Echolocation in Bats: A Fascinating Array

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The paper discusses the process of use of sound to distinguish the objects present in our environment known as echolocation. It can also be defined as the process of visualizing with the aid of sound, which is remarkably utilized by those organisms lacking efficient vision power. It is very astonishing that the diverse range of vertebrates uses sound to acquire their food and shelter supplemented with the aim to escape from their enemies to ensure the continuity of their race. These include the bats (Chiropterans), dolphins, whales (Odontocetes), birds, shrews, swift lets, porpoises, etc.

Key Words: Morphological modifications, Echo call

Introduction

The process of use of sound to distinguish the objects present in our environment is known as echolocation. It can also be defined as the process of visualising with the aid of sound, which is remarkably utilised by those organisms lacking efficient vision power. It is very astonishing that the diverse range of vertebrates uses sound to acquire their food and shelter supplemented with the aim to escape from their enemies to ensure the continuity of their race. These include the bats (Chiropterans), dolphins, whales (Odontocetes), birds, shrews, swift lets, porpoises, etc.

Fig. 1: Examples of echolocating birds and mammals

Basic principle behind echolocation

Echolocation, also referred to as biosonar, is a biological process employed which involves the emission of sound by the concerned animal into the environment which after striking the obstacles gets bounced back as echoes.

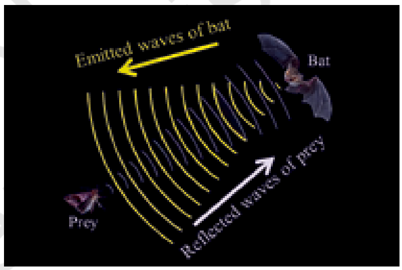

Fig. 2: Basic principle of echolocation

These echoes created by the surrounding objects are received by the animal to acquire an accurate representation of the surroundings. The range and the horizontal angle (azimuth) of the objects can be calculated to a high degree of accuracy by utilising the time delays and sound intensity of the received echoes thereby facilitating efficient communication, orientation, navigation and foraging of the respective animal. There are significant differences in the method of production, reception and interpretation of sound processing from animal to animal. In a nutshell, echolocation is a process conducted by the auditory brain circuit where the ascending brain pathways in the brain stem allow the brain to calculate the differences between the receptions of two ears even to a level of small fractions of a second. The approximate echo level (EL) returning to the echolocating animal can be estimated using the active SONAR equation, i.e. $EL = SL + TS - 2 \times TL$, where TS denotes the target strength, SL denotes the source level of the emitted sound pulse, and TL represents the transmission loss. Appropriate detection of the returning echoes is possible when the EL is higher than the hearing threshold of the echolocating animal or higher than the ambient clutter levels.

Echolocation in Bats

The unique wing structure and the specialised muscular coordination of bats facilitate appreciable flight manoeuvrability – crucial to their survival due to their extraordinary dependency on the small, quick moving insects. The task of hunting their prey becomes increasingly difficult for them due to their restricted activities at night, dusk and dawn. Their adaptation to this — against the clock — lifestyle is attributed to their tendency to escape the capture of their fierce flying predators who are exceptionally active during the day time. Hence, bats utilise the advantage of the abundant nocturnal insects to which they get access by their remarkably astonishing navigation system, i.e. echolocation.

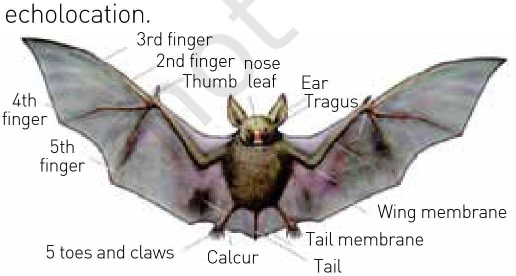

Fig. 3: Morphological features of a bat

Morphological Modifications

Bats have specialised larynx (voice box), the contraction of which produces sound. The vibrations of the vocal cords within the larynx which is tensed by cryco-thyroid muscle leads to sound production. The clicking of tongue by certain species invariably accomplishes sound production. In a few species, a basal fleshy horseshoe or leaf like structure is adhered to

Fig. 4: Head of a bat

the base of the nostrils which too aid in the emission of echo calls. Hence, bats can be regarded as mouth emitters or nostril emitters. The ears and the brain cells of the bats which are attuned to the sound emitted and the echo produced; contain dense concentration of the receptor cells within, which in turn make it tremendously sensitive by aiding it to detect even minute frequency variations, 0.0001 kHz. The ears of the bats are especially designed to get adapted to endure high frequency calls without getting any damage. To prevent deafening, the middle ear muscle called stapedius dampens the sound and contracts to separate three bones (ossicles), i.e. malleus, incus and stapes which normally conduct the received sound waves between eardrum and cochlea, thus reducing the hearing sensitivity. This contraction of muscle occurs about 6 ms before the larynx muscle contract to commence the process of sound production. The middle ear muscle relaxes 2- 8 ms later, at an instant, when the ear is ready to receive the echoes of the surrounding objects. The reception and funneling of the echoes bounced back by the obstacles is perfectly accomplished by the bats due to the presence of large variations in sizes, shapes, folds and wrinkles in their external ears.

Nature of Echolocation Calls

Extensive research in the branch of chiropterology confirms that the source filter theory is applicable in bats. According to it, the vibration of tissue masses lead to sound production where certain frequencies are attenuated while the rest are left for propagation. As voice is considered a distinguishing feature of a particular person, similarly the echolocation calls also have certain variations in terms of frequency, intensity, harmonics, pitch, pulse interval, call duration, etc.

The echo calls generally have a frequency range from 9 – 200 kHz, majority of the range encompassing the human audible range which extends up to 20 kHz. In terms of loudness, bats exhibit significant variations ranging from 50 dB to 120 dB. Though some of the squeaks and squawks produced by the bats can be heard by the humans, but these are not echo calls. An echolocation call can be composed of FM or CF. FM or frequency modulation sweep is a broadband signal consisting of a range of frequencies, which allows for better resolution of time delay between call and returning echo thereby improving the cross-correlation of the two. Additional imposition of harmonic frequencies enhances the precision of localisation.
The distribution of energy of the call over a wide range of frequencies decreases the operational range of the FM call. Any echo returning at a particular frequency can be evaluated for a minute fraction of second due to fast downward sweep of the call which doesn't remain at a particular frequency for a considerable interval. CF or constant frequency is a narrow band signal composed of a constant frequency throughout the call duration and consequently has extended operational range as the summation of the echoes returning from within the narrow frequency band over the entire length of the call remains consistent for a considerable time. CF signals have adaptive structures that allow these bats to detect both the velocity and fluttering of the target. Hence FM and CF components are suitably used to prey in cluttered environment and open sky respectively due to their characteristic features without calls overlap.

A single echo call can persist from 0.2 to 100 milliseconds in duration depending on the stage of the prey catching behaviour in which the bat is engaged in. The call duration decreases in the final stages of prey capture which enables the bats to emit calls more rapidly with simultaneous reception of echoes without overlap.

The pulse, i.e. the time interval between successive echo calls is an important aspect to be controlled. Bats increase the repetition rate of their calls, i.e. decrease the pulse interval as they locate a target in order to get updated information about the target's location. Hence, the approach of the bat towards the prey transforms their echo calls into a terminal buzz or train of clicks. The pulse interval also determines the maximum range of bat's detection capacity as the bats can keep a track of the echoes from one call at a time which then gets expunged after the reception of subsequent echoes from the next calls.

Structures involved in Echo Call Reception

The process of accurate orientation of the objects in the brain is accomplished by the bats with the aid of specialised neuro-auditory circuits and capable of interpreting the calls generated by its own species. Although the bats exhibit remarkable structural similarities in their auditory organs with those of the mammals, however certain bats have specialised modifications of the inner ear to amplify its responsiveness to a particular ultrasonic frequency. The bats with CF component have a narrow frequency tuning corresponding to that of the predominant frequency and harmonic of CF vocalisation supplemented with an especially large area responding to the frequency of bat's returning echoes. All these specialisations are concentrated within the basilar membrane in cochlea. A large membranous section is present in the brain of bats which is extraordinarily sensitive to the frequency of the returning echoes called the *acoustic fovea* that possess dense aggregation of the primary auditory neurons. The stimulated basilar membrane which is connected to the auditory pathways transmits the signals to the primary auditory neurons and results in elicitation of considerable degree of response.

The process of conduction of the integrated signals received from the auditory processing pathway to the auditory cortex is performed by the inferior colliculus present in the bat's midbrain. As the collicular neurons maintain high time accuracy hence the interneuron localised in that region are highly sensitive to the time delay which provides an idea about the distance. This extraordinary degree of responsiveness is attributed to their low threshold of activation. Besides, after getting activated, they respond with one or two action potentials. This short duration of response ensures extreme precision in the calculation of time delays.

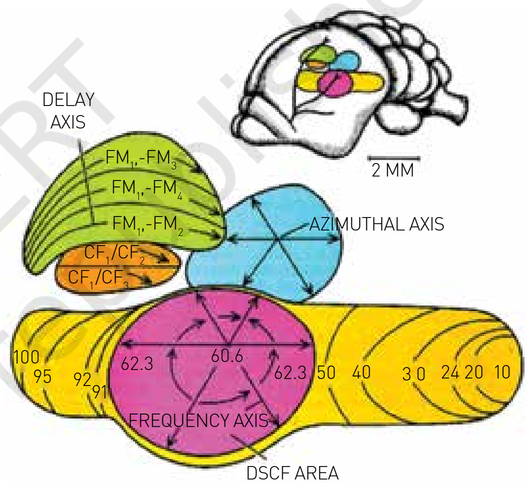

Fig. 5: FM, CF and DSCF areas in the brain of bat

A large space is occupied by the auditory cortex which being composed of a series of maps organised systematically based on acoustic functions, houses the response sites of different signals. A dense aggregation of neurons are localised there which responds to those specific frequency-timing (sound echo delay) and hence known as combination-sensitive neurons. The elicitation of a response requires the exposure of neurons to at least two specific stimuli. The maps are basically of three types: FM-FM, CF-CF, and DSCF (Doppler shifted constant frequency). FM area is FM sensitive combination neurons arranged in columns which respond to the two FM sweeps: a call and its causes possessing sensitivity for one harmonic in the original call and a different in the returning echo. CF area consists of neurons sensitive to specific CF calls. The DSCF area is a large section of the cortex constituting a map of acoustic fovea which is organised into radially arranged columns containing neurons responding to specific combination of frequency and amplitude. Neurons in this region respond to Doppler shifted CF signals (only echoes) which lies within the same narrow frequency range of response of acoustic fovea and hence play a vital role in frequency discrimination.

Bat's Perception and Sensing

Bats emit their echolocation calls due to passage of air through the vocal cords which gets vibrated and produces sound. This sound when emitted causes fluctuations in the rushing air and generates a longitudinal sound wave which requires a medium for propagation. The transmission of sound wave in the air is accomplished by the conduction of vibration to the surrounding air particles thereby generating a series of compressions and rarefactions. When the wave propagates, the energy of the disturbed particle is

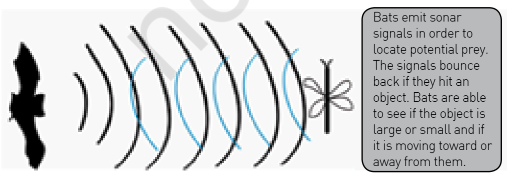

Fig. 6: Location of prey by signals

transmitted to the adjacent particle thereby disturbing the latter from its equilibrium position. This particle soon displaces its adjacent particle on striking with it. The restorations of the disturbed particles occur with the wave continuously striving forwards. These waves however can get reflected, refracted or attenuated by the medium. The waves when strike a solid, preferably a

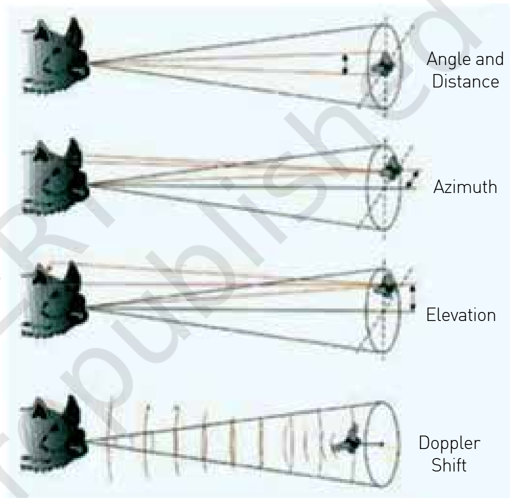

Fig. 7: Discrimination using echolocation

large obstacle, get bounced back as echoes which can again be perceived by the emitter provided the time of reflection and distance of obstacle are coherent. For example, in case of humans, the audible sound persists for one-tenth of a second and speed of the sound in air is 340.29 m/s and hence the object from which echoes can be received should be located at least at a distance greater than 17 m otherwise the echoes will be received too early and cannot be distinguished from the originally emitted sound. The distance varies from organism to organism depending on the characteristic persistence of successive sounds.

By minutely listening to the echoes, bats can very accurately determine the position, shape, size and direction of motion of the objects. The bat can have the idea whether the insect is to the right or left by comparing the relative moment of the sound reaching the left and right ear. If the sound reaches the right ear prior to the left ear, then the insect is definitely present on the right side. The intricately designed ear folds perform the task of determination of an insect's vertical position. Echoes escalating from beneath will strike the outer ear folds at a different point than those descending from an elevated obstacle, which in turn produce different sounds after propagating into bat's inner ear. The estimation of elevation of obstacle detected is done by the interpretation of the interference patterns caused by the echoes getting reflected from the flap of skin on the external ear, the tragus. The idea about the size of the insect can be obtained by the analysis of the echo intensity. A smaller object will reflect less of the original sound wave thereby producing a less intense echo. The determination of the pitch of the echo can pave the way to sense the direction of movement of the prey. A prey moving away from the bat will result in the production of the echo with a pitch lower than the original sound while those originating from the insect moving towards the bat will have a higher pitch. This difference is distinct due to the phenomenon of Doppler Effect— a popular concept of acoustics. This information received is processed unconsciously in their brain, as we process the visual and aural information, by forming an echolocation image in its head.

Defense Mechanism of the Prey

Evolutionary studies of certain animals reveal a significant advancement in the cultivation of certain characters aimed to escape from their predators by hoodwinking them. The target prey exhibit strategies to impede its detection, one of which is associated with the increment in noise levels in the environment thereby minimising the echo/clutter ratio. The moths flying close to vegetation escape from the bats by auditory camouflage. In other words they hide themselves acoustically in certain environments where the echoes originating from them are predominated by other echoes. The small muscular mass and size of prey lower the target strength. If the prey gets aware of the fact that it has already been detected by the bat using its inherent aural and vibration sensing qualities, it starts exhibiting secondary defense mechanisms. The insects that are capable of tracing the bat's echolocation calls possess evasive manoeuvres. Some insects, such as, tiger moths emit anti-bat signals which are species-specific in function. These signals serve as a mode of advertisement of moth's toxicity in some species while startling the bats in other species. The anti-bat signals can also jam the bat's biosonar. Hence, the insects which evolve features to respond to ultrasonic frequency remain mostly undetected leaving their contemporaries encounter considerable selection pressures.

The bats can also detect their predators and enemies like cats, snakes, etc., by minutely analyzing the characteristics of the approaching organism by getting reference from the echoes received. It is probably the size of the organism which helps the bat procure an idea about the presence of a predator or prey approaching it.

Echolocation Jamming

Bats hunt by echolocation which refers to the phenomenon where they listen to the bouncing back echoes generated by the high-frequency ultrasonic sound emitted by them. The universal system of competition prevalent in our ecosystem transforms the predator-prey interactions into amazing aerial dogfights. In order to sustain in the increasingly shrewd environment, bats of a few species have evolved strategies to emit certain typical calls quite distinguishable from normal echolocation calls. A close observation has revealed that the emission of those special calls occur on the occasions of approach of another bat towards their prey. It is hence concluded that these bats emit the calls to interfere with other's echolocation calls and the echoes, thereby causing jamming and confining the located prey within its own dish. Recent study on the habits of Mexican free-tailed bats (*Tadarida brasiliensis*) has confirmed the use of this jamming technique which is prominently observable while another bat emits the distinct feeding buzz.

Evolutionary Deductions

While a few bat species lack the power of vision but it cannot be negated that echolocation is often used in conjunction to vision. These abilities are not disjoint sets. Paleontology of bats provides evidences indicating the inability of bats to exhibit the echolocation powers approximately 52 million years ago. This makes us believe that the process has evolved in them to enable them to thrive in their habitats. Two hypotheses have been proposed regarding the evolution of echolocation in bats. The first suggests that the evolution of laryngeal echolocation has occurred twice in Chiroptera, once in Yangochiroptera and once in the Horseshoe bats, i.e. Rhinolophidae. The second proposes single origin of it in Chiroptera, which was subsequently lost in the family Pteropodidae (all megabats) and later evolved as a system of tongue-clicking in the genus Rousettus. The possession of echolocation ability has enabled the Microchiropterans to occupy a diverse set of ecological conditions and simultaneously get adapted to the specific environments. These processes which are linked together so as to be carried out in a coordinated way promote the process of decent with modification escalating diversity of Microchiropterans as is visible today.

Conclusion

The advancement of science and technology in the present century is creating countless ways to conserve non-renewable natural resources often turning an ignorant attitude towards its negative impacts on the ecosystem. The construction of windmills to guarantee uninterrupted power supply has aggravated enormous problems for the bats, thus disturbing the natural ecosystem and obstructing the food chain and in turn the food web. Though the God gifted creatures are blessed with features to protect themselves from these stresses but the rampant and reckless expansion of the modernisation strategies is posing a genuine threat by disturbing the natural ratios. As human beings, we should take an oath to respect the wildlife resources of earth. We should be focused enough to undertake determined endeavors to conserve wildlife. Our motto should be to satisfy our needs and not our greed and we should strictly abide by this path until it is too late where the situation becomes irreparable. We have only one mother earth to live in and hence we should not leave a single stone unturned to transform it into a golden planet.

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Further reading

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