

Echolocation in bats

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Abstract

This article describes echolocation in bats from several points of view. Acoustical properties such as the temporal and frequency domain qualities of echolocation signals are examined in depth, and different echolocation signal types are described. Also the echolocation voice production and perception capabilities of Chiroptera including the vocal organs and ear anatomy, voice control capabilities and neurological aspects, are discussed. Then, the performance of bat echolocation is described. Finally, some overview of identification of bat species and specimen and technological applications of airborne echolocation are discussed.

1. INTRODUCTION

1.1. Bats in folklore and religion

Bats have aroused the interest of people throughout the history. Their unique qualities have made them special among all living creatures. They fly like birds, bite like beasts, hide by day, and see in the dark, so surely they could be neither “flesh, fowl, nor good red herring” (Allen, 1940). Their peculiar habits and features have placed them in folklore of numerous cultures. The Greek storyteller Aesop, the Latin people, some Nigerian tribes and the North American Cherokee Indians all had similar tales, in which the bat in bird council claimed he was a mouse, and in the animal council declared he was a bird. While the European and African stories end up with bats being shunned by both animals and birds, in the Cherokee tales the agility of the bat actually helped him score a victorious goal in a ballgame between birds and animals. In this game, the bat played on the birds’ side.

The strangeness of bats has also given them many religious connotations among different cultures. For example, the Votiaks had a belief that during sleep the soul frees itself from the body and may then appear as a bat. This would explain the bats’ disappearance by day, and should a bat come near anyone, it was believed to be in fact the spirit of some kinsman or acquaintance. Also among the Chinese bats are held in high regard, and by the Buddhists they are sometimes considered sacred. Also among the ancient Mayans of Central America the Bat God was a powerful deity who also controlled fire. On the other hand, in cultures of Roman and Christian origin, the bat has always had a sinister significance. Divius Basilius, an old Latin writer, states that the nature of the bat is kin with that of the Devil. Allen (1940) also notes that the Bible has several passages, in which the bats are described as unholy creatures, and that this presentation of the satanic form

was so familiar, that when the British first saw large fruit bats in Australia, they thought they had met with a real live devil.

The attributes and abilities associated with bats can be seen to originate in actual notes of bats' features and habits. For example, the Indians valued the nimbleness of the bat, while the Europeans shunned its fondness of caverns and night and its habit of sleeping upside down. However, as Allen (1940) notes:

“Frequently the observations are correctly made but quite as often their interpretation is wholly fanciful, for among simple people credulity is large and critical analysis rare.”

Thus, the rest of this literature review concentrates on sources with less fanciful interpretations, less credulity, and among which critical analysis is commonplace.

1.2. Overview of bats

Bats are one of the most extraordinary mammal orders. Not only are they the only mammals having wings and being capable of true flight, but they also possess the capability of advanced echolocation.

Bats are the second largest mammalian order with 966 species, to be outnumbered only by rodents with about 1700 species (Altringham, 1996). However, bats display unparalleled diversity in their order. They are distributed all around the world, including the higher latitudes and remote islands such as New Zealand where they are the only native mammals.

Bats range in size from the smallest mammal (the bumblebee bat, *Craseonycteris thonglongyai*, 1.5–2 g) to 1 kg flying foxes (*Pteropus* spp.) with wingspan approaching 2 m.

Even among all animals, echolocation is quite rare. Of all mammals, the *Cetacea* (whales and dolphins) along the bats have the most advanced echolocation capabilities, although some other small insectivores (shrews and tenrecs) have rudimentary capability of ultrasonic echolocation (Altringham, 1996). There exist also some birds that echolocate with lower frequency sounds. Best known examples are the cave dwelling birds: the South American oilbird and the South-East Asian swiftlets, which use 2–10 kHz sounds to locate their nests in dark caves.

First experiments on bats' navigation and location methods were performed already in 1793 by Lazzaro Spallanzani, who noted that, contradictory to his hypothesis, bats were fully able to navigate with their eyes covered and in total darkness (Griffin, 1959). Series of experiments made by Spallanzani made him conclude in 1799 that even though bats did not have much use for their eyes, covering or damaging their ears would prove invariably fatal to them, as they would stumble on any and all obstacles and be utterly unable to catch any prey. This conclusion was ridiculed in his time, as bats were thought to be mute and his findings contradicted common sense. The problem remained unsolved until sufficient ultrasonic technology was developed for bat sound detection. Only some 130 years later, in 1932, a Dutchman Sven Dijkgraaf noticed the ability of bats to avoid obstacles using sound. The puzzle was finally solved by Griffin in 1938, who demonstrated together with Pierce and subsequently with Galambos, that bats emit ultrasound frequency sounds and listen to echoes from objects in the path of the sound beam, allowing them to orient in the dark and exploit food sources of the night sky. He also coined acoustic orienting behavior as “echolocation” (Griffin, 1944, 1958; Surlykke & Moss, 2000).

This literature review will present the echolocation capabilities of bats in detail.

1.3. Structure of the article

This article is structured as follows. First, a general introduction of order *Chiroptera*, bats, is given in Section 2. The overview consists of general taxonomy of the order *Chiroptera*, a description of bat anatomy, their area of distribution and a description of their social behavior. Then, in Section 3, the acoustical properties of bat echolocation signals are described: different signal types, frequency ranges, temporal structures, energy levels and various other relevant phenomena. After that, in Section 4, the production of echolocation signals is described. The Section handles bat vocal organs and how the echolocation signals are generated. In Section 5, bat ear anatomy and neurological aspects in echolocation signal perception are discussed. Section 6 discusses the social aspects of bat voice use: how bats communicate with sound, how those signals differ from echolocation signals, etc. Finally, the paper is concluded in Section 7.

2. BAT BIOLOGY AND ANATOMY

2.1. Classification of bats

All bats are included in the order *Chiroptera* (meaning hand-wing), which has two suborders, the *Megachiroptera* (megabats) and the *Microchiroptera* (microbats). All of the megabats belong to the same family, *Pteropodidae* (the Old World fruit bats or flying foxes), while the microbats have been distributed across four superfamilies and a total of 17 families (Altringham, 1996). The phylogeny of living bat families is shown in Figure 1.

A brief introduction of the two suborders follows.

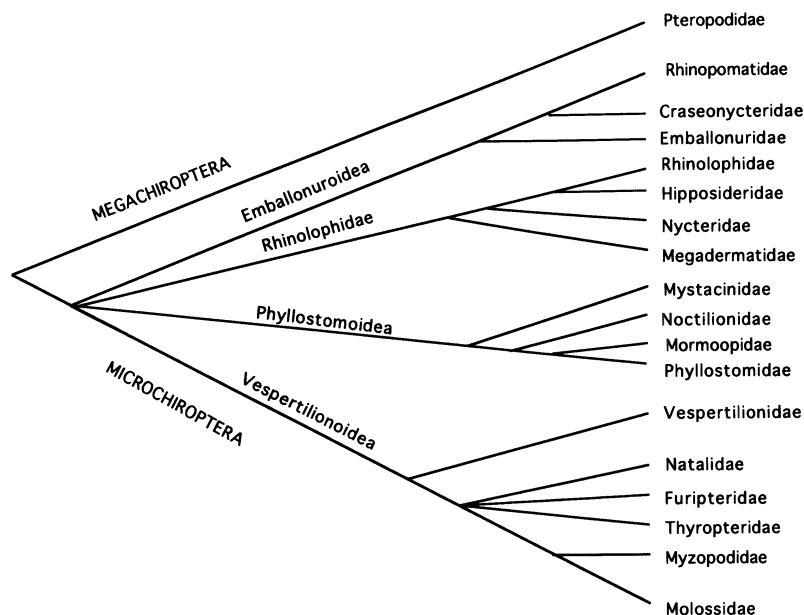


Figure 1: Phylogeny of the families of living bats after Fenton (1995), adapted to represent current understanding of Chiropteran monophyly.

2.1.1. *The megabats*

The Old World fruit bats, or flying foxes, are confined to the Old World tropics and feed exclusively on fruit, flowers, nectar and pollen. They are generally larger than microbats, with forearm lengths of 40–220 mm.¹ They weigh from 20 g to 1.5 kg, with wingspan approaching 2 m. Most megabats have rather dog-like faces, hence the name flying foxes. They generally have large eyes, simple ears and simple muzzles. Skull and jaws are typically adapted to deal with tough-skinned fruit. Although most megabats are brown in color, some are patterned or otherwise brightly colored. Figure 2 shows a roost of the megabat *Rousettus aegyptiacus*.

With the exception of genus *Rousettus*, megabats do not echolocate, but rely on vision and smell for orientation (Altringham, 1996; Nowak, 1999).

Megabats inhabit Sub-Saharan Africa, South-Asia and western parts of Oceania, including northern Australia.

2.1.2. *The microbats*

The microbats, as the name states, are generally smaller than megabats. Forearm length ranges from 22 to 110 mm. While all Microchiropteran families prey upon insects to some extent, a minority have evolved to feed on fruit, nectar and pollen, vertebrates and blood (Altringham, 1996). The ears are often large and complex, and many species have noseleaves. Both features are associated with echolocation, and all species of the order *Microchiroptera* have advanced echolocation capabilities. Although most species have small eyes, they often have a good vision. Some species are even able to locate their prey without echolocation, by listening for prey generated sounds or by using vision. Microbats probably have insectivorous ancestry, and their teeth reflect this, despite their diversification into a wide range of diets. Figure 3 illustrates a microbat, *Trachops cirrhosus*, in action.

Microbats inhabit all continents except Antarctica and the arctic regions.

2.2. **Bat anatomy**

Bats are mammals and, as such, possess all of the features characteristic of this vertebrate class (Hill & Smith, 1984). These features include most notably possession of a fur as opposed to scales or feathers, mammary glands for milk production, the single replacement of at least a portion of the dentition, and the ability to maintain a constant body temperature. In addition, bats give birth to young after a substantial period *in utero*.

Since bats are mammals, it is true that their form is basically like that of any other mammals. However, because of their adaptation to flight, they possess an easily recognizable form and appearance.

The wing is the most obvious adaptation of a bat. Unlike birds and the extinct flying reptiles in which the bony structure of the wing consists of greatly modified forelimb bones, the wing skeleton of bat is in comparison not much different from that of the forelimb of most mammals (Hill & Smith, 1984). The skeletal structure of bat wing is illustrated in Figure 4.

The wing consists of elongated hand and finger bones, which are connected to each other by a flexible membrane. The short thumb points forward and includes a claw used

¹Altringham (1996) states that the body length of a bat, excluding the head, is generally similar to its forearm length.



Figure 2: A communal roost of Egyptian Fruit Bat, *Rousettus aegyptiacus*. The picture is taken from below, with the bats hanging upside down. (Photograph courtesy of the Centre for the Conservation of Specialized Species.)



Figure 3: The frog eating bat, *Trachops cirrhosus*, closing in on an unsuspecting victim. (Photograph by Merlin D. Tuttle.)

in locomotion, and even food handling and fighting. The other fingers form the ribs of the wing and are clawless. Furthermore, depending on the species, there may or may not be a flight membrane connecting the hindlimbs and the tail (Hill & Smith, 1984; Altringham, 1996).

The hindlimbs of the bats are also very much specialized. The upper leg bone has rotated 180° from its normal position, so that the knee is directed rearwards in bats. While the hindlegs have lost their weight-bearing capabilities, the adaptations are useful in controlling the posterior parts of the wing membrane in flight.

According to Hill & Smith (1984), the heads of the bats show perhaps a wider range of variation than any other group of mammals, due to their different diets and food capture methods. The shapes of their skulls vary according to their diet: Insectivores generally have long, pointed noses, although some beetle-eating species have somewhat shorter and deeper muzzles. Carnivorous bats generally have somewhat dog-like head shapes, while the piscivorous bats tend to have short, deep faces and high-domed heads like bulldogs. Frugivorous (fruit-eating) bats have a wide range of head shapes, depending on their diet. The snouts may be long, deep and pointed, or extremely short with high doming of the braincase. Bats that eat nectar and pollen have long and tubular muzzles suited for reaching deep into flowers. Figure 5 illustrates heads of several bat species.

Features of the head that affect the echolocation capabilities in bats are discussed in Section 5.

The muscular system of bats is highly adapted to flight. Altringham (1996) states that the fact that the muscles are used both in flight and terrestrial locomotion makes the flight musculature of bats more complex relative to that of birds. In bats, there are

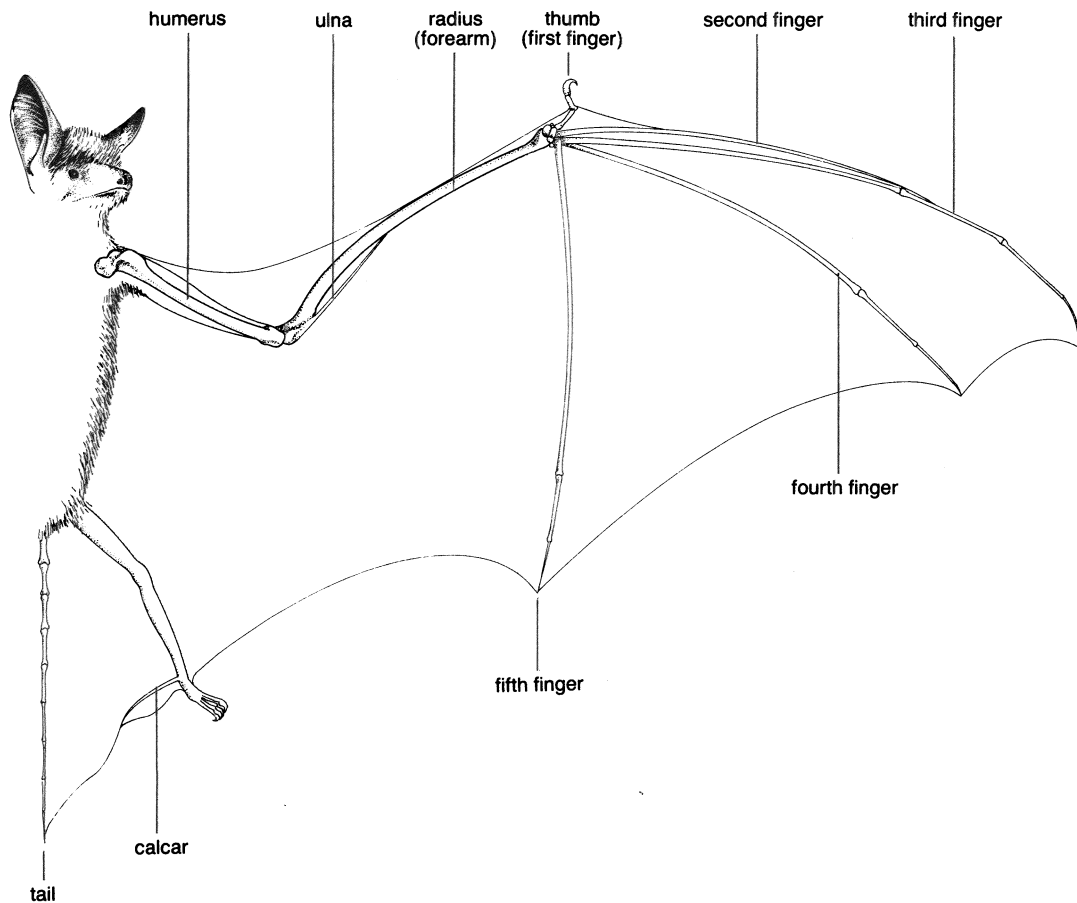


Figure 4: Structure of bat wing (after Hill & Smith, 1984).

five major downstroke muscles and two major upstroke muscles, while birds have one major downstroke muscle, assisted by one other. Otherwise, the musculature is typically mammalian, and since they must be capable of sustained activity, they are highly aerobic.

Also the respiratory and cardiovascular systems are very adapted to flight. In flight, the oxygen consumption per kg per time unit is approximately twice that of running mammals, and comparable to flying birds. When a bat takes off, its breathing rate rapidly increases to match its wing beat frequency (around 10 Hz for an average sized microbat according to Altringham, 1996). This rate, as high as 1000 Hz for average-sized Microchiropterans, is higher than those of running mammals and comparable with those of flying birds. Also the bat's heart is as much as three times as large as that of a terrestrial mammal of comparable size, so that the circulatory system is able to pump around the oxygen required for sustained flight.

Torpor and hibernation are phenomena greatly affecting Chiropteran energy balance (Altringham, 1996). To conserve energy during the long daytime inactive periods, most temperate region microbats are heterothermic—they are able to let their body temperature fall to the ambient temperature and then rapidly raise it again to normal level. This enables bats to dwell in harsh climate conditions. Figure 6 illustrates the advantages of heterothermicity. During the winter all of the bats in temperate zone either hibernate or migrate to warmer regions. The hibernation of bats is like prolonged torpor, so that bats wake up when handled and also arouse spontaneously many times throughout the

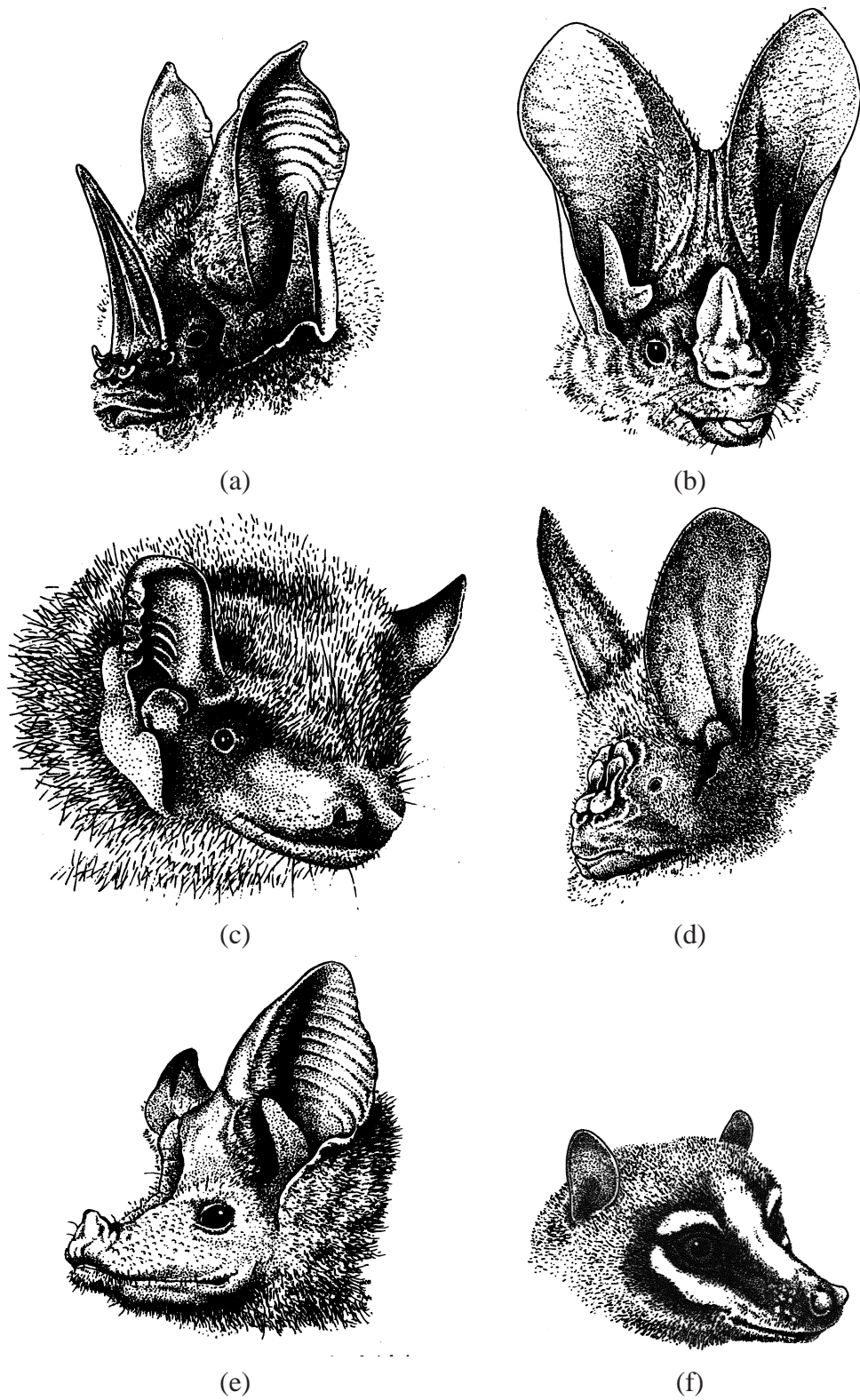


Figure 5: Illustrations of heads of several bat species: (a) *Lonchorhina aurita*, (b) *Macroderma gigas*, (c) *Nyctalus noctula*, (d) *Nycteris grandis*, (e) *Rhinopoma hardwickei*, and (f) *Pteropus personatus*. *P. personatus* is the only megabat illustrated here. Illustrations after Hill & Smith (1984).

hibernation period.

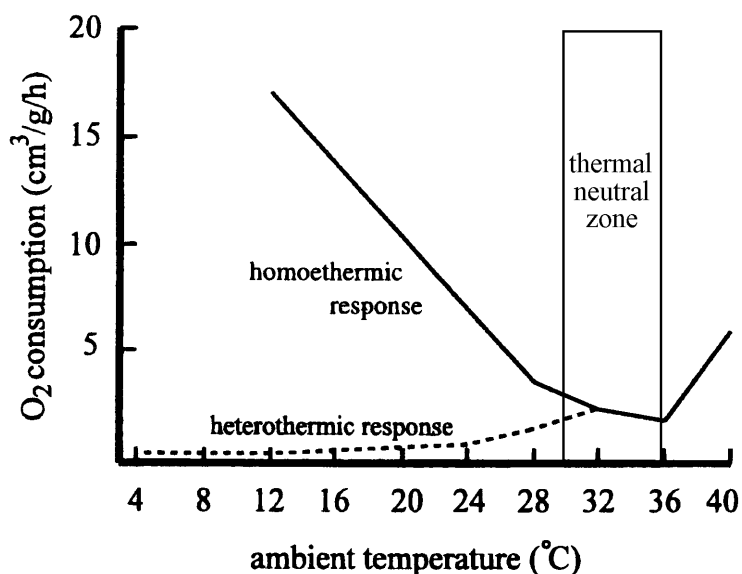


Figure 6: Energy expenditure in the western pipistrelle, *Pipistrellus hesperus* (after Hill & Smith, 1984).

2.3. Evolution of bats

The habit of roosting within caves in large colonies facilitates the preservation of bat bodies after their death. Some of the water dripping into caves has high mineral-content, and thus slows the rate of decay and, in time, helps to form a deposit over the dead bats. Despite of this, the ratio of known extinct to living species is low for bats, and it is generally said that bats are not well represented in the fossil record (Nowak, 1999; Altringham, 1996).

Even the earliest fossils tell us quite little about Chiropteran evolution. The oldest fossil records date back 50 million years before the present. Other remarkable specimens date back about 45 million years. These ancient fossil bats were insectivorous, and have a remarkable resemblance to modern microbats. No fossil bats are known which are in any way intermediate in form between a modern microbat and some early tree-living ancestor. According to Altringham (1996), if time is allowed for the evolution of bats, then microbats may have made their appearance 65–100 M years ago. If so, they shared the world with the dinosaurs, and watched their extinction at the end of the Cretaceous period.

Microbats show no close affinities to any other mammalian order. The nearest, but still distant order, may be the Edentantes—anteaters and sloths, themselves a very ancient group! These are unlikely ancestors for the bats, and they probably evolved from something similar to modern tree shrews (Altringham, 1996).

Why did bats then evolve? Altringham (1996) states, that there was a free ecological niche available. At the time bats are thought to be evolving, the flowering plants were in the first stages of their massive diversification. They became dominant over more primitive plants 100–95 M years before present, and by the end of the Cretaceous the insects supported by these plants were abundant. Insectivorous mammals and birds were

already well established, but few creatures preyed insects during the night. However, it would be logical that insectivorous birds had filled this niche, and Speakman (1995) also claims that competition with diurnal birds or animals is the least likely explanation for Chiropteran nocturnality. Other possible causes given by Speakman are the avian predation hypothesis and the hyperthermia hypothesis, although none of these is able to explain bat nocturnality by themselves.

According to Simmons (1995), there are two separate theories on the origin of powered flight in bats. It was suggested by Jepsen (1970) that proto-bats captured insects by jumping and hovering, and selection favoring to hovering may have led to the evolution of true powered flight. On the other hand, Smith (1977) argued that bats evolved from gliding rather than hovering ancestors, and this has also received support based on the relative energetic requirements of gliding, hovering and slow flapping flight (Clark, 1977). Since no fossil records of proto-bats have been found, the issue has not been resolved, although the gliding theory is the widely favored option (Rayner, 1991).

As proto-bats became more agile, they would have had to improve their nocturnal orientation skills to be successful night fliers. Vision is of limited use in dense forests during the night, and the other senses used by mammals—smell, hearing and tactile senses—are of limited use in flight. Altringham (1996) states that echolocation probably evolved alongside flight. The evidence gathered from the very earliest fossil microbats suggest that they had a well developed echolocation system (Novacek, 1985), but again, as no proto-bat fossils have been found, the evolution of echolocation is subject to speculation.

2.3.1. *Bat monophyly controversy*

Until the 1980s it was agreed among the bat research community that the common ancestor of all extant bats was a flying mammal, a hypothesis which implies that bats are monophyletic (i.e., developed from a single common ancestral form) and powered flight evolved only once in mammals (Simmons, 1995). However, bat monophyly has been questioned recently by authors suggesting that Megachiroptera and Microchiroptera may not be closely related (e.g. Pettigrew, 1995).

While it was widely accepted that primates and Chiropterans were closely related (“sister orders”), findings in 1980s and 1990s indicated that megabats shared a substantial amount of features with primates. The contradictory hypothesis was that bats were not monophyletic, but diphyletic. Thus, the ability of mammal flight would have developed not once but twice, and similarities of megabats and microbats would have been due to convergent evolution. It was suggested that megabats actually would have evolved from primates.²

The features causing monophyly controversy initially included a number of advanced visual pathway characteristics and certain distinctive features of penis anatomy, but lots of other evidence contrasting the differences of megabats and microbats and emphasizing features of megabats shared with primates has been collected since. Both Pettigrew (1995) and Simmons (1995) present extensive lists of these features. However, the viewpoints supporting Chiropteran monophyly have fallen into minority, as conclusive evidence supporting bat monophyly has emerged from molecular and morphological studies (Simmons, 1995). Martin (1999) summarizes:

As molecular evidence now overwhelmingly indicates that bats are mono-

²Seems like the childhood dream and vain attempts to fly by flapping one’s hands were not that far-fetched after all.

phyletic, the 'flying-primate hypothesis' must be regarded as severely disabled.

3. ACOUSTIC PROPERTIES OF BAT ECHOLOCATION SIGNALS

While bats are known for their exceptional echolocation capabilities (which will be described in detail in this and future sections), it has to be noted first that they are not the only animals having this ability. A number of other animal groups possessing echolocation capabilities were mentioned in Section 1.2.

Even in bats, echolocation is not a pervasive trait. While all microbats do echolocate, of megabats only those of the genus *Rousettus* echolocate. However, they generate sound by clicking their tongue, and while their navigational abilities are well developed, they do not match that of the microbats (Altringham, 1996). The rest of this literature review concentrates on the echolocation capabilities of microbats.

The frequencies used in echolocation by bats fall usually between 25 kHz and 100 kHz, although some species emit and analyze principal components as high as 150 kHz (Grinnell, 1995).

In following, echolocation signal types and temporal structures are described.

3.1. Echolocation signal types

3.1.1. FM bats

According to Altringham (1996), bats emit echolocation sounds in pulses. The pulses vary in properties depending on the species, and can be correlated with different hunting strategies and mechanisms of information processing (Grinnell, 1995). Most families use short, downward frequency-modulated (FM) sounds that sweep through about an octave. The signal bandwidth is further increased by one or more harmonics.

3.1.2. Long CF/FM bats

Another common echolocation signal pattern are constant-frequency (CF) signals. Long CF/FM pulses are used by a much smaller number of species belonging to three different families. These signals have a long (10–100 ms) constant-frequency component preceding an FM sweep (Grinnell, 1995). In the two best-studied species, the CF components are approximately 60–62 kHz and 83 kHz. Although individual bats exhibit slight frequency differences, the signals are very consistent in any given bat.

Long CF/FM bats are very specialized for detailed analysis of sounds in the range of the emitted CF. A large fraction of the inner ear and most of the neurons in auditory neural centers are devoted to analysis of a narrow range of frequencies around the CF. This neural configuration has been termed an "acoustic fovea" (Schuller & Pollak, 1979; Grinnell, 1995). These bats control the frequency of the emitted signal to compensate for Doppler shifts of returning echoes so that the echo CF stays within the acoustic fovea (Grinnell, 1995; Fenton, 1995).

Long CF/FM bats usually hunt in cluttered environments where prey detection is harder for bats that use only FM signals.

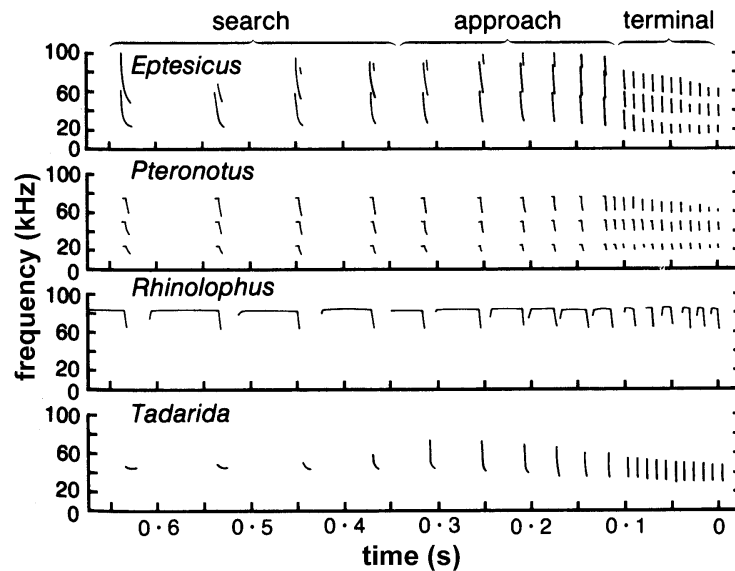


Figure 7: Schematic illustrations of sonograms of echolocation signals of different bats (after Hill & Smith, 1984). *Eptesicus* and *Pteronotus* are typical FM bats, while *Rhinolophus* is a stereotypical long CF/FM bat. *Tadarida* changes its signal form along the attack.

3.1.3. Short CF/FM bats

There also exists numerous species that employ an intermediate pulse design, with pulses containing a short CF component of up to 8–10 ms and terminating in a FM sweep (Grinnell, 1995). They may use Doppler shift information to some degree, but are less specialized for the CF frequency band analysis than long CF/FM bats.

It is also common for bats to modify the pulse structure according to the environment. Some species emit pure FM signals when close to vegetation, but in uncluttered environments prolong the pulse and reduce the amount of sweep to be able to detect faint echoes from remote targets.

3.2. Temporal structure of the echolocation signals

There exist two different approaches to microchiropteran echolocation (Fenton, 1995). These approaches are reflected in the duty cycles of their calls, i.e. the percentage of time that signals are being produced. All FM and short CF/FM bats have duty cycles of less than 20%, and they appear to be unable to process echoes overlapping with the pulse. These are the so-called low duty cycle bats. On the other hand, the long CF/FM bats have duty cycles that regularly exceed 80%, and they can tolerate overlap between pulses and their echoes.

Next, these two approaches are described.

3.2.1. Low duty cycle bats

Low duty cycle bats adjust the durations of individual calls according to the situations in which they are operating. When hunting airborne targets, the ultrasonic sound bursts last typically 5–20 ms and are emitted 10 times per second while the bat searches for

prey. The signals are synchronized with wing beats and respiration to minimize breathing effort. After the bat detects a target of interest, it enters the approach phase, in which the distance between the bat and the prey decreases, and the frequency of the pulses increases. Simultaneously, the duration of the pulses also becomes shorter. In the terminal phase, pulses may be emitted at frequencies of more than 200 Hz, and each pulse may be only a fraction of a millisecond long. This pulse behaviour may be explained by the aforementioned fact that most FM bats are unable to tolerate overlap between pulse and echo. So, when the biosonar of the bat is in long-range mode, the bat emits long pulses and allows sufficient time between the pulses. When a target becomes closer, the pulses have to shorten progressively to avoid pulse-echo overlap, and at the same time the bat is able to update the target location more often.

The duration and the intervals of the pulses define the maximum operational ranges of bat echolocation. Depending on the species, the range could be from 2.4 m to 62 m, although these intervals may provide no indication of the active use range of bat echolocation.

3.2.2. *High duty cycle bats*

While still having the capability of processing FM type signals, the high duty cycle species in the families Hipposideridae, Rhinolophidae and Mormoopidae are specialized for exploiting Doppler-shifted echoes generated by fluttering targets (Fenton, 1995). They produce calls that vary in duration from around 10 ms to more than 50 ms depending on the species. During attacks on airborne targets, the high duty cycles are maintained, although the durations of individual calls are decreased.

3.2.3. *Intensity of echolocation calls*

Intensities of the echolocation calls vary greatly from species to species. Measured from 10 cm in front of the bat, the sound pressure levels vary from less than 60 dB to 120 dB (Griffin, 1958; Altringham, 1996), with many species producing calls of intermediate strengths. The environment and hunting behaviour of the species influences call intensity. Bats searching for airborne targets usually produce intense echolocation calls, while those searching for prey on surfaces (gleaners) depend more on quieter calls. Furthermore, at least one species, *Myotis emarginatus*, adjusts its call intensity depending on the situation (Schumm et al., 1991).

Fenton (1995) notes that differences in call intensity pose challenges to people studying the echolocation of bats. Species using high-intensity calls are easily monitored with microphones sensitive to the call frequencies, while those using low-intensity calls remain virtually undetectable.

4. PRODUCTION OF ECHOLOCATION SIGNALS

In common with other mammals, microbats generate their sonar calls in the larynx (Altringham, 1996). Although the larynx is proportionally larger in microbats than in most other mammals, the mechanism of action is the same. Mergell et al. (1999) note that in many Microchiropteran bat species there exist vocal membranes, which are thin upward extensions of the membraneous portion of the vocal folds. Vocal membranes are illustrated in Figure 8. It has been suggested that they act as independent low-mass oscillators, and thus support generation of ultrasonic sonar calls (e.g. Griffin, 1958). Another

hypothesis is that the vocal membranes increase vocal efficiency (Schön-Ybarra, 1995). In their modeling experiments, Mergell et al. (1999) concluded that both theories are correct; vocal membranes both allow bats to produce higher-pitched sounds, but also to produce a given sound louder and more efficiently.

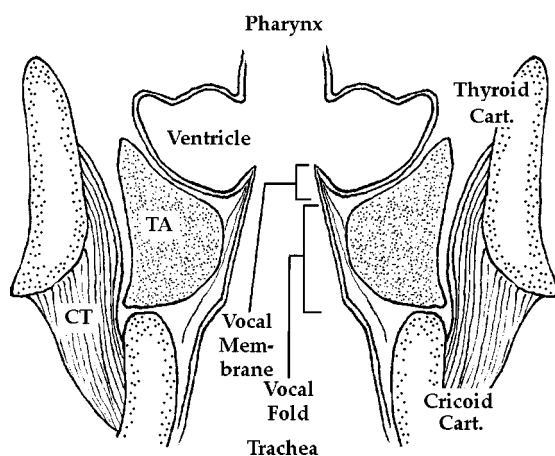


Figure 8: Schematic illustration of the anatomy of the vocal membrane (after Mergell et al., 1999).

By observing upward frequency shifts of the harmonic components of Microchiropteran sound in helium-oxygen atmospheres, it has been concluded e.g. by Hartley & Suthers (1988) that the sound production of bats follows the same source-filter model that was proposed for human speech production by Fant (1970). For example, by studying CF/FM-type horseshoe bats (*Rhinolophus hildebrandti*), it has been shown that the vocal tract attenuates the first and third harmonics as much as 40 dB compared to the second harmonic, which is the dominant frequency in the echolocation call of the said bat (Hartley & Suthers, 1988). Thus, the different chambers present in the bat vocal tract have an impedance matching role at the second harmonic.

Bats are able to modify the echolocation signal according to their needs. A prime example of this is the final “buzz” in the terminal hunting phase described in Section 3.2, in which the short distance and the need for accurate locationing abilities necessitate rapid pulse sequences. Furthermore, several FM bats modify the pulse form according to environment, so that while gleaning, they use short broadband pulses of medium intensity, while in open spaces the FM modulation is weaker and pulse duration longer and intensity higher (Fenton, 1995). Tests performed by Wadsworth & Moss (2000) indicate that the FM bat *Eptesicus fuscus* is able to actively modify the call signal according to the given task so that in echo delay tasks mainly short broadband signals were used and in Doppler discrimination tasks long and relatively shallow signals were used.

It is also well known that CF/FM bats are able to adjust their signal frequency so that the Doppler-shifted signal frequency falls within the frequency range of their acoustic fovea (Grinnell, 1995; Fenton, 1995). This frequency regulation is accurate to within 50 Hz in 83 kHz. For comparison, a respective ability for a singer would be to control the pitch of a 440 Hz “A” tone with an accuracy of 0.26 Hz. These bats appear to be sensitive to the small frequency and amplitude oscillations caused by insect wingbeats and are able to use these oscillations not only to detect but also to discriminate prey (Schnitzler & Flieger, 1983).

The directionality of echolocation calls appears to vary greatly between different species. Simmons et al. (1995) state that the directionality of the calls of big brown bat, *Eptesicus fuscus*, is quite low, so that at 30° off the centerline the call attenuation is only -7 dB at 60 kHz. In many species possessing noseleaves (facial ornaments) these actually form acoustic lenses, which focus the sound into a narrow beam in front of the bat (Altringham, 1996).

The emission of high-intensity sounds is energy-wise pretty expensive process. The emission of high intensity sounds at a pulse rate of 10 Hz costs a resting pipistrelle ten times its resting metabolic rate (Altringham, 1996). By comparison, flying costs a pipistrelle around 15–20 times its resting metabolic rate—the emission of echolocation signals costs the bat more than half of the flying metabolic rate! However, a flying bat get echolocation for free. In flight, breathing is locked to wing flapping, and it costs the bat next to nothing to emit ultrasonic sound during expiration.

5. PERCEPTION OF ECHOLOCATION SIGNALS

5.1. Bat ear anatomy

Microchiropteran ears resemble the ears of other mammals in form and function, although several special adaptations are present and common in different species.

5.1.1. Outer ear

Several different Microchiropteran outer ears are illustrated in Figure 9. The pinnae are large and flap-like, sometimes many times the size of the head of the animal. The inside surface of the ear pinna frequently has several transverse ridges or a series of longitudinal ridges, which are presumed to provide structural support for the pinna (Hill & Smith, 1984). Two other ear components are also found in Microchiroptera. The first of these is tragus, a small 'earlet' in front of the ear canal. Tragus, when present, has considerable impact on sound localization. Lawrence & Simmons (1982) conducted experiments, in which the tragus of *Eptesicus fuscus* was deflected and compared the vertical sound localization capabilities of these bats to intact ones. The vertical discrimination performance clearly deteriorated when the tragus was deflected. The second commonly found ear component is the antitragus, which is a broad flap that is continuous with the outer margin of the pinna (Hill & Smith, 1984). Some long-eared bats also have a peculiar ability to coil their ears during roosting and torpor, presumably to reduce heat and water loss.

5.1.2. Middle ear

The middle ear of microbats, illustrated in Figure 10, is similar in structure to other mammals, although small differences are present. The tympanic membrane (eardrum) is relatively thinner than that of other mammals with comparable membrane areas (Hill & Smith, 1984). The area of the tympanic membrane does not correlate with the body size, but bats that operate with high frequencies (50–125 kHz) generally have smaller eardrums than bats that operate at lower frequencies. There is a similar correlation with the mass of middle ear ossicles: the higher the operating frequencies, the smaller their mass is.

There exist two muscles in the middle ear: the tensor tympani (attached to the malleus and serving to tighten the tympanum) and the stapedius (attached to the stapes and serving to pull the stapes away from the oval window) (Hill & Smith, 1984). Especially the

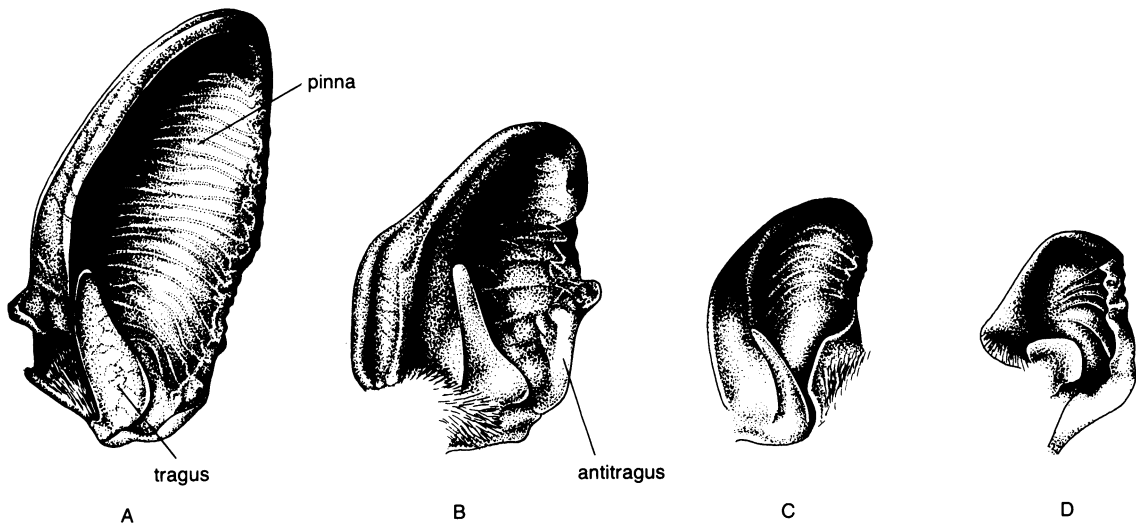


Figure 9: Pinnae of several Vespertilionidae (after Hill & Smith, 1984). (A) *Plecotus auritus*. (B) *Barbastella barbastrellus*. (C) *Myotis daubentonii*. (D) *Nyctalus noctula*.

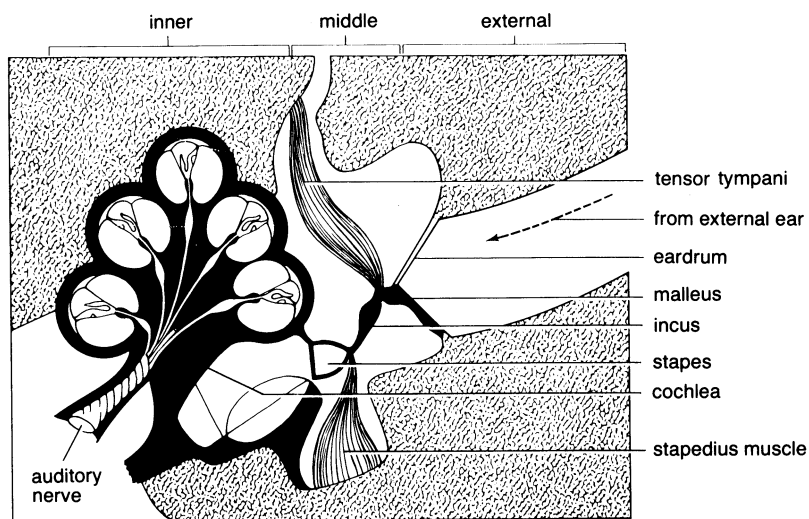


Figure 10: Auditory apparatus of bats (after Hill & Smith, 1984).

stapedius is important. FM bats use it to control the signal amplitude entering the cochlea by contracting it 10 ms before pulse emission and gradually loosing it after the emission (Hill & Smith, 1984). In the final stages of taking an insect, the stapedius muscle may operate at a frequency of more than 200 Hz—one of the highest rates recorded in vertebrate muscle. Furthermore, the stapedius muscle acts as an automatic gain control for the signal entering the cochlea. Contraction of the stapedius muscle strongly attenuates sensitivity to the emitted signal, weakly attenuates response to echoes from nearby targets, and leaves the auditory systems maximally sensitive to echoes from distant objects (Grinnell, 1995). Because the echo energy falls sharply with distance, the cumulative result of these phenomena is a form of an automatic gain control in bat hearing, so that the level of the echolocation signal entering the cochlea stays approximately equal.

5.1.3. Cochlea

The cochlea of microbats, while conforming to the general mammalian model, is specialized for the use of high frequencies and, in CF/FM bats, for hyperacuity around the CF (Grinnell, 1995). As a more general comment, it is interesting to note that the acquisition of highly developed cochleae that are able to analyze low-level signals at many different frequencies is a recent development, and only confined to higher vertebrates (Kössl & Vater, 1995). To compare, the high-frequency hearing capabilities of reptiles and birds are restricted to frequencies below 12 kHz³. In cochleae of Microchiroptera, mechanisms for sensitive and sharp tuning at high frequencies up to 160 kHz are fully exploited.

The obvious fact that hearing is an integral part of bat echolocation is reflected in the sheer size of the cochleae of bats employing different echolocation strategies (Habersetzer & Storch, 1992): in some CF/FM bats, the cochlea diameter may be more than 1/3 of the skull width! Relative sizes of cochleae in different bat families are shown in Figure 11. Also, according to Altringham (1996), the number of complete turns in the organ of Corti (2.5–3.5 complete turns) is higher in microbats than in megabats and primates (1.75 complete turns).

The basilar membrane performs the first important steps in cochlear frequency analysis. As with other mammals, the increasing width and the decreasing thickness of the basilar membrane produce a stiffness gradient that creates a frequency representation along the membrane. High-frequency signals maximally displace basal cochlea regions with high stiffness, and vice versa (von Békésy, 1960). According to Kössl & Vater (1995), the basilar membrane of *Microchiroptera* is narrower and thicker than in most non-echolocating mammals, which reflects adaptation to high-frequency sensitivity. In FM bats with unspecialized tuning properties, both the width and the thickness of the basilar membrane change gradually toward the apex as seen in most non-echolocating species, although the absolute gradients in basilar membrane width of non-echolocating species can be considerably larger than in bats (Kössl & Vater, 1995). However, the gradients encountered in CF/FM bats differ considerably from those in other mammals due to the development of the acoustic fovea. The basilar membrane of CF/FM bats commonly has very abrupt changes in thickness, and very large parts of the membrane have nearly constant thickness and width, reflecting adaptation to analyzing signals with frequencies close to the CF₂.

In contrast to the great adaptations in basilar membrane dimensions, the structural organization of the receptor cells in bat cochlea conforms to the patterns seen in most

³This also explains why the calls of even the tiniest birds are well within human auditory range.

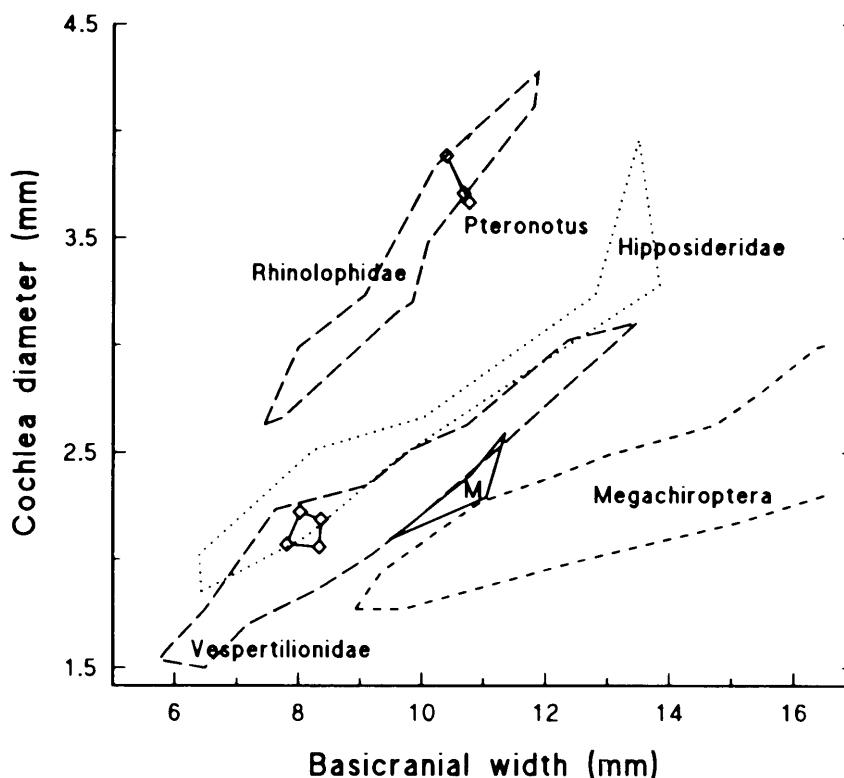


Figure 11: Measured diameters of the cochlea of different Chiropteran families. The open symbols represent the *Pteronotus*, of which one species uses long CF/FM calls and the others are pure FM bats. The relatively larger cochlea of CF/FM bats is clearly visible. The region marked with the letter M represents the cochlea of bat fossils found in Messel, Germany. This extinct bat dates from 53 million years before present. After Kössl & Vater (1995).

non-echolocating mammals (Kössl & Vater, 1995). There exists one single row of inner hair cells, which is located medial to three rows of outer hair cells. However, the dimensions of the receptor cells in *Microchiroptera* are considerably smaller than in other mammals. For example, the maximal length of outer hair cells in the cochlea of the CF/FM bat *Hipposideros bicolor* is lower than the minimal length measured in the guinea pig cochlea. The short hair cell size corresponds to the extended high-frequency hearing range of the bat species. On the other hand, the densities of outer hair cells of bats fall in the range reported for other mammals, although the density of inner hair cells appears slightly higher.

5.2. Threshold of hearing

While the behavioral threshold of hearing of non-echolocating mammals can extend up to about 100 kHz (e.g. Ehret, 1974), FM bats may not only be able to hear higher frequencies, but at extremely low levels as well. For example, the auditory threshold of *Megaderma lyra*, shown in Figure 12 (A), remains close to 0 dB up to frequencies of about 100 kHz (Kössl & Vater, 1995), and the threshold of hearing between frequencies of 10 and 25 kHz is below -20 dB! It has to be noted that the hypersensitive region of the

frequency range is used for passive listening and communication because it does not fall within the range used for echolocation signals.

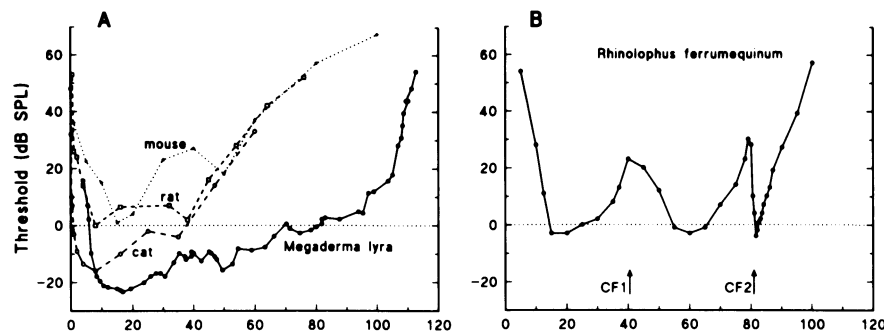


Figure 12: Auditory thresholds of (A) *Megaderma lyra* and several non-echolocating animals, and (B) *Rhinolophus ferrumequinum* (After Kössl & Vater, 1995). See text for discussion.

The auditory threshold curves of long CF/FM bats are lot more varied in nature. As an example, the auditory threshold curve of a CF/FM bat (*Rhinolophus ferrumequinum*) is shown in Figure 12 (B). According to Kössl & Vater (1995), there are sharp maxima and minima in the threshold curves that are related to the CF frequencies. Typically there is a narrow threshold peak coinciding with the range of the second-harmonic CF component (CF_2), and just above that threshold peak there is a sharp threshold valley. Another threshold peak, broader in shape, is found close to the fundamental frequency of the CF signal (CF_1). Depending on the bat species, there may be a formation similar to that at CF_2 at CF_3 as well. The reason for these strange formations is quite intriguing. Since long CF/FM bats emit sound concurrently while receiving it, there is an obvious need to filter out the emitted signal. This is done using the Doppler-shift and sharp maxima and minima of the auditory threshold curve: the frequency of the emitted signal is actively tuned so that the returned echo of interest falls precisely into the sharp threshold valley, while the emitted signal itself falls into the insensitive region of hearing.

5.3. Directionality

While it is sometimes assumed that the sonar of bats is sufficiently directional for separating echoes from different targets so that the bat can aim the sonar broadcasts and ears towards one target rather than the other, this does not hold true. For the directionality of the echolocation to be useful in target separation, the directionality of either hearing or broadcasts would have to be great enough to segregate echoes from different targets. In studies of *Eptesicus fuscus*, neither the observed directionality of hearing nor the directionality of sonar support this assumption (Simmons et al., 1995). As noted in Section 4, the directionality of transmissions is quite broad. Furthermore, it has been noted that not only is the directionality of the ear broad as well, but these two are linked in a close manner. Figure 13 shows that the combination of call and ear directivity is practically constant for a range of at least 30 degrees to one side, so that the echolocation system is equidirectional in sensitivity for signals arriving within the 60° wide cone in front of the bat.

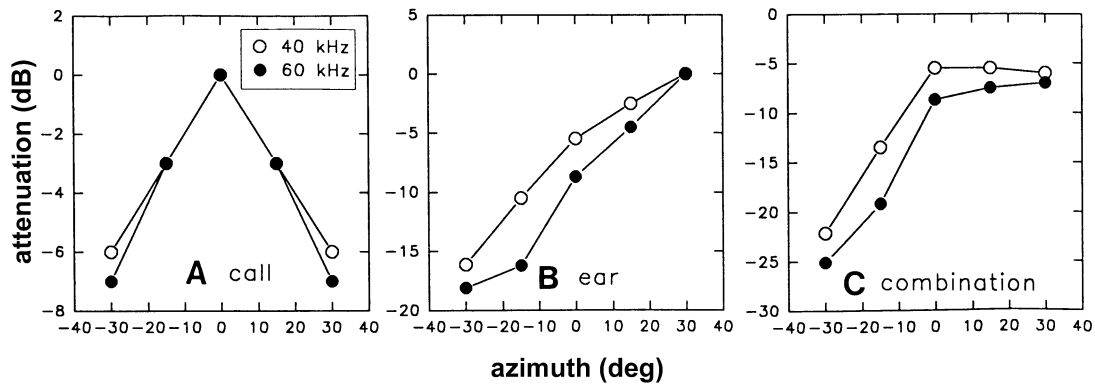


Figure 13: Directivity of (A) calls, (B) ear, and (C) combination directivity, measured from *Eptesicus fuscus*. (After Simmons et al., 1995.)

5.4. Angular resolution

In several studies conducted both by observing the performance of bats capturing or pointing their heads directly at flying insects and in laboratory behavioral experiments it has been noted that bats appear to be able to determine the direction of an echo source to within $\pm 2^\circ$ – 5° (Grinnell, 1995). For example, the big brown bat, *Eptesicus Fuscus*, is able to discriminate targets at a separation of 1.5° in the azimuth. Even though most mammals have much worse lateral resolution, forced-choice experiments show vertical localization of the *Eptesicus* to be about 3° —almost as accurate as the horizontal separation.

The horizontal spatial hearing is mostly affected by interaural time and level differences as in other mammals. The large pinnae, further complicated by the presence of the tragus, create strong shadows at ultrasonic frequencies. A target 10° – 20° to one side of the axis of a bat's head returns an echo that may be 30–40 dB louder at one ear than at the other (Grinnell, 1995). Furthermore, binaural inhibitory interactions exaggerate interaural differences within the nervous system.

For airborne echolocating creatures, vertical localization is as important as horizontal. As mentioned earlier in this Section, tragus has great effect on vertical angular resolution of bats. This implies that vertical localizations are performed at least in part using the cues from the spectral shaping characters of the pinna. However, long CF/FM bats rapidly flick one pinna forward and the other backward with each pulse emission. This alteration permits correlation of ear position with echo direction, thus enabling binaural processing of vertical localization (Grinnell, 1995). In experiments conducted by Mogdans et al. (1988) it was noted that immobilization of the pinnae of *Rhinolophus ferrumequinum* caused its vertical sound localization abilities to deteriorate notably, thus verifying the significance of pinna movements on vertical localization.

When there are multiple simultaneous targets (such as multiple insects, a tree branch, etc.), the situation becomes more complicated. Simmons et al. (1995) argue that intensity and spectral cues are useless for localization in situations in which there are multiple targets present. For example, to distinguish two reflections (glints) at approximately same distance and angle but on opposite sides of the lateral plane (a common situation e.g. when a bat has to fly between two wires or branches perpendicular to its flight path), the bat has to distinguish signals arriving within a few microseconds. Since the integration

time of the bat ear is 300–400 μs , a simple measurement of interaural loudness difference would result in false target localization (Grinnell, 1995). Instead, Simmons et al. argue that echoes are localized by the interference patterns caused by overlapping echoes from different targets (or glints from parts of targets). The overlapping echoes modify the spectral characteristics of the echo. The resultant signal can in principle be deconvoluted and processed to obtain the direction of each echo source.

5.5. Discrimination of targets

The bats are able to discriminate airborne targets with great sophistication. In experiments performed by Webster & Brazier (1965), two inedible plastic discs were thrown in the air along with an edible mealworm so that the bat is able to catch any of them. In tests of this kind, bats achieve 80%–90% correct captures (Simmons et al., 1995). This is a remarkable achievement, since the targets are well within the ear integration time of each other, and the bat receives only about half-dozen echoes during its approach, from which it has to determine whether the target is a mealworm or a disk.

In practice, the discrimination abilities are even far more sophisticated than described above. Bats appear to discriminate targets by the variations of the Doppler effect caused by insect wing flutter rates (Altringham, 1996). Long CF/FM bats appear to be extremely specialized in Doppler analysis, being able to detect slightest insect movements from the foliage or grass. Moss & Zagaeski (1994) noted that the sounds emitted by FM bats are too short to carry information during an insect's complete wingbeat cycle, and so it was assumed that FM bats only use amplitude differences caused by prey flutter and temporal characteristics of glints to discriminate prey. In subsequent studies by Grossetête & Moss (1997), there have been indications that even FM bats (*Eptesicus Fuscus* in their case) may utilize Doppler-induced changes in echo delays in perception of flying insect prey.

In behavioral field studies it has been noted that different bats substantially select prey both according to their size and their species. The distribution of insect species eaten by bats commonly greatly varies from the distribution of available insect species (Altringham, 1996).

It appears bats are able to create an auditory image of their environment, with which they are able to see and react to different targets and obstacles and track them accordingly. According to Simmons et al. (1995), targets are first discriminated by segregating glints making up the scene and then comparing the echo streams at the two ears in a glint-by-glint manner. These separate targets are then individually tracked using sophisticated auditory scene analysis methods (Moss & Surlykke, 2001).

5.6. Separation echolocation signals

One interesting feature of Microchiropteran echolocation is their ability to use echolocation concurrently with other bats without being confused by other bats' signals. The need for this is still increased due to the gregarious nature of most bat species. While extraneous sounds do influence bat's performance level, echolocation appears to have evolved to overcome many of the problems (Altringham, 1996).

The moustached bat, *Pteronotus parnellii*, overcomes interference by suppressing the first harmonic in its sonar pulse to about -20 dB of the total signal energy. It is then so weak that other bats may not even hear it. The bat itself still hears its own first harmonic directly through the tissue between vocal membranes and cochlea (Altringham, 1996).

The first harmonic is used to open a neural gate which enables the bat's auditory system to receive and process the echo from that call.

Altringham (1996) continues: The small fisherman bat, *Noctilio albiventris*, uses paired CF and CF/FM pulses for echolocation. In experiments, it is able to discriminate its own echo from simulations of CF or FM components of its own CF/FM pulses. However, when presented entire simulations of the CF/FM pulses, the bat could not discriminate the signals reliably any longer. Further research suggests that the bat could only receive and process the FM component to determine the target range, if it was preceded by the correct FM component. The CF component is presumed to open a neural gate of short duration, thus enabling the bat to process the echoes from its own pulses. In many long CF/FM bat species, each bat is assumed to have its own call frequency.

6. INFORMATION TRANSFER IN BAT VOICE USE

It is clear that the signals one bat produces are available not only to itself but to other bats and animals as well, making information leakage a reality of echolocation (Fenton, 1995). This leakage is in large part unintentional, but also intentional communication between bat specimen occurs. This section will discuss different aspects of information transfer (both intentional communication and information leakage) in bats.

Given the gregarious nature of many bat species, it is hardly surprising that they have fairly developed communication skills, both intentional and unintentional.

Because echolocation pulses give hints about the feeding activity and success of a bat specimen, eavesdropping of them is commonly used by conspecifics for acquiring information about good foraging sites (Wilkinson, 1995). It has been demonstrated with playback experiments that eavesdropping leads to group formation for *Myotis lucifugus* which approached speakers broadcasting echolocation calls. There are differences, however, whether the bats respond to calls of other species, or only to conspecifics. Another method for locating feeding sites is to follow conspecifics. This behavior is quite common, and is well shown by clustered departures of roosting sites.

Observing of conspecifics' echolocation calls are also used in situations mutual for both parties. For example, in many cases group foraging is much more efficient than solitary hunting. Some bat species such as *Myotis daubentonii* advertise prey availability by lowering the frequency of the terminal buzz in an attack sequence (Kalko & Schnitzler, 1989). Also co-ordinated tandem flight requires monitoring the location of conspecifics, presumably by eavesdropping on echolocation pulses (Wilkinson, 1995). Furthermore, it has been demonstrated in several cases that individual recognition also occurs in bats, both to find preferred roostmates and to bind foraging groups together.

Also imitative learning has been reported for several bat species (Wilkinson, 1995). Naive bats allowed to search for mealworms suspended on a wall found the mealworm faster and more confidently when a knowledgeable bat was present. Observations of extreme similarity in echolocation pulses between mother and young *Rhinolophus ferrumequinum* also suggest that imitative learning influences echolocation calls as well.

There exists also quite some intentional signalling. Many bat species use audible calls during courtship and copulation. Furthermore, alarm calls, while reported only for one species, are assumed to be more common among bats (Wilkinson, 1995). Also, when captured, many bats emit loud low-frequency vocalizations, maybe to startle the predators or to attract conspecifics.

There exist intentional calls both for defending and advertising foraging sites. Many

species have territorial calls for defending feeding sites, especially when food density is low. On the other hand, some species give audible vocalizations at feeding sites without evidence of territorial behavior. Several bats also have audible screech calls, which attract conspecifics, and which are used to recruit conspecific bats into foraging groups. These calls are given at times when group members will hear them.

7. CONCLUSIONS

The hearing capabilities of any other land animal do not match that of bats. The *Microchiroptera* have developed such elaborate echolocation skills, that field observations and behavioral experiments document remarkable, sometimes seemingly impossible skills at detecting, localizing and discriminating the nature of targets by echoes of emitted sounds. Both CF/FM and FM bats have developed unique, ingenious ways of extracting information from acoustical signals. These traits, together with the unique capability of powered flight, have made bats one of the most successful, and probably the most diverse mammalian order.

Bats may possess the most advanced hearing of any land animal. They behave as if they can construct a full, remarkably detailed, acoustic image of nearby objects in space by the echoes of each pulse.

Research of bat hearing, driven to large extent by behavioral experiments, continuously sheds new light on mammalian hearing and the neuroethology of mammalian auditory structures.

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