Bat Biosonar

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Bats (the order Chiroptera) are a huge and very diverse family of mammals. There are approximately 1000 species of bats, meaning that they make up about one fifth of all the mammals (Au et al, 2007). One of the most interesting aspects of bats is their ability to use echolocation to sonically “see” their surroundings and detect prey. Not all bats use echolocation; the Megachiropterans (flying foxes), of which they are about three hundred species, are not echolocaters, but the remaining seven hundred species, the Microchiropterans, are.

The bats get information about their surroundings by sending out brief, high pitched calls and listening for echoes. The sound bounces off of the environment (trees, the ground, and hopefully insects) and returns to the bat, which can determine information about the size and location of different objects from the amplitude (volume) and frequency (pitch) of these incoming waves. Bats produce the calls using the larynx, and they are emitted through the nose or the mouth (Fenton et al, 2012)(Schnitzler and Denzinger, 2011). The bats can focus and control the sound waves they send out to get focused, sensible information back from the echoes.

There is a considerable amount of variation in the particulars of echolocation between bat species. One of the main splits arises from how bats deal with the problem of acoustical masking. The sounds that the bats are emitting are much louder than the echoes returning from the environment. If the bat is constantly releasing sound, it would not be able to hear the sound of the returning echoes over the much louder sound that it is producing. There are two main strategies to deal with this; that of the high duty cycling bats and that of the low duty cycling ones (Fenton et al, 2012).

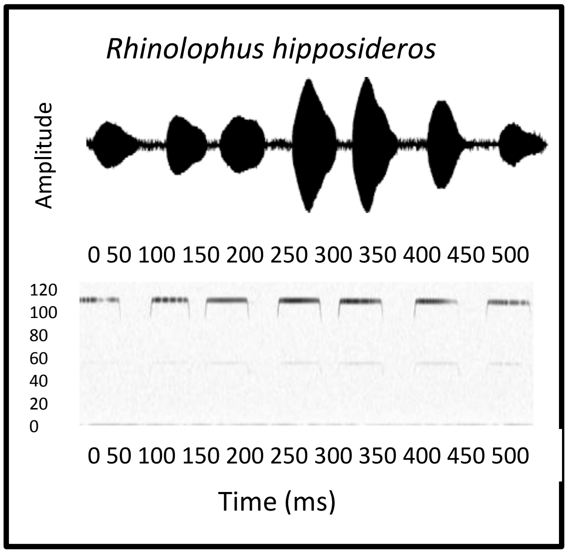

Figure 1 : Top; oscilligram and bottom; spectrograph of the call of *Rhinolophus hipposideros*, the lesser horseshoe bat. It is a high duty cycling bat. The oscilligram on top shows the amplitude of the sound wave produced. The spectrograph on the bottom shows the frequency of the same call in kHz. The overall constant frequency of each call can be easily seen on the spectrograph. From Fenton et al, 2012.

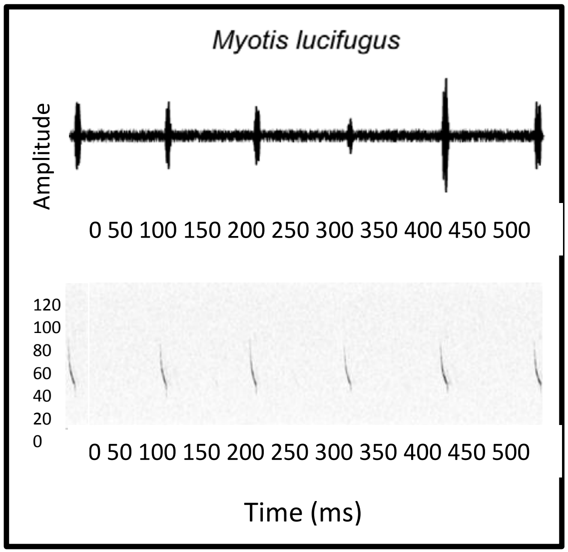

Figure 2 : Top; oscilligram and bottom; spectrograph of the call of *Myotis lucifugus*, the little brown bat. It is a low duty cycling bat. The oscilligram on top shows the amplitude of the sound wave produced. The spectrograph on the bottom shows the frequency of the same call in kHz. The short calls with the high variability of frequencies are characteristic of the low duty cycling bats. From Fenton et al, 2012.

The duty cycle is the ratio of the time spent calling and the time spent in silence. The low duty cycling bats have longer silences between their calls because they use time to separate the calls and the echoes. The high duty cycles differentiate between them using the frequency of the sound, and hence spend more time during the call cycle actually producing sound. Because the bats separate call from echo in different ways, they produce different types of calls.

The low duty cycling bats use frequency modulated calls (frequency modulated waves are sometimes called broadband). These calls use a wide range of frequencies. A frequency modulated sweep can cover about an octave in under five milliseconds (Jones, 1999). These bats emit calls that last for only 1 to 20 milliseconds (Fenton et al 2012). This is the call structure that is used by most bat species. It well suited for localization of objects and prey.

High duty cycling bats are much rarer. This call structure is used by about 160 species in the families Rhinolophidae and Hipposideride, as well as in one species of Mormoopid (Fenton et al 2012). It uses separation of frequency rather than separation in time to clearly distinguish between incoming and outgoing sounds. High duty cyclers emit calls of a much longer duration, 10 to 50 milliseconds. These calls are constant frequency (narrowband) calls, with a short frequency modulated burst at the end of the call. These high duty cycle calls, while more rare, allow these bats to determine location of objects and prey as well as the type of prey and the direction it is moving. It also increases these bats' ability to distinguish their fluttering prey from more cluttered surroundings. This is done by the bats' manipulation of acoustical physics.

Because echolocation is mostly done while moving, one of the interesting issues that the high duty cycling bats run into is the Doppler effect. The Doppler effect is the change in frequency when a sound source is approaching or moving away from the listener. When the sound source is approaching the listener, the frequency heard by the listener increases, and when the sound source is moving away from the listener, the frequency decreases (Speaks, 1996)(Stephens and Bate, 1996). This is not important for the low duty cycling bats because frequency is less important in their analysis of echo data and because their calls are so short. It is,

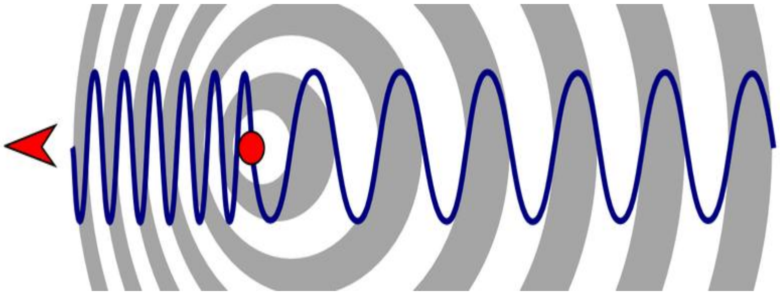

Figure 3 : Graphic representation of the Doppler effect with the red point moving to the left of the page.

however, understandably an important thing for the high duty cycling bats because they use frequency changes to distinguish between incoming and outgoing sounds.

For an example from nature, let us consider a lesser horseshoe bat (Rhinolophus hipposideros) flying in the positive x direction at a velocity of 5 meters per second. This bat, one of the high duty cycling bats, emits a constant frequency call at frequency 110 kHz. The emitted sound wave bounces off of a stationary insect located 10 meters in front of the bat. What will the frequency of the call be at the location of the bug?

The new frequency is determined by the equation

$$f' = f(\frac{s}{s - s_{source}})$$

where f' is the new frequency, f is the frequency emitted by the sound source, s is the velocity of a sound wave in air (at sea level, this is approximately 340 meters per second) and s_{source} is the velocity of the sound source (Speaks, 1996). So,

$$f' = 110kHz\left(\frac{340\frac{m}{s}}{340\frac{m}{s} - 5\frac{m}{s}}\right)$$

$$f' = 111.6\,kHz$$

The sound then has to bounce off the insect and return to the still moving bat for the bat to gain information from the call.

To find the frequency when the call reaches the bat, we use the following equation:

$$f'' = f'\left(\frac{s + s_{receiver}}{s}\right)$$

where f'' is the frequency when the call reaches the bat, f' is the frequency being bounced off of the insect, s is still the velocity of the sound wave in air, and $s_{receiver}$ is the velocity of the bat. This time, the insect is the sound source and the bat is the listener.

$$f'' = 111.6\ kHz \left(\frac{340\frac{m}{s} + 5\frac{m}{s}}{340\frac{m}{s}} \right)$$

$$f'' = 113.2\ kHz$$

when the sound has made its way back to the bat.

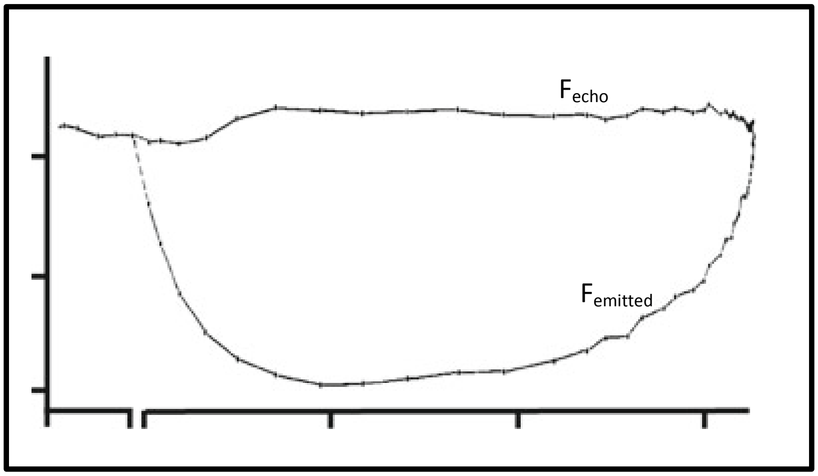

Figure 4 : A figure showing the frequencies of both the emission from *Rhinolophus ferrumequinum*, the greater horseshoe bat and the returning echo off of a stationary target for the same call. It is easily seen that the bat is reducing and modulating the frequency of its own call to keep the echo at an optimally audible level. From Schnitzler and Denzinger, 2011.

When the high duty cycling bats lock on to a target, they have to modulate their calls to mitigate the Doppler effect. What they do is lower the frequency of their calls so that the echoes coming back stay at a constant frequency (Schnitzler and Denzinger, 2011). This has two functions.

First off, it allows them to filter out some background noise (Schnitzler and Denzinger, 2011). It is easy to see that in crowded environments like close forest it is more difficult to distinguish a fluttering bug from the moving leaves. It is especially difficult for low duty cycling bats that do not use Doppler effect modulation. Because of this, most of the echolocating bats are aerial-hawking bats. This means that rather than hunting in the cluttered environment of a forest, they hunt on forest edges or in open fields. For high duty cycling bats, being able to handle this background noise allows them to exploit underutilized niches in the forest community, giving them an evolutionary advantage.

It also allows them monitor whether they are gaining on the insect or not more easily. If we look again at the bat example, we can calculate the amount they need to lower their frequency to modulate their movement towards the insect.

So, we set up the same set of equations:

$$f' = f\left(\frac{s}{s - s_{bat}}\right) \qquad f'' = f'\left(\frac{s + s_{bat}}{s}\right)$$

And then combine them and solve for f.

$$f'' = \left(f\left(\frac{s}{s - s_{bat}}\right)\right)\left(\frac{s + s_{bat}}{s}\right)$$

$$f = \frac{f''(s - s_{bat})}{(s + s_{bat})}$$

Let us see what the original call frequency needs to be to keep the echo frequency at 200 kHz.

$$f = \frac{200kHz\ (340\frac{m}{s} - 5\frac{m}{s})}{(340\frac{m}{s} + 5\frac{m}{s})}$$

$$f = 194.2\ kHz$$

High duty cycling bats also have another advantage from their long calls. The duration of the call is 10 to >50 milliseconds. The period of an insect’s wingbeat is also 10 to 50 milliseconds. During the wingbeat of the insect, there is one point where the insect’s wings flare out perpendicularly to the direction of the propagation of the sound wave from the bat as it moves them back to start another wingbeat. These flared out wings reflect more sound back towards the bat, and the insect’s wings are moving backwards from whichever way the insect is flying. This causes a “glint” in the echo that the shows up in both the amplitude and frequency of the echo. The glint shows up in the amplitude because there is more area for the sound waves to bounce off. The change in the frequency is even more useful. The movements of the wings indicate the direction of the insect’s flight, and the bat can pick up on that by detecting the tiny changes in frequency caused by the Doppler shifts made by the wings (Schnitzler and Denzinger, 2011) .

Continuing from the earlier example, we can calculate how much the frequency spikes during this glint.

If we assume that the insect is preparing to flee from the bat but is not actually moving yet. It is flaring its wings backwards towards the bat at the rate of 10 meters per second. The following equation is the basic Doppler effect with both sound source and listener moving.

$$f' = f\,\frac{(s + s_{receiver})}{(s - s_{source})}$$

When this is adapted to find the frequency of the echo.

$$f'' = f\left(\frac{s + s_{wing}}{s - s_{bat}}\right)\left(\frac{s + s_{bat}}{s - s_{wing}}\right)$$

$$f'' = 194.2\ kHz\left(\frac{340\frac{m}{s} + (-10\frac{m}{s})}{340\frac{m}{s} - 5\frac{m}{s}}\right)\left(\frac{340\frac{m}{s} + 5\frac{m}{s}}{340\frac{m}{s} - (-10\frac{m}{s})}\right)$$

$$f'' = 188.6\ kHz$$

The frequency of the glint decreases when the insect is moving away. Now, let's model the glint if the insect is (foolishly) moving towards the bat. This means that the backstroke on the wings when they flare out is in the positive x direction.

$$f'' = f\left(\frac{s + s_{wing}}{s - s_{bat}}\right)\left(\frac{s + s_{bat}}{s - s_{wing}}\right)$$

$$f'' = 194.2\ kHz\left(\frac{340\frac{m}{s} + 10\frac{m}{s}}{340\frac{m}{s} - 5\frac{m}{s}}\right)\left(\frac{340\frac{m}{s} + 5\frac{m}{s}}{340\frac{m}{s} - 10\frac{m}{s}}\right)$$

$$f'' = 212.1\ kHz$$

This ability allows these high duty cycling bats to sense fluttering insects, their food of choice, more easily. They can also actually identify the kind of insect they are targeting from the pattern of the wingbeats, which allows them to be "picky eaters" and avoid noxious prey, a distinct advantage in evolutionary terms.

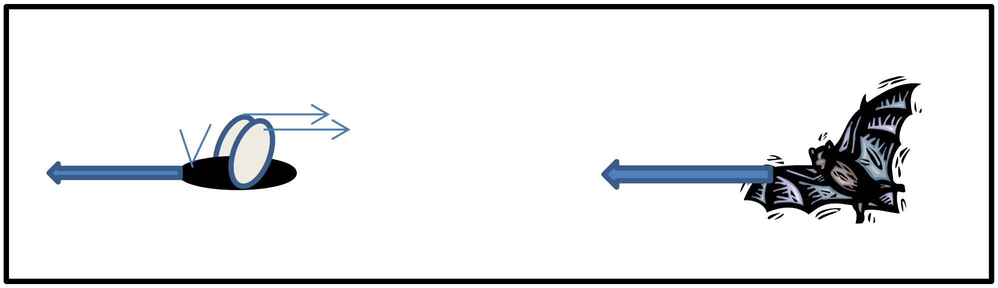

Figure 5 : Diagram of bat chasing a fluttering bug. During its wingstroke, the insect must move its wings backwards in relation to its body to reset the wingstroke. This movement turns more of the wing towards the bat and produces an acoustic blip on the bat's radar.

Figure 6 : The Ziama horseshoe bat *(Rhinolophus ziama)* shows elaborated noseleaf structures. Arkive.com

Frequency modulation is not the only method that bats have to control their echolocation. Another method is the use of noseleaves to modulate the pattern of the beam of sound released. Noseleaves are elaborated structures around the mouth and nose that some bats have. They have some slight mobility and are used to focus the beam of sound produced (Feng et al, 2012). The outer ears, also called pinnae, are also often large and mobile. They can be used to focus on incoming sounds from a specific area. The noseleaves help define the beam pattern, or the pattern of sound intensity emitted by the sound source at a long distance(Muller, 2010)(Koblitz et al, 2011). At long distances, the beam pattern varies with the frequency of the sound wave and at close distances it is a much more complicated function involving frequency and position (Muller, 2010). Receivers also have a beam pattern that they receive sound

Figure 7 : The Plecotis auritus, or brown long eared bat, exhibits a beautiful example of the exaggerated pinnae often seen in the echolocating bat species. Wikimedia Commons.

from.

Echolocation is an impressive adaptation in all the bats, but it reaches even more impressive heights from the physics perspective when one considers the bats that use primarily constant frequency calls with a high duty cycle rather than short, spaced, frequency modulated calls. They are able to more effectively find, track and identify fluttering insects even in cluttered backgrounds, which can slow bats that use frequency modulation. Their adroit manipulation of something as simple as the Doppler effect is a truly amazing feat of adaptation to exploit resources in cluttered environments.

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