Echolocation

• Diversity
  – Organisms
  – Sound production and reception

• Information decoded from echos
  – Distance
  – Velocity
  – Prey size and location

• FM vs CF bat adaptations
Echolocating animals

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

Microchiroptera: 1000 species, 15 families, all echolocate
Megachiroptera: 100 species, 1 family, 1 genus echolocates
Not all bats are aerial insectivores.
Nose leaf and ear diversity in bats
Ear pinna amplifies selected frequencies

- Pinna acts as a horn
- Larger pinna transmit lower frequencies better
- Wavelength of the resonant frequency equals $4 \times$ length of the ear canal
Ear and nose leaf focus sound

(A)

(B) Emitted sound field
(C) Received sound
(D) Sonar beam
Information decoded from echoes

Target detection
Distance
Angular direction
Velocity & trajectory
Target size & shape
Bat sounds are emitted only during wing upbeat to minimize physiological costs.

Air pressure in calls is just below blood pressure in lungs—physiological maximum.

60 kHz pulse
19 mm target at 3 m
Wavelength depends on media

• Wavelength depends on the speed of propagation (c)
• Wavelength = cT or c/f
  – Speed of sound in air = 340 m/s, wavelength of 34,000 Hz = 10 mm
  – Speed of sound in water = 1450 m/s, wavelength of 14,500 Hz = 100 mm

<table>
<thead>
<tr>
<th>Frequency</th>
<th>10 Hz</th>
<th>1 kHz</th>
<th>10 kHz</th>
<th>100 kHz</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wavelength</td>
<td>3.4 m</td>
<td>34 cm</td>
<td>34 mm</td>
<td>3.4 mm</td>
</tr>
</tbody>
</table>
Attenuation is due to spherical spreading, medium absorption, and scattering.
Wavelengths for echolocation
Echolocation call design

FM = frequency modulated

CF = constant frequency
Why produce FM calls?

• FM is best for determining target distance
  – Measure time delay between pulse and echo return
  – FM sweep labels each part of pulse with a frequency value
  – Average time delay between pulse and echo over all frequencies
  – Must not overlap pulses and echoes

• FM is best for determining target properties
  – Object size and shape cause frequency-dependent scattering
  – Can compare frequency spectra of pulse and echo
  – Most information with broadband pulse
FM calls during prey capture

Big brown bat
*Eptesicus fuscus*

Note low duty cycle, bandwidth increases as bat approaches prey
FM bats shorten call duration to prevent pulse-echo overlap with target approach.

![Graph showing the relationship between sound duration and distance to target. The graph illustrates how the sound duration decreases as the distance to the target decreases, with a line indicating the echo overlap zone.](image-url)
Suggests that species that use high frequency must hunt closer to prey and, therefore, need to use shorter calls to avoid pulse-echo overlap.

Figure 26.7  Maximum pulse duration versus average frequency in search pulses of various vesperilionid bats. The line shows result of the regression of pulse duration on the logarithm of frequency. Code to species plotted: Cg, Chalinolobus gouldii; Cv, Chalinolobus variegatus; Ec, Eptesicus capensis; Ef, Eptesicus fuscus; En, Eptesicus nilssonii; Ep, Eptesicus pumilus; Es, Eptesicus serotinus; Gt, Glisochropus tylopus; Hs, Hypsugo savii; Hb, Hesperopterus blandfordi; La, Laephotos angolensis; Lc, Lasiurus cinereus; Ln, Lasionycteris noctivagans; Ma, Miniopterus australis; Ms, Miniopterus schreibersii; Nl, Nyctalus leisleri; Nn, Nyctalus noctula; Ns, Nycticeinops schlefferi; P4, Pipistrellus sp1; P5, Pipistrellus sp2; Ph, Pipistrellus hesperus; Pk, Pipistrellus kuhlii; Pn, Pipistrellus nathusii; Pr, Pipistrellus ruepelli; Pu, Pipistrellus nanus; Sg, Scotorepens greyii; Sn, Scotophilus nigriga; Sv, Scotophilus viridis; Tp, Tylonycteris pachyprous; Tr, Tylonycteris robustula; Vm, Vesperilieio murinus. (From Waters and Jones 1995, © Springer-Verlag.)
How do bats estimate time delay?

- Could compare pulse and echo at a single frequency, but echo frequency depends on object size.
- Better to compare pulse and echo at all frequencies and average. This would provide the best estimate of time delay.
- Can use cross-correlation for this purpose.
Cross-correlation function can be used to measure echo delay time in FM bats

Figure A  Typical autocorrelation function between a signal and a copy of itself at varying lags. Lags can be negative (copy begins before signal) or positive (copy begins after signal).

If bats cannot detect phase, then the correlation function is the envelope
Autocorrelation and bandwidth

Narrow band; 1 ms, 25-20 kHz pulse

Broad band; 1 ms, 50-20 kHz pulse, should permit better range resolution
Call bandwidth and target ranging

Fig. 3.10. Relationship between call bandwidth and target ranging acuity. Target ranging resolution should theoretically be equal to the reciprocal of the bandwidth, the dotted line in the figure. The 4 species studied by Simmons (1973) have target ranging abilities very close to those expected. Lower diagram shows what is meant by resolved difference distance.
Why produce constant frequency calls?

- CF is better for long range detection
  - More energy at a single frequency will carry further
- CF is better for detecting target motion
  - 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*, hunts from a perch.

Note high duty cycle, repetition rate increases as bat approaches prey.
CF bats exhibit doppler-shift compensation

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.
CF bats detect wing flutter as echo glints
Inner ear (cochlea) adaptations

Basilar membrane is longer and thicker at base

A basilar membrane that is thicker at the base increases sensitivity to high frequencies
Middle ear adaptations

Tympanum: oval window area = 53:1 in Tadarida, 35:1 in a cat
Malleus: incus = 3-5:1 in bats, 1.5:1 in a cat
Ear tympanum speed

Faster at high frequencies because it is much thinner
*Rhinolophus ferrumequinum*
Hearing is tuned to echolocation frequency

CF bats are tuned to dominant frequency

FM bats show broad frequency sensitivity
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 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 combined with varying CF$_1$. Neurons along the black lines respond to Doppler shifts corresponding to a specific relative target velocity. The bottom graph (right) shows...
Tonotopic representation varies by species

Inferior colliculus frequency maps
Call design and 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).
Echolocation in toothed cetaceans

- Use clicks for echolocation
  - Very short duration produces broadband sound
- In porpoise, click produced by air moving between sacs, focused by oil-filled melon
- Echo received by fatty jaw that conveys sound to ear
Information decoded from echos

Target detection
Distance
Angular direction
Velocity & trajectory
Target size & shape

Frequency of echo
Pulse-echo time delay
Ear amplitude difference
Pulse-echo frequency change
Frequency of echo