Echolocation and hearing in bats

• Sound transmission
  – Sound properties
  – Attenuation

• Echolocation
  – Decoding information from echoes
  – Alternative calling strategies

• Adaptations for hearing in bats

• Websites
How does a cicada sing?

Sound is produced by changes in pressure.
Frequency and wavelength

- Wavelength of a sound is the distance traveled in one cycle.
- Frequency (in cps or Hertz) = 1/period, \((f = 1/T)\)
Wavelength depends on media

- Wavelength depends on the speed of propagation \((c)\)
- \(Wavelength = cT \) or \(c/f\)
  - Speed of sound in air \(= 340 \text{ m/s} \), so wavelength of 340 Hz \(= 1 \text{ m}\)
  - Speed of sound in water \(= 1450 \text{ m/s} \), wavelength of 340 Hz \(= 4.3 \text{ m}\)
Wavelength problem

• Which sound has a shorter wavelength: 1 kHz in air or 3 kHz in water?
• Wavelength = speed of sound / frequency
• Air: 340 m/s / 1000 cycle/s = 0.34 m/cycle
• Water: 1500 m/s / 3000 cycle/s = 0.5 m/cycle
• Therefore, the answer is 1 kHz in air
Source movement

- When the sound source is moving, the frequency of the sound will be altered. This is known as the Doppler shift
- Approaching sounds are higher in frequency
- Departing sounds are lower in frequency
Amplitude measurement

- Sound pressure is measured in decibels (dB) on a $\log_{10}$ scale relative to a reference level.
- $\text{dB} = 20 \log_{10} \frac{P_1}{P_r}$ where $P_r$ is a reference pressure level, usually the threshold of human hearing at 4 kHz. This is referred to as sound pressure level (SPL).
- A sound with twice the SPL is 6 dB louder: $20 \log_{10} (2) = 20(0.3) = 6$. 
Sample sound pressure levels

- soft whisper \(20 \text{ dB}\)
- nearby songbird, office hum \(50 \text{ dB}\)
- barking dog \(70 \text{ dB}\)
- roaring lion, heavy truck \(90 \text{ dB}\)
- echolocating bat \(100 \text{ dB}\)
- jet take-off \(120 \text{ dB}\)
Amplitude measurement

Peak  Peak-to-peak  Root-mean-squared (RMS)
Amplitude problems

• If sound A has 10 times the SPL of sound B, how much louder is A than B in dB?
  \[ dB = 20 \log_{10} 10 = 20 \text{ dB louder} \]

• If sound A is 100 db and sound B is 80 db, how much louder is A than B?
  • 20 db

• If an 80 db sound is combined with a 40 db sound, how loud is the sound (approximately)?
  • 80 db
Phase shifts

- Sounds that arrive out of phase cancel each other out (negative interference)
- Sounds that arrive in phase increase in amplitude (positive interference)
- Sounds partially out of phase create varying amplitudes (beats)
Sound spectrum

Time domain

Frequency spectrum

Frequency domain

Sound pressure or voltage vs. time

Amplitude vs. frequency
Frequency domain of a complex wave

Frequency spectrum

Phase spectrum
The Fourier series

• Any continuous waveform can be partitioned into a sum of sinusoidal waves

\[ P(t) = P_o + \sum P_n \sin (2\pi f_n t + \Phi_n) \]

• \( P_o \) is the ambient pressure
• \( P_n \) is the pressure of the \( n \)th sine wave
• \( f_n \) is the frequency of the \( n \)th sine wave
• \( \Phi_n \) is the phase of the \( n \)th sine wave
Harmonic series

• Harmonic frequencies are integer multiples of the fundamental frequency, i.e. $w, 2w, 3w, 4w \ldots$

• Dirichlet’s rule states that the energy in higher harmonics falls off exponentially with the frequency of the harmonic.

• Note, however, that some bats alter the amplitude of harmonics by selective filtering during sound production.
Sound attenuation

- Spherical spreading
- Absorption
  - Temperature and humidity effects
- Scattering
  - Reflection, refraction, diffraction
Spherical spreading

- Loss in sound intensity follows the inverse square law: pressure halves for each doubling of distance, i.e. - 6 dB for each doubling of distance.
Atmospheric attenuation

Increases with temp. & square of frequency

Nonlinear with humidity
Diffraction

Reflected wave is out of phase with creeping wave. Occurs when wavelength is similar to object diameter.
Sound reflects off objects when wavelength is less than the size of the object.
Echolocating animals

http://www.youtube.com/watch?v=0ne00CWf6kc
http://www.youtube.com/watch?v=_aXF_FZm1ag
Bat echolocation

60 kHz pulse
19 mm target at 3 m
Information decoded from echos

Range
  pulse-echo time delay
Velocity
  pulse-echo frequency change
Target size
  frequency of echo
Location
  ear amplitude difference
FM calls during prey capture

Big brown bat
*Eptesicus fuscus*

Low duty cycle
FM bats shorten call duration to prevent pulse-echo overlap with target approach
Echolocation call diversity

FM = frequency modulated

CF = constant frequency
Echolocation strategies

CF, considerable pulse-echo overlap
FM, no pulse-echo overlap
Why produce constant frequency calls?

• More energy at a single frequency will carry further
• Target shape change will cause amplitude fluctuations in echoes
• Movement of target will cause frequency shift of echo due to the Doppler shift
• Need to overlap pulse and echo to measure frequency shift accurately
CF calls during prey capture

Greater horseshoe bat, *Rhinolophus ferrumequinum*

High duty cycle
CF bats detect wing flutter as echo glints.
DOPPLER-SHIFT COMPENSATION is demonstrated by placing a mustached bat on a pendulum. During the forward swing the animal lowers the frequency of its emitted pulse (red) such that the echo stays at a "reference" frequency. The animal does not compensate for Doppler shift during the backward swing. O'Dell W. Henson, Jr., of the University of North Carolina at Chapel Hill first performed the experiment.
Call design fits foraging strategy

Fig. 3.24. Foraging strategy in relation to echolocation calls and auditory characteristics. Foraging height is plotted against the best frequency of audition. Bats are loosely divided into gleaners (ground and foliage), above canopy hawkers, low level open-air hawkers, and hawkers in cluttered habitats, and the characteristic sonograms of each group shown (adapted from Neuweiler, 1990).
The auditory pathway
Tonotopic map in the auditory system

Auditory cortex

Gray areas correspond to call frequencies

Auditory cortex is expanded at frequencies associated with echolocation
Neuronal tuning in little brown and horseshoe bats

\[ Q_{10} = \text{best freq/ bandwidth at -10 dB} \]
Pteronotus parnellii
Individual *Pteronotus* bats use unique CF frequencies

Combination-sensitive neurons encode range and velocity in CF bats

Each neuron responds to a specific echo delay and amplitude. In the CF/CF area (tan), neurons along the blue lines respond to a specific CF$_1$ combined with varying CF$_2$. Neurons along the black lines respond to Doppler shifts corresponding to a specific relative target velocity. The bottom graph (right) shows...
Developers:
Dr. Rob Houston
Dr. Stuart Parsons
Dr. Gareth Jones
Dr. Andy Bennett

BIOSONAR
Seeing with sound

http://www.biosonar.bris.ac.uk/
http://www.werc.usgs.gov/bats/searchphasecall.html

Bat Vocalizations - Search Phase Call

![Bat Image](http://www.werc.usgs.gov/bats/searchphasecall.html)

Photo courtesy of Merlin D. Tuttle © Bat Conservation International.

Most of the vocalizations produced by bats are search phase calls. These calls are used to detect what is present in the vicinity of a bat, be it food or obstacles that the bat must navigate around. These calls are often species specific and can thus be used to identify the type of bat making the call.

Even within a species, search phase calls typically vary depending on the information that the bat needs. For example, when flying in an area with lots of vegetation, the bat produces more search phase calls, which tend to be higher pitched, and sweep through a greater range of frequencies. More frequent calls provide more rapid information on something that the bat might need to avoid as it flies along. The higher pitch results in a sound with a shorter wavelength and thus provides a finer resolution when an echo is received. Hence, while it is possible to characterize the calls of most species of bats, there is a considerable amount of variation depending on where it is flying and what type of information the bat is trying to obtain.

**About the Recordings and Graphs**

Each recording is a series of bat calls. With one exception, the pitch (frequency) has been lowered by a factor of 16 so the calls fall within the range of human hearing. For example, a call that was originally 64 kHz is played back at 4 kHz. The Western mastiff bat calls are not lowered since they are already within the range of human hearing. For most of the files, playback speed has not been altered, so you are hearing the calls at the speed they were produced.