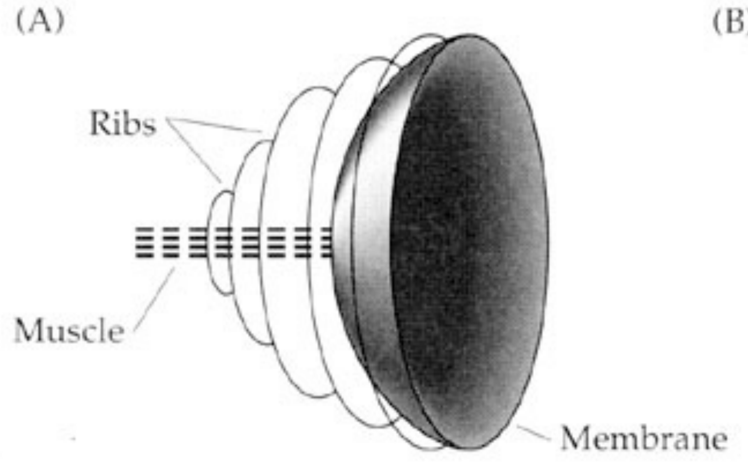
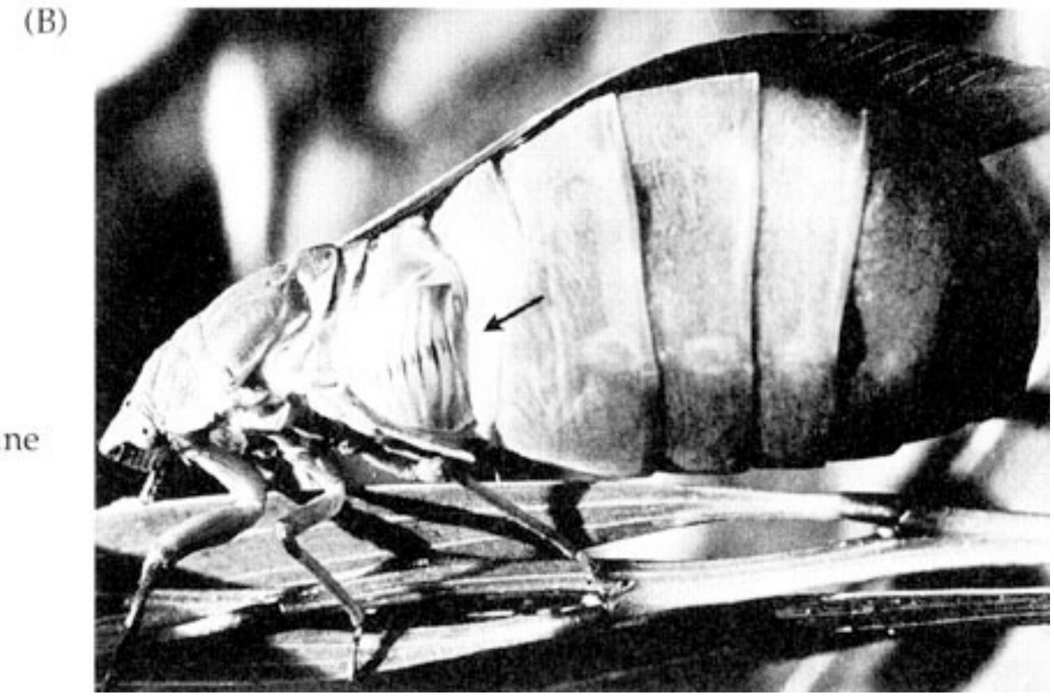
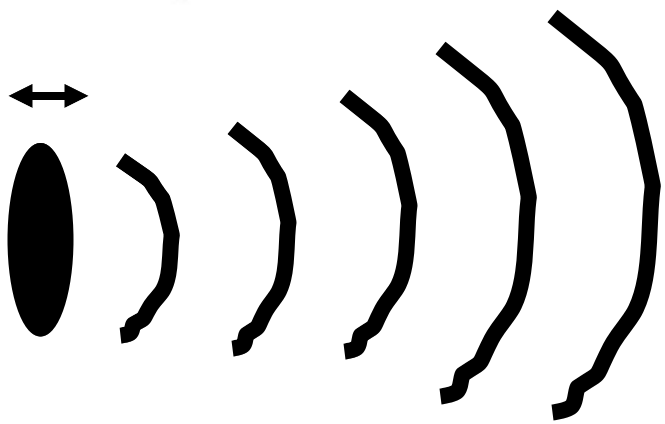
Echolocation and hearing in bats

- Sound transmission
  - Sound properties
  - Attenuation
- Echolocation
  - Decoding information from echoes
  - Alternative calling strategies
- Adaptations for hearing in bats
- Websites

How does a cicada sing?

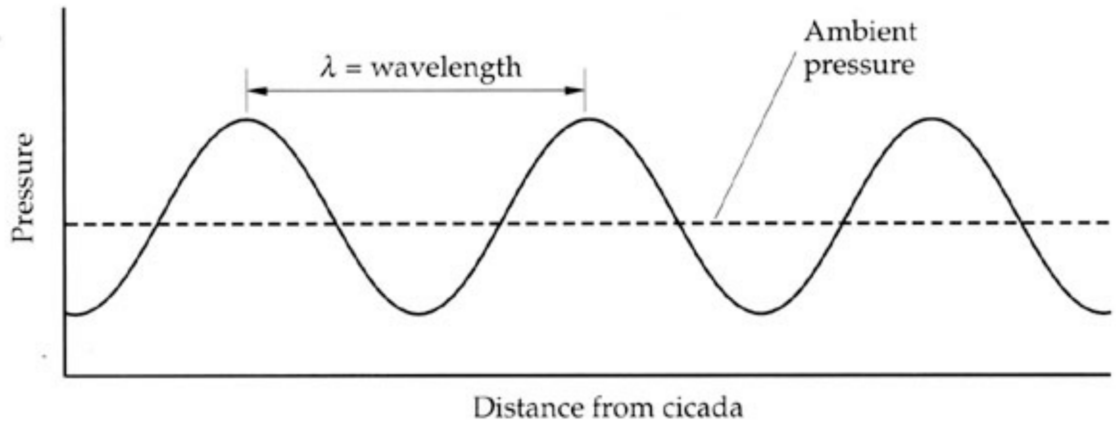






Sound is produced by changes in pressure

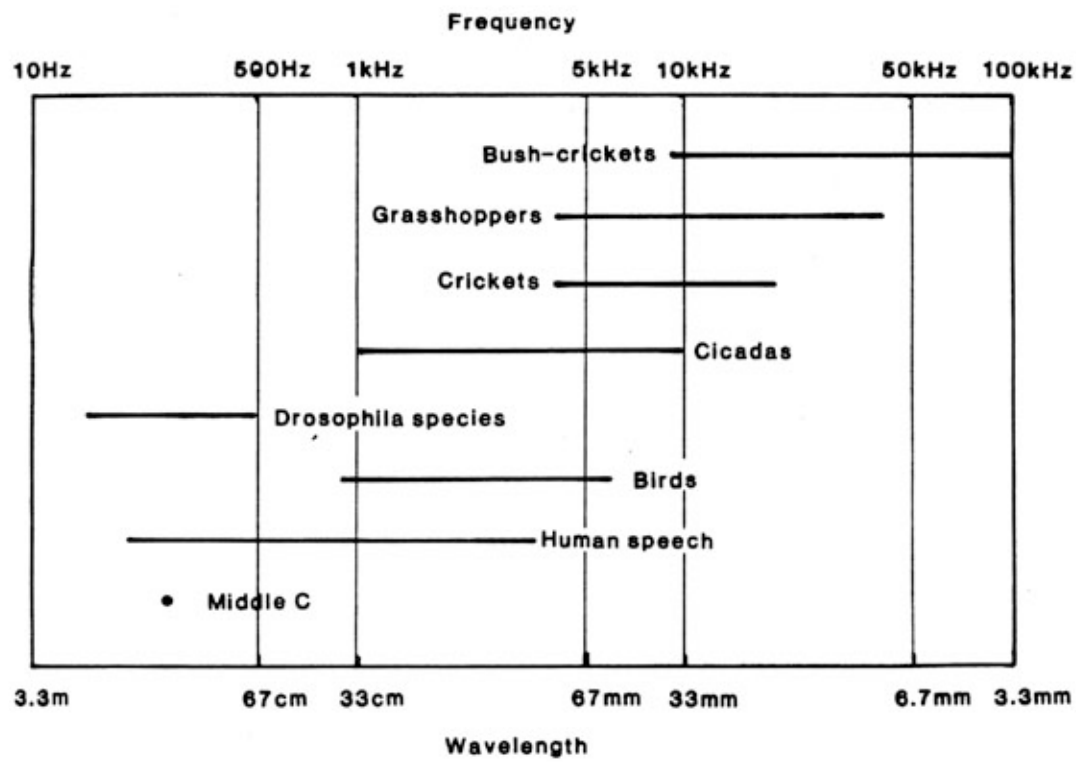
Frequency and wavelength



- 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 m/s, so wavelength of 340 Hz = 1 m
  - Speed of sound in water = 1450 m/s , wavelength of 340 Hz = 4.3 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

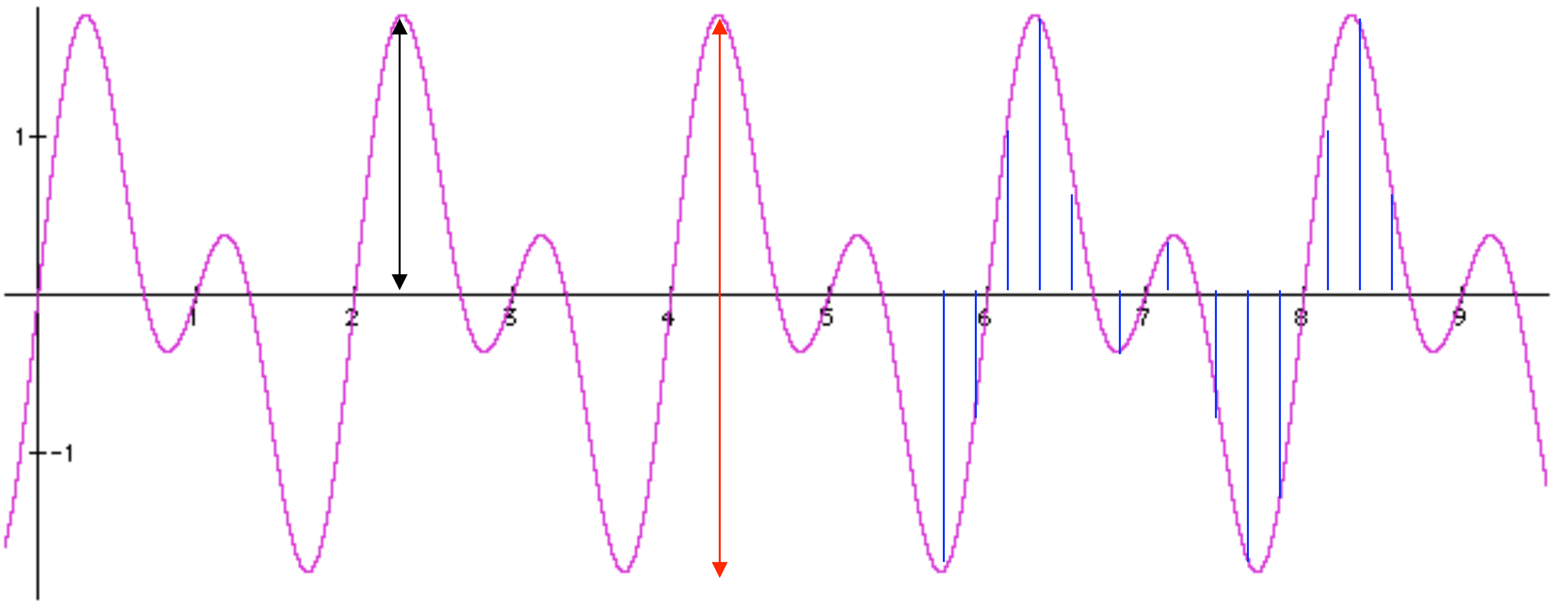
- Sound pressure is measured in decibels (dB) on a $\log_{10}$ scale relative to a reference level
- $dB = 20 \log_{10} P_1/P_r$ where P_r is a reference pressure level, usually the threshold of human hearing at 4 kHz. This is referred to as sound pressure level (SPL)
- A sound with twice the SPL is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

Sample sound pressure levels

- soft whisper 20 dB
- nearby songbird, office hum 50 dB
- barking dog 70 dB
- roaring lion , heavy truck 90 dB
- echolocating bat 100 dB
- jet take-off 120 dB

Amplitude measurement

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



Amplitude problems

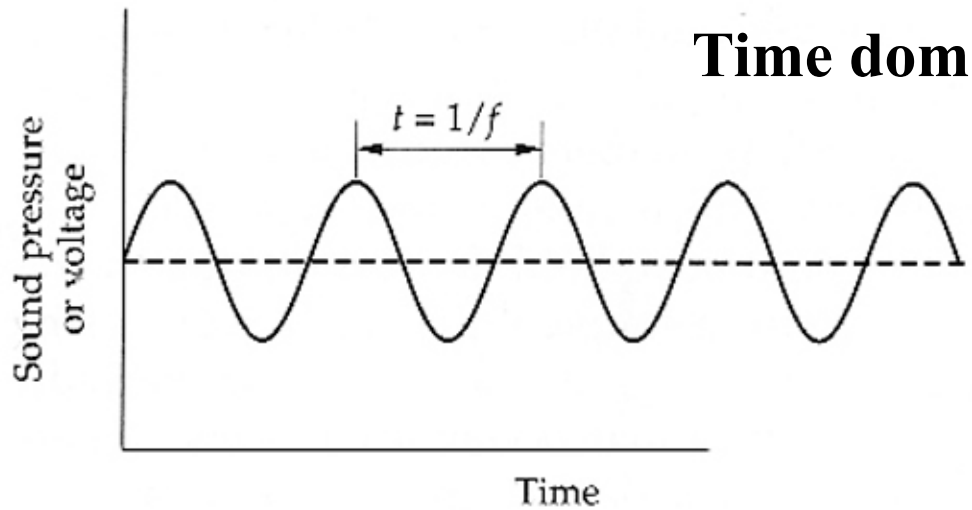
- If sound A has 10 times the SPL of sound B, how much louder is A than B in dB?
- dB = 20 $\log_{10}$ 10 = 20 dB louder
- If sound A is 100 db and sound B is 80 db, how much louder is A than B?
- 20 db
- If an 80 db sound is combined with a 40 db sound, how loud is the sound (approximately)?
- 80 db

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)

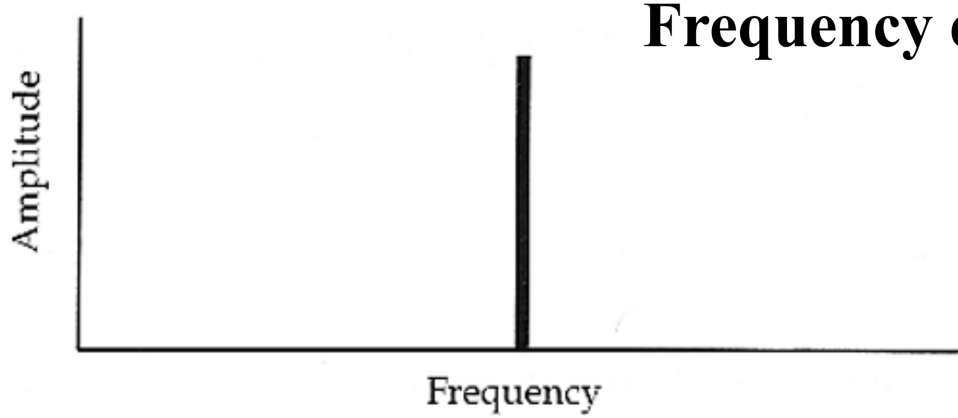
Sound spectrum

Time domain



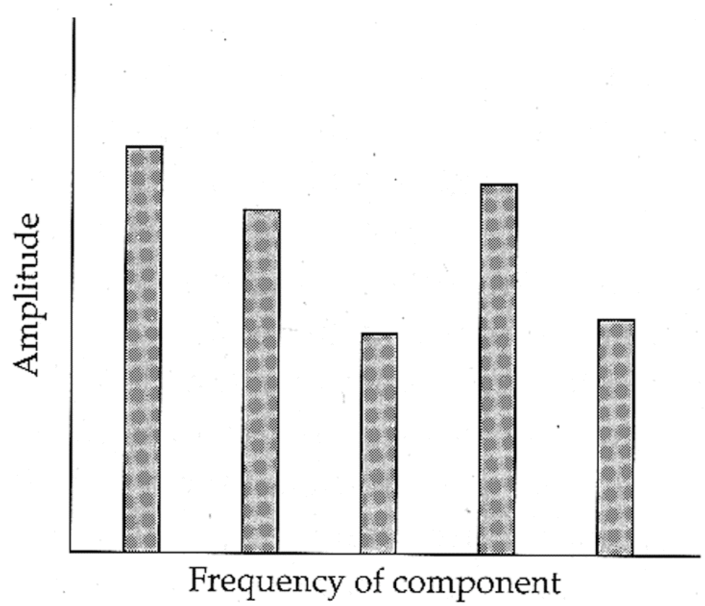
Frequency domain

Frequency spectrum

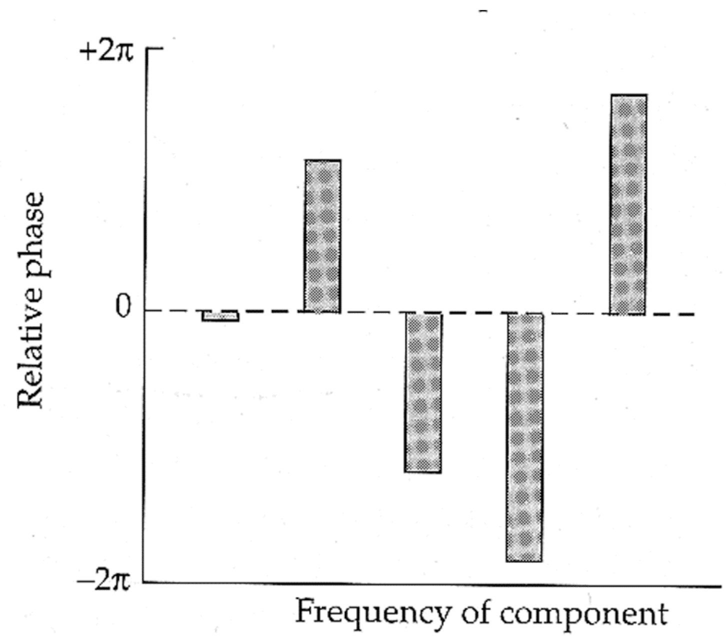


Frequency domain of a complex wave

Frequency spectrum



Phase spectrum

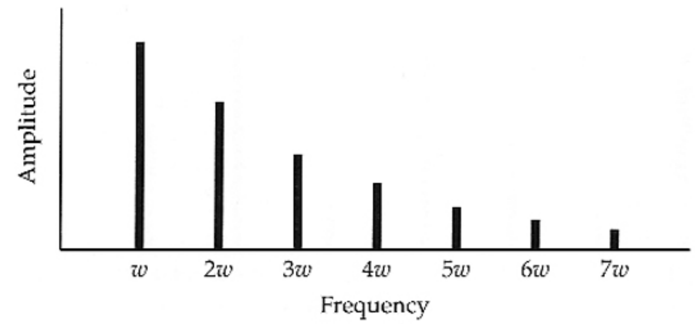


The Fourier series

- Any continuous waveform can be partitioned into a sum of sinusoidal waves
- $P(t) = P_o + \Sigma P_n \, sin \, (2\pi f_n t + \Phi_n)$
- P_o is the ambient pressure
- P_n is the pressure of the nth sine wave
- f_n is the frequency of the nth sine wave
- Φ_n is the phase of the nth sine wave

Harmonic series

- Harmonic frequencies are integer multiples of the fundamental frequency, i.e. w, 2w, 3w, 4w …

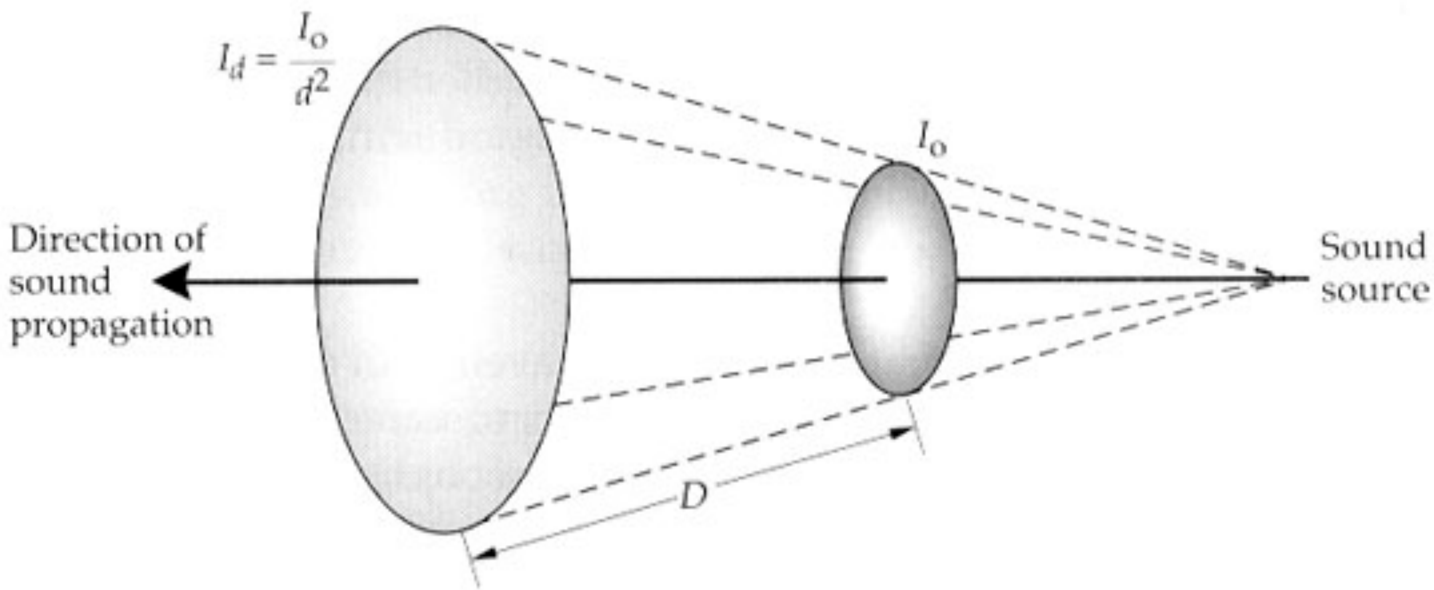


- Dirichlet's rule states that the energy in higher harmonics falls off exponentially with the frequency of the harmonic
- Note, however, that some bats alter the amplitude of harmonics by selective filtering during sound production

Sound attenuation

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

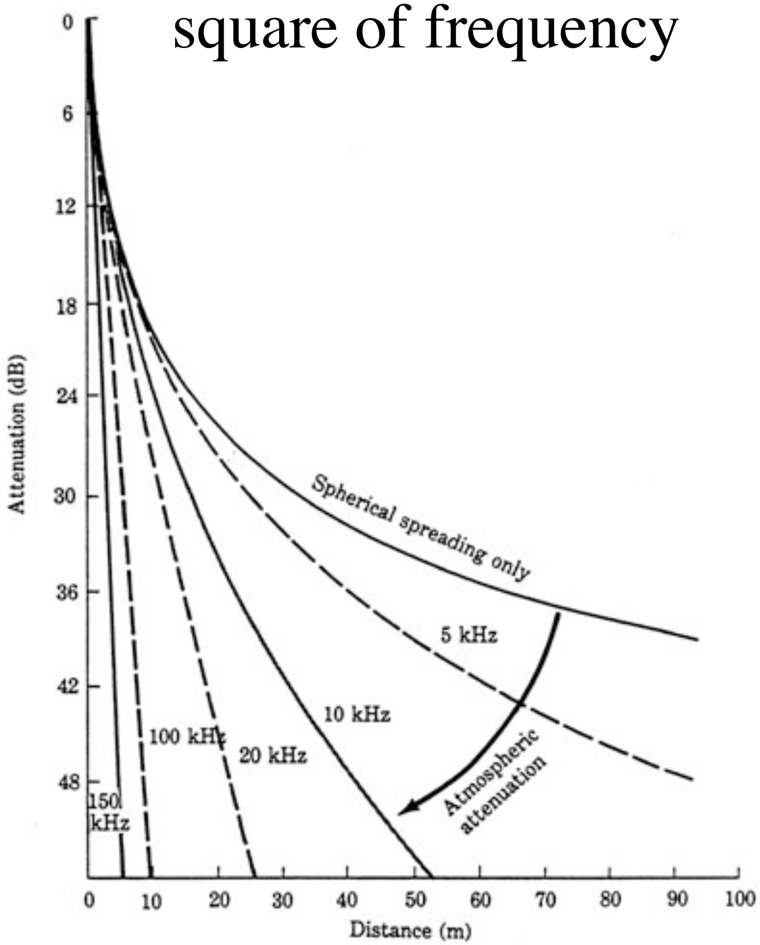
Spherical spreading



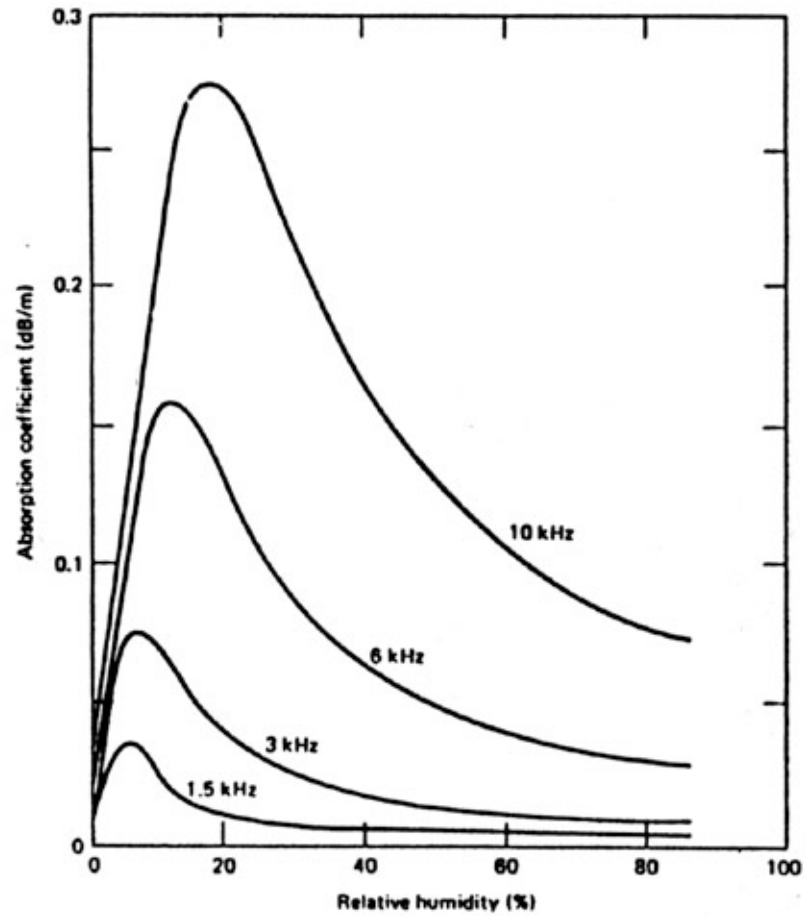
- Loss in sound intensity follows the inverse square law: pressure halves for each doubling of distance, i.e. - 6 dB for each doubling of distance

Atmospheric attenuation

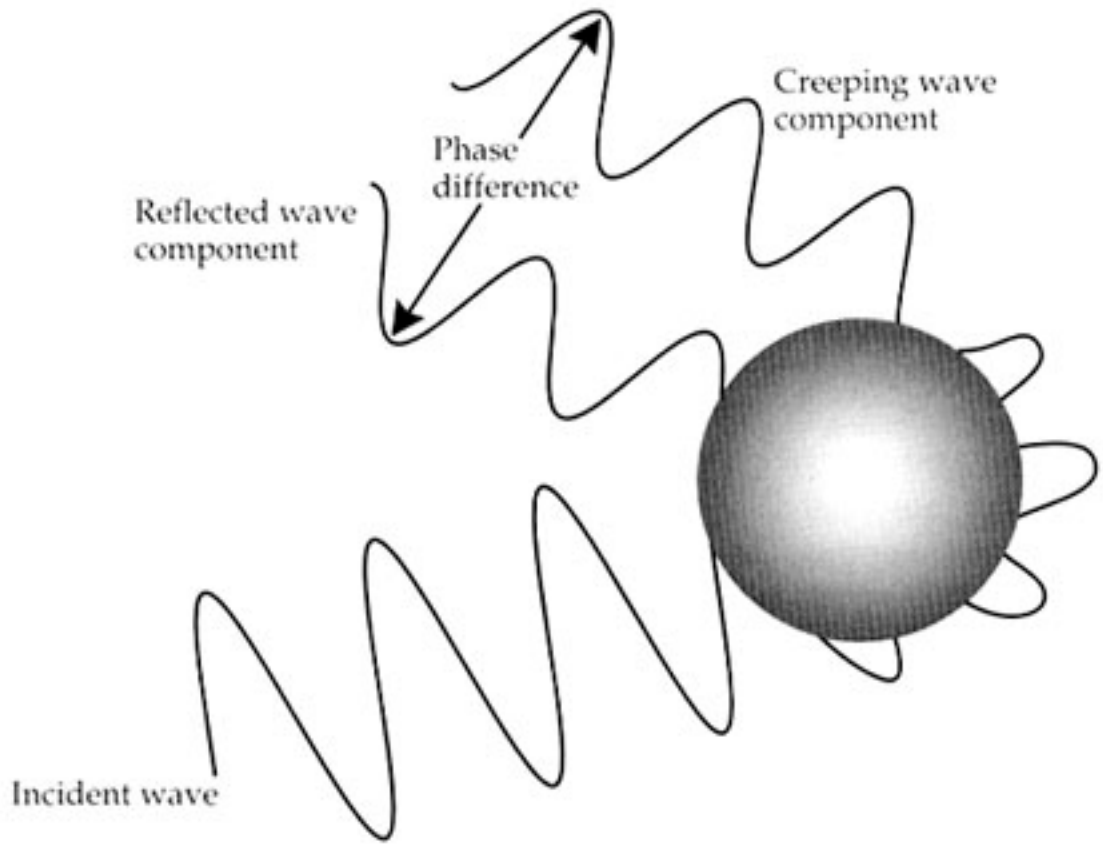
Increases with temp. & square of frequency



Nonlinear with humidity

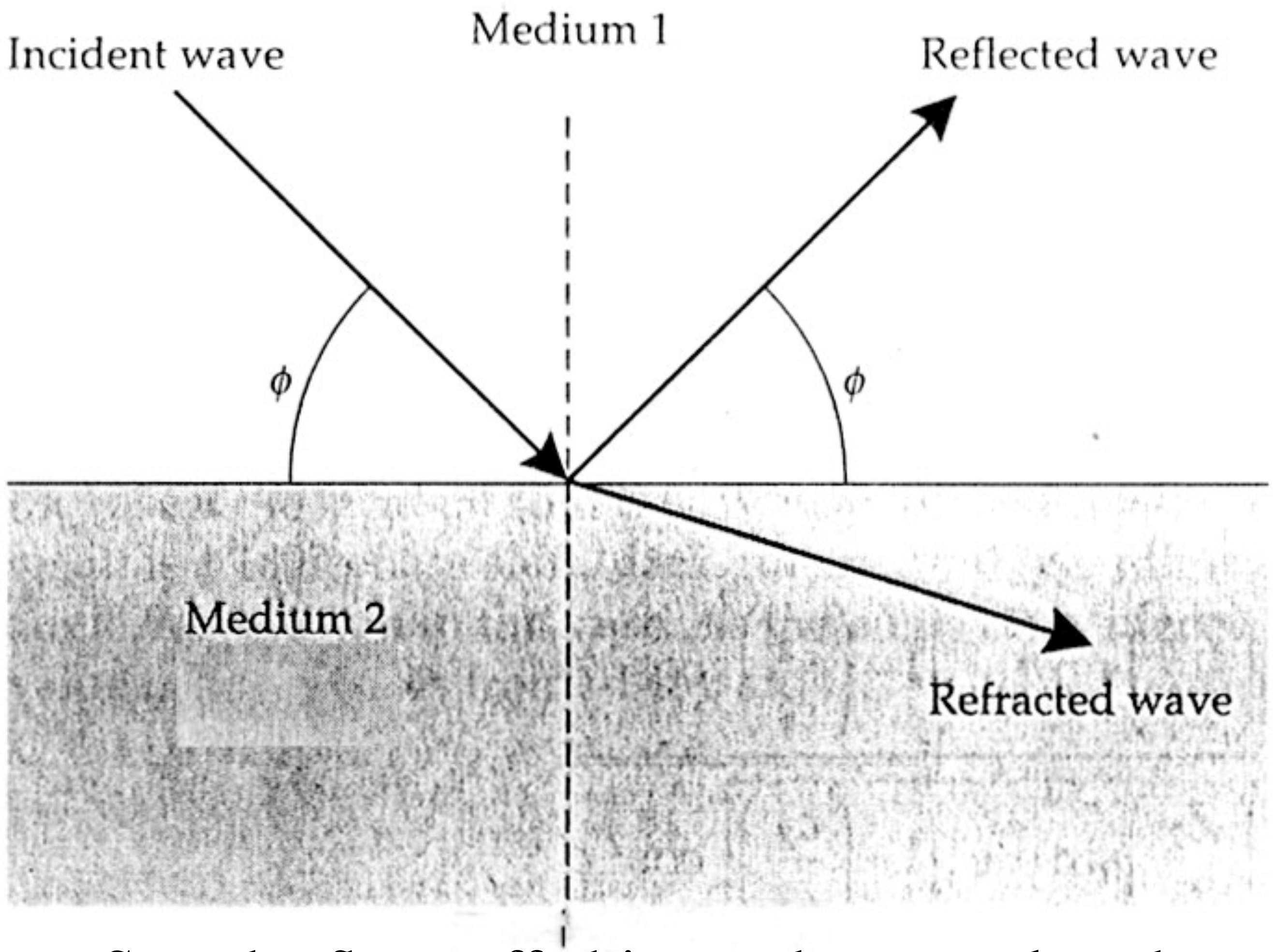


Diffraction



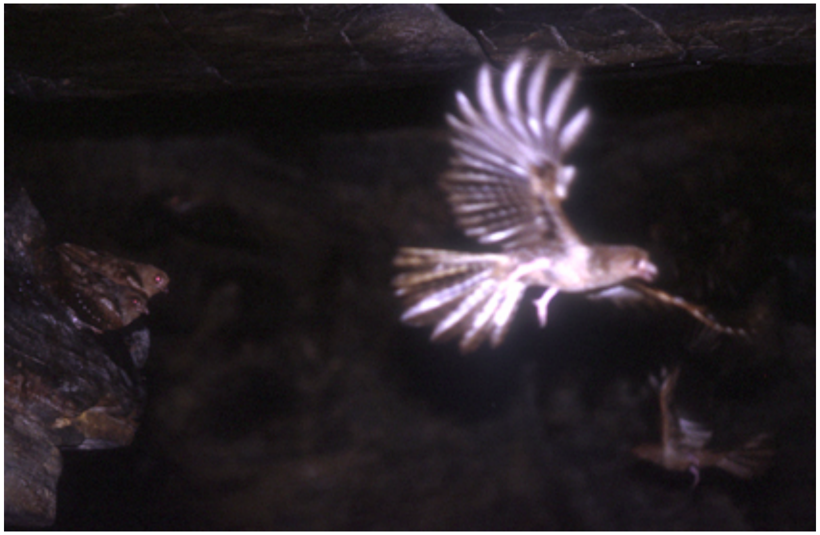
Reflected wave is out of phase with creeping wave.
Occurs when wavelength is similar to object diameter

Reflection and refraction



Sound reflects off objects when wavelength
is less than the size of the object

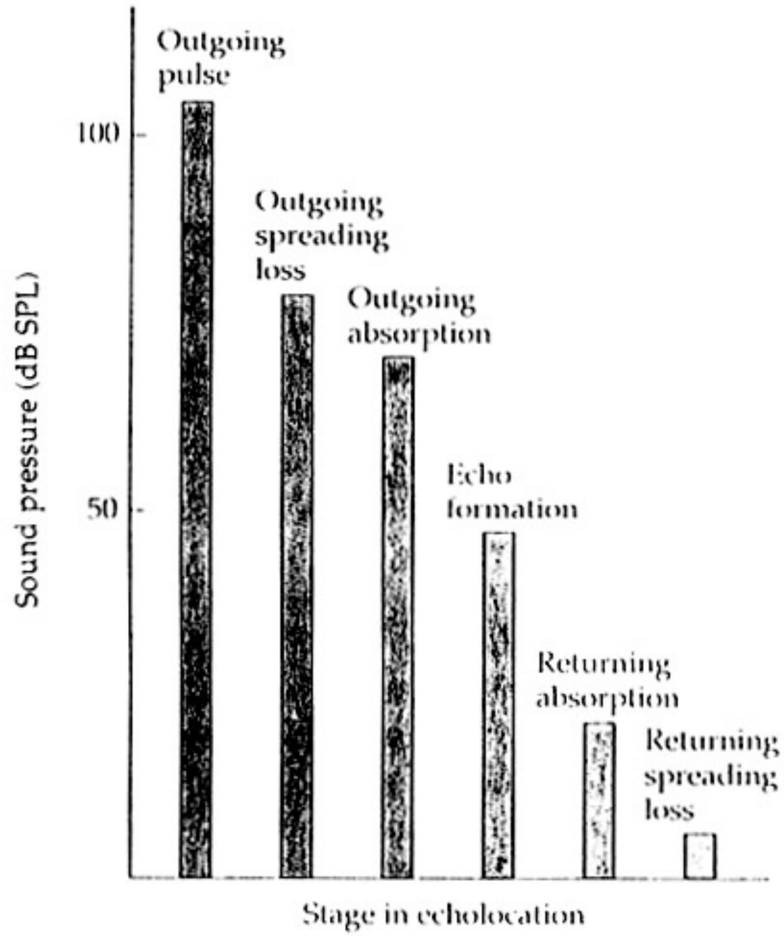
Echolocating animals



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

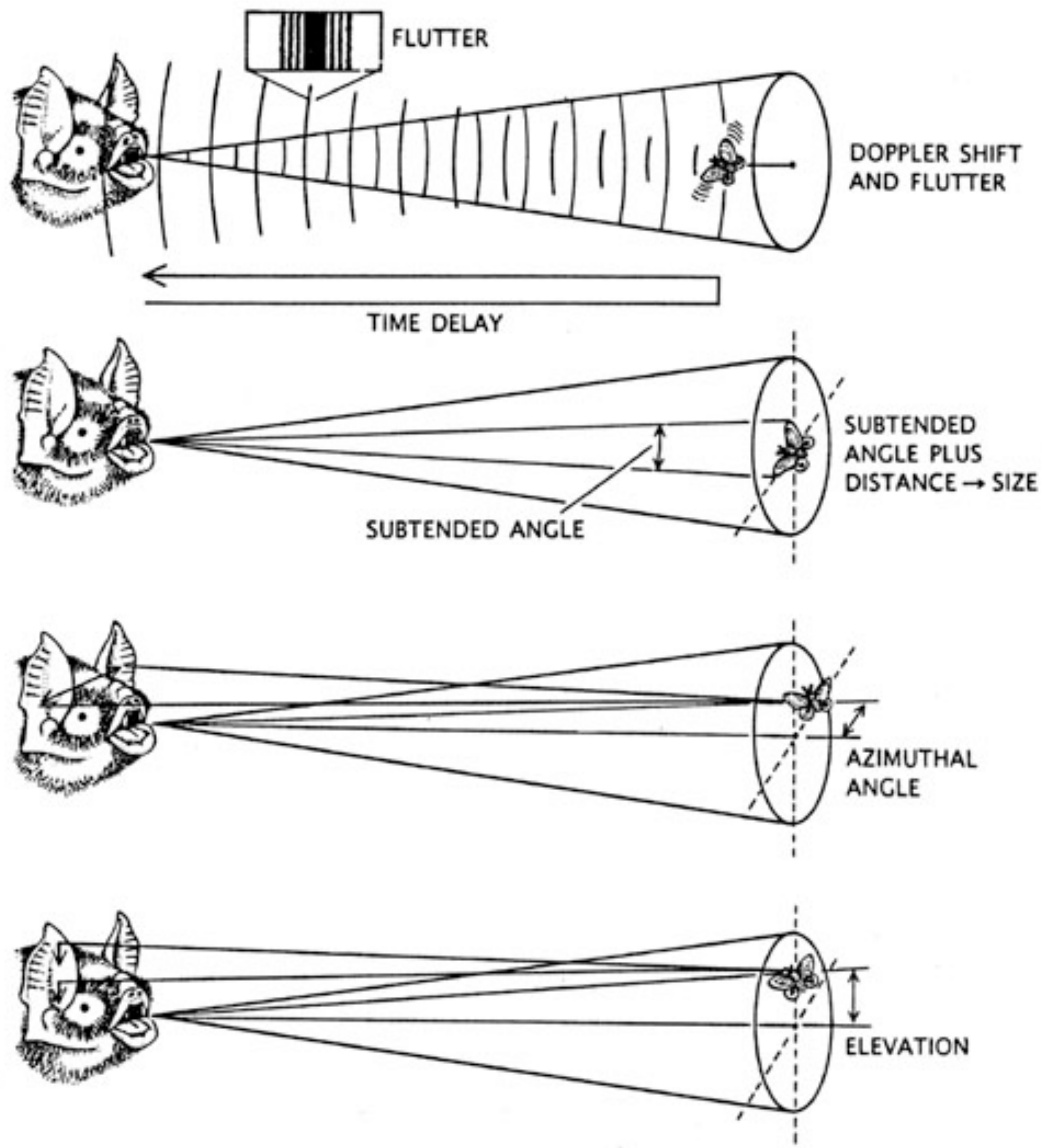
Information decoded from echos

Range
- pulse-echo time delay

Velocity
- pulse-echo frequency change

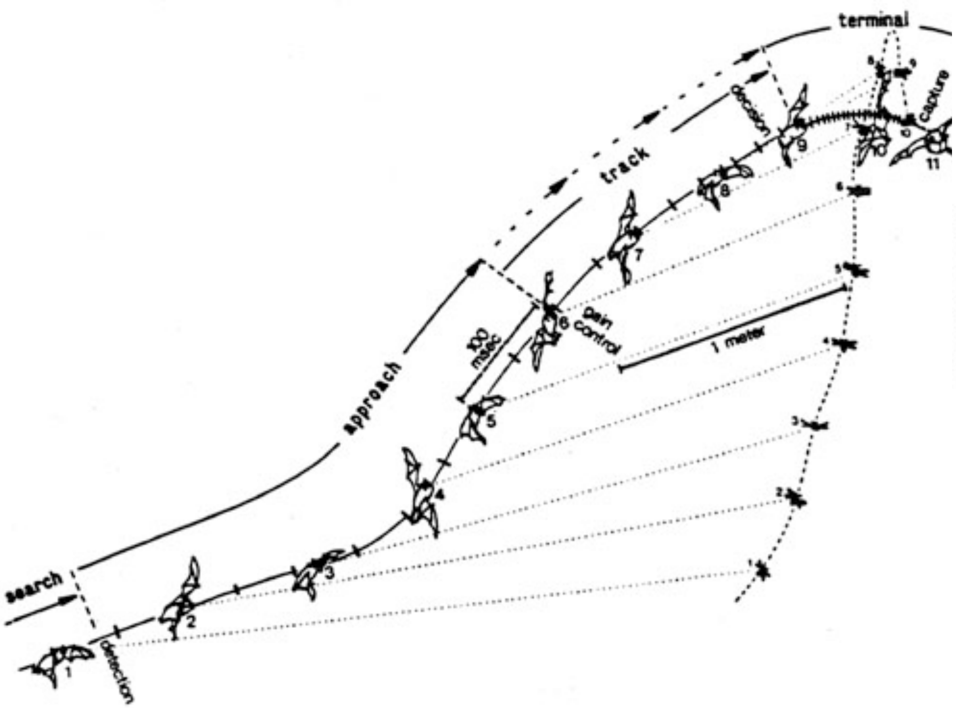
Target size
- frequency of echo

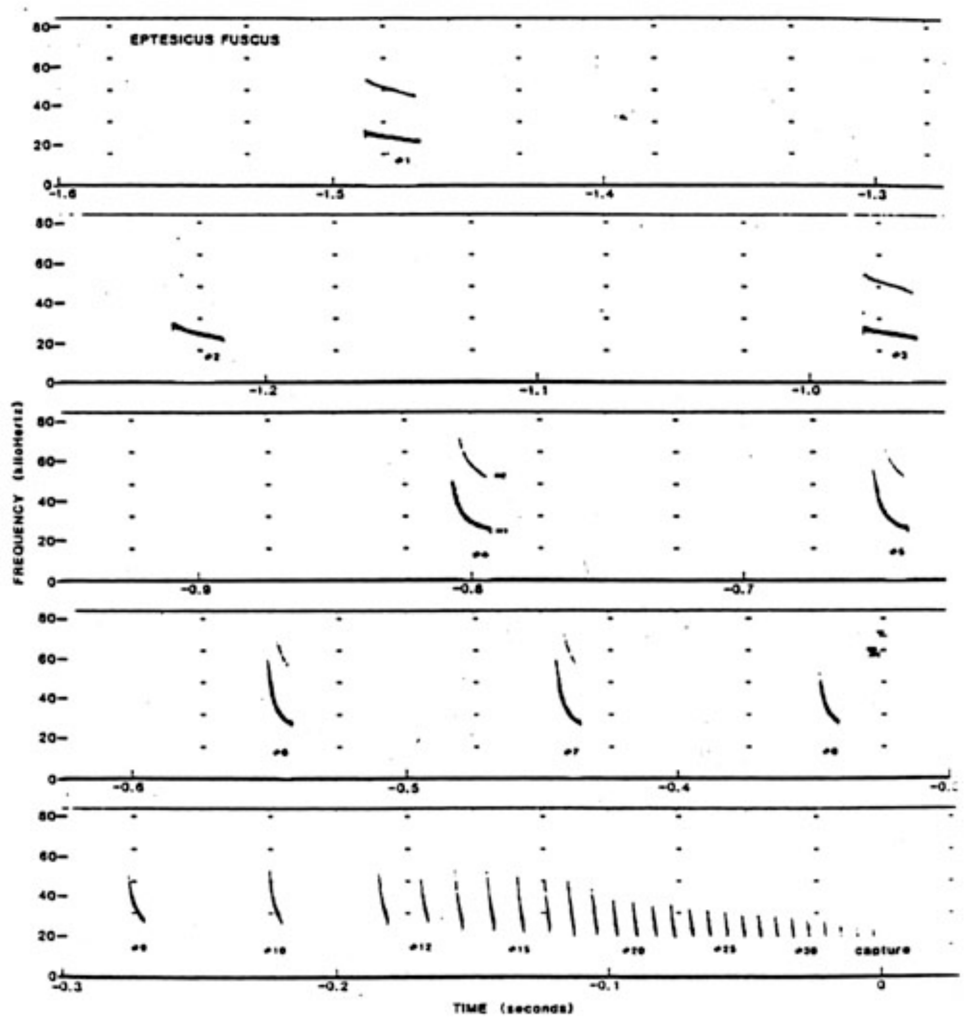
Location
- ear amplitude difference



FM calls during prey capture

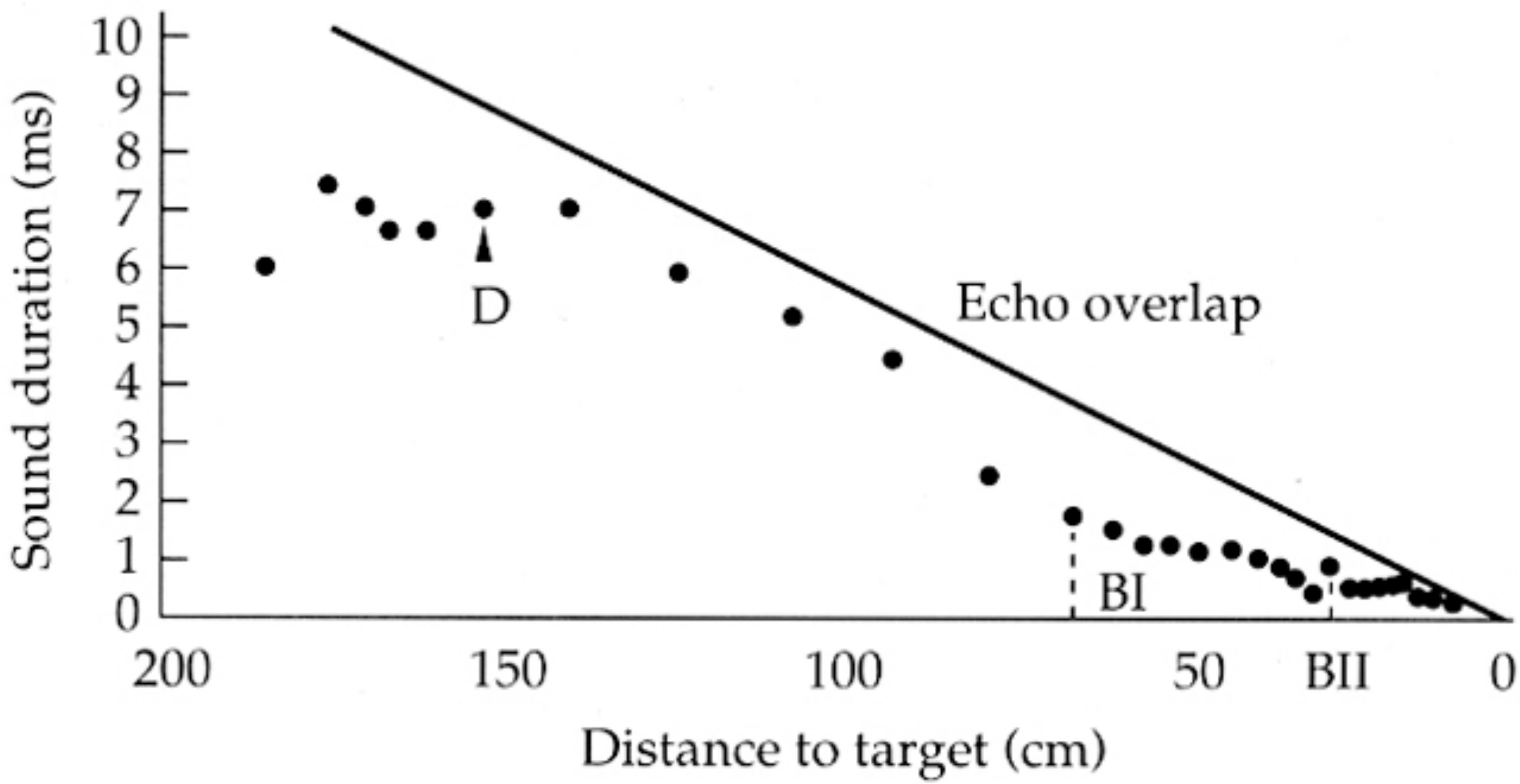
Big brown bat
Eptesicus fuscus





Low duty cycle

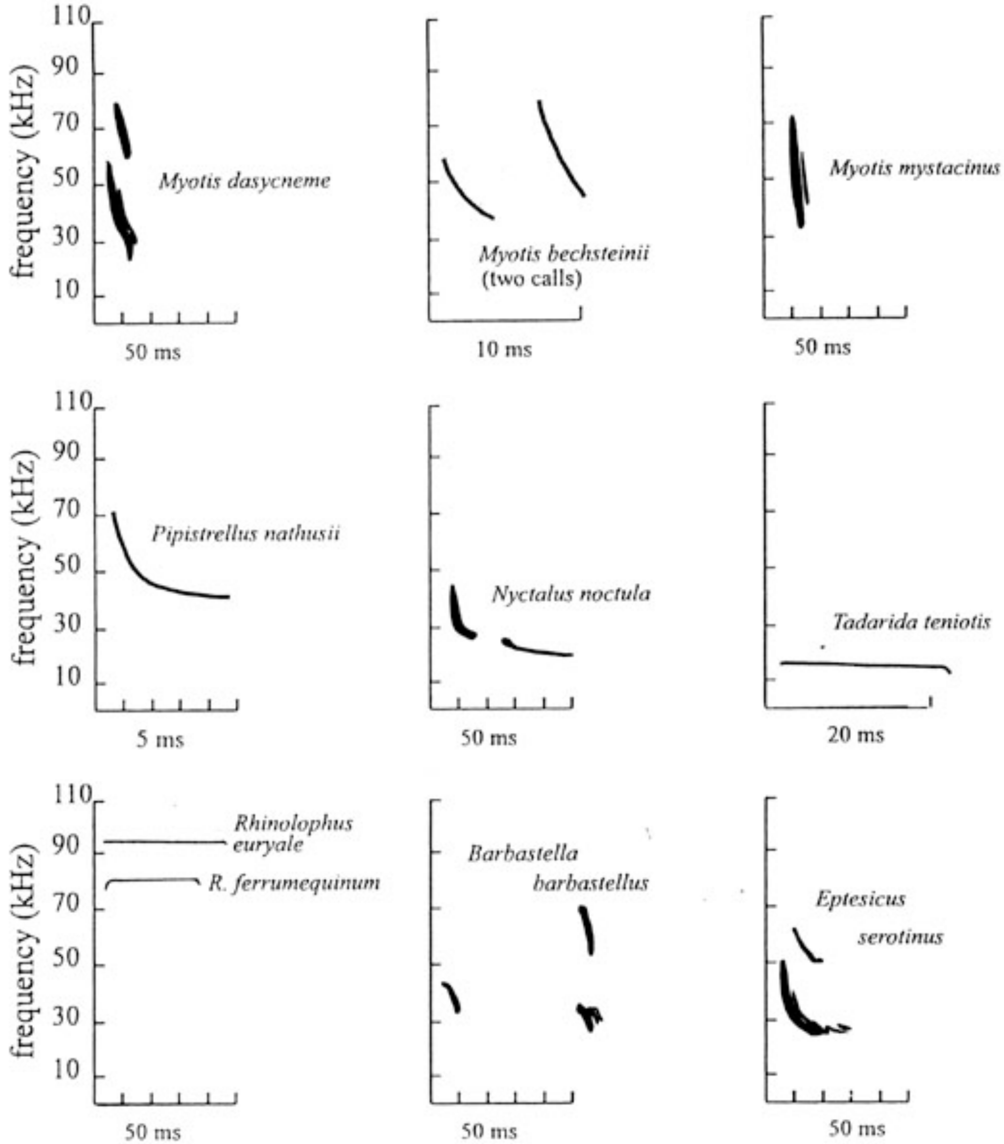
FM bats shorten call duration to prevent pulse-echo overlap with target approach



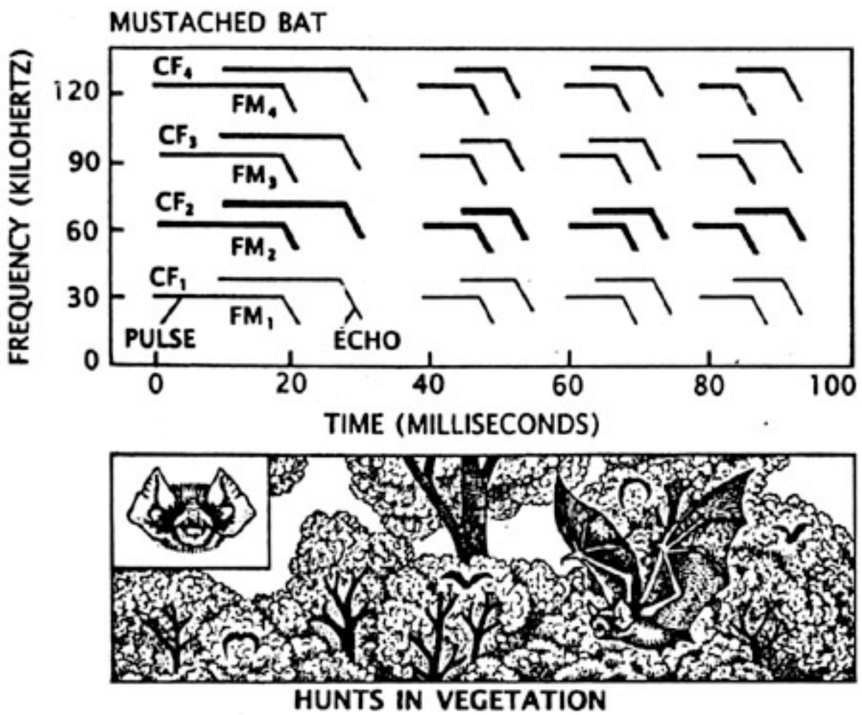
Echolocation call diversity

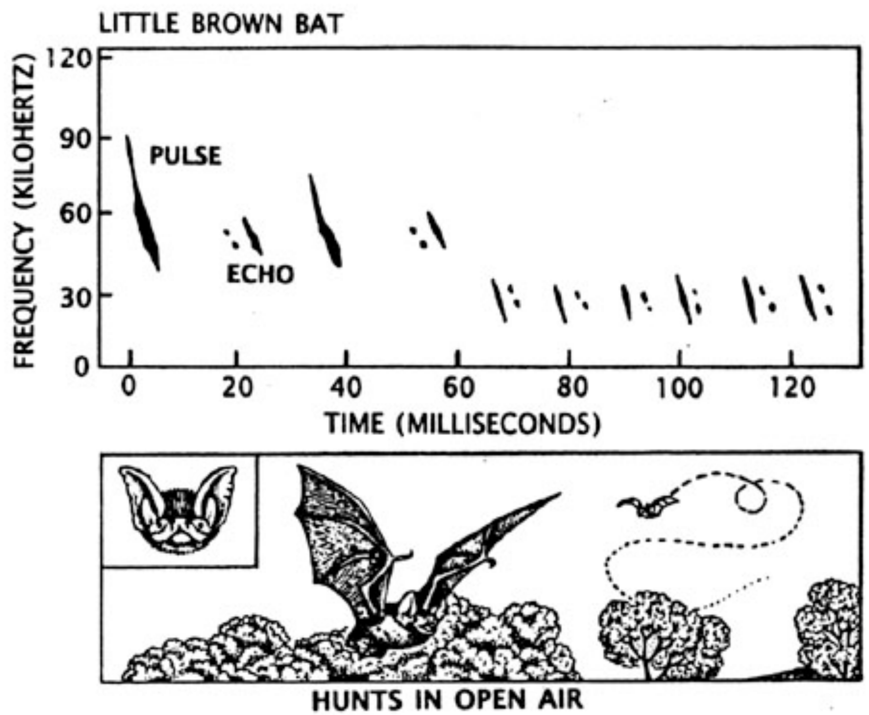
FM = frequency modulated

CF = constant frequency



Echolocation strategies





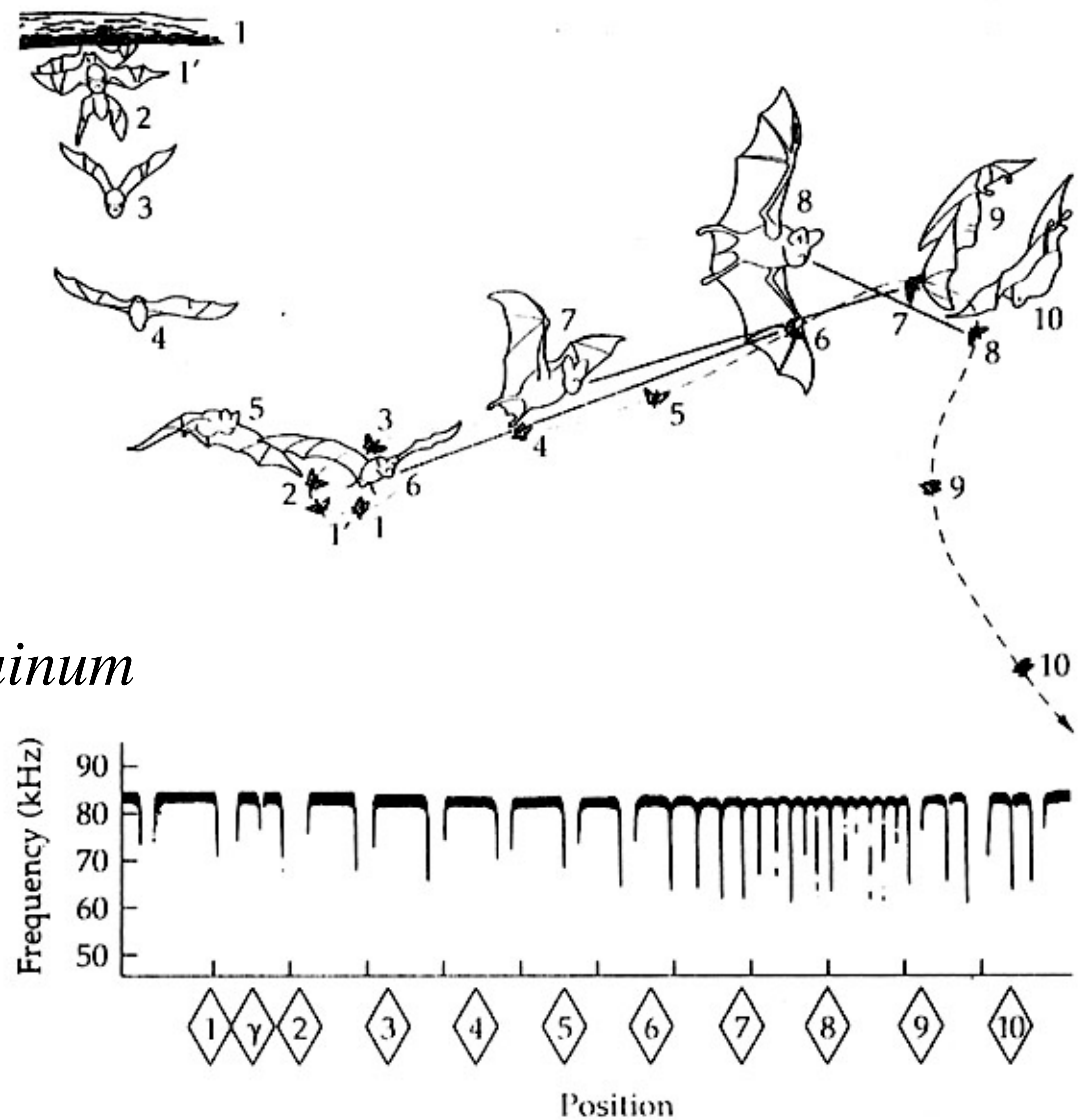
CF, considerable pulse-echo overlap

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

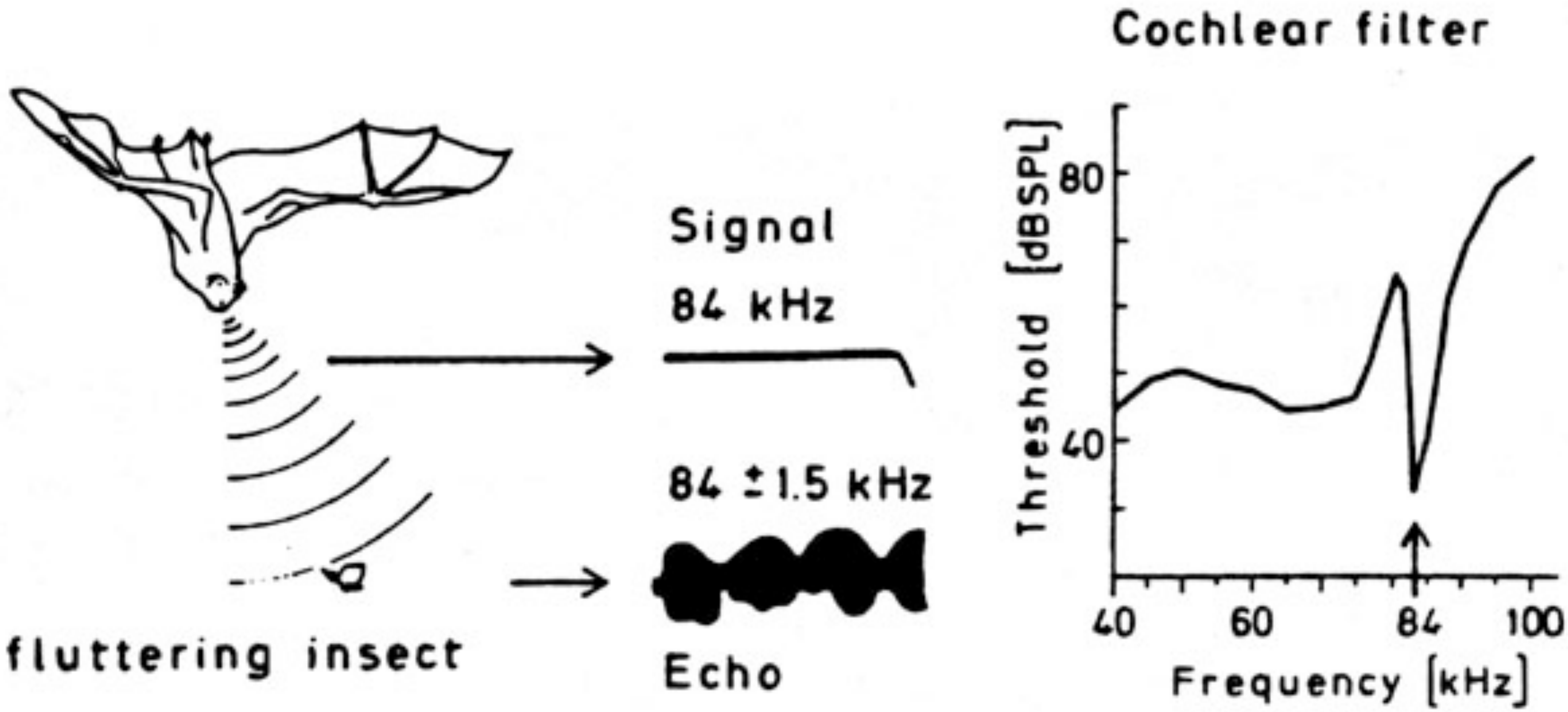
CF calls during prey capture



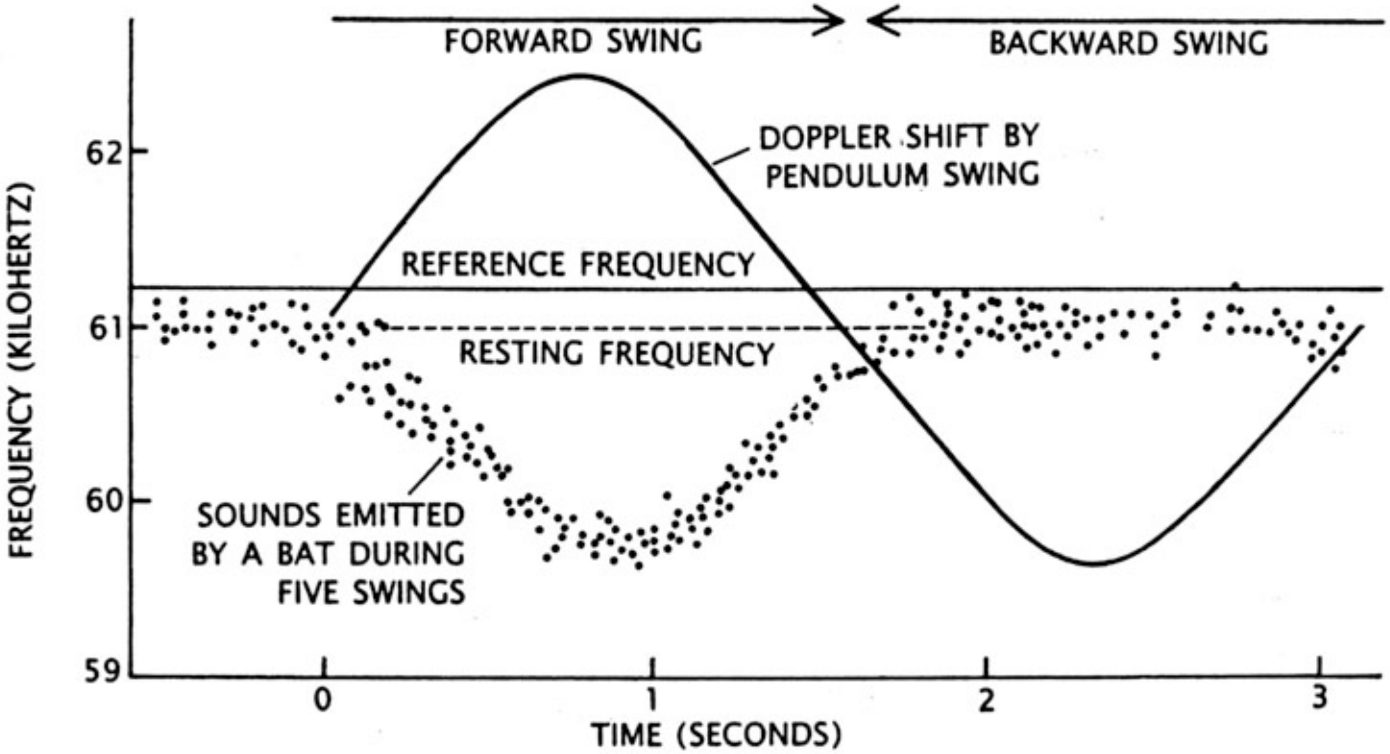
Greater horseshoe bat,
Rhinolophus ferrumequinum

High duty cycle

CF bats detect wing flutter as echo glints



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.

Call design fits foraging strategy

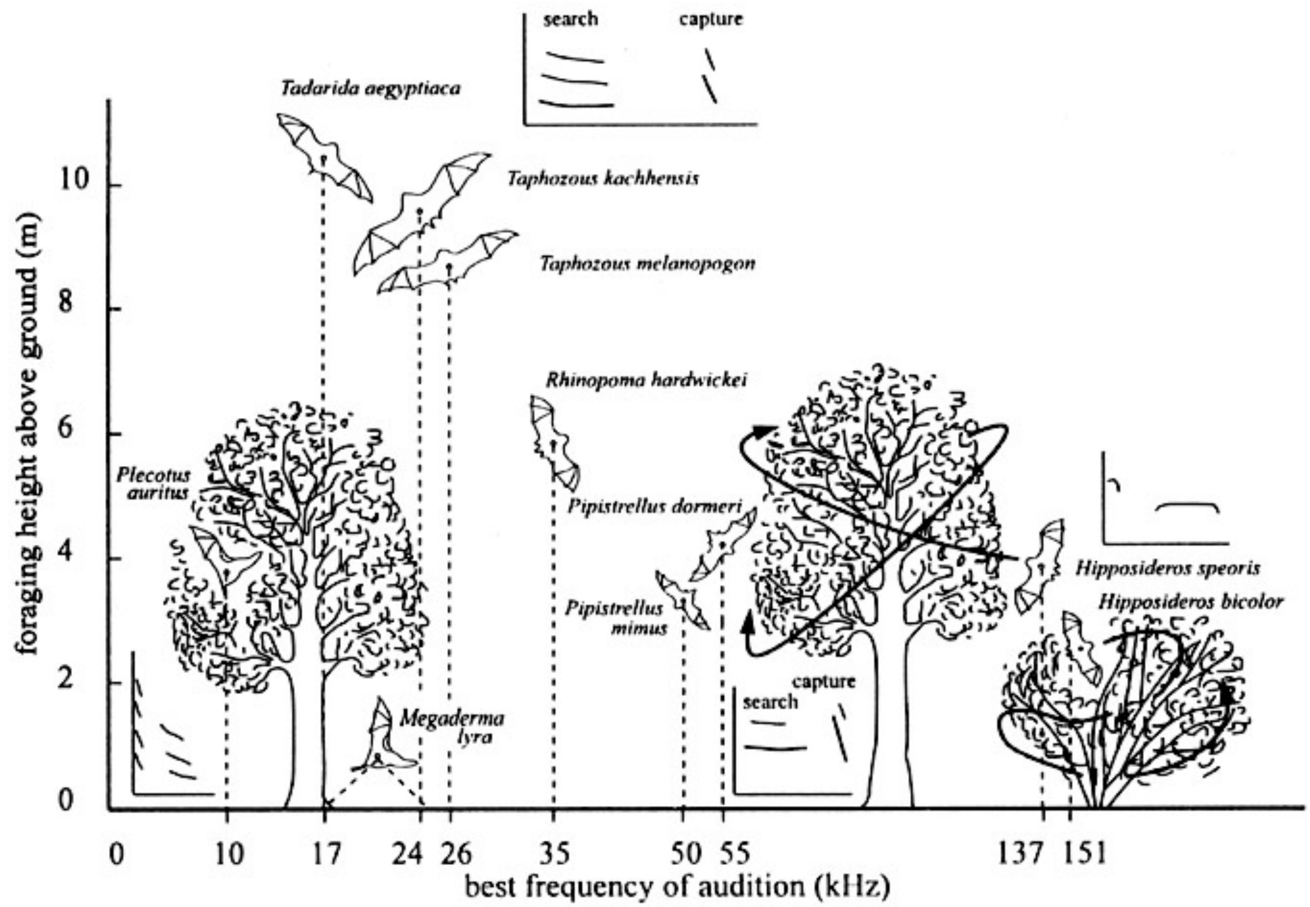
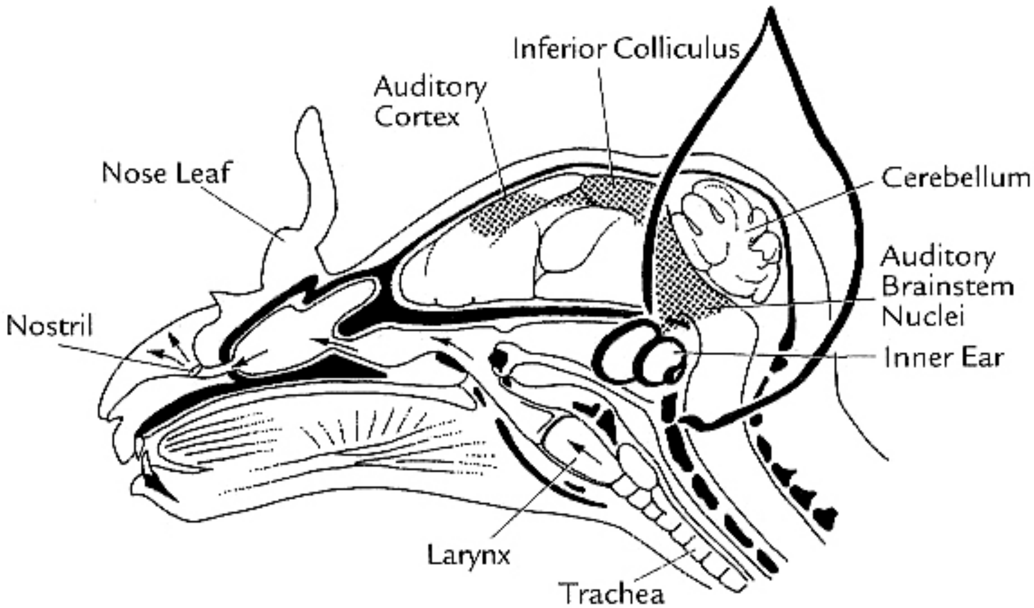
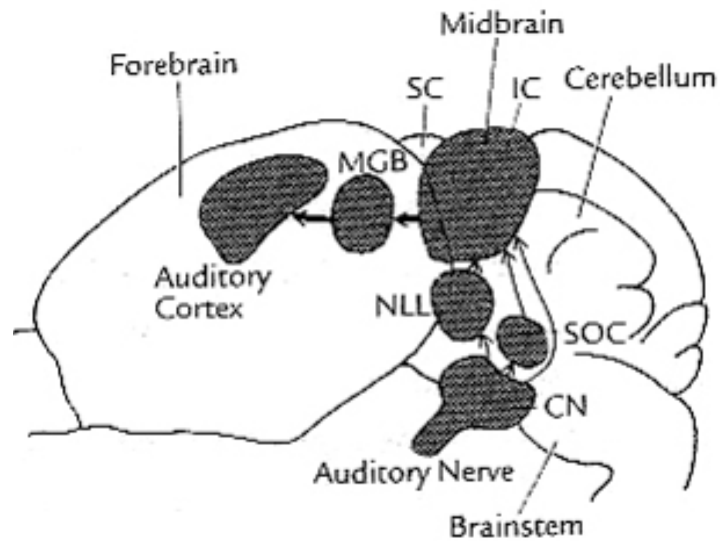


Fig. 3.24. Foraging strategy in relation to echolocation calls and auditory characteristics. Foraging height is plotted against the best frequency of audition. Bats are loosely divided into gleaners (ground and foliage), above canopy hawkers, low level open-air hawkers, and hawkers in cluttered habitats,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

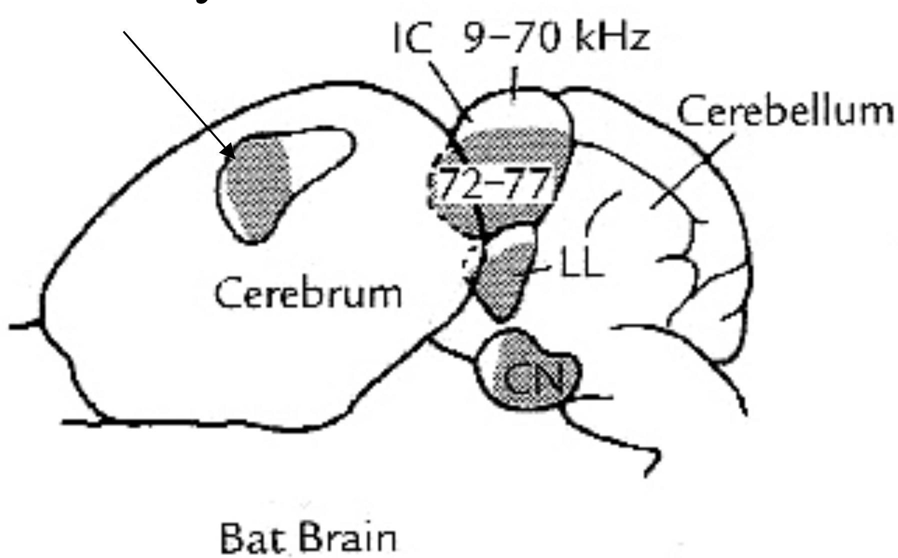
The auditory pathway

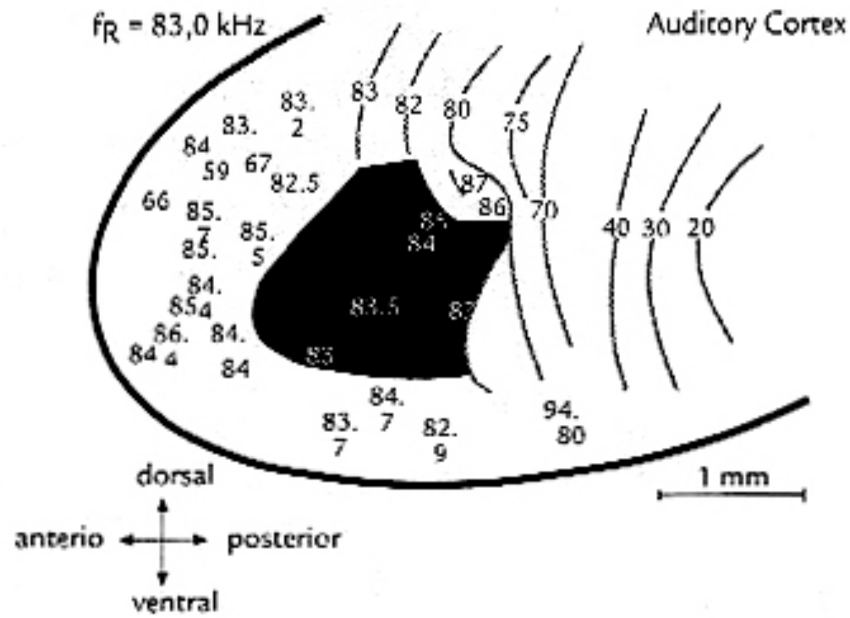




Tonotopic map in the auditory system

Auditory cortex

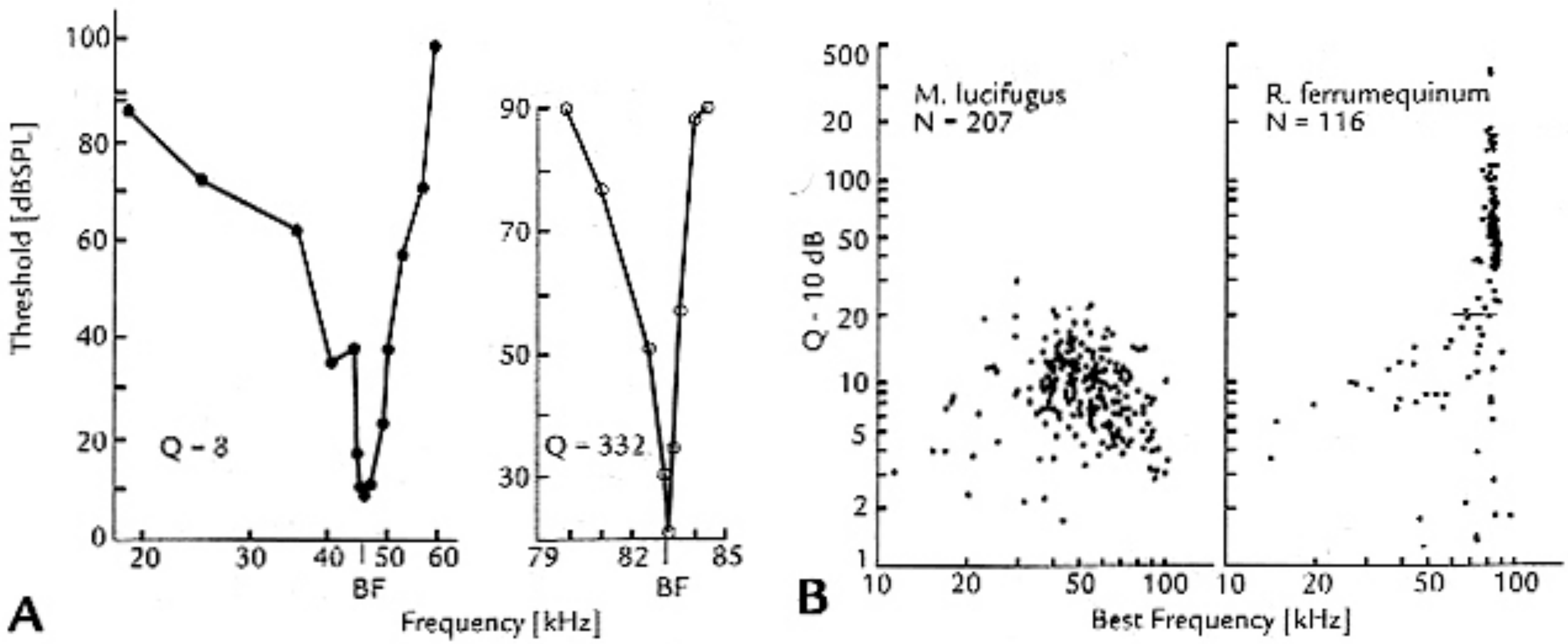




Gray areas correspond to call frequencies

Auditory cortex is expanded at frequencies associated with echolocation

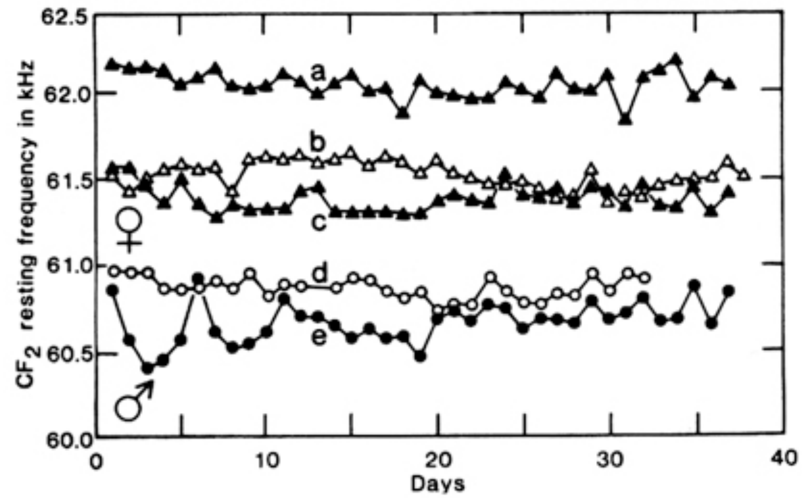
Neuronal tuning in little brown and horseshoe bats

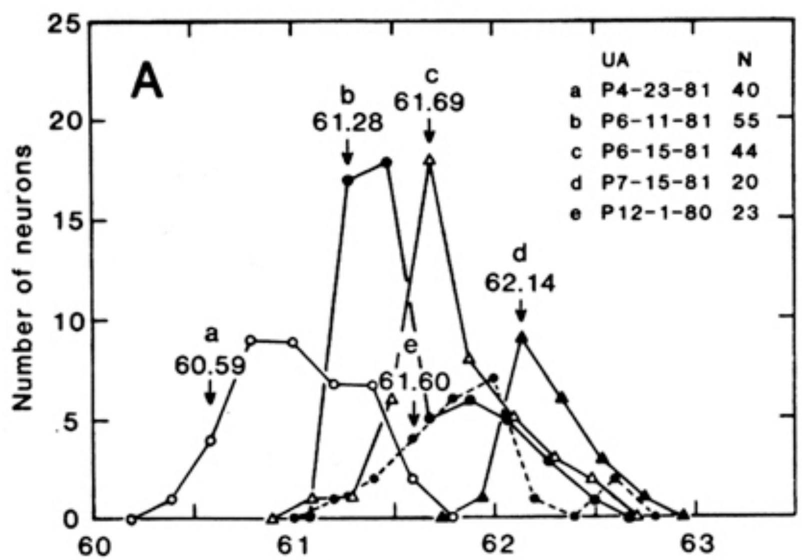


Q_{10} = best freq/ bandwidth at -10 dB


Pteronotus parnellii

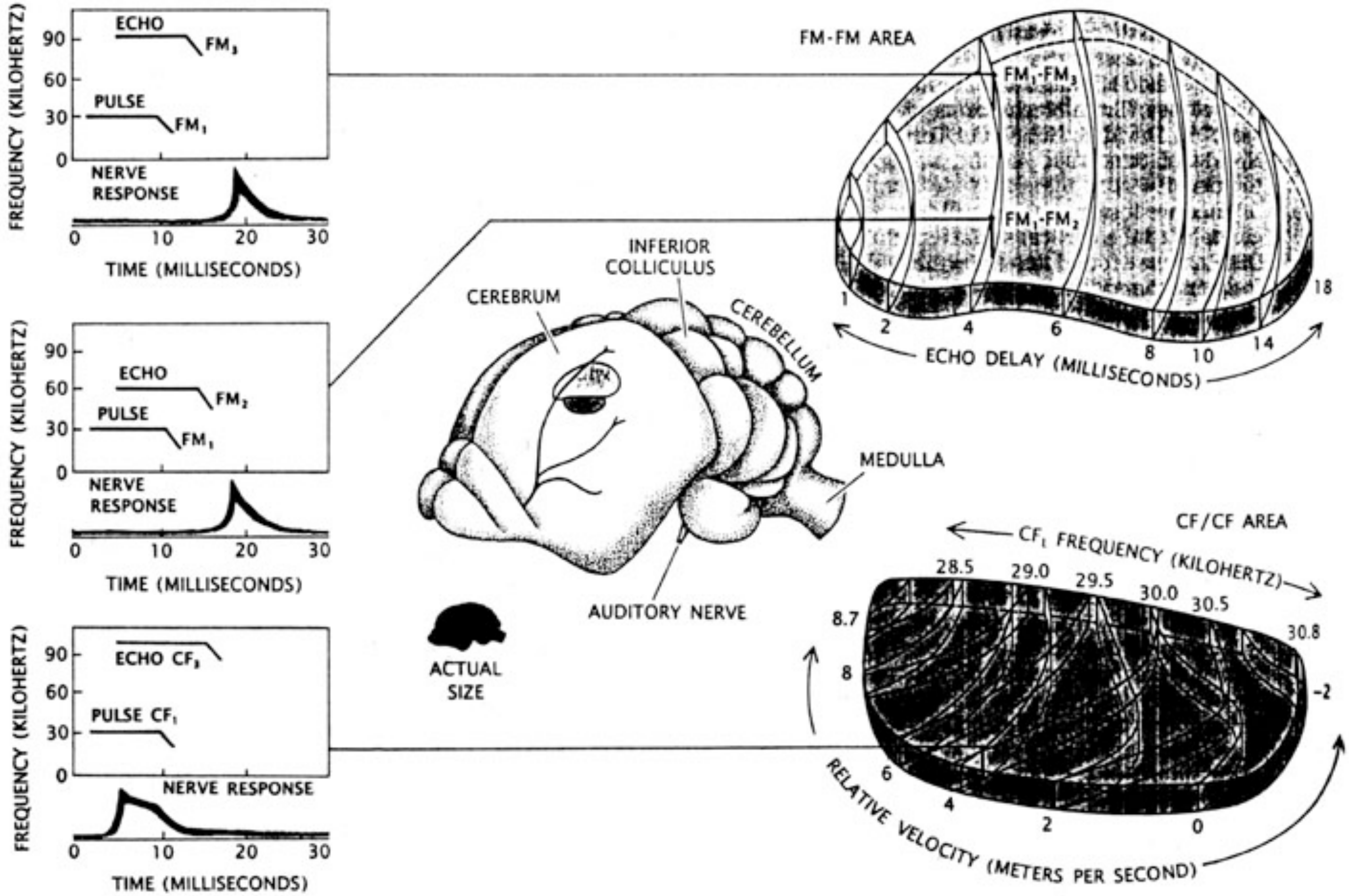
Individual *Pteronotus* bats use unique CF frequencies





Suga, N., H. Niwa, I. Taniguchi, D. Margoliash 1987 J. Neurophys. 58:643-654

Combination-sensitive neurons encode range and velocity in CF bats



COMPUTATIONAL MAPS in the auditory cortex of mustached bats represent echo delay (or distance) and Doppler shift (or relative velocity). In the FM-FM area (*green*), neurons along each black line respond to a specific echo delay. The top graph (*right*) shows the delay-tuning curves of six FM-FM neurons; 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

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http://www.biosonar.bris.ac.uk/

Western Ecological Research Center

http://www.werc.usgs.gov/bats/searchphasecall.html

Bat Vocalizations - Search Phase Call

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.