FURTHER STUDIES OF HEARING IN THE GEKKONID LIZARDS*

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One of the most distinctive groups of lizards is the family Gekkonidae.[1] Most members of this group produce vocal sounds in the form of squeaks or chirps, are of nocturnal habit, have large lidless eyes with vertical pupils, and have adhesive pads on the feet that enable them to climb about on vertical walls and even on rough ceilings.

We have already reported observations by the cochlear potential method on the auditory capabilities of one species of this family, the Tokay gecko (*Gekko gecko*).[2] The present study includes results on two other species, the warty gecko, *Hemidactylus turcicus turcicus*, and the banded gecko, *Coleonyx variegatus bogerti*.   Hemidactylus belongs to the same subgroup as *Gekko gecko*, which is the subfamily Gekkoninae or true geckos, whereas Coleonyx is in the subfamily Euplepharinae or ground geckos.   Coleonyx is unusual among the geckos in that the eyes have movable lids.   Both these lizards are small; our specimens of warty geckos measured 4.7 cm from snout to vent, 10 cm over all, and the banded geckos measured 6.0 cm from snout to vent, 10.6 cm over all.

Procedure.—Our method of recording the cochlear potentials was the same as described earlier for the Tokay gecko, and as used on other lizard species.[3] The animals were anesthetized with ethyl carbamate, the round window was exposed through an opening in the throat region, and a fine bead electrode was placed on the round window membrane.   Sounds were delivered to the ear through a tube sealed over the external auditory meatus, and the resulting potentials were amplified and finally measured with a selective voltmeter.
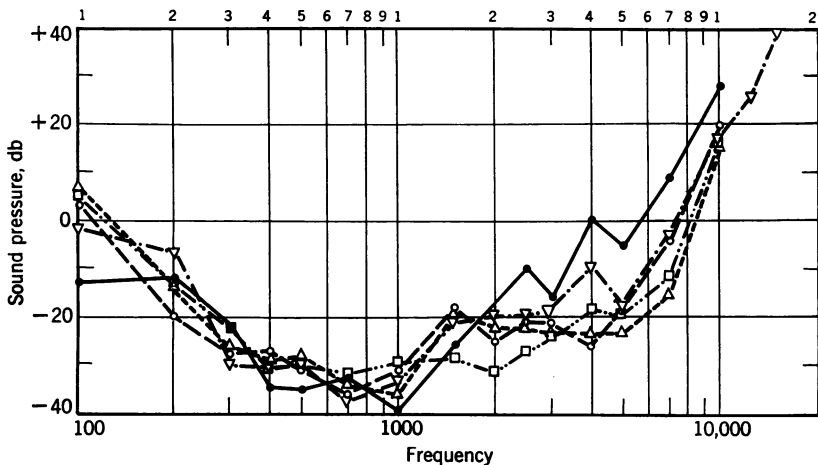

Fig. 1.—Sensitivity functions for 5 specimens of *Hemidactylus turcicus turcicus.* Each curve shows, for a given animal, the sound pressure required at various frequencies to produce a standard response of 0.1 microvolt.
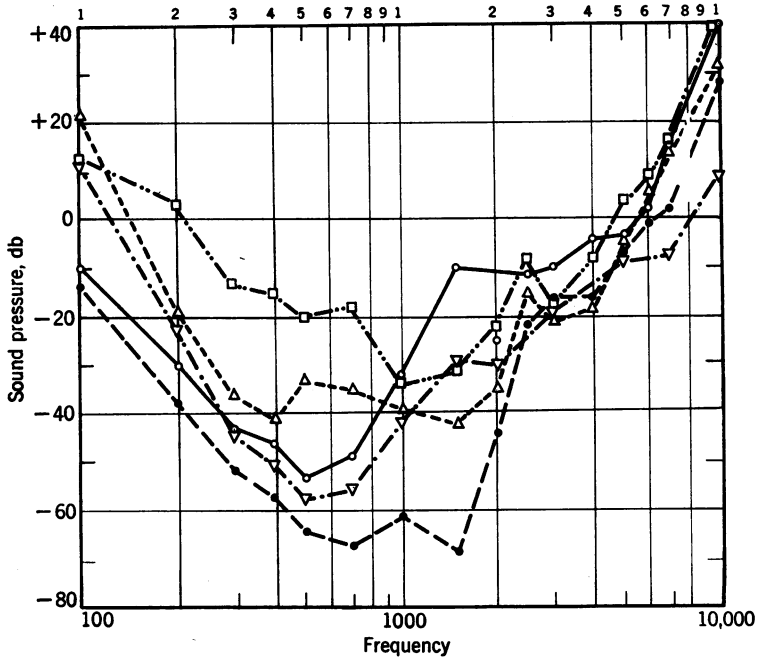
Fig. 2.—Sensitivity functions for 5 specimens of *Coleonyx variegatus bogerti*, plotted as in the preceding figure.
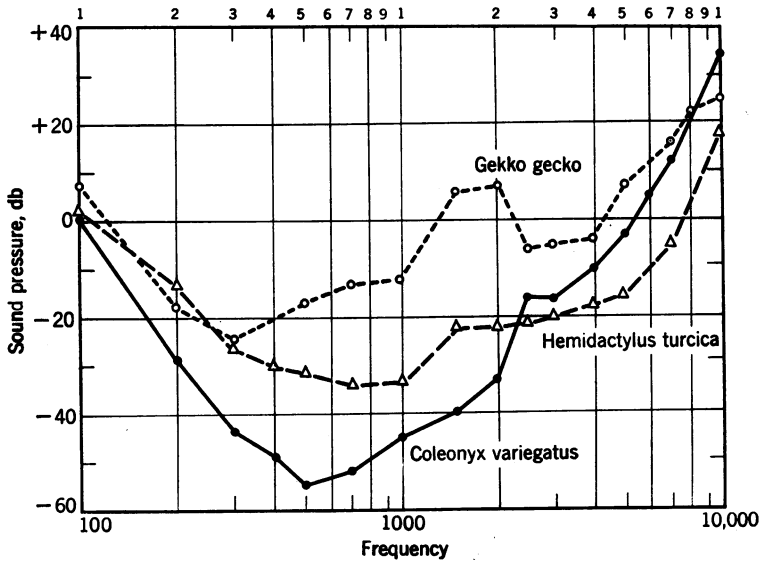

Fig. 3.—Mean sensitivity curves for three species of geckos.

Our base level for the sensitivity measurements was 0.1 microvolt, and to attain so low a level it is necessary to reduce as far as possible all sources of background noise, both instrumental and physiological. Sounds more intense than those necessary for this base level were found often to produce considerable variability of
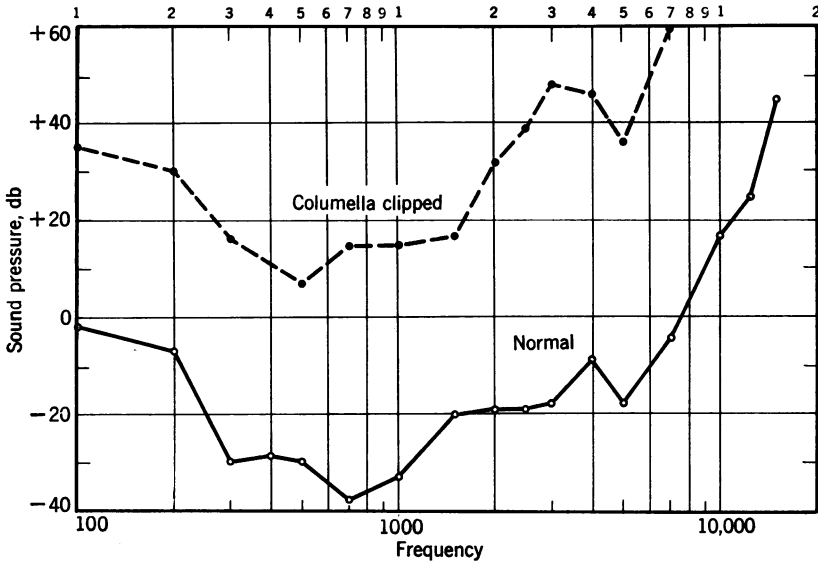
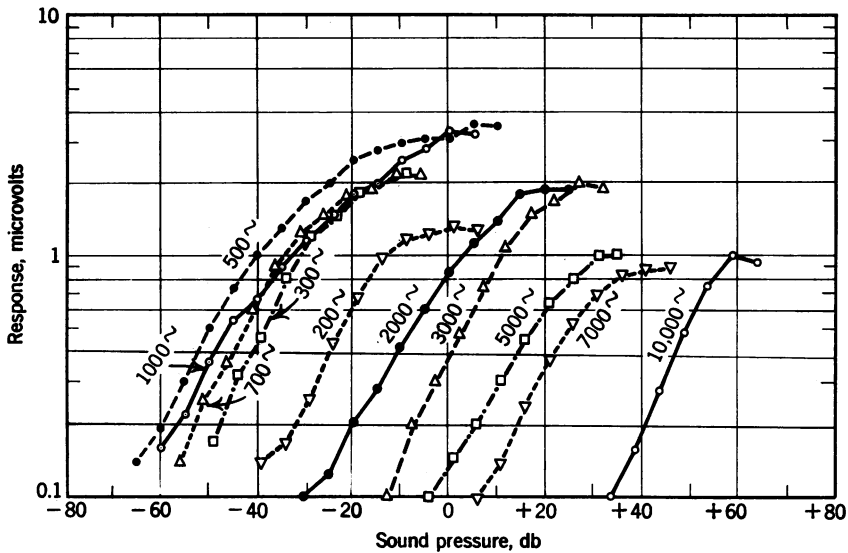FIG. 4.—The effects on sensitivity of an interruption of the columella in a specimen of Hemidactylus.

FIG. 5.—Intensity functions for various tones in a specimen of Coleonyx. Each curve shows, for a given frequency, the varying response in microvolts as the sound pressure is altered.

response, in part, as we believe, because of the arousal of aural muscle action. Extreme levels of stimulation caused damage as shown by the rapid deterioration of the electrical responses. With all animals our first concern was the determination of a sensitivity function, after which various other procedures were carried out.

The animals were maintained at a temperature of approximately 21 °C.

Results.—We show in Figure 1 the sensitivity curves for 5 specimens of *Hemi-*
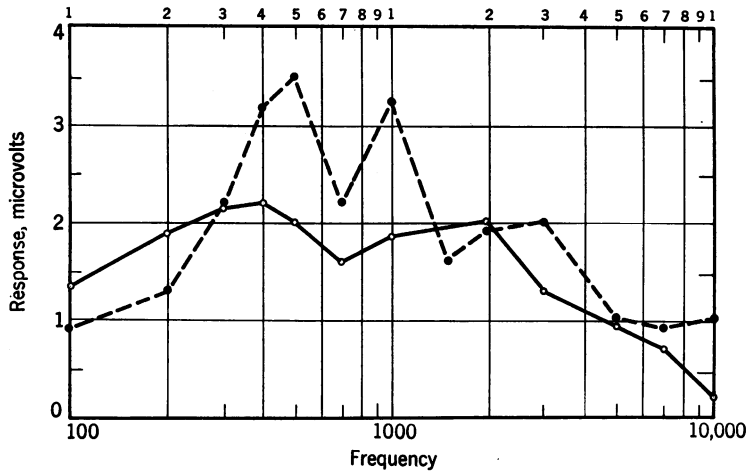
Fig. 6.—Maximum values of response as a function of frequency, in two specimens of Coleonyx.

dactylus turcicus turcicus. The ordinate indicates the sound pressure, in decibels relative to 1 dyne per sq cm, required to produce the standard response of 0.1 microvolt. As may be seen, the curves run fairly close together, with a little more dispersion in the extreme frequencies than elsewhere. The range extended from 100 to 10,000 cycles per sec, except in one animal where measurements were possible up to 15,000 cycles.

Sensitivity curves for Coleonyx are given in Figure 2, likewise for 5 animals. These curves show the same frequency range as the ones for Hemidactylus, but they differ in some other respects. The dispersion is considerably greater, especially in the low and middle frequencies, and for 3 of the animals the sensitivity in the middle range, from 400 to 1000 cycles, is superior to that of any other lizard that we have observed.

We can best compare the sensitivity of these species by averaging the data for the two groups. Figure 3 shows the results of this procedure, and a third curve representing the Tokay gecko has been added from our earlier paper. There are clear differences in the forms of the functions and in the degree of sensitivity exhibited, with the Tokay gecko the poorest and the banded gecko the best in the middle frequency region.

In one of the specimens of Hemidactylus the columella was sectioned, and Figure 4 shows the effects on the sensitivity. The loss varied from 37 db at 100 cycles to 65 db at 7000 cycles, and averaged 48.8 db. It is clear that the middle ear mechanism is of great importance in the reception of sounds.

In a specimen of Coleonyx the sound pressure was varied systematically for a number of tones to obtain intensity functions, as given in Figure 5. These curves show the usual form: the response increases with the sound pressure, in approximately linear fashion, until at a high level it departs from linearity and passes through a maximum. Most of these curves show only a slight decline beyond the maximum because we stopped the run at the first indication that the maximum had been passed. Stimulation beyond the maximum incurs a great risk of damage to
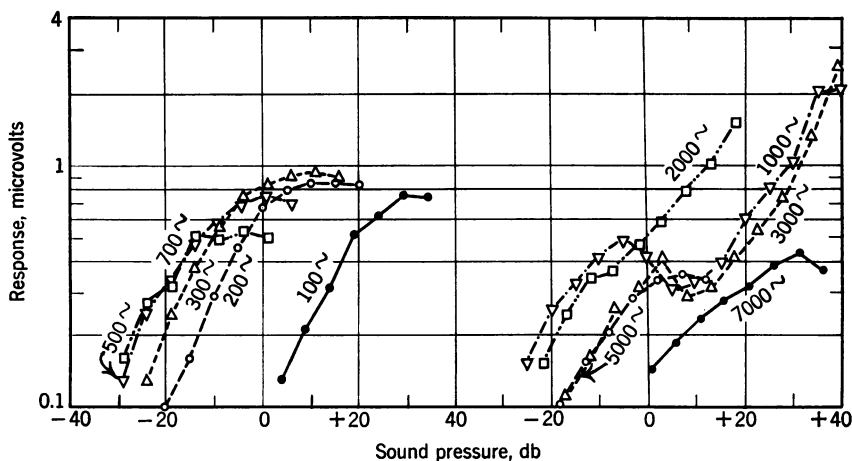
FIG. 7.—Intensity functions for a specimen of Hemidactylus showing certain irregu-
larities of form.

the ear, and such damage must be avoided if the curves for a series of tones are to
be compared. In a number of animals we carried the stimulation well beyond the
maximum, and the result was damage from which there was only partial recovery
over the course of several minutes of rest.

From a set of functions such as those of Figure 5 we may plot a curve to show the
maximum values of response as a function of frequency. Two such curves are
given in Figure 6 for different Coleonyx specimens. These curves show the largest
values in the midfrequency range, and then in the higher frequencies present the
usual decline as the frequency rises.

It is interesting that we find in the responses of the lizard ear the two features
that in the mammals have given support to the conception of changing forms of the
response on the basilar membrane as a function of frequency.[4] The first of these
features is the variation in the form of bending in the region of the maximum, and is
to be seen in the curves of Figure 5. The low tones bend gradually, the high tones
more abruptly. The second feature is the decline in the values of the maximums
for the high tones, and this trend is clearly evident in Figure 6, though there are
some irregularities. The irregularities are at least partly due to our caution in
seeking to avoid injury, which we are sure has sometimes led us to terminate a run
before the full maximum value of response was attained.

The conclusion to be drawn from these features is that the low tones have a pat-
tern of stimulation that involves a great many hair cells in varying degrees, whereas
the high tones have patterns in which fewer cells are strongly stimulated and there
is a sharp transition to other cells that are more moderately stimulated. More-
over, the peaked patterns for the high tones become sharper as the frequency is
increased.

This is the same pattern of differentiation in the cochlea that has been worked
out for the mammalian ear, except that the degree of frequency differentiation in
the lizard cochlea is much less than it is in the mammals. Yet the differentiation
indicated by these results is surprising in view of the anatomical simplicity of the
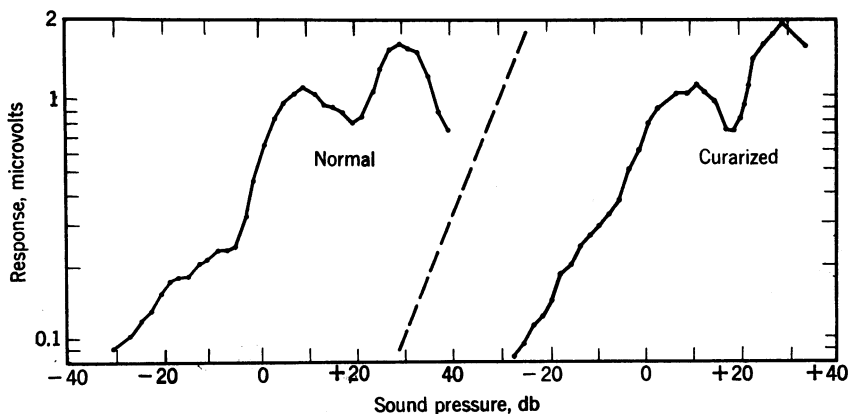inner ear structure.

FIG. 8.—Intensity functions for a specimen of Hemidactylus for a tone of 1000 cycles. On the left is a curve obtained under normal conditions, and on the right a curve obtained after muscle action had been stopped by curarization. For reference, the broken line in the middle of the graph indicates a linear slope on this plot.

The intensity functions are not always as regular as those shown in Figure 5. We show in Figure 7 a series obtained from a specimen of Hemidactylus in which there are two kinds of departure from what we have come to regard as the typical form. One is a failure of the function to show linearity even in its lower portion. The most obvious example in Figure 7 is the curve for 7000 cycles. The second departure is seen in this figure for 1000, 2000, and 3000 cycles; for these tones the curves exhibit a flexure in midcourse, after which they rise rapidly and attain a linear slope at their upper ends. Such curves will eventually bend over if the intensity is carried to a sufficiently high level, but always such levels produce severe and irrecoverable damage.

We have carried out a number of experiments in the attempt to account for these irregularities. The results of one of these experiments are shown in Figure 8. On the left is an intensity function obtained in the usual way in a specimen of Hemidactylus stimulated with a tone of 1000 cycles. This curve from −30 to −5 db has a slope of about 0.26, far below linearity, and it then shifts abruptly to practically a linear form from −5 to +3 db, after which it bends and passes through a maximum. In earlier observations of such behavior we have offered the suggestion that the initial depression of slope is the result of a progressive contraction of middle ear muscles. To test this hypothesis, after the results shown on the left of Figure 8 had been obtained, the animal was given an injection of curare (Intocostrin) to suppress muscle action. An effect was seen in 15 min, and continued for more than one hr. The right-hand curve shows an intensity function obtained after 20–30 min from the injection of the drug. As a result, the slope of the lower part of the curve has increased considerably. It has not attained linearity, and it still fails to do so if we take account of the background noise, but these results show that muscle action is a significant feature in the initial departure from linearity. Some other cause of nonlinearity is yet undisclosed; we can surmise that at these low levels there is sometimes an instability in the action of the hair cells that disappears when the stimulation becomes more vigorous. We have

not seen this feature in the response of mammalian ears, perhaps because in their large populations of hair cells the irregularities of individual cells are ironed out.

A further feature of Figure 8, as seen also in the curves for 1000, 2000, and 3000 cycles in Figure 7, is the flexure beyond the first maximum. The curve of Figure 8 then goes on to pass through a second maximum. This feature does not vanish after curarization, and hence is not a result of muscle action. Such behavior has also been encountered at times in the responses of mammalian ears, both normal and curarized.

The explanation of this feature involves a consideration of the nature of a maximum of response. Such a maximum represents a stage at which many hair cells are being severely overloaded and for a given small increase of stimulus are producing negative increments that are balanced by the positive increments produced by other hair cells that are still in the linear portion of their response curves. A further increase in stimulus intensity depresses the response because the negative increments of these overloaded cells become greater and still other cells enter the overloading region. Finally the most severely stimulated cells are damaged and fall out of the action. The total response then rises because the negative increments of the damaged cells have now been removed. The function rises as before, now involving a somewhat different population of cells, and it passes through another maximum as many of the remaining cells suffer overloading.

Summary.—Our study of hearing in the lizards has been extended to two further species of geckos, the warty gecko *Hemidactylus turcicus turcicus* and the banded gecko *Coleonyx variegatus bogerti*. The sensitivity curves of these species are distinctive, yet follow the general form that has been found for most lizards.

A consideration of the forms of the intensity functions for various tones, and the values of the maximum potentials obtained, lead to the conclusion that tones of different frequency involve the cochlear hair cells in somewhat different response patterns. The frequency differentiation is far less than that of mammalian ears, but is sufficient to indicate that the basic conditions responsible for such differentiation are already present in this primitive ear.

[1] Smith, Hobart M., *Handbook of Lizards* (Ithaca, New York: Comstock Publishing Co., 1946).

[2] Wever, E. G., J. A. Vernon, E. A. Peterson, and D. E. Crowley, "Auditory responses in the Tokay gecko," these PROCEEDINGS, **50**, 806–811 (1963).

[3] Wever, E. G., D. E. Crowley, and E. A. Peterson, "Auditory sensitivity in four species of lizards," *J. Auditory Research*, **3**, 151–157 (1963); Wever, E. G., and E. A. Peterson, "Auditory sensitivity in three Iguanid lizards," *J. Auditory Research*, in press.

[4] Wever, E. G., and M. Lawrence, "The patterns of response in the cochlea," *J. Acoust. Soc. Am.*, **21**, 127–134 (1949); *Physiological Acoustics* (Princeton, N. J.: Princeton University Press, 1954), pp. 300–316.