of a wild avian population. In this case, premigratory hyperphagia would be of particular interest. Previous studies of energy input in migratory species have been limited to captive populations (*3*). However, daily variations in environmental stimuli (for example, temperature or precipitation) as well as the more gross changes of season may elicit adaptive changes in energy input which could be missed in captive birds. In wild populations of birds like the mourning dove which may feed in a way amenable to quantitative evaluation, the influence of such environmental factors may be evaluated. If analyses of energy input could be combined with techniques for evaluation of the metabolism of migratory birds in their natural habitat (*4*), a complete picture could be obtained of the bioenergetics of migratory habit.

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5. Research supported in part by NSF grant G-16830 and by a University of North Dakota faculty research stipend.

12 August 1965

Electrical Output of Lizard Ear: Relation to Hair-Cell Population

Abstract. *Cochlear potentials measured in several species of lizard show a close correlation between maximum electrical output and number of hair cells, whereas there is no uniform relation to sensitivity. These results are interpreted as indicating structural differentiation and frequency discrimination in spatial terms in the more advanced lizard ears.*

We have reported measurements of cochlear potentials on 11 species of lizards (*1–5*), and data are now available on two other species. The most represented families in our observations are the Iguanidae with five species and the Gekkonidae with three (Table 1).

Our object has been to investigate the character of hearing in this group of reptiles, and especially to explore the range of species variations in auditory function in relation to the structure of the ear. Such a study is related to the problem of the evolution of the vertebrate ear, and may provide clues concerning the origins of the more complex auditory mechanisms found in birds and mammals. This paper presents results on two basic aspects of ear performance, sensitivity and maximum output, in relation to the level of inner-ear development.

Sensitivity is measured as electrical output compared to sounds of known magnitude; more truly stated it is the sound pressure required to produce some constant amount of cochlear potential. Sensitivity, when measured in this way, is the inverse of the required sound pressure: the less sound required the greater the sensitivity. For the range of frequencies for which responses were obtainable, our measurements show the sound magnitude in decibels, relative to a pressure of 1 dyne/cm^2, that must be applied to produce a standard potential of 0.1 μv at the round window of the cochlea.

The maximum output for a given sound stimulus is taken as the first point on the intensity function beyond which an increase in stimulus intensity leads to a reduction in electrical potential. This is a maximum in a mathematical sense, and it is often possible to drive the ear to yield outputs greater than this maximum value, though always at the risk of permanent injury.

Our measure of the degree of inner ear development is the number of hair cells contained in the auditory papilla resting on the basilar membrane. This number varies greatly among lizard species, from less than 100 in most iguanids to about 1600 in the Tokay gecko (*Gekko gecko*).

For the study of electrical potentials the round window of the cochlea on the right side was approached through an incision in the throat region, and an active electrode was placed on the round-window membrane, with another electrode in indifferent tissue near by. A curve for sensitivity was obtained by presenting pure tones of various frequencies at the sound pressures necessary to produce a potential of 0.1 μv (root mean square). These potentials were read directly on a selective voltmeter. The changes in the magnitude of the electrical response were then observed over a range from the minimum detectable up to where the response showed overloading and passed through a maximum.

When intensity functions are determined for a number of tones throughout the range of a given animal, it is then possible to draw a curve of maximum responses for this ear. Such curves have been obtained for several of our animals, and observations on others are sufficient to show the general level of the maximums though they do not represent the complete function. The maximums produced in the different species varied significantly from 0.4 μv in the alligator lizard (*Gerrhonotus multicarinatus*) to over 50 μv in the Tokay gecko.

After the observations of cochlear potentials were completed a number of the animals—usually three or four of each species—were prepared for histological examination. While still under anesthesia the animals were perfused through the heart, first with Ringer's solution for a few moments to clear the blood vessels and then with a form of Maximow's solution for a period of 20 to 40 minutes to fix the tissues. The head, with only moderate trimming, was prepared by the celloidin process and sectioned serially in a plane transverse to the long dimension of the auditory papilla. Through the ear region every section was stained and mounted. For most of the specimens a staining procedure was used (hematoxylin, orange G, and azocarmine) that provided special differentiation of the hair cells.

The hair cells of the auditory papilla were counted in every section; they were observed with an oil immersion objective (×1400). Hair-cell counts were made on both ears, though electrical measurements had been made only in the right ear.

For each species electrical potentials were measured in some ears, but the ears were not prepared histologically. Alternatively, for many ears (all left ears plus both ears of a few other animals), the histological preparation was not preceded by electrical study. Consequently there are two ways of handling the data. In one way ("same ear" method) the electrical measurements may be compared with the hair-cell counts in the very same ears.

This is the most straightforward procedure, though it leaves out many of the data. By the other method ("species average") the data obtained from a given animal, whether cochlear potential measurements or hair-cell counts, are considered representative of the species, and the averaged potential data are compared with the averaged hair-cell counts for each species. This procedure includes all the observations, but the ears contributing to the averages that are compared are only partly the same.

In our calculations we have used the best sensitivity for each ear: this is the sound level in decibels required for the standard potential in the region of frequency where the animal is the most sensitive. This region varies in different species from 300 to 400 cy/sec in the Tokay gecko to 1500 to 2500 cy/sec in the Colorado sand lizard *Uma notata*. We have also used the largest value of the maximum observed in a given ear, which likewise varies in its region of frequency for the different species. In general, this region is the same as the region of best sensitivity or is the region immediately below.

Figure 1 shows a graph of best sensitivity relative to hair-cell count, the "same ear" method being used. A correlation for these data determined according to the Pearson product-moments formula has a value of 0.33. A correlation obtained by the "species average" method has a value of 0.24. These correlation coefficients reflect the wide scatter of the data and indicate a slight relation (not significant) between sensitivity and numbers of hair cells. Indeed, the correlation that appears is determined to a considerable extent by the presence of the three specimens of Persian lacerta (*Eremias velox persica*) that appear in Fig. 1 at the lower left. As shown, these animals have few hair cells and extremely poor sensitivity. Their sensitivity is so poor that their inclusion in this group is questionable, and some factor yet undiscovered may impair their hearing. If these three animals are excluded the correlation falls to 0.22 for the "same ear" method and to 0.19 by the "species average" method, even more insignificant values.

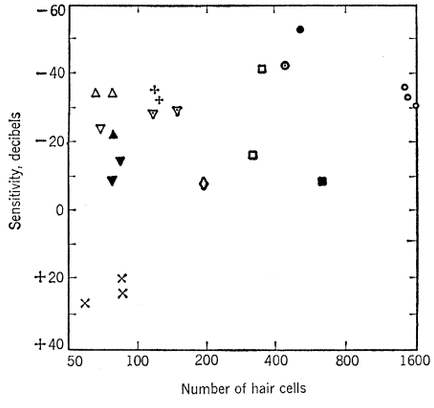

Fig. 1. The relation between best sensitivity and numbers of hair cells in 22 lizard ears, representing 13 species (correlation coefficient, 0.33). In this figure and the next, species are identified as follows: *Sauromalus obesus*: inverted dotted triangles; *Sceloporus magister*: inverted filled triangles; *Sceloporus clarkii*: upright filled triangle; *Uma notata*: upright open triangles; *Urosaurus ornatus*: inverted open triangles; *Gekko gecko*: open circles; *Coleonyx variegatus*; filled circles; *Hemidactylus turcica*: dotted circles; *Gerrhonotus multricarinatus*: plus signs, *Ophisaurus ventralis*: diamonds; *Eumeces obsoletus*: filled squares; *Cnemidophorus tesselatus aethiops*: open square, *Eremias velox persica*: Xs.

Figure 2 shows a graph of the largest maximum values of cochlear potentials relative to hair-cell count, the "same ear" method being used. The correlation coefficient for these data is 0.82. The coefficient obtained by the "species average" method is 0.90. This relation is highly significant: a large hair-cell population in a given ear leads to the production by an intense sound of a large maximum of cochlear potential.

If the ear of an animal were quite undifferentiated and every hair cell were stimulated equally well and in the same fashion by every tonal stimulus, we should expect the sensitivity as measured by the cochlear potentials to be a direct function of the number of hair cells present.

The results of these experiments do not show any significant improvements in sensitivity with an increase in hair-cell population. We must look for a differentiation of the lizard ear through which some of the hair cells are more readily stimulated than others by a given sound.

There are three types of variation in the physical properties of the responsive structures that could produce this differentiation. These are variations in mass, elasticity, and friction. Our preliminary examinations of the structure of the inner ears of the various species of lizards used in these experiments indicates that these three physical characteristics do indeed vary in the different species. In some species there is considerable uniformity

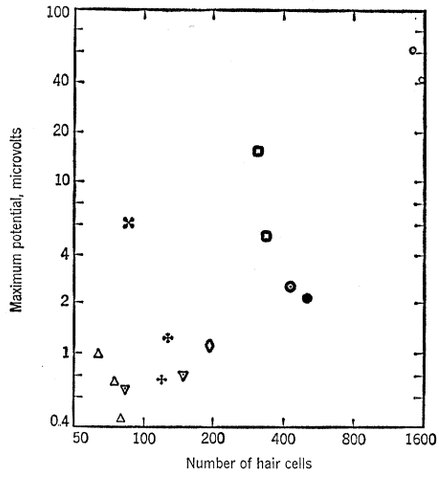

Fig. 2. The relation between the largest maximum of cochlear potential and numbers of hair cells in 15 individual lizard ears, representing ten species (correlation coefficient, 0.82).

along the basilar membrane in its width and thickness and in the bulk of the sensory structures borne by the membrane. In other species these properties vary widely along the basilar membrane. Thus the conditions for differentiation are present in the more advanced types of ears. A sound stimulus acting upon a differentiated ear will involve certain hair cells strongly and others less so, and the action will show an intensity pattern with some degree of focusing.

These same conditions will produce a frequency differentiation as well. Not

Table 1. Lizards on which cochlear potentials have been measured.

Genus and species	No. of specimens
Iguanidae	
Sauromalus obesus	5
Sceloporus magister	5
Sceloporus clarkii	3
Uma notata	5
Urosaurus ornatus	2
Gekkonidae	
Gekko gecko	7
Coleonyx variegatus	6
Hemidactylus turcica	5
Anguidae	
Gerrhonotus multicarinatus	4
Ophisaurus ventralis	4
Scincidae	
Eumeces obsoletus	2
Teiidae	
Cnemidophorus tessellatus aethiops	3
Lacertidae	
Eremias velox persica	5

only will a given tone produce a varied pattern of amplitudes, but different tones will have patterns that differ from one another. A particular tone will act most strongly upon a region of the basilar membrane where the mechanical conditions are most favorable. The sensitivity to this tone will be determined by the general conditions of tuning and the size of the region responding to this tone, and it will not be influenced to any considerable extent by the total number of hair cells in the cochlea. Another ear that is less differentiated may show equal sensitivity to this tone because all or a large proportion of the hair cells present enter vigorously into the action.

A difference in the performance of differentiated and relatively undifferentiated ears will appear, however, when the sound intensity is raised to high levels. The ear with few hair cells, all performing in much the same manner, will reach a limit early, when perhaps half the hair cells have passed their individual maximums and are giving decrements as the stimulus intensity is increased. Raising the sound to still higher levels carries the remaining hair cells into the decremental portions of their individual functions, so that the total response undergoes a rapid decline (*6*).

In the ear with many hair cells and frequency differentiation, the response to a given tone will continue to rise as the intensity is increased because large numbers of hair cells on the fringes of the principal region are able then to make a significant contribution to the output. At moderate levels of stimulation their contributions are small, but, as the stimulation increases and the hair cells in the favored region pass their maximums and produce negative increments of response, these fringe cells continue to increase their output, and assume a new importance in the total action. A maximum is reached when all their contributions are balanced by the large negative increments of the overstimulated cells of the primary region. At this high level of stimulation all the cells of the cochlea are making significant contributions to the output. Hence a close correlation exists between the total number of hair cells and the highest value of the maximum.

The presence of a large maximum in the ears of certain lizards points to an extended dynamic range in these animals. The more extended range has an obvious value in the greater variety and precision of representation of the intensive aspects of acoustic stimuli.

The existence of a measure of structural differentiation in some of the lizard species is perhaps unexpected. Up until now the reptilian ear has generally been regarded as primitive and lacking in many of the important qualities that make hearing one of the dominant senses in birds and mammals. Our evidence suggests the need for a new evaluation of the lizard ear and of the reptilian ear in general and a consideration of how this ear serves in adaptive behaviors. The value of an ear depends directly upon the number and nicety of the discriminations that may be made on a basis of the information that it presents. From our evidence it appears that many of the lizards have progressed far beyond an elementary stage in the process of hearing, and have reached a level of development in which there is both intensity and frequency differentiation of considerable degree.

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24 August 1965

Heterothallism in Biflagellate Aquatic Fungi: Preliminary Genetic Analysis

Abstract. *Genetic analysis of several hundred progeny from crosses of two heterothallic species of* Achlya *and* Dictyuchus *provides preliminary information about the life cycle and pattern of sexuality in the biflagellate Phycomycetes. Extensive testing of mycelial progeny indicates a diploid life cycle. Control of sexual expression and mating competence appears to be based on a complex genetic system.*

A distinctive pattern of sexuality characterizes the heterothallic members of the biflagellate, phycomycetous orders, Saprolegniales, Leptomitales, and Peronosporales (*1, 2*). Each heterothallic species of these orders typically consists of a linear series of sexual strains, each of which, with the exception of the two terminal strains, interacts as male or as female, depending upon its position in the series relative to that of its mate. The two terminal strains typically react in a single sexual capacity. In addition, the sexual reproduction process in *Achlya*, and probably in the other genera, is initiated and coordinated throughout its entire course by a series of specific, diffusible hormones (*3*).

Genetic analysis of this system has been thwarted for many years by our inability to induce significant numbers of oospores to germinate. Sansome (*4*), however, has published cytological evidence that indicates strongly that meiosis occurs during the maturation of the antheridium and oogonium in *Pythium debaryanum*, rather than during oospore germination (*5*), with the result that the gametes are the only haploid phase in the life cycle. Sansome also reported "similar unpublished evidence for *Phytophthora cactorum* and *Achlya sp*" (*4*).

We have succeeded in germinating several hundred oospores from two typical heterothallic species belonging to the genera *Achlya* and *Dictyuchus*.

Mature oospores, held at 2°C for several weeks, thinly spread upon water agar, and incubated at 23°C, germinated at very low frequency (less than 1 percent) in 1 to 3 days (*6*). Each germling consists of a multinucleate germ tube that develops into a germ sporangium if transferred to water or into an extensive coenocytic mycelium if it is in the presence of nutrients. The established mycelium can also be induced to form zoospores by transfer to water.

It is thus possible to test either the mycelium directly derived from the germinating oospore or many mycelia mitotically derived via uninucleate zoospores. For example, with *Achlya ambi-*