The Oilbird: Hearing and Echolocation

Abstract. *Oilbirds can navigate in total darkness by echolocation. The sound energy in their sonar cries is unevenly distributed over the range from about 1 to 15 kilohertz, with a dominant frequency range of 1.5 to 2.5 kilohertz. This corresponds to the most sensitive range of their hearing as determined by neurophysiological methods. Behavioral tests in their home cave indicate that the smallest object avoided by them is a disk 20 centimeters in diameter.*

The oilbird, *Steatornis caripensis*, is endemic to the neotropical region. Since its description by von Humboldt in 1799, this inhabitant of the dark has fascinated naturalists (*1*). The ability of the oilbird to navigate in totally dark caves, where it roosts and nests, requires that it possess some sort of nonvisual guidance system. The use of sonar by oilbirds is suggested by the sharp audible clicks they produce as they fly in their caves and while under dark canopies during nightly foraging excursions. Griffin (*2*) confirmed that the oilbird uses echolocation: He observed that three captive oilbirds collided with the walls of a darkened room when their ears were plugged, whereas they avoided the walls when their ears were unplugged.

Several important questions about the nature of echolocation in this species remain unanswered. What sound frequencies can the oilbird hear? How is sound energy in the sonar signal distributed? How small an object can the oilbird detect by echolocation? In order to answer these questions we carried out laboratory and field experiments on oilbirds in Trinidad.

Five birds were collected at the Oropuche Cave, which contained a colony of about 600 birds (*3*). The birds were brought to an outdoor aviary for behavioral observations (*4*). In the aviary were many beams, pillars, and large hanging objects; the only light sources were the stars of a moonless night (*5*). Nevertheless, upon release the birds could fly and avoid all obstacles without emitting any sound. When a blindfold blocked their frontal visual field, however, the captive birds began to produce clicks continuously during flight. They ceased to click upon landing on the ground or on perches. These observations indicate that the production of clicks is associated with nonvisually guided flight. Since the blindfolded birds tended to hover in one place, however, it was impossible to determine whether they were in fact using their clicks for echolocating obstacles.

After the behavioral tests, the auditory physiology of these same birds was studied to determine their hearing range. The birds were anesthetized with urethane (*6*). Cochlear potentials and evoked potentials from the forebrain auditory nucleus were recorded with Teflon-coated tungsten electrodes (*7*). Cochlear potentials were recorded through a hole made in the bone near the round window. Sound stimuli were tone bursts delivered from a loudspeaker with a special adapter that guided the sound into the ear canal in a closed system (*8*).

Auditory evoked potentials as well as cochlear potentials vary according to the threshold of hearing. Although absolute

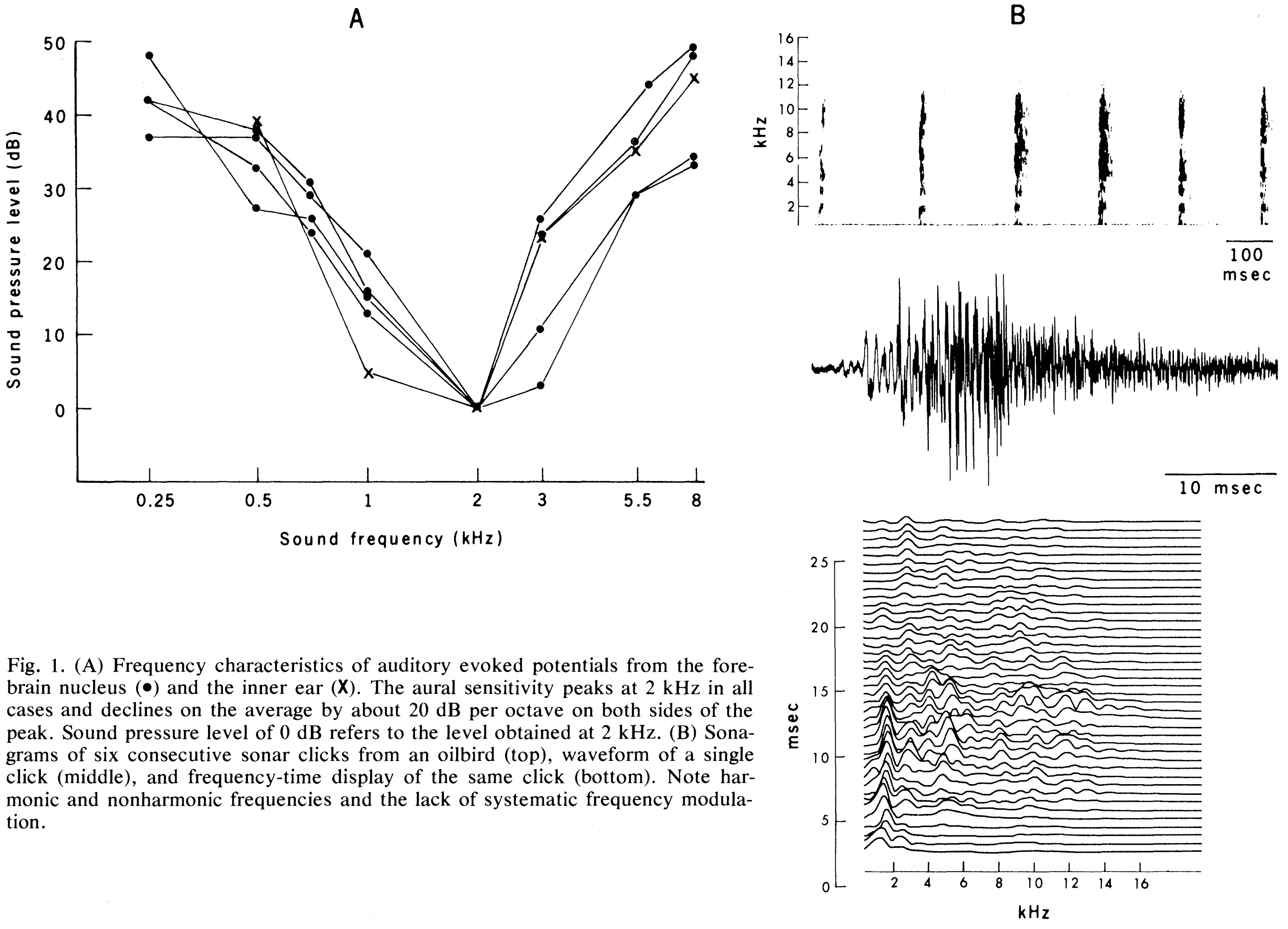

Fig. 1. (A) Frequency characteristics of auditory evoked potentials from the forebrain nucleus (●) and the inner ear (X). The aural sensitivity peaks at 2 kHz in all cases and declines on the average by about 20 dB per octave on both sides of the peak. Sound pressure level of 0 dB refers to the level obtained at 2 kHz. (B) Sonagrams of six consecutive sonar clicks from an oilbird (top), waveform of a single click (middle), and frequency-time display of the same click (bottom). Note harmonic and nonharmonic frequencies and the lack of systematic frequency modulation.

0036-8075/79/0427-0425$00.50/0

auditory thresholds cannot be directly derived from these potentials, the shape of the function can be established by determining how the sound level to evoke a constant potential varies with frequency. The frequency-intensity functions of the auditory potentials, determined in five separate measurements in four birds, are presented in Fig. 1. Auditory sensitivity reaches a maximum at 2 kHz, beyond which it declines by about 20 dB per octave. The oilbird's ear is insensitive to frequencies above about 6 kHz. Correlated with these results are differences in the dynamic range (*9*) of the potentials for different frequencies. At 1 and 2 kHz the dynamic range was as much as 35 dB, whereas at 8 kHz it was less than 15 dB.

The results suggest that the oilbird must use relatively low frequencies for echolocation. According to Griffin (*2*), the oilbird's sonar signal consists of bursts of very brief (1 to 1.5 msec) pulses containing a mean dominant frequency of 7300 Hz. If this were true, the emitter and receiver would be poorly matched indeed. In order to obtain more precise information about their temporal and spectral structure, sonar signals of three captive oilbirds were tape-recorded at close range as each bird hovered in the nearly anechoic enclosure of a small outdoor aviary (*10*). The amplitude-time display of sample signals exhibits some pulsatile structure to which Griffin referred; the interval between major sound pulses may be rather constant in some cases (Fig. 1). Griffin called these pulses clicks. It would seem, however, more appropriate to call a whole burst of pulses a click because (i) the "burst" contains a complex waveform with some pulsatile elements rather than a series of discrete pulses, (ii) it is this burst unit that increases in its repetition rate during echolocation and not the pulses within it, and (iii) what the human ear registers as an oilbird click is not one of the pulses but the whole burst.

A click, as we propose to redefine it, has a fast rise time and a slower decay, its main sound energy being contained in the first 15 to 20 msec. Spectral analysis of sample clicks confirms the subjective impression that they contain a great deal of energy at relatively low frequencies (< 6 kHz) (*11*). The sound energy is unevenly distributed over the range from about 1 to about 15 kHz, with a dominant frequency range in the first half of the click of 1.5 to 2.5 kHz (Fig. 1). This frequency distribution corresponds well with the oilbird's audible range.

The amount of sound reflected is a function of object size and signal wavelength. Since the oilbird uses low frequencies (long wavelengths) in echolocation, objects resolved by its sonar system must be relatively large. This prediction was borne out by obstacle avoidance tests performed within the cave. The tests required that oilbirds detect and avoid plastic disks strung across their main passageway (Fig. 2). As our test site we chose a narrow section of the cave about 3 m wide and about 7 m high, so that the birds were forced to approach the disks normal to their surface. Protruding from the corridor ceiling were many stalactites of various lengths and diameters. Birds usually increased the rate of clicking as they approached these natural obstacles and passed through the space just under them. The test objects were hoisted up to occupy that space (*12*).

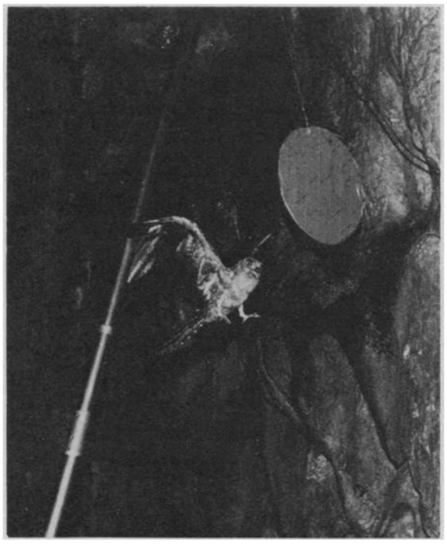

Fig. 2. An example of obstacle avoidance tests. In this photograph an oilbird comes to a rapid stop in midair and hovers momentarily before a disk 35 cm in diameter.

Disk diameters of 5, 10, 20, 25, 30, 35, and 40 cm were tested, one at a time (*13*). Small disks (5, 10, and 20 cm) were presented in a square array consisting of rows and columns of disks affixed to a fine nylon netting. The size of the array was adjusted so that disks were spaced apart by 5*d*, where *d* is disk diameter. The number of disks in each array was adjusted to maintain the total disk surface area at 1256 cm^2; hence, 64 disks of 5 cm, 16 of 10 cm, and 4 of 20 cm were used. The larger disks were tested singly by suspending them with fine wire (Fig. 2).

The tests were performed on three separate nights. On the first night, we observed the birds' reactions to a wide range of disk sizes in order to determine roughly the smallest diameter to which birds showed avoidance responses. On the second and third nights, previous observations were confirmed with a narrower range of disk diameters. We observed the birds with an infrared telescope (Javelin 221) as they hit or dodged the disks. Hits were those cases in which the bird's body collided with the disk. Dodges referred to active avoidance of the disk; passes without any sign of avoidance were not regarded as dodges. Because our presence at the testing site seemed to disturb the birds, we could not accumulate large numbers of trials. We thus relied more on the qualitative observations of behavior than on quantitative criteria to determine whether or not they avoided a given disk. Usually only one bird passed the test area at a time in the direction of the cave entrance, bird traffic in the other direction being rare. This implies that the same bird seldom came back to the testing site during the experiment.

All birds hit 5- and 10-cm disks as if nothing had existed in their paths. The first sign of avoidance appeared when 20-cm disks were presented and all birds avoided the 40-cm disk. Prior to an avoidance maneuver, we often noted an increase in the rate of sonar clicks. Many birds came to a rapid stop, hovered momentarily in front of the disks, then turned around and flew away. Some birds swerved under or to the side of the disks after detecting them (Fig. 2).

Since the obstacles were placed in their familiar passageway, inattention on the part of the birds might have resulted in their colliding with disk sizes that they might otherwise have avoided. Their tendency to increase their click rates as they approached the corridor, however, suggests that the birds were paying attention to a fair degree.

Other factors that affect echolocation are the many sources of sonic interference present in a cave: the highly echoic surrounding of a cave causes multiple echoes from a single click; simultaneous or closely spaced clicks from other birds can cause jamming; and noises from water running in a cave are often loud enough to produce masking effects. Animals that use ultrasonic sound solve some of these problems by directional broadcasting and hearing of signals. Some bats use special anatomical structures to beam their sonar signals, and they restrict the area they sample with their highly directional external ears (*14*). The oilbird, on the other hand, has no pinnae and uses low frequency sonar signals, features that reduce the directionality of their echolocating system (*15*).

The direct and correlated evidence

presented in this report shows that the role of echolocation in the oilbird is the detection of relatively large objects. The oilbird's sonar system is crude in comparison with those of many insectivorous bats. Other animals known to use low frequency sonar systems include cave swiftlets *Collocalia* and the fruit bat *Rousettus*. Like the oilbird these animals echolocate only when the light is too dim to permit navigation by vision, and their signals are band-limited noises lacking systematic frequency modulation. The only aspect of echolocation in which these species differ radically from the oilbird is their reported ability to detect very small objects. *Collacalia vanikonensis granti*, using frequencies between 4.5 and 7.5 kHz, was said to have detected wires as thin as 6 mm in diameter. Similarly, one *Rousettus aegyptius* using perhaps 10 to 12 kHz, avoided wires as fine as 0.46 mm in diameter (*16*). It is difficult to reconcile these results with our observations of the oilbird (*17*).

MASAKAZU KONISHI
ERIC I. KNUDSEN
Division of Biology, California Institute of Technology, Pasadena 91125

References and Notes

1. D. R. Griffin, *Listening in the Dark* (Yale Univ. Press, New Haven, 1958).
2. ———, *Proc. Natl. Acad. Sci. U.S.A.* **39**, 884 (1954).
3. A collecting permit was obtained from the Forestry Division, Trinidad.
4. The aviary was a wire net enclosure 8 m wide by 10 m long and located at the former William Beebe Tropical Research Station, Simla, Trinidad.
5. Film rated as ASA 400 exposed for 1 second at F 1.4 did not show any sign of exposure. The luminence computed from the above data is less than 0.318×10^{-2} cd/ft^2.
6. When 1.6 ml of 20 percent urethan (20 g of ethylcarbamate in 100 ml of water) was injected in a single dose into a bird weighing about 450 g, good anesthesia was induced, but no evoked potentials could be recorded from the forebrain nucleus. Cochlear potentials were still present, however. The same amount of urethan injected in many steps over a period of 1 hour did not abolish forebrain evoked potentials.
7. In order to reduce frequency biases due to the tonotopic organization in the forebrain nucleus, evoked potentials were recorded with a large electrode (1 mm of tip exposed) at several different loci in the nucleus.
8. A special battery-operated instrument containing oscillator, pulse generator, and electronic switch circuits was used. Cochlear potentials were obtained with continuous tones; forebrain potentials were evoked with tone bursts. For frequencies higher than 1 kHz, the duration of tone bursts was 4 msec with rise and decay times set at 1 msec. Longer durations were used for lower frequencies to include more cycles per burst. Sound frequencies were measured with a digital counter. Evoked as well as cochlear potentials were amplified with an amplifier (Grass P15) and displayed on an oscilloscope (Tektronix) for voltage measurement. Sound pressure level was controlled with a decade attenuator and was monitored with a calibrated 12 mm condenser microphone (Bruel and Kjaer), the output of which was displayed on the oscilloscope for voltage measurement. Since the sensitivity and stability of the condenser microphone was susceptible to high humidity, we also calibrated the loudspeaker with our own ears (E.K.), which were later calibrated with an audiometer.
9. The dynamic range is that range over which evoked or cochlear potentials vary as a function of stimulus sound level.
10. Sonar clicks were recorded with a tape recorder (Nagra 111) and a microphone (Sennheiser MKH 105) at a tape speed of 39 cm/sec. The frequency response of both instruments was essentially "flat" from 50 Hz to 20 kHz. Since the aviary was on top of a hill and was made of fine wire netting, it was largely free of echoes in the frequency range involved.
11. The spectral analysis of sonar clicks was made by W. Heiligenberg using a Fast Fourier Transform program on a computer (PDP 11/40). The recordings were played back on the same tape recorder at one-half the recording speed. The analog data were sampled at 50 kHz.
12. This part of the cave was totally dark at night.
13. The disks smaller than 20 cm were made of plastic sheet 6 mm thick. The larger disks, made of 6-mm Masonite sheet, were covered with plastic tape to reduce sound absorption and water damage.
14. J. A. Simmons, *J. Acoust. Soc. Am.* **46**, 1054 (1969).
15. A rough test of aural directionality was made by comparing the amplitude of cochlear potentials as a function of speaker location. We also brought back a dead specimen to our laboratories in Pasadena for this purpose. The original shape of the ear canal and drum was carefully restored before these measurements. A curved probe tube 1 mm in diameter and 3 cm long was inserted through the external meatus so as to place its open end in front of the eardrum. The tube was connected through an adapter to a calibrated 12-mm condenser microphone (B & K). Sound level was measured with a wave analyzer as a function of speaker location. A special device was used to move a 5-cm speaker around the bird's head as described by E. I. Knudsen, M. Konishi, and J. D. Pettigrew [*Science* **198**, 1278 (1977)]. The results show little directionality for frequencies lower than 4 kHz and some location-dependent irregularities in sound level at 6 kHz.
16. D. R. Griffin and R. A. Suthers, *Biol. Bull.* **139**, 495 (1970).
17. The sonar signal of *Rousettus* contains frequencies from about 10 kHz to about 50 to 60 kHz [G. Sales and D. Pye, *Ultrasonic Communication by Animals* (Wiley, New York, 1974)]. There is some disagreement as to its hearing range; in *R. aegyptius*, A. M. Brown [*J. Comp. Physiol.* **83**, 407 (1973)] found that auditory sensitivity is maximum at 11 to 12 kHz, and declines sharply on both sides of that range, while A. D. Grinnell and S. Hagiwara [*Z. Vergl. Physiol.* **76**, 82 (1972)] found a broad response range from 10 to 100 kHz in *R. amplexicaudatus*.

18. We thank D. R. Griffin, W. Heiligenberg, G. A. Manley, I. Lambie, J. Price, J. Simmons, and N. Suga. Supported by a grant from the National Geographic Society.

26 December 1978

Thyroxine Increases Nerve Growth Factor Concentration in Adult Mouse Brain

Abstract. *The effects of thyroxine and propylthiouracil on nerve growth factor concentrations in cerebral cortex, cerebellum, and brainstem of adult male mice were assessed by using a sensitive radioimmunoassay for the β-subunit of mouse nerve growth factor. Thyroxine administration significantly increased the concentration of nerve growth factor in all three brain areas compared to control values, whereas propylthiouracil was without effect. These results suggest that thyroid hormones stimulate nerve growth factor synthesis in the mature central nervous system, and raise the possibility that the influence of thyroid hormones on central nervous system development might be mediated or influenced by nerve growth factor.*

Nerve growth factor (NGF) is a protein that is essential for the maturation and maintenance of adrenergic neurons in sympathetic ganglia (*1*). The recent observations that brain tissue contains both NGF (*2*) and NGF membrane receptors (*3*) suggest that NGF may play an important role in central nervous system (CNS) function [reviewed in (*4*)]. We have found that administration of thyroid hormone to adult male mice significantly increases NGF content and concentration in submaxillary gland and liver (*5*). Because thyroid hormones affect brain growth and maturation in postnatal rodents (*6, 7*), we conducted a study in adult male mice to examine the possibility that thyroid hormones affect NGF in the mature CNS, using a recently developed specific and highly sensitive radioimmunoassay (RIA) for the biologically active β-subunit of NGF.

Table 1. Body and thyroid gland weights in control, PTU-treated, and T_4-treated adult male mice. Each value is the mean ± S.E. (N = 10).

Group	Body weight (g)	Thyroid weight (mg per 100 g body weight)
Control	38.2 ± 1.4	7.6 ± 0.8
PTU-treated	36.8 ± 1.2	41.8 ± 2.7*
T_4-treated	42.5 ± 1.9	7.2 ± 0.6

*Significantly different from controls at $P < .001$.

The β-NGF was purified by the method of Mobley *et al.* (*8*) and was used as both iodination and reference preparations. The antiserum to 2.5*S* NGF used in this study was provided by H. Herschman. The sensitivity of the RIA is 13 pg per assay tube with an intraassay coefficient of variation of 7 percent. Of the substances tested for immunological cross-reactivity (*9*), only mouse epidermal growth factor produced significant displacement (11 percent at a dose of 100 μg/ml). Parallel labeled ligand displacement was observed for all tissues studied, including brain.

Three groups of ten adult male Swiss-Webster mice were used. One group served as controls; the second was treated with 12 daily intraperitoneal injections of 25 μg of L-thyroxine (T_4); the third group received 0.05 percent propyl-