

THE SENSITIVITY OF THE TURTLE'S EAR AS SHOWN
BY ITS ELECTRICAL POTENTIALS*

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Little is known about the performance of the ear of the turtle. Andrews¹ in 1915 succeeded in training five individuals of the genus *Chrysemys* to distinguish the sound of a whistle from that of a bell when one of these was made the positive signal for feeding. Poliakov² reported the establishment of conditioned head withdrawal in three specimens of *Emys orbicularis* in response to a variety of tones and noises. On the other hand, Kuroda³ in two experiments, one of which used the same method as Andrews, failed to obtain any evidence of hearing in the Japanese turtle, *Clemmys japonica*.

Three experiments have dealt with the turtle's ear by electrophysiological methods. Foà and Peroni⁴ in 1930 recorded from the facial-auditory nerve of the giant sea tortoise, *Thalassochelys caretta*, and obtained impulses on stimulation with strong tones from organ pipes with frequencies of 16¹/₂, 33, and 132 cycles. Wever and Bray⁵ in 1931 obtained synchronized responses from the eighth nerve of the painted turtle, *Chrysemys picta*, for all tones up to 1,000 or 1,200 cycles, though the responses were feeble beyond 500 cycles. Adrian, Craik, and Sturdy⁶ obtained similar responses from the eighth nerve of the box turtle, *Cistudo*, and a land turtle *Testudo graeca*, on stimulation with tones up to 400 cycles, and in two specimens they obtained inner-ear potentials also for tones up to 700 or 800 cycles.

The electrophysiological experiments are in agreement in indicating that the turtle's ear is responsive to low tones. But despite this evidence and the positive results obtained by Andrews and Poliakov, many herpetologists have held the opinion that turtles are completely deaf and that their ear is only a vestigial organ. Such a view was expressed by Pope⁷ in 1939 and by Carr⁸ in 1952.

The present experiments have made use of the electrophysiological method, with measurements of the inner-ear potentials produced by sounds of known intensities. The results reported here were obtained on twenty-one animals belonging to three related species: four wood turtles, *Clemmys insculpta* (Le Conte), nine painted turtles, *Chrysemys picta picta* (Schneider), and eight "Cumberland" turtles, *Pseudemys scripta*. The individuals comprising the last group showed some race variations and included *P. scripta scripta* (Schoepff), *P. scripta elegans* (Wied), and *P. scripta troostii* (Holbrook), as well as some intergrades among these but for present purposes these variations are of no significance. All these species belong to the family Emydidae.

METHOD AND PROCEDURE

The animals were anesthetized with 25 per cent ethyl carbamate in turtle Ringer's solution, injected into the leg muscles in the amount of 6.5 cc. per kilogram body weight. The head was held by a clamp fixed to the lower jaw, and movement was further restricted by anchoring the shell and closing all leg openings with tape.

Three different positions for the active electrode were used, and the operative procedure varied accordingly. In these procedures bleeding was sometimes a

problem, and it was found helpful to tie a string tightly around the neck and to leave it in place for a short time—2–5 minutes, usually—until the bleeding stopped. This constriction did not entirely block the circulation to the head, and the animal remained in good condition. In a test experiment we found that leaving the ligature in place for as long as 90 minutes had no effect upon the inner-ear potentials. A radiofrequency cautery was useful also in controlling hemorrhage from small vessels.

Early in the experiment the active electrode was placed on the cranial wall of the otic capsule, near the point of penetration of the posterior root of the eighth nerve. Sometimes also it was placed in a small hole drilled in this wall. This approach requires a dorsal skin incision and removal of the bony cranial roof in the region of the cerebellum. It was found best to avoid any opening of the dura mater, which causes troublesome bleeding. The cerebellum can be pushed to one side, and then the two roots of the eighth nerve can be located deep in the cavity as they leave the otic capsule and enter the medulla. The best position for the indifferent electrode was found to be beneath the skin in the dorsal part of the cranium, at a point remote from any muscles.

Later on, a simpler and more satisfactory procedure was worked out for approaching the otic capsule. A skin incision was made along the dorsal crest of the squamous bone, at the most lateral insertion of the temporalis muscle, and then this muscle was elevated to expose the suture between the paroccipital and supraoccipital bones. Midway along this suture and extending medially is a clear area in the otherwise white bone, and this area marks the most dorsal course of the bony channel for the posterior semicircular canal. A fine steel needle, insulated except at the tip, was pushed into the suture at this place to make contact with the perilymph of the bony canal. The utricle also is close to the surface here, and the saccule, lagena, and cochlea are only about 3 mm. below, so that it is possible to record from such of these endings as are responsive to sounds. This dorsal location in the otic capsule was used in most of the experiments.

A third and more elaborate procedure, used only in a few ears, permitted a recording from the round window membrane. The posterior extension of the tympanic cavity (the so-called "mastoid antrum") is first entered by removing its dorsal wall, which is formed by the squamous bone. Then along the medial wall of this cavity there can be seen through the bone a broad dark line that represents the course of the cavernous sinus, in which are included the carotid artery, internal jugular vein, and facial nerve. By drilling into the bone just above this sinus, carefully avoiding its vessels, the pericapsular recess is entered. This recess is a bent tube that borders on the otic capsule along its posterior and lateral aspects and incloses both oval and round windows. It is filled with fluid. If the fluid is removed by applying pledgets of absorbent cotton, the round window membrane may be seen at the posterior end of the recess. This window bounds the fluid of the inner ear, just as in the higher forms. A platinum-foil electrode was passed through the exposed cavity of the recess to make contact with this membrane.

After the electrode was fixed in one of these positions, a sound tube leading from a loud-speaker was placed firmly against the head in such a manner as to inclose the tympanic membrane without touching it, with a piece of rubber tubing over the end to serve as a gasket. Further, to insure that the fit to the head was sound-

tight, the end of the rubber tube was covered with petroleum jelly, and sometimes strands of cotton covered with the jelly were wound around the end of the tube. A probe tube from a condenser microphone entered the sound tube from the side and then ran concentrically with this tube to a point near its tip, and by means of this probe tube and microphone the sound pressures applied to the tympanic membrane were measured.

As will be brought out presently, the inner-ear potentials of the turtle are small in magnitude, and, as usual in low-level recording, it is necessary to use precautions to avoid artifacts. The stimulating sounds were confined in tubes as described and were not permitted to pervade the experimental room. The condenser microphone and its associated apparatus were attached only for a calibration run at the beginning or the end of an experiment and were not in position near the ear during the measurements of its potentials. In spite of these precautions it was possible to obtain potentials representing the microphonic action of tissues when sounds of extreme intensities were applied, but these intensities were beyond any required for our measurements and indeed were such as to produce severe injury to the ear. With the sound intensities normally employed, these spurious potentials were not measurable, and numerous checks were applied from time to time throughout the experiment to guard against their appearance.

The stimulating tones usually extended from 100 to 3,000 cycles. Sometimes higher tones were used, but it was found that if such tones were delivered in sufficient strength to produce measurable potentials, they almost always caused injury to the ear, as shown by a reduction in the response to all tones. Our standard procedure for determining the sensitivity was to present various tones at the intensities necessary to produce a certain small potential, usually 0.3 or 0.1 microvolt, beginning with the low tones and then progressing upward toward the more hazardous frequencies. Often the high-tone presentations were alternated with retests at 400 cycles to discover whether any damage had been done. The results that are given for tones above 3,000 cycles were obtained at the end of the series of measurements on a given ear, so that other portions of the function would not be affected, with the presentations made as brief as possible to minimize the injury.

The measurements were made at a room temperature of about 20°–22° C.

RESULTS

General Physiological Conditions.—We shall begin with a consideration of the condition of the animal in relation to the ear's generation of potentials. It is common in experimental studies on reptiles to make no attempt to maintain the circulation, or otherwise to give attention to the general physiological condition. For example, in the experiments of Adrian, Craik, and Sturdy, mentioned above, the animal was decapitated, the head dissected widely, and the brain almost wholly removed. Nevertheless, these authors reported that the preparation remained in satisfactory condition for hours, and nothing was gained by attempts to preserve the circulation. It should be noted that in these experiments the recording was from the eighth nerve during stimulation with sounds that may have been of extreme intensities, and under such conditions a variation in the performance of the sensory cells may not have been revealed.

Our observations of the inner-ear potentials show an essential dependence upon the state of the animal. Two of our animals died in the course of the observations, evidently from an overdose of anesthetic, and in both of these the responses declined rapidly. In another animal, after the usual measurements had been made, a tone of 400 cycles was presented and steadily maintained at the intensity necessary to produce a response of 1 microvolt. Normally this response will continue for hours. In this instance, after a number of observations had been made to establish the stability of the response, the head was cut off and the observations continued over a period of 30 minutes. The results are given in Figure 1. As will be seen, the response failed rapidly and at the end of the 30-minute period had sustained a loss of 10 db. Moreover, at that time the decline was still continuing at a rapid rate. It is clear that for precise determinations of the performance of the turtle's ear it is necessary that the circulation be maintained and, in general, that the animal be kept in good condition.

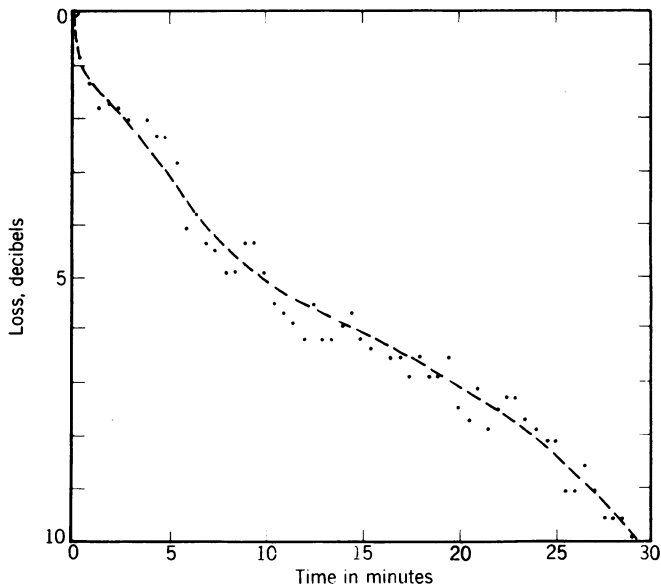


FIG. 1.—The loss of inner-ear potentials in the turtle after death. The test tone was 400 cycles, presented at a constant intensity.

Intensity Functions.—As has been found for mammals and birds, the inner-ear potentials show a progressive and regular increase with sound pressure at the lower levels and then at higher levels begin to bend, attain a maximum, and finally decline. Figure 2 shows some representative intensity functions. These curves are approximately linear in their lower portions: an increase of sound pressure by some fractional amount gives an increase of potential of nearly the same fractional amount. In these curves the departure from linearity in the upper portion of the curve is rather gradual. This is the typical condition, though for some of the functions, more often for the high frequencies, the decline beyond the maximum is more rapid.

Sensitivity Functions.—The next three figures present sensitivity curves for representative ears among the three species studied. Each figure contains three curves for different animals. Two of these (*solid and short-dashed lines*) were obtained with the active electrode in the dorsal position in the otic capsule, and the remaining one (*long-dashed line*) with the electrode on the cranial wall. The solid line represents one of the most sensitive animals of its group, and the short-dashed line a more typical animal. Figure 3 shows results for *Chrysemys picta*, Figure 4 for *P. scripta*, and Figure 5 for *Clemmys insculpta*. These curves show the sound pressures required at various frequencies to produce a constant potential of 0.3 microvolt.

It will be noted that in all these ears the sensitivity is fairly uniform for the low tones, up to 500 or 700 cycles, and then decreases at a rapid rate as the frequency is raised. The general form of the sensitivity function is the same for all three species. In absolute sensitivity the *Chrysemys* and *Pseudemys* groups are similar, and the *Clemmys* group shows somewhat greater sensitivity for the low tones. In general, the measurements made with the dorsally placed electrode show greater sensitivity than those made with the electrode on the cranial wall of the otic capsule, evidently representing better contact with the electrical fields of the sensory cells.

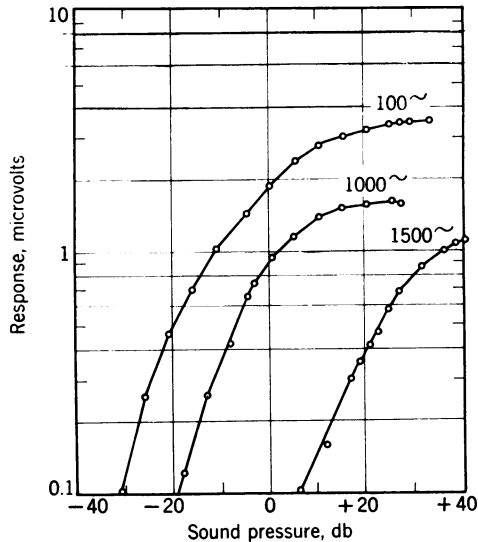


FIG. 2.—Intensity functions. The sound pressure is represented in decibels relative to 1 dyne per square centimeter.

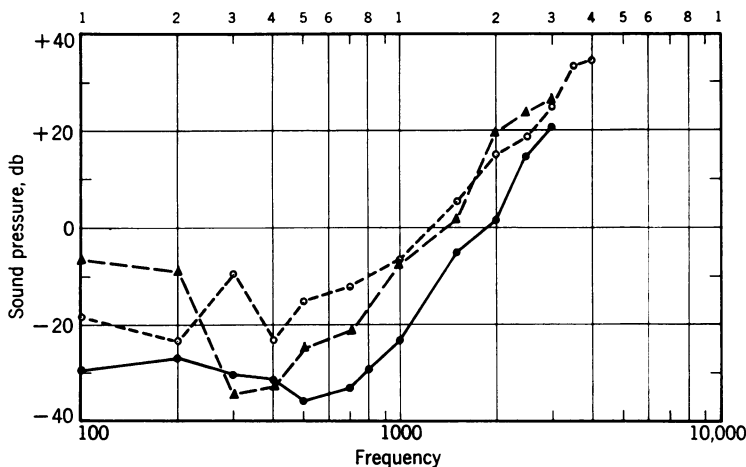


FIG. 3.—Sensitivity curves for three turtles of the species *Chrysemys picta*. The sound pressure is represented relative to 1 dyne per square centimeter.

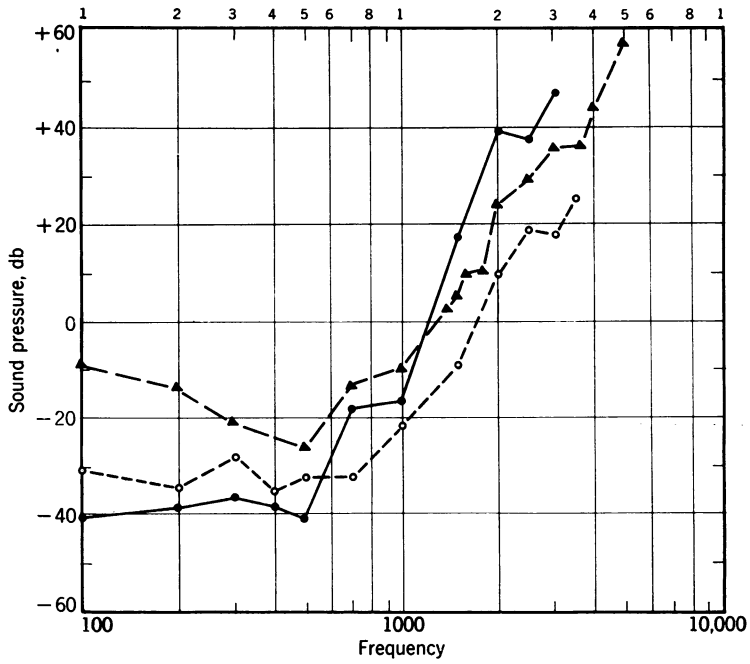


FIG. 4.—Sensitivity curves for three turtles of the species *Pseudemys scripta*.

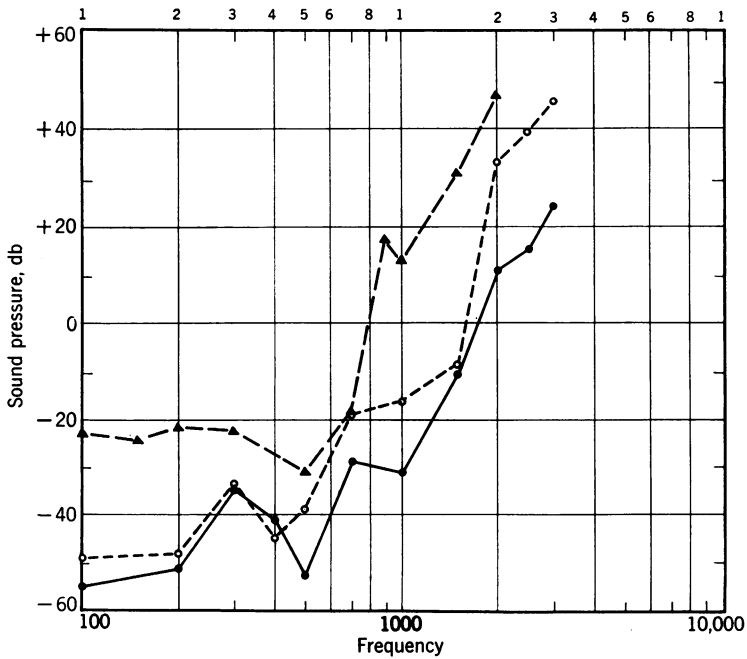


FIG. 5.—Sensitivity curves for three turtles of the species *Clemmys insculpta*.

When the electrode was a platinum foil on the round window membrane, the responses were increased about 5 db over what they were with the dorsally placed needle electrode, irrespective of the stimulus frequency. This fact suggests that the active cells are located in the inferior division of the labyrinth, in the endings of the cochlea, lagena, and saccule.

It is of interest to compare the sensitivity of the turtle's ear as shown in its electrical potentials with that found by the same method in the cat.⁹ This comparison is made more fairly if for both forms we use results obtained with the electrode on the round window membrane. On this basis, the turtle's ear measures favorably in relation to the cat's in the low-tone region. For *Chrysemys picta* and *P. scripta* the sensitivity for tones up to 500 cycles is nearly the same as for the cat and for *Clemmys insculpta* it is a little better. In fact, in terms of sound pressure this last species shows about the same sensitivity for these low tones as the cat does in the higher part of the scale—in the region of 1,000–2,000 cycles—where the cat attains its maximum sensitivity.

This near-equality in the responsiveness of turtle and cat to the low tones holds only for the smaller values of sound intensity. As the intensity is raised, the cat's ear increases its output over a wide range, remaining linear from 0.1 microvolt to as much as 200 microvolts for the low tones, whereas for the same tones the turtle's ear rarely produces over 1 microvolt before showing a significant departure from linearity.

Maximum Potentials.—The maximum values of potential obtained for intense stimuli have already been indicated in a preliminary way in Figure 2. More complete data for two ears are given in Figure 6. Some irregularities appear at the two lowest frequencies, but in general the values of the maximums show a progressive decline with frequency. The values are about 8–10 microvolts for the lowest tones and then fall to about 1 microvolt for the highest tones.

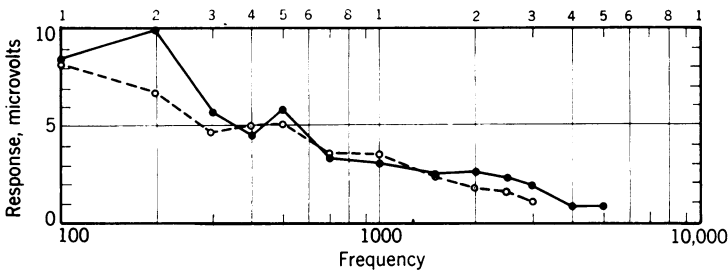


FIG. 6.—Maximum-response curves for two turtles of the species *Chrysemys picta picta*.

These maximum values are to be compared with the ones obtained in mammals, especially in guinea pigs and cats, in which potentials approaching 1,000 microvolts may be measured from the round window membrane for tones below 700–1,000 cycles. The difference of about 100-fold is only in a minor way to be attributed to differences of recording and mainly represents the large increase in the number of sensory cells as we go from reptile to mammal. Beyond 700–1,000 cycles the maximums for the guinea pig decline progressively with frequency, and the same is true for the cat for tones beyond 1,500 cycles. It is interesting to find this same feature

in the performance of the turtle's ear, though with the function displaced downward in the frequency scale.

SUMMARY AND CONCLUSIONS

Electrical potentials in response to sounds were recorded from the inner ear of three species of turtles of the family Emydidae. The recording electrode was given three locations: on the cranial wall of the otic capsule, in the dorsal part of the perilymph space close to the posterior semicircular canal and utricle, and on the round window membrane. These locations are increasingly efficacious in the order named, but the second is the most practical for systematic measurements.

The turtle's ear is highly sensitive, and rather uniformly so, for faint tones in the region up to 500 cycles. For higher tones, however, the sensitivity falls off with great rapidity, and beyond 3,000 cycles a measurable potential can be obtained only at the risk of injury by overstimulation. The sensitivity for low tones is of the same order as that determined by similar methods in the cat, and in one of the species studied (the wood turtle, *Clemmys insculpta*) is nearly equal to that of the cat for higher tones, where this animal has its maximum sensitivity.

For intense stimuli the turtle's ear makes a poorer showing. It has only a limited dynamic range; its potential is a linear function of sound pressure only at low levels, and as the intensity is raised overloading quickly set in. Measured from 0.1 microvolt, the lowest level at which reliable observations have been made, the turtle's range of linearity is about 20 db and its maximum range of response is about 40 db, whereas the cat's range of linearity for low tones is about 66 db and its maximum range is 80 db. It seems reasonable to suppose that the turtle has relatively poor loudness discrimination for any but the faintest sounds.

The general correspondence of the inner-ear potentials of the turtle to the cochlear potentials of birds and mammals evidently represents a basic similarity in the nature and operation of the auditory sense cells.

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