these deliberations will come further suggestions, ideas, appraisals, and statement of the problem. The methods developed in this country for measurement and all the data collected are available to everyone. It is our hope and intention that this problem, like others of the atomic age, will come to be generally understood.

Fallout is normally considered an aspect of atomic warfare and nuclear armament. There is some similarity, however, between the weapons fallout and the hazard from a reactor accident, in which radioactive products would be disseminated over a limited area but would never reach the stratosphere or undergo anything like the world-wide tropospheric dissemination. As it has so often been observed in the past, so it is again true in this instance, that a new fact of nature is likely to have its beneficent as well as its somber and frightening aspects. As we learn about the way the world-wide fallout particle, probably as tiny as a virus molecule, wends its way from the stratosphere through the tropopause into the troposphere and, within a few weeks, collides with a water droplet and thus is brought to the earth's surface by rain, we shall learn more about the questions which will naturally arise more and more frequently as the world's population increases world-wide pollution of the atmosphere not only with fission products but with the other by-products of our new technological age.

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³ Stanley Greenfield, Rand Corporation.

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AUDITORY RESPONSES IN THE COMMON BOX TURTLE*

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We have previously reported observations of inner-ear potentials in response to sound in three species of turtles, *Chrysemys picta picta*, *Pseudemys scripta*, and *Clemmys insculpta*.¹ Sensitivity curves were obtained for these ears by measuring the sound pressure necessary to produce a standard amount of potential, and these curves were found to be similar in form for all three species. The sensitivity is rather uniformly keen for tones between 100 and 700 cycles and then grows progressively poorer for the higher tones up to 3,000 cycles, beyond which a response cannot be obtained at any intensity that is safe to apply to the ear.

We have now extended our observations to a fourth species, the common box turtle *Terrapene carolina carolina*. This species, like the others mentioned, belongs to the extensive family of Emydidae, but anatomically it presents a number of variations from the general type. Of particular interest are the variations in the form of the skull in the region of the ear. Also, this turtle is relatively small, rarely exceeding 5 inches in length of carapace. Our specimens were mostly adult and varied from 4 to 5 inches in carapace length.

The observations reported here were made on eight animals, and in four of these on both ears. In addition, a number of animals were tested which on subsequent examination were found to be suffering from middle-ear infections. In these the sensitivity was 20-40 db. poorer than in healthy animals.

The experimental procedure was similar to the one used principally in our earlier As before, the active electrode was a steel needle, insulated except at the studies. tip, which was inserted into the perilymph space of the ear. However, the placement of this electrode was considerably more difficult than in the other species. The bones of the temporal region of the skull are relatively thick in this species, and usually we were unable to find the sutures that in the other forms served as reliable landmarks for the location of inner-ear structures. The most satisfactory procedure was first to remove the temporal muscle and then to open the posterior part of the middle-ear cavity (a procedure that itself has no significant effect upon the sensitivity).² Thereupon two features are revealed: a dark area that represents the shadow of the cavernous sinus lying deep beyond the inner wall of the middle-ear cavity and a translucent area that marks the location of the posterior portion of the pericapsular recess. With the aid of these points a hole was drilled through the bone in the region of the posterior semicircular canal, and the needle electrode was tightly fitted into this hole to prevent the escape of perilymph. An indifferent electrode was inserted beneath the skin of the head.

Tones were applied to the ear through a rubber tube sealed over the tympanic membrane, and observations were made of the sound pressures necessary to produce a standard potential of 0.3 microvolt. Results for two of the animals are shown in Figure 1. Here the solid line represents one of the more sensitive animals and the broken line one of the less sensitive. These curves follow the form already described for the other species of turtles, showing good sensitivity over a range from 100 to 600 cycles and progressively poorer sensitivity for higher and lower tones. As observed earlier, it usually was not possible to obtain measurable potentials for tones above 3,000 cycles at intensities that were safe to apply to the ear. The auditory sensitivity of this species, as measured by the inner-ear potentials, is closely similar to that of *Chrysemys picta picta* and *P. scripta* and somewhat below that of *Clemmys insculpta* in the most favorable region of 100-600 cycles.

Some of our observations have dealt with the mode of action of the tympanic membrane. This membrane consists of a cartilagenous disk (the extracolumellar disk) lying beneath the largely undifferentiated skin at the side of the head and attached to this skin by a loose network of fibrous and fatty tissue. The attachment of the disk to the edges of the tympanic opening in the skull is very loose except at the posterior edge, where there is a heavy ligament, the posterior ligament, connecting to the quadrate and squamous bones. A gross displacement of the tympanic membrane causes the extracolumellar disk to move as on a hinge at the posterior ligament. This motion is transmitted through the medial process of the extracolumella to the columella, which is a thin bony rod leading inward to the otic capsule, where it expands to a funnel-like stapes lying in the oval window. The rocking motion of the tympanic membrane produces a piston-like motion of the stapes in the oval window. The question arises whether this rotational mode of movement of the tympanic membrane holds also for the much smaller displacements produced by sounds.

To study this movement, we set the tympanic membrane into vibration by applying to its surface the point of a needle that was driven by a piezoelectric crystal. The crystal vibrator was constructed so as to have great stiffness in the direction of the vibrations and so that the moderate loading involved in this application had only a negligible effect upon the vibratory amplitude. The inner-ear potentials produced by driving the tympanic membrane in this manner were observed as the needle was applied at various points over the membrane surface. A heavy manipulator with graduated scales was used to hold the vibrator and to control its placement. Care was taken to restrict the driving amplitudes to the linear range of operation of the ear.



FIG. 1.—Sensitivity curves for two turtles of the species *Terrapene carolina carolina*. The sound pressure is represented in decibels relative to 1 dyne per square centimeter.

The results of a typical experiment are shown in Figure 2. Here the vibrating needle was first applied at a point somewhat in front of the anterior edge of the extracolumeler disk and then was moved posteriorly by small steps until it was well behind the posterior edge of this disk. At every position the driving current for the crystal was adjusted to produce a constant inner-ear potential of 0.3 microvolt. The result was a curve, as shown, containing sharp breaks at the two ends. Subsequent measurements, made after removing the superficial skin layer, proved that these breaks appeared as the driving point was moved over the anterior and posterior edges of the extracolumellar disk and onto the neighboring tissues, which then communicated the motions to the columellar system in a complicated way. As may be seen, the vibratory amplitude necessary to produce the standard response fell off in a systematic manner as the driving point was moved along the anteroposterior dimension of the disk. If the position on the extreme anterior edge is taken as a reference (0 db.), as indicated in the figure, the necessary amplitude falls

to a value of 40.7 db. less at the extreme posterior edge of the disk. This observation means that the lever ratio of the system is continually changing along this dimension, and the driving point is being moved toward a fulcrum located at the posterior end. It follows that the normal action of the tympanic membrane in response to sound is a rocking motion about the posterior ligament. It is of interest to note that a similar motion of this membrane occurs in higher animals, including man, as best shown by the observations of Békésy.³



FIG. 2.—Relative amplitude of vibration of the tympanic membrane necessary to produce a standard response of 0.3 microvolt when the driving point was varied along the antero-posterior axis. This amplitude is shown in decibels relative to the least effective position at the anterior edge of the extracolumellar disk. Distances from this position are shown on the abscissa in thousandths of an inch. Below the graph a cross-sectional view of the extracolumellar disk is represented on the same scale as the abscissa.

Summary.—The auditory sensitivity of the common box turtle, T. carolina carolina, was measured in terms of the inner-ear potentials. This ear resembles that of other species of turtles studied previously in that it shows keen sensitivity in the region of 100–600 cycles and progressively poor sensitivity for higher and lower tones. The tympanic membrane was found to undergo a rotational mode of movement in response to applied forces, swinging about a hinge formed by its posterior ligament.

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¹ E. G. Wever and J. A. Vernon, "The Sensitivity of the Turtle's Ear as Shown by Its Electrical Potentials," these PROCEEDINGS, **42**, 213–220, 1956.

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³ G. von Békésy, "Über die Messung der Schwingungsamplitude der Gehörknochelchen mittels einer kapazitiven Sonde," *Akust. Z.*, 6, 1–16, 1941.