tion times, which is not surprising since the relaxation times must for large velocities behave as $1/vn\sigma$, and the cross section σ is constant for hard spheres. It seems likely that in the interval $(-4\pi^2, 0)$ there are at least some discrete eigenvalues related to the viscosity and heat conduction of the gas, but no proof is available.[8]

[1] First shown by Hilbert in *Integral Gleichungen* (New York: Chelsea Publishing Co., 1953), chap. 22, p. 276. We will follow the presentation of Carleman, T., in *Problèmes Mathématiques dans la Théorie Cinétique de Gaz* (Uppsala: Almquist and Wilsells, 1957).

[2] Pekeris, C. L., these PROCEEDINGS, **49**, 38 (1963).

[3] Carleman, T., *op. cit.*, p. 77.

[4] For the appropriate theorems concerning completely continuous operators, see, for example, Schatten, R., in *Norm Ideals of Completely Continuous Operators* (Berlin: Springer Verlag, 1960), pp. 16–18.

[5] Carleman, T., *op. cit.*, p. 74.

[6] Although the estimate given here does not preserve the symmetry of $G_3(v, v_1)$, it is easy to show by the same methods that

$$|G_3(v, v_1)| < C\left(\frac{1}{(1+v)^{1/2}(1+v_1)^{3/2}} + \frac{1}{(1+v)^{3/2}(1+v_1)^{1/2}}\right),$$

which is symmetric, and so on for the higher iterates.

[7] Cf. Riesz, F., and Sz.-Nagy, B., in *Functional Analysis* (New York: F. Ungar Publishing Co., 1955), p. 367. The theorem as used here is as follows "THEOREM. If a completely continuous symmetric transformation B is added to a symmetric transformation A, the set of limit points of the spectrum remains invariant." We are indebted to Professor M. Schreiber for pointing this theorem out to us.

[8] *Note added in proof:* Similar results have been obtained by a different method by Grad, H., in *Third International Rarified Gas Symposium* (New York: Academic Press, 1963), vol. I, pp. 26–58.

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*AUDITORY RESPONSES IN THE TOKAY GECKO**

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Most lizards do not produce any vocal sounds, and the faint hiss occasionally heard from a number of them is perhaps only the result of a sudden expiration of air. A notable exception to this rule is the family Gekkonidae, whose members utter cries usually described as chirps or squeaks. Indeed, the name "Gecko" is supposed to be an imitation of the call of the animal.

All geckos are nocturnal, and it has been suggested that the development of vocal capabilities is in some sense a compensation for the lack of visual cues, especially in the mating process. Nearly all species in this family lack eyelids and are provided with an iris that closes almost completely under ordinary daytime illumination.

The species investigated here is the Tokay Gecko, and its scientific name is *Gekko gecko*. One feature is the presence on the dorsal surface of numerous randomly distributed scales that are larger than the others and usually bear a small knob or crest, giving a rough texture to the skin. These animals are distributed

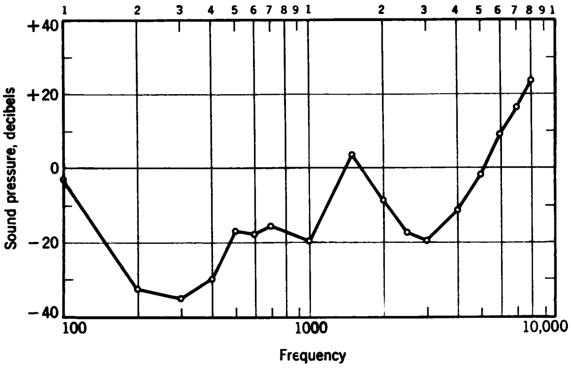

FIG. 1.—Sensitivity function for a lizard, *Gekko gecko*. The curve shows the sound pressure in decibels relative to 1 dyne per sq cm necessary to produce a cochlear potential of 0.1 μv at the frequencies indicated.

throughout Southeast Asia and are one of the commonest species there. They are now found also in a few regions of the United States, having stowed away in ship cargo and then escaped to establish themselves in some of the seaports of the South. Some of our specimens came from India, and others were collected in this country. This is a rather large species of lizard; our specimens measured from 20–23 cm over all, 11–13 cm from snout to vent, and weighed 42–73 gm.

Their attitude is belligerent; when disturbed they open the mouth to its fullest extent, utter a fairly loud cry that may be compared to the sound of a squeaky hinge without high-frequency components, and often follow by making quick lunges at an intruder. Also, if the opportunity is offered, they seize a finger and deliver a vigorous pinch.

The structure of the lizard ear has been studied by a number of anatomists, though not in the detail that is desirable, and many features remain obscure. Evidently there are large species variations in some portions of the mechanism.

In the gecko there is an external auditory meatus of oval cross section, measuring about 2 by 4 mm and obliquely placed at the side of the head. The orifice is provided with a constrictor muscle, and we have observed its closure when the

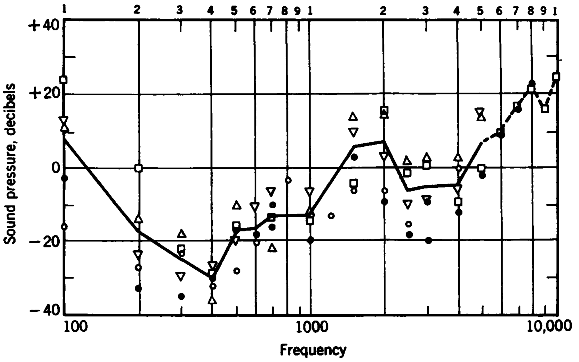

FIG. 2.—Sensitivity data for five geckos, as in Fig. 1. The curve represents mean values.

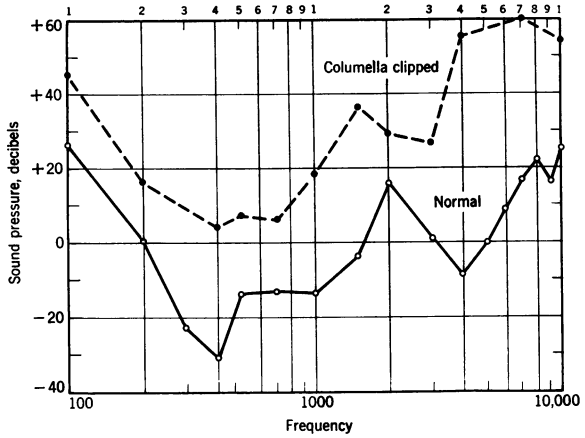

FIG. 3.—The sensitivity of a gecko ear under normal conditions and after interrupting the columella.

animal is disturbed. The opening leads inward about 3 mm to a tympanic membrane 4 by 7 mm in size. Extending from this membrane to the otic capsule is a columellar system made up of two portions. An extracolumella is attached to the tympanic membrane and continues medially to a thin rod, the columella proper, which expands at its innermost end to form the stapes lying in the oval window. There is a round window opening into the pharyngeal cavity, a space only slightly separated from the mouth.

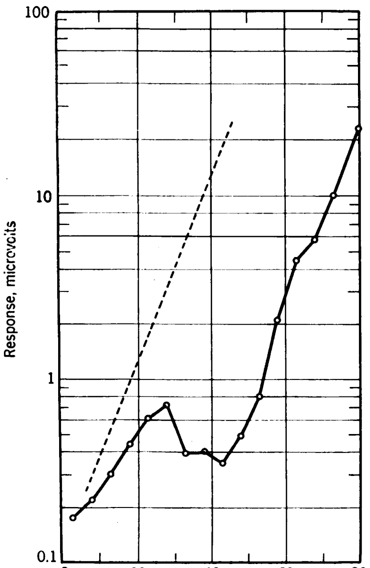

FIG. 4.—Variations of response as a function of sound pressure (solid line). The sound pressure is in decibels above 1 dyne per sq cm. The dotted line shows the slope of a linear function.

Procedure.—Our study of auditory sensitivity in this animal was carried out by placing an active electrode on the round window membrane, with an indifferent electrode in other tissue nearby, and observing the potentials produced on stimulating the ear with tones. The animals were anesthetized with 5% urethane (ethyl carbamate) in Ringer's solution. The dose level was 0.04 cc per gm of body weight. The round window was approached on the right side by an opening made through the lower jaw close to the posterior end of the mandible. The electrode was a silver bead about 0.1 mm in diameter, made by briefly heating a wire of 0.05 mm diameter in a flame.

Sounds were produced with a Western Electric 555 loudspeaker and conducted to the ear through a tube that ended in a sound cannula sealed tightly over the external meatus. A probe tube attached to a condenser microphone ran through the sound cannula and ended near its tip, and this system was calibrated to give measurements of sound pressure for the stimulating tones.

The body temperature of the animals was

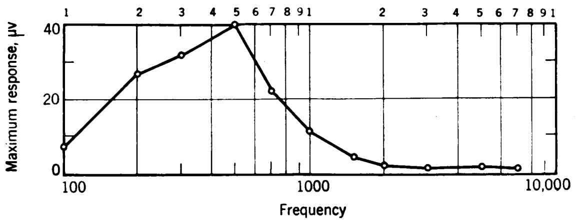

FIG. 5.—Maximum responses obtained for tones over the range 100–7000 cycles.

measured during the experiment and was found to remain in the region of 24 °C.

Results.—The sensitivity was determined by presenting various tones at the sound pressure necessary to produce a response of 0.1 μv. Results for one animal are given in Figure 1. As indicated, responses were obtained over a range from 100–7000 cycles per sec, with the greatest sensitivity in the low tones from 200–400 cycles, and rapidly decreasing sensitivity for tones above 3,000 cycles.

Similar results for five animals are given in Figure 2. Here the different kinds of points represent the individual ears, and the curve shows the mean values. The individual variations are of the order of 20–30 db, but the forms of the functions are much the same for the different ears.

The role played by the columellar system in the transmission of sounds to the inner ear is reflected in the results of Figure 3. The solid line shows a normal sensitivity curve, with the columellar system intact, whereas the dashed curve shows the sensitivity after an interruption of the system made by clipping the columella in two places, leaving a gap. The losses as a result of this interruption range from 16 to 62 db, with a mean value of 31 db. In the cat a similar interruption of the ossicular chain has been found to impair the ear's sensitivity by an average amount of 28 db.

In numerous animals the cochlear potentials have been found to increase linearly as a function of sound pressure at low and intermediate levels, and then for extreme pressures to depart from linearity, pass through a maximum, and then decline sharply as overloading becomes severe. An attempt was made to obtain intensity functions of this kind for the gecko, but with little success. We found that when the sound pressure was raised even moderately above the level necessary to produce potentials of 0.1 μv the responses became highly irregular and often varied as much as 30 db during a single observation. We attribute these variations to the action of middle ear muscles.

An attempt to exclude the action of these muscles by increasing the depth of anesthesia—a procedure that works fairly well in mammals—was unsuccessful within the limit at which respiration was impaired and the animal died. We had the impression that the variability was reduced at deeper levels of anesthesia, but not to the point where reliable measurements were possible. Also, we were unable to fatigue the muscle action by the protracted application of strong tones; rather, this procedure seemed to produce a sensitization of the action so that even the fainter tones for a time gave variable responses.

Some results that illustrate the effects of the muscle action are given in Figure 4. Here the sound pressure was varied over a range of nearly 80 db for a tone of 500 cycles. The response rose at first at a rate a little below linearity, then fell sharply over a range of nearly 20 db before rising again, after which it continued to rise at practically a linear rate as the sound pressure was increased further. We interpret these results to mean that the middle ear muscles underwent in the beginning a slight increase of tonus and then contracted sharply around 30 db so as to reduce the transmission appreciably, increasing this contraction for the next two steps of stimulation. At this point it appears that the muscles had reached their limit of contraction, where they remained as the stimulation was further increased. The response therefore follows a linear course for this upper portion of the function, though it is about 35 db below what it would be without the muscle action. The dotted line on this graph suggests what the course of the response would be if the response continued to be linear beyond its lowermost values up to a sound pressure of 50 db (316 dynes per sq cm). We should not expect the linear course of the function to extend much farther than this because of the entrance of overloading at high levels.

We have referred here to "middle ear muscles," but we are not able at this time to be as specific as we would like about their number or identity. The anatomical literature on the gecko and on lizards in general gives scanty information on the aural muscles. There is evidence that a muscle is present in the gecko that is variously called a stapedius muscle (Killian[1]), or musculus laxator tympani (Gaupp[2]), but perhaps better named the musculus extracolumellaris (Versluys[3]). It runs from the hyoid arch to the posterior accessory process of the extracolumella. The extracolumellar structure is highly complex, and it is possible that other muscles are concerned in the restraint of the columellar motions. This question is being studied further.

Because of the irregularities in the auditory potentials at high levels we were usually not able to determine maximum responses to the different tones with any great degree of reliability. Figure 5 shows the results of our attempts at such measurements in one animal. Plotted here are the largest potentials that we were able to record under the conditions. The values shown for frequencies above 500 cycles we regard as fairly close to true maxima, but those for lower tones are probably reduced appreciably by muscle action and might well approach 40 μv if such action were excluded.

Discussion—The sensitivity shown by this ear is somewhat below that found by the cochlear potential method in mammals[4] when the comparison is made between the most favorable regions of frequency for each species. The cat, for example, shows the greatest sensitivity in the region of 7,000 cycles, and is superior to the gecko's sensitivity at 300 cycles by about 30 db. If we make the comparison in the low frequencies, the difference is less, though still in favor of the cat's ear. In comparison with other reptiles the gecko shows up a little more favorably. Its sensitivity lies about midway between that of snakes[5] and turtles;[6] it is about 10 db better than snakes and 10 db poorer than most turtles. However, it is inferior to the caiman[7] by about 30 db. Thus, we find among the reptiles a considerable range of sensitivity, with the lizards occupying an intermediate position. No doubt these variations will be found to correspond to differences in structure of the middle and inner ears, but these points remain for further exploration.

* This investigation was supported by grants from the National Institute of Neurological Diseases and Blindness, U. S. Public Health Service, aided by a contract with the Office of Naval Research, and by Higgins funds allotted to Princeton University. Permission is granted for reproduction and use by the United States Government.

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COMPOSITION OF THE NUCLEUS AND CHROMOSOMES IN THE LAMPBRUSH STAGE OF THE NEWT OÖCYTE*

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A lampbrush chromosome is metabolically active at many sites all along its axis.[1, 2] This is in marked contrast to other interphase chromosomes, in which a few loci are active while most are relatively inactive,[3, 4] and also in striking contrast to mitotic chromosomes, which appear to be metabolically inert, though they are being moved about.[5] Since lampbrush chromosomes are so active metabolically, it is of interest to know about their composition and to compare it with the composition of other chromosomes. In this paper we present determinations of the deoxyribonucleic acid (DNA), ribonucleic acid (RNA), and protein contents of lampbrush chromosomes and of the nuclei containing these chromosomes.

Lampbrush chromosomes occur in the growing oöcytes of many different animals.[6] In our work we have used oöcytes of the newt, *Triturus viridescens*. Chromosomes of ordinary size are present in the oöcyte both before and after the period of growth; presence of giant lampbrush chromosomes in the oöcyte only at the time of growth points, therefore, to a correlation between the massive synthesis of cytoplasm and the formation of the enormous chromosomes with their lateral extensions, the so-called loops.[7, 8]

Other well-known giant chromosomes are the polytene chromosomes of dipteran larvae.[3] The puffs of these chromosomes are sites of marked accumulation of protein and nucleic acid,[9, 10] and puffs of polytene chromosomes may perhaps be compared with the loops of lampbrush chromosomes, for both puffs and loops are