*HEARING IN THE BLACKFOOTED PENGUIN, SPHENISCUS DEMERSUS, AS REPRESENTED BY THE COCHLEAR POTENTIALS**

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Communicated May 14, 1969

Abstract.—A study of the hearing of the penguin *Spheniscus demersus*, in terms of the cochlear potentials, showed sensitivity over a range at least of 100 to 15,000 Hz, with the best sensitivity in the region of 600 to 4000 Hz. The form of the sensitivity function is consistent with the vocalizations of these animals. In general, this species of penguin shows good agreement with other birds in both the form and range of auditory sensitivity.

The auditory capabilities of one species of penguin, *Spheniscus demersus*, commonly called the Blackfooted or Jackass Penguin, were investigated by means of the cochlear potentials. This is one of the smaller penguin species, breeding on islands off the western coast of South Africa. Three animals were used for the observations.

The animals were anesthetized with ethyl carbamate, administered intraperitoneally in a 20 per cent solution at a dosage of 0.01 cc per gram of body weight. During the experiments the animal rested on a heating blanket, and a body temperature of 38°C was maintained by means of a temperature probe in the cloaca that led to a regulating instrument.

The middle ear cavity was exposed by a lateral approach, as indicated in Figure 1. The right side of the head is shown, with the region of the skin incision indicated. The removal of skin and muscle tissue in this region exposed the poster-

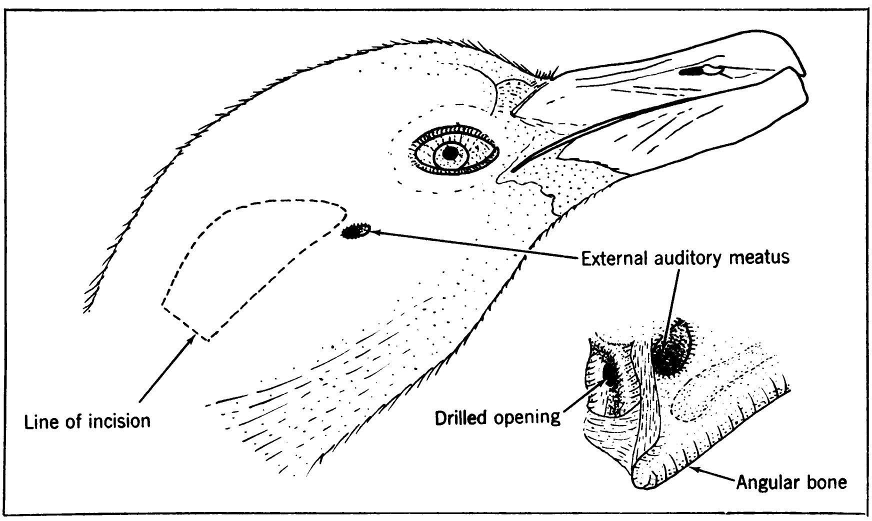

Fig. 1.—Outline drawing of the head of *Spheniscus demersus*, seen from the right side. The region of the incision is indicated. *Inset:* the area exposed by removal of skin and muscle tissues.

olateral surface of the exoccipital bone, as shown in the inset at the lower right of the figure. A hole drilled in this bone exposed the middle ear cavity. Figure 2 gives the view through this opening from a posterior direction and shows the oval window with the stapedial end of the columella largely covering it and the columellar shaft extending forward and laterally. The round window lies lateral and ventral to the oval window, with an interfenestral process separating the two. An active electrode, consisting of a wire tipped with a silver bead of 0.3-mm diameter, was placed in contact with the round-window membrane. Two other electrodes, located in inactive tissues in the same region, provided a differential recording of the round window potentials.

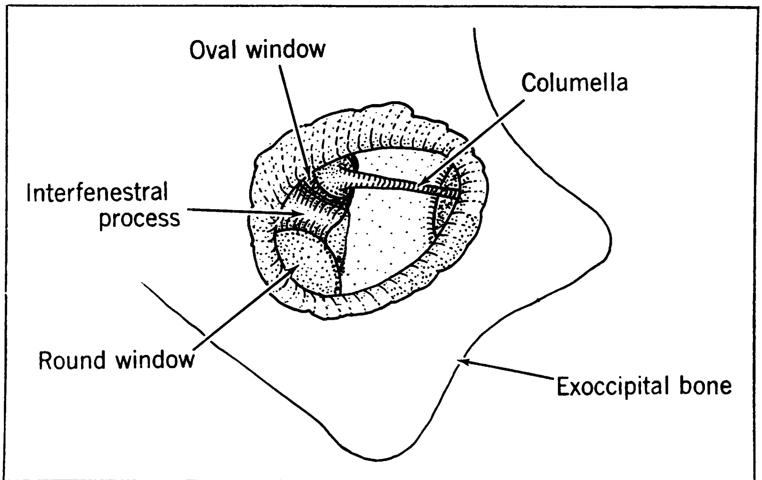

FIG. 2.—View of the middle ear cavity, obtained by drilling a hole in the lateral surface of the exoccipital bone.

The preparation was located in a soundproofed and electrically shielded chamber, and sounds from a loudspeaker were conveyed through the wall of the chamber by a tube with its end sealed over the external ear opening. Running concentrically with the terminal portion of this sound tube was a probe tube that led to a condenser microphone, and the probe tube and microphone system were calibrated to indicate sound pressures at the terminus of the tube and hence at the entrance to the external auditory meatus. All the observations were made on the right ear.

Sounds were produced by a dynamic type of loudspeaker (Western Electric type 555) and covered a range of 100 to 15,000 cycles per second (Hz). Tones below 100 Hz were not employed because of the high level of physiological noise for such tones, and tones above 15,000 Hz were avoided because the required intensities involved the risk of damage to the ear. A tone synthesizer, used to generate alternating currents over this range, gave precise determination of frequencies (within 1 cycle). These currents were passed through a variable attenuator to a power amplifier and then through a second variable attenuator to the loudspeaker. The two attenuators were controlled with a special switch that included a totalizing mechanism with a numerical display; this device afforded rapid setting of tonal intensity and eliminated the human error of reading and summing a number of dials.

Figure 3 gives the sensitivity curves for the three animals. These curves show on the ordinate, for a number of tones, the sound pressures in decibels relative to a level of 1 dyne/sq cm required to produce a standard response of 0.1 μv at the round window.

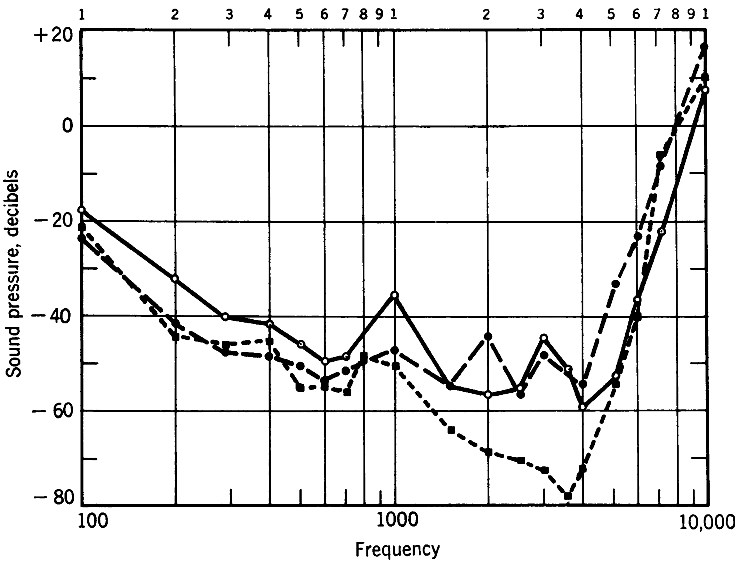

FIG. 3.—Sensitivity curves for three specimens of the Blackfooted penguin *Spheniscus demersus*. Shown is the sound pressure, in decibels relative to 1 dyne/sq cm, necessary to produce a cochlear potential of 0.1 μv.

The three functions are in good agreement over most of the frequency range, but one of them shows significantly keener sensitivity in the region from 1500 to 4000 Hz. For all three ears the range from 600 to 4000 or 5000 Hz seems to show the best auditory acuity. Above this range the acuity falls off precipitously. The observations at 15,000 Hz are not indicated on the graph, but their points fall precisely on the projected curves. The rate of decline of sensitivity beyond 4000 Hz is about 60 db per octave.

In two of the animals intensity functions were obtained by observing the varying output while increasing the sound level in steps of 5 db. Three of these functions for one of the animals are given in Figure 4. As has been observed in a great variety of animals, the electrical output of the ear is a linear function of sound pressure (except as it may be disturbed by noise) at low and intermediate levels and becomes nonlinear at high levels. We see here a good approximation to linearity in the lower portion of the curves, and then a departure from linearity that is at first slight and increases progressively. In these tests the sound intensity was not carried high enough to produce the flattening and then the decline of the function that are often seen, since we wished to avoid the damage to the ear that may result from a very high level of stimulation. In a single instance, for one of the animals, a tone of 1000 Hz was carried to a level of 1000 dynes/sq cm, at which the curve began to bend downward.

At the end of these experiments the ears were perfused in preparation for a histological study of details of the structures of the middle and inner ear.

Our animals produced vocalizations that are best described as grunts and brayings. To our ears the sounds seemed predominantly low-pitched. Tape recordings made on other individuals of this same species by Dr. P. P. Kellogg of the Laboratory of Ornithology of Cornell University were studied by means of a sound spectrograph. This analysis showed, in line with our preceptions, that the principal energy of the vocalizations lies below 2000 Hz. It was somewhat surprising, however, to find that there is appreciable energy in the range above 2000 Hz all the way to 6000 Hz and a little beyond. The spectrographs showed further that the "grunt" and the "bray" have about the same frequency composition and differ only in duration. Another component of the "bray," which is the inspiration phase following the prolonged expiration phase of 1.5–1.7 sec, mainly contains frequencies between 1200 and 1700 Hz, with a lesser admixture of frequencies around 3000 Hz.

The vocalizations reported here are probably not the only ones of which these birds are capable; they are the ones that were readily noticed and that could easily be recorded. There is reasonable agreement between the frequency pattern of these vocalizations and the region of best sensitivity of the ears as measured by cochlear potentials.

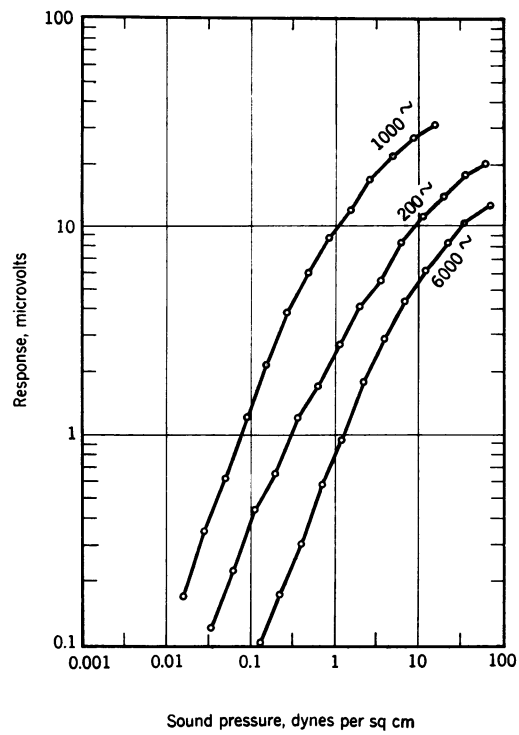

FIG. 4.—Intensity functions for a specimen of *Spheniscus demersus*.

The form of the sensitivity function as observed for these penguins is surprisingly similar to what we know about the auditory sensitivity of other bird species. Wever and Bray in 1936 used the cochlear potential method to study the auditory sensitivity of the pigeon and found maximum sensitivity at 3000 Hz.[1] In 1948, Schwartzkopff determined the threshold sensitivity of bullfinches (*Pyrrhula p. minor*—Brehm) by a training method, and found the best sensitivity at 3200 Hz.[2] In a summary of observations on a number of different species of birds, Schwartzkopff showed that for most the best sensitivity lies in the region of 1000–3000 Hz, although in a few—especially the owls—it lies appreciably higher.[3] Our penguins therefore show good agreement with the smaller birds in their region of best sensitivity.

They show good agreement also in their upper frequency range. In general, birds appear to have upper limits of frequency around 12,000 to 20,000 Hz, though a few may go a little higher—to as much as 25,000 Hz. In this respect it is notable that birds are inferior to most of the mammals whose hearing has been suitably investigated in the high frequencies. Many of these hear tones up to 50,000 Hz and some as far as 100,000. Our penguins were so poorly responsive at 15,000 Hz that we did not wish to run the risk of damage to their ears by testing at still higher frequencies, and we consider that 15,000 Hz may be regarded as their practical limit.

We express our thanks to Dr. P. P. Kellogg of the Laboratory of Ornithology, Cornell University, for the use of tape recordings of penguin vocalizations.

* From the Department of Psychology. This investigation was supported by grants from the National Institute of Neurological Diseases and Stroke, U.S. Public Health Service, and was also aided by a contract with the Office of Naval Research and by Higgins funds allotted to Princeton University.

[1] Wever, E. G., and C. W. Bray, "Hearing in the pigeon as studied by the electrical responses of the inner ear," *J. Comp. Psychol.*, **22**, 353–363 (1936).

[2] Schwartzkopff, J., "Die Hörschwellen des Dompfaffen," *Naturwissenschaften*, **35**, 287 (1948).

[3] Schwartzkopff, J., "Uber die Gehörsinn der Vögel," *J. Ornithol.*, 91–103 (1952).