VOLUME 9, NO. 2 Summer 1991

SEEING IN THE DARK
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by M. Brock Fenton

Bats perform at night many of the activities necessary for their survival, sometimes accomplishing the feat in total darkness. Without using their vision, many bats can find food and avoid obstacles with great ease. Man has long marvelled at this ability, but it remained a mystery until only recently.

Lazarro Spallanzani, an Italian scientist in the late 1700s, provided the first insights on how bats operated in the dark. He put a bat and an owl in a semi-dark room and found that both could orient well in low light. The bat also flew effortlessly in complete darkness, but the owl bumped into objects in its flight path. When he placed a sack over the bat's head it, too, became disoriented. Spallanzani concluded that bats used a "sixth sense" to orient, but he was not satisfied that he had the answer. He shared his results with other scientists and encouraged them to conduct experiments of their own to solve the problem.

Charles Jurine, a Swiss zoologist, added significant information by showing that blocking one of the bat's ears also prevented it from orienting. Spallanzani then devised new experiments, later concluding that bats could "see" with their ears, perhaps using sound. The idea seemed preposterous and was rejected by most of his colleagues. Spallanzani's conclusion remained an interesting, but untestable, hypothesis.

It was not until 150 years later, in the 1930s, that Donald R. Griffin, then an undergraduate at Harvard University, went to work on Spallanzani's "bat problem." Using special microphones, Griffin showed that bats produce sounds above the human range of hearing. His discovery revealed that they use the *echoes* of these ultrasonic, high frequency calls to *locate* objects. He coined the term "echolocation" to describe this behavior, referring to the ability of bats to orient themselves by using the echoes of sounds they produce. Echolocation, the sonar "sight" of bats, is analogous to the sonar* used by the military. Because it is produced by living organisms rather than by machines, it is often called "biosonar."

Although we most often associate echolocation with bats, other animals have also developed this sense. Toothed whales, porpoises, some species of shrews and tenrecs, oilbirds, and several species of swiftlets all use echolocation. It is also sometimes attributed to seals, rats, and humans, but the evidence for this is not conclusive.

Contrary to popular belief, not all bats can echolocate, nor, as we shall see, do they all use the same approach to echolocation. The order to which bats belong, the Chiroptera, consists of two suborders, the Microchiroptera and the Megachiroptera. Microchiropterans typically are small insectivorous bats, are found worldwide, and have well-developed echolocation

abilities. Nearly 70% of the world's bat species fall into this group.

Megachiropteran bats are found only in the Old World tropics, are usually large-bodied, and feed on fruit, nectar, and pollen. They rely mainly on vision and olfaction to find food and are often referred to as flying foxes because many have dog-like faces. Most do not echolocate, although Egyptian fruit bats (*Rousettus aegyptiacus*) use echolocation to find their way in the caves where they roost.

The elaborate facial ornamentations of some microchiropteran bats are thought to be associated with echolocation, but a direct relationship between the two is not always clear. Bat facial structures show enormous variation, ranging from small triangular shaped noseleaves, to spear-shapes, to convoluted labyrinths of folds and wrinkles. They abound in most of the Old World and New World leaf-nosed bats, horseshoe bats, and false vampire bats, but are absent in most north temperate bats--the species with which most of us are familiar. Research with the short-tailed fruit bat (*Carollia perspicillata*), a tropical New World species, reveals that the position and shape of its noseleaf affects the pattern of sound radiation from the bat.

Not all vocalizations produced by bats are echolocation calls. The squeaks and squawks that bats make in their roosts do not fall into this category, nor do the calls that mother and young make to one another, or those that feeding bats make to defend their foraging territories. To echolocate, a bat must produce a particular type of sound and be able to hear and use the echoes that rebound from objects in its path.

An echolocating bat registers each outgoing sound pulse and compares the originals to returning echoes. The time lapsed between generating the outgoing sound and receiving an incoming echo provides an accurate assessment of a target's distance from the bat. Changes in the amplitude (intensity) and frequency (pitch) of the outgoing sound provide data about the nature of the target (e.g., size, shape, surface structure, velocity, etc.).

All microchiropteran bats produce echolocation calls using vocal cords in their voice boxes, or larynges. In contrast, echolocating Egyptian fruit bats make echolocation sounds by clicking their tongues. Different species broadcast calls in different ways, some emitting calls from the mouth and others through their nostrils. Oral emitters fly with their mouths open, and nasal emitters fly with their mouths closed. Remarkably, both kinds of bats can chew food and vocalize at the same time.

Incoming sounds, including echoes, are collected by the bat's external ears, or pinnae, before they are funnelled into the rest of a bat's hearing system. The great variation in bat ear design reflects differences in sound-collecting ability and the requirements of different species, and this in turn reveals something about the diversity of bat echolocation strategies.

Processing information from returning echoes involves an overwhelming array of complex operations in a bat's brain. In this respect, bats are biotechnical marvels, and not surprisingly, the subject of considerable study by biologists, medical doctors, the U.S. military, and others interested in the study of how animals hear. The military alone spends hundreds of thousands of dollars each year to study echolocation in bats and marine mammals.

The echolocation calls of bats can be classified in several ways. Although the calls of most are not audible to the human ear, the loudness of bat echolocation calls can still be measured. This is expressed in decibels (dB), and for comparison is usually measured at a

fixed distance from a bat's mouth (at 10 centimeters or about four inches). Intense echolocation calls measure 110 dB or more (equivalent in strength to a smoke detector alarm). Faint echolocation calls measure as little as 60 dB (the intensity level of a normal human conversation).

Little brown bats (*Myotis lucifugus*) and big brown bats (*Eptesicus fuscus*) are examples of high intensity, or "shouting," echolocators, while northern long-eared bats (*Myotis septentrionalis*) or common vampires (*Desmodus rotundus*) are examples of low intensity, or "whispering," bats. In many cases, call intensity is related to foraging habitat. Bats that feed in open spaces produce the most intense calls. In contrast, those that forage in cluttered areas, such as deep in a forest, usually produce lower intensity calls.

If some bats produce sounds equivalent in strength to a smoke alarm, why then can we not hear bat echolocation? The answer lies in the frequency or pitch at which the calls are produced. Frequency is measured in kilohertz (kHz). Humans hear sounds ranging up to 20 kHz, while most bats use a broader range (from about 9 kHz to 200+ kHz). Most bat echolocation calls are high in frequency, well beyond the range of human hearing, but we can hear the echolocation calls of some species. Spotted bats (*Euderma maculatum*), for example, produce calls that cover frequencies from 9 kHz to 15 kHz. Like the calls of many free-tailed *(Tadarida* spp.) and sheath-tailed bats (e.g. Old World *Taphozous* spp.), they are clearly audible to us.

Most echolocating bats do not produce calls at a constant frequency (CF). Calls usually start at one frequency and sweep down to another (frequency modulated, or FM, calls). In some cases, bat calls have both a CF and an FM component. The FM portion of a call provides a bat with information about the texture of an insect target and its position in horizontal and vertical space, while the CF component relays information about the insect's velocity. Harmonics or overtones, which are multiples of the sound frequencies used by the bat, further assist in pinpointing the insect's location.

Calls that span many frequencies are called broadband and are typical of the many microchiropterans that hunt flying insects in uncluttered open spaces. Narrowband calls, as the name implies, cover a narrower frequency range, focusing a lot of energy within a small range of frequencies. According to engineers studying call design, echoes from broadband signals provide an echolocator with the most detailed information about its target.

These different types of echolocation calls provide bats with different information. Low frequency, narrowband calls increase a bat's detection range, but because lower frequencies have longer wavelengths, they provide less detail about a target. The advantage is that they increase the echolocation signal's effective range. To obtain complete information about a target's distance and about the target itself, bats often switch from narrowband to broadband signals as they detect and close in on their prey.

Flexibility in call design is directly related to flexibility in hunting behavior. Bats that prey on airborne insects in open areas face a relatively straight-forward problem. They must find, follow, and evaluate hard targets moving against a soft background (the air). In contrast, species that hunt prey near or on vegetation have a more complex acoustical environment to cope with. Surface-gleaning bats therefore use different echolocation call types than bats that take insects from the air. The calls of gleaners are shorter, more broadband, and lower in intensity than those of bats that hunt airborne prey. Some bats combine both foraging tactics, but others are more limited in their flexibility and therefore are more restricted in their hunting repertoires.

Echolocation allows bats to evaluate targets with precision. Despite this, it has serious drawbacks for animals that operate in the air. Air absorbs, or attenuates, the energy contained in sound waves. High frequency sounds have relatively short wavelengths and are much more vulnerable to atmospheric attenuation than are those of low frequency, which have long wavelengths. The booming bass of a stereo illustrates how low-frequency sound can carry for considerable distance (much more so, for example, than the high frequency sound of a flute).

Atmospheric absorption reduces the operational range of echolocation in air and appears to limit its effectiveness to a maximum of about 50 feet. Only the few bat species that emit very low frequency echolocation calls are able to reach even this distance. Laboratory studies with big brown bats (covering frequencies of 60-30 kHz), have shown that these animals are quite "near-sighted," first detecting a 3/4-inch sphere at about 16 feet.

The length of each echolocation call, and the rate at which they are produced, changes according to the situation. Calls can be relatively long, up to 50 milliseconds (ms, or thousandths of a second), or very short (less than one ms long). A bat searching for an insect typically produces longer calls than one going in for a kill. For example, when a red bat (*Lasiurus borealis*) is looking for insects (the search phase), it produces calls 8-12 ms long, averaging about 10 calls per second. As it zeroes in on a target (the approach phase), it shortens the length of its calls as well as the interval between them. In the terminal phase of an attack, right before a bat makes its kill, calls are only one or two ms long and are produced in a rapid volley of about 200 per second. Electronic devices called bat detectors allow the human ear to perceive these various components of a bat's echolocation bouts (see "Tuning in with a bat detector," page 15).

When a long, narrowband echolocation call strikes the body of an insect that is beating its wings, the returning echoes reflect a rhythmic, but constant, pattern. When the insect's wings are at the top or bottom of a wingstroke, for example, they reflect sound from a larger surface than when they are in a horizontal position. The ability to distinguish the flutter patterns of flying insects is well developed in bats using constant frequency echolocation calls. Included in this group are horseshoe bats (*Rhinolophus* spp.), Old World leaf-nosed bats (*Hipposideros* spp.), and Parnell's mustached bat (*Pteronotus parnelli*). There are about 120 species of *Rhinolophus* and *Hipposideros*, which live only in the Old World. In the New World, Parnell's moustached bat is unique in using this CF approach to echolocation.

Structures within the ears of these bats, and accompanying concentrations of nerve cells, tune their auditory systems to very narrow and specific frequencies. Although they can hear many other frequencies, this specialization gives them great powers of resolution at the frequencies with which they hunt.

For bats calling at a constant frequency, the Doppler effect (a phenomenon produced as objects move toward or away from each other) provides a significant potential source for error. The auditory specializations of *Rhinolophus, Hipposideros,* and *Pteronotus* allow them to actually exploit the Doppler-shifted echoes from their fluttering targets, giving them an excellent way to find flying insects.

The most thoroughly studied echolocating bats are those preying on flying insects. But bats that hunt non-flying animal prey use echolocation for more than just locating or assessing potential food items. Central America's frog-eating bat (*Trachops cirrhosus*) is one species

that does this. Merlin Tuttle and Michael Ryan demonstrated that these bats use frog calls to find and identify their prey whether the frog is sitting in water or on land.

Frog-eating bats produce echolocation calls when they approach their target, yet they can be fooled into attacking a speaker playing frog calls. Surely if the bat were using echolocation to collect information about its target, it would not make such a mistake. Biologists presume that frog-eating bats, like many other species, use echolocation to find out about the surrounding background, rather than to locate and assess their targets.

So echolocation is invaluable in pinpointing a potential meal or gaining information about the surrounding landscape. But it also has its drawbacks. The high intensity of echolocation calls and the large number of calls produced advertise a bat's presence, making them conspicuous to potential prey. It is not surprising, therefore, to find that many insects have ears that are sensitive to bat echolocation calls. This anti-bat system provides early warning of an approaching peril [see "Predator and Prey: Life and Death Struggles," page 5].

As a countermeasure, bats, such as pallid bats (*Antrozous pallidus*), California leaf-nosed bats (*Macrotus californicus*), and Indian false vampire bats (*Megaderma lyra*), use foraging strategies that avoid echolocation call production when other sources of information are available. *Macrotus* and *Megaderma*, for example, have excellent vision and can use this to locate and identify their targets whenever there is enough light.

This is a small sampling of what we have learned about the echolocation abilities of bats since Spallanzani began to unravel the mystery of how bats are able to "see" with their ears. The more we learn about these animals, the more they continue to amaze and intrigue us with the many and varied ways in which they accomplish their remarkable sensory feats. We have come a long way, but there is still much to learn before we completely understand the phenomenon of echolocation.

[bio]
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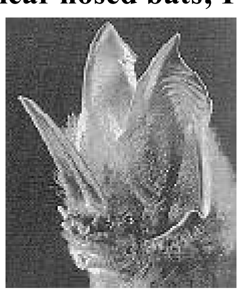
*an acronym for Sound Navigation Ranging

New World leaf-nosed bats; Family: Phyllostomidae

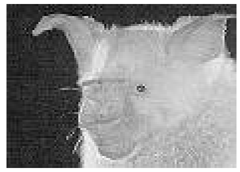
Tent-making bat, *Uroderma bilobatum* (Latin America)



Sword-nosed bat, *Lonchorhina aurita* (Latin America)

False Vampire bat, *Vampyrum spectrum* (Latin America)

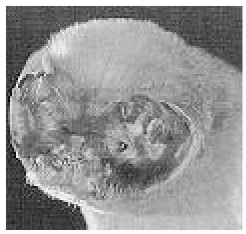
Giant mastiff bat,
Otomops martiensseni
(Africa)



Giant leaf-nosed bat,
Hipposideros commersoni
(Africa)

Australian ghost bat,
Macroderma gigas
(Australia)

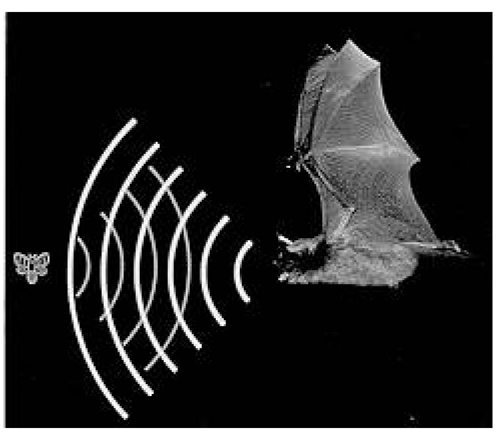
Dobson's horseshoe bat,
Rhinolophus yumanensis
(Asia)



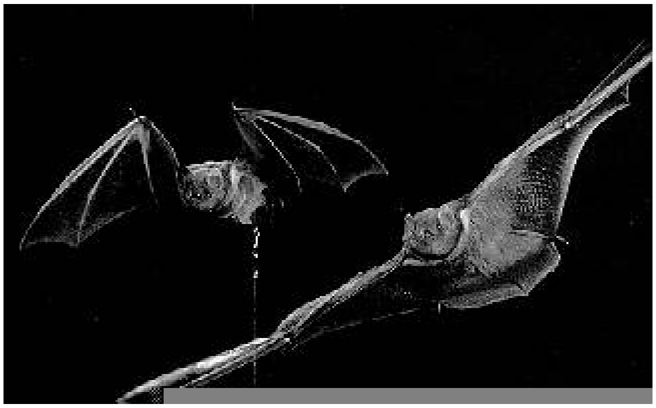
Antillean ghost-faced bat,
Mormoops blainvilii
(Latin America)

Evening bat,
Nycticeius humeralis
(Genus is widely distributed throughout
the world, including North America)

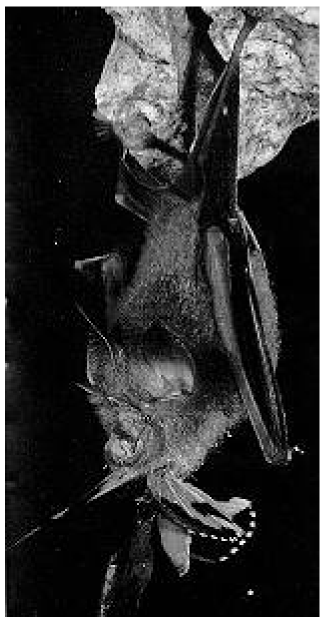
The diverse and elaborate facial features and ears of many insectivorous bats are thought to be associated with echolocation. Bats in the family Vespertilionidae, with their plain, unadorned faces, are the type with which those of us who live in temperate climates are most familiar.



As this little brown bat produces echolocation calls, it registers each outgoing sound pulse and compares the originals to the returning echoes, giving it information about its target.



Bats that fly with their mouths open may look ferocious, but in reality, they are merely echolocating. These red bats are in search of a meal.



Bats that hunt in dense foliage use different hunting strategies than bats that hunt in the open. Horseshoe bats produce long, constant frequency echolocation calls, enabling them to distinguish the rhythmic, fluttering wings of insects from leaves and twigs oscillating in the wind.

All articles in this issue: