

Echolocation

The Strange Ways of Bats

G Marimuthu



G Marimuthu has studied the behaviour of bats for almost two decades. His pioneering experiments have led to an understanding of how bats catch frogs in total darkness.

Bats are capable of avoiding obstacles that they encounter, even in complete darkness. This is because they emit ultrasound (high frequency sound) and analyse the echo produced when the sound hits objects on their path. This article describes the hunting flight of bats and how echolocation is useful in prey capture. Prey capture without the aid of echolocation by some bats is also described.

The March 1996 issue of *Resonance* introduced us to the fascinating world of bats, the only flying mammals of the world. As opposed to traditional views on bats, they are a harmless and interesting group of animals. Awareness about bats and the need to conserve them has increased considerably in recent years. A very interesting feature which was only briefly mentioned in *Resonance* Vol.1, No.3, is the ability of bats to 'see' through their ears. The microchiropteran bats use a special property called 'echolocation', both to avoid obstacles on their way and to locate and capture their prey.

Echolocation is a specialized process of orientation used by bats. Bats emit high frequency sound waves while navigating, and process the echo that comes back from obstacles. This method assists prey location and capture.

The Discovery of Echolocation

During the year 1790, Lazzaro Spallanzani, an Italian naturalist, first observed that bats were able to avoid obstacles while flying even in total darkness. He also found that despite the surgical removal of eyes, bats could fly without bumping into obstacles. Later, Charles Jurine, a Swiss zoologist, plugged the ears of bats

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and observed their inability to perform these correct orientations. Spallanzani repeated these experiments and obtained similar results. Both of them concluded that bats could 'see' through their ears! The French naturalist Cuvier disagreed with this statement. He explained that a sense of touch in the wing membrane caused the bats to avoid obstacles. In 1920, Hartridge, a British physiologist put forward the hypothesis that bats emit ultrasound and listen to the echoes of these sounds. After 18 years, the American zoologist, Donald R Griffin along with Pierce, a physicist, used a microphone sensitive to ultrasound and demonstrated that bats do emit trains of ultrasonic pulses while flying. They showed that the number of sound pulses increased as bats approached obstacles on their flight path. They also noticed that the bat's mouth was always open when the sounds were emitted. Griffin continued the experiments and found that closing the mouth of the bat resulted in disorientation. He established that bats emit sounds through their mouths. It was Griffin who coined the term 'echolocation' in 1938. In 1958, he published his classic book, 'Listening in the Dark' which documents many details about the discovery of echolocation. Echolocation is one of the methods of orientation mainly used by the microchiropteran or insectivorous bats. While flying, these bats emit high frequency ultrasound. These sound pulses hit obstacles like rocks, trees, walls etc. and their echoes are heard by bats. By analysing these echoes, bats are able to find their way even deep into underground caves in which there is absolutely no light.

Vocalizations of Bats

Like other mammals, including humans, bats emit sound through the voice box or larynx. Sound is produced when the vocal chords vibrate as air passes over them. Hence these sounds are called vocalizations. The muscles in the larynx adjust the tension on the vocal chords. This controls the rate of vibration of the vocal chords which explains the frequency or pitch of the sound emitted. Some of the characteristics of sound are shown in the



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Figure 1 The face of the Indian false vampire bat *Megaderma lyra*. It is a microchiropteran and carnivorous bat. It weighs about 40 g. While flying, it emits ultrasounds through its nostrils, which help to beam the sound pulses. The huge pinnae are able to collect the faint noise created while the prey moves.

box. Most of the species (eg. Indian pygmy bat, free-tailed bat, tomb bat) emit their echolocation sounds through the mouth. A few other species (eg. Indian false vampire bat, leaf nosed-bat, horseshoe bat) produce their vocalizations through the nostrils. The latter species have grotesque facial ornamentations. This is known as the noseleaf (*Figure 1*). It is a shallow, parabolic portion surrounding the nostrils and a spear shaped, rounded or fleshy superior portion. The structure of the noseleaf varies from species to species. The noseleaf serves to narrow and focus the outgoing beam of sound.

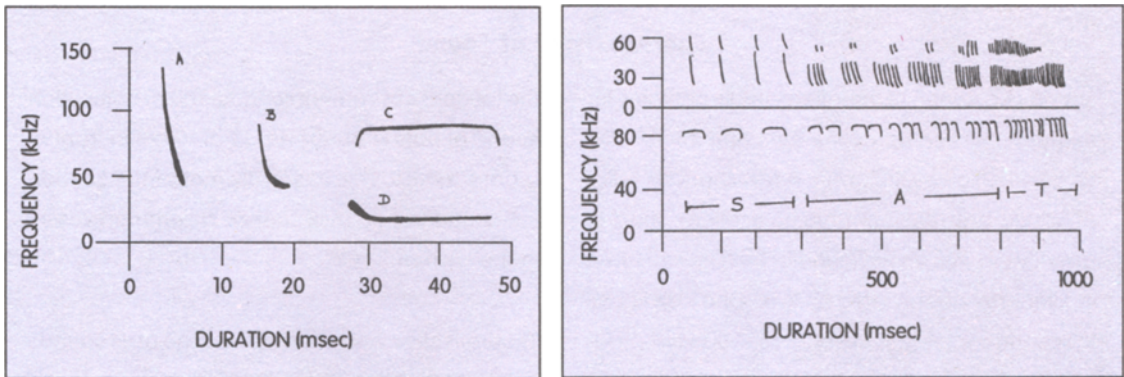
Vocalizations used in echolocation are generally divided into two categories.

- **Broadband signals** These cover a wide range of frequencies, from 20 to 140 kHz and have shorter durations of less than 5 milliseconds. They are technically called frequency modulated (FM) pulses. Each pulse starts at a high frequency and sweeps down to lower frequency within a short duration.
- **Narrowband signals** These have a constant frequency (CF) and longer durations of about 100 milliseconds.

Functions of Echolocation

Even though there are two such distinct kinds of sounds (*Figure 2*), bats use either one or combinations of both depending on the situation and gather detailed information on their flight path. The hunting flight of bats is divided into three stages: the search stage, the approach stage and the terminal stage (*Figure 3*). During the search stage, bats emit sound pulses with a low repetition rate of about 10 pulses per second. Actually a correlation exists between the habitat in which a species regularly forages and the type of signal it emits at this stage. Usually short CF pulses, with or without an FM tail, are found in species that forage in open spaces where vegetation and other obstacles are not found. Bats that hunt close to vegetation or the ground, emit pulses which mainly have an FM sweep. Theoretically, the

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amount of information available from a signal is proportional to its bandwidth. A broadband outgoing sound pulse would cause a greater number of altered frequencies in the returning echoes. Bats use such echoes to analyse the features of the target, for example to differentiate prey from the background clutter and to differentiate smooth and rough surfaces suitable for landing. They can accurately discriminate between targets that are within 10-15 mm of each other. To estimate the target range (distance), bats analyse the time delay between the emission of sound and its return as echo just like a radar detects objects several metres away.

A few other species like horseshoe bats which emit narrowband signals with longer CF component use an alternative strategy of echolocation. They distinguish the moving prey from nonmoving obstacles by means of the Doppler effect (see box and *Resonance*, Vol.1, No.2, Page 14).

The main function of the search stage is to detect the potential prey among obstacles. The big brown bat *Eptesicus fuscus* can detect a sphere having a diameter of 2 cm, at a distance of 5m. The same bat detects a 0.5 cm sphere at a distance of 3 m.

The onset of the approach stage represents the first visible reaction of the bat to the target. This stage begins when the bat is between 1 or 2 metres away from the target. The bat turns its head and ears towards the target. It also increases the repetition rate of the echolocation sounds to about 40 pulses per second. In

Figure 2 Sonograms of different types of echolocation sounds shown as frequency in the ordinate and duration in the abscissa scales : (A). Steep broadband FM signal starts at a higher frequency and ends in a lower frequency in a short duration. (B). Steep FM signal ends with a shallow FM component. (C). A long CF narrowband signal with an initial increasing FM and a decreasing FM tail at the end. (D). Signal starts as a shallow FM with a long CF component.

Figure 3 Pattern of the emission of echolocation pulses by bats which emit only FM signals (top) and bats which emit a combination of both CF and FM signals (bottom) at three different stages. (S) - search stage, (A) - approach stage, (T) - terminal stage.

Characteristics of Sound

Sound is a series of vibrations in air or water for example, picked up by the ears and interpreted as a sensation by the brain. A few characteristics of sound are relevant to echolocation. The *frequency or pitch* of the sound of bats is measured in kilohertz, abbreviated as kHz. One kHz is one thousand cycles per second or 1000 Hertz. Humans can hear up to 20 kHz. Sounds having a higher frequency than this are called ultrasound. The echolocation calls of bats are inaudible to humans and hence called *ultrasonic*. Since high frequency sounds are more rapidly absorbed by the atmosphere, the echolocatory system works within a limited distance. The *intensity* of sound is measured in decibels, abbreviated as dB. This unit is related to the ratio of the sound intensity to a standard, which is taken to be the threshold sound intensity detectable by the human ear. *Table 1* provides the decibel scale to measure

the loudness of various sounds. The echolocation sound of bats is about 110 dB at 10 cm in front of a bat's mouth. This is slightly more intense than the sound from a milk cooker, a common vessel in the kitchen.

Theoretically a bat receives the echo of its sounds within 500 milliseconds (1000 milliseconds = 1 sec). The obstacles could be away at a maximum distance of about 85 m. The bat detects the distance of the target by measuring the time interval between the emitted signal and its echo. The range of frequencies of the echolocation pulses is the bandwidth of the signal. The power spectrum explains the distribution of energy on the frequencies of the signal (see *Figure 4*). A bat collects detailed information about targets by comparing the power spectra of the emitted sound and its echo.

Table 1. The decibel scale

<i>dB</i>	<i>Examples</i>	<i>dB</i>	<i>Examples</i>
10	Rustling leaves	80	Vacuum cleaner
20	Whisper	90	Classroom in a school
30	-	100	-
40	Voices in city night	110	A road drill
50	Normal speech	120	-
60	A busy super market	130	Jet aircraft take off
70	-	140	Painful sounds

The hearing sensitivity of bats is much higher than other mammals.

In addition to these changes, a qualitative change in the pulse pattern also occurs. In species (eg. *Myotis myotis*) which emit only FM pulses, the slope of the FM sweep becomes steeper, the duration of the pulse becomes shorter but the bandwidth of the

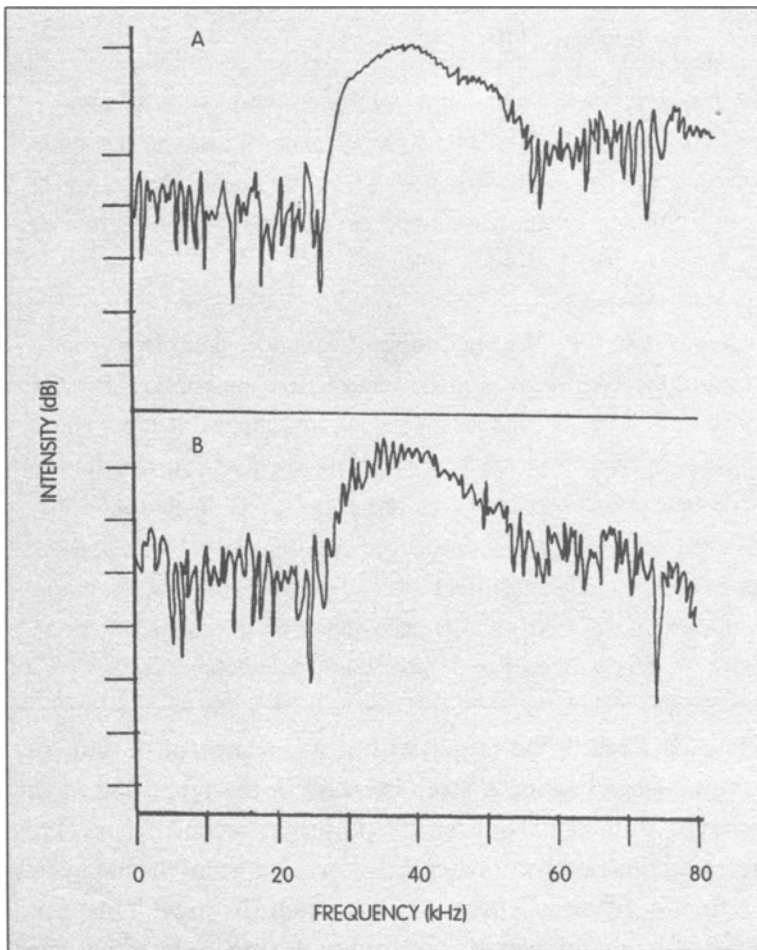


Figure 4 The spectrogram of the echolocation call (A) and its echo (B). The spectral difference between the pulse and the echo provides detailed information about the target structure.

signal remains the same. In a few other species like *Nyctalus noctula* which emit only CF pulses during the search stage, an abrupt switch to emitting brief FM pulses occurs. The CF component is dropped. Horseshoe bats which use long CF-FM pulses during the search stage do not drop the CF component at the approach stage. Their pulses become shorter with an increase in bandwidth of the FM component.

Thus a shift towards emission of FM pulses is discernible at the approach stage. Since the information content is greater in the broadcast (FM) signals, this shift is useful to decide whether to catch a prey or to avoid an obstacle or to land on a roosting site.

The big brown bat *Eptesicus fuscus* can detect a sphere having a diameter of 2 cm, at a distance of 5m. The same bat detects a 0.5 cm sphere at a distance of 3 m.

Doppler Shift

Our ears hear a changed sound when we listen to a sound source which moves rapidly towards or away from us, eg. a car passing us with its horn blowing. We experience a sudden drop in frequency as the car passes away from us. Even though we hear a sudden change in frequency, the horn actually sends out sound waves at a regular interval. If we stand ahead of the car (person 'A' in *Figure 5*) our ears receive more than the normal number of sound waves and we hear a higher frequency than the real tone of the horn. After the car passes, our ears receive fewer sound waves (person 'B' in *Figure 5*) so that the frequency becomes lower, with a sudden drop at the moment the car passes us. The faster the car

moves, the greater the change in frequency. This effect of motion on the frequency of sounds was first pointed out by an Austrian scientist Christian Doppler and it is named after him as *Doppler shift*.

The long constant frequency signal of the echolocation sounds emitted by a few species of bats is used for measuring the Doppler shift but is not suitable for target description. Bats are able to analyse the shifts that occur in the echo frequency produced by a flying insect. They use this method to detect the insect prey from the large amount of echo clutter produced by the dense foliage or other background objects.

When bats reach the target within a distance of 50 cm, the terminal stage begins. A steep increase in the repetition of the emission of about 100 or even 200 pulses per second occurs. This increased rate rapidly updates the information and the bat makes the final decision whether or not to catch the prey. This rapid increase in the emission of sound pulses during the terminal stage is termed as 'final buzz'. In most bat species, the sound pulses emitted at this stage are only FM sweeps with three or four harmonics. These are of lower duration of within 0.5 milliseconds. In bats which use the Doppler shift, like the horseshoe bats, the CF component still remains but is reduced in duration and is about 10 milliseconds (compared to 60 milliseconds during search stage). After detecting the insects, bats capture them by using their wing membranes and transfer them to their mouth.

A few other species like horseshoe bats distinguish the moving prey from nonmoving obstacles by means of the Doppler effect.

The hearing sensitivity of bats is much higher than other mammals. This specialization allows bats to receive and analyse faint echoes. When the echoes return to them, they are received by the auditory system similar to other mammalian patterns.



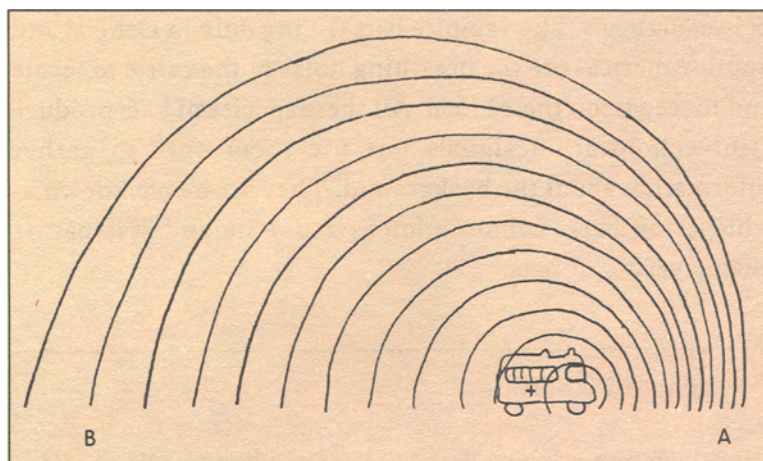


Figure 5 Each sound wave starts out as a circle. Since the horn is moving forward continuously, the centre of each circle is a little farther along the road than the previous one. This makes the wave 'crowded' (high frequency) in front (A) and 'stretched out' (low frequency) at the back (B).

Echolocating bats have prominent external ears. Their pinnae are specialized to amplify the faint echoes. The mechanical vibrations of the echoes travel through the ear drum, middle ear and reach the cochlea of the inner ear. A helical ribbon, known as the basilar membrane, present in the cochlea contains hair cells. These are the receptor cells that convert the mechanical vibrations of the echoes into electrical signals and transmit them to the brain along the auditory nerve. Processing of the echoes takes place in the brain. The processing includes information such as the pulse-echo delay and comparison of spectral features of the original sound and its echoes. From this process a bat gets an 'acoustic picture' of its flight path.

Prey Capture without Echolocation

Recent studies show that some species of bats do not use echolocation to detect their prey. These are the false vampire bats in India, Australia and Africa, long eared bats in North America, mouse eared bats in Europe, fringe lipped bats in Panama and slit-faced bats in Africa. The Indian false vampire bats listen passively to the noise associated with the movement of the prey (frogs, mice, larger insects, etc.). The fringe-lipped bats use the songs of male frogs to locate and capture them.

They can distinguish the calls of edible frogs from those of

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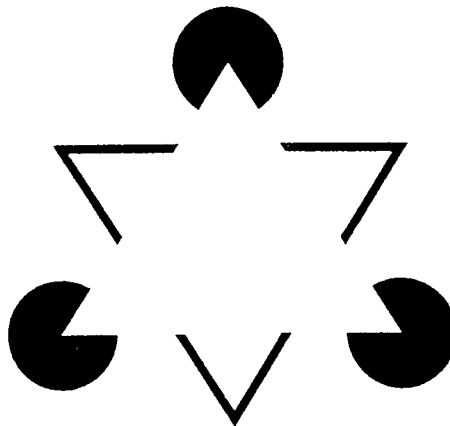
poisonous toads. The vampire bats (living only in Central and South America) use the breathing noise of the cattle to locate and to feed upon their blood. All these species of bats produce faint echolocation signals but use them only to gather information about the background. They are hence known as whispering bats. Echolocation is a unique and fascinating characteristic of bats.

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Suggested Reading

- D R Griffin. *Listening in the Dark*. Yale University Press, New Haven. 1958.
G Neuweiler. *Echolocation and Adaptivity to Ecological Constraints*. In:
Neuroethology and Behavioural Physiology. (Eds) F Huber and H Markl.
Springer Verlag, Berlin. 1983. 280-302.
D Young. *Nerve Cells and Animal Behaviour*. Cambridge University Press.
Cambridge. New York, Sydney. 1989.



Kanizsa triangle ... consists of illusory contours. A normal visual cortex sees a triangle even though interconnecting lines are missing. Such illusions show that the visual cortex must resolve conflicts between different functional areas.

Honeybees can see optical illusions ... Brazilian researchers have found that bees rewarded with a sugar solution can be taught to "see" Kanizsa triangles.