtles begin their rapid ascent at 500 or 700 Hz, whereas for *Chelonia mydas* they do so around 400 Hz. When we consider the great size of this animal and the correspondingly large mass of its auditory structures, it is surprising that the difference is no greater than it is. Again we must ascribe the principal determination of the ear's sensitivity to the cochlear structures.

A comparison of this turtle with other animals in terms of cochlear potentials is of interest. In relation to the pigeon, *Chelonia mydas* is about equal in sensitivity at 100 and at 600 Hz, but in the region between it is definitely superior. In relation to the cat, this turtle shows about the same degree of sensitivity in the low tones, but becomes inferior, and increasingly so, as the frequency is raised above 400 Hz.

We conclude from these observations that the giant sea turtle has a serviceable ear, with a reasonable degree of sensitivity within a restricted range. Its ear is clearly a low-frequency receptor, with a useful span of perhaps 60 to 1000 Hz. Both on land and in the sea, this ear no doubt enables the animal to perceive many important signals.

* This investigation was carried out in the Auditory Research Laboratories, Department of Psychology, Princeton University, with support by a contract with the Office of Naval Research (Washington, D.C.) and by the Naval Undersea Research and Development Center (Point Mugu, Calif.). Some of the facilities were provided by grants from the National Institute of Neurological Diseases and Stroke, Public Health Service. The first and last authors are from the Marine Bioscience Facility, the others from the Auditory Research Laboratories.

¹ Foá, C., and A. Peroni, "Primi tentativi di registrazione delle correnti d'azione del nervo acustico," *Archivi di Fisiol.*, **28**, 237 (1930).

² Wever, E. G., and J. A. Vernon, "The sensitivity of the turtle's ear as shown by its electrical potentials," these PROCEEDINGS, **42**, 213 (1956).

³ *Ibid.*, "Sound transmission in the turtle's ear," p. 292.

⁴ *Ibid.*, "Auditory responses in the common box turtle," p. 962.

⁵ Patterson, W. C., "Hearing in the turtle," *J. Auditory Res.*, **6**, 453 (1966).

⁶ W. L. Gulick, and H. Zwick, "Auditory sensitivity of the turtle," *Psychol. Record*, **16**, 47 (1966).