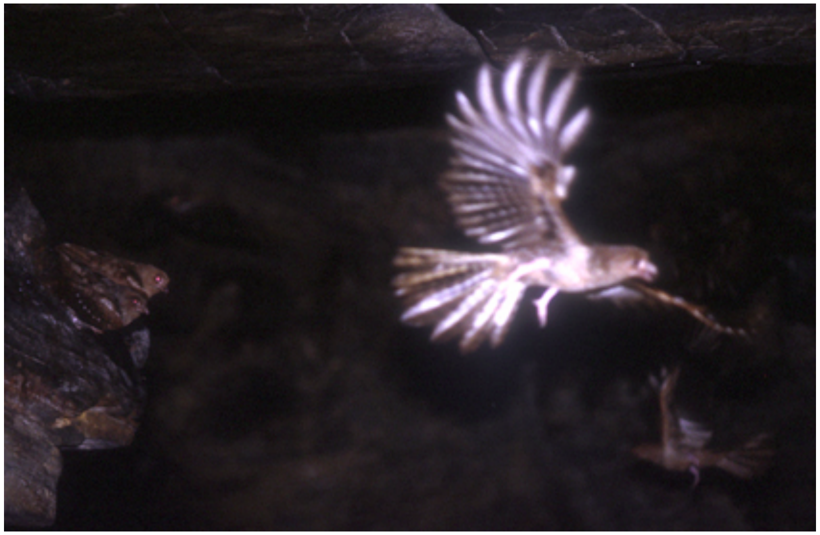
Echolocation

- 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

Fig. 2.19. Brown long-eared bat, *Plecotus auritus*, a gleaner.

Fig. 2.20. A hovering nectar feeder, the long-tongued bat, *Glossophaga sorici...*

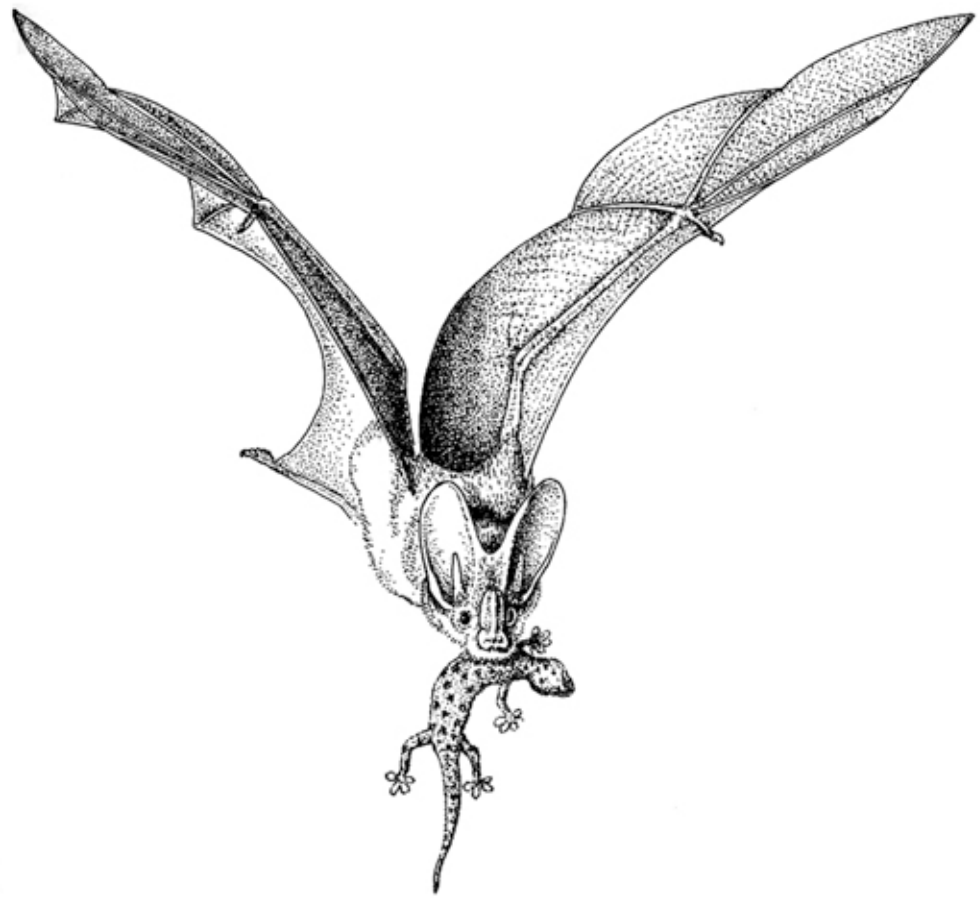
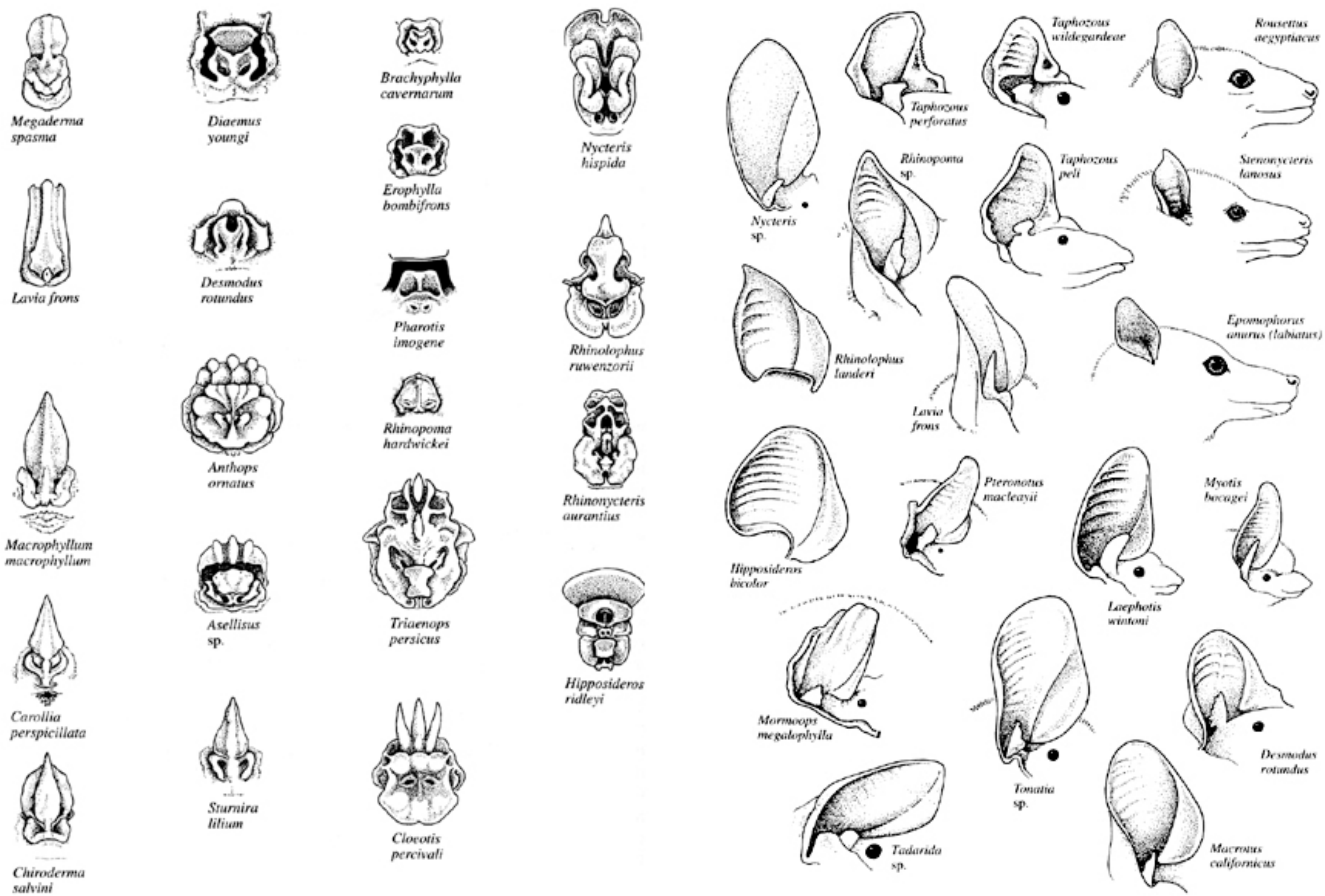
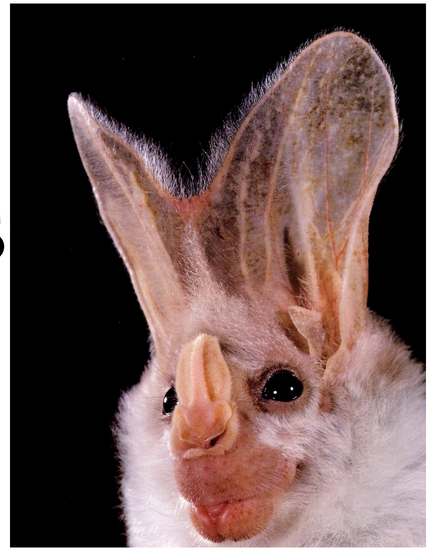


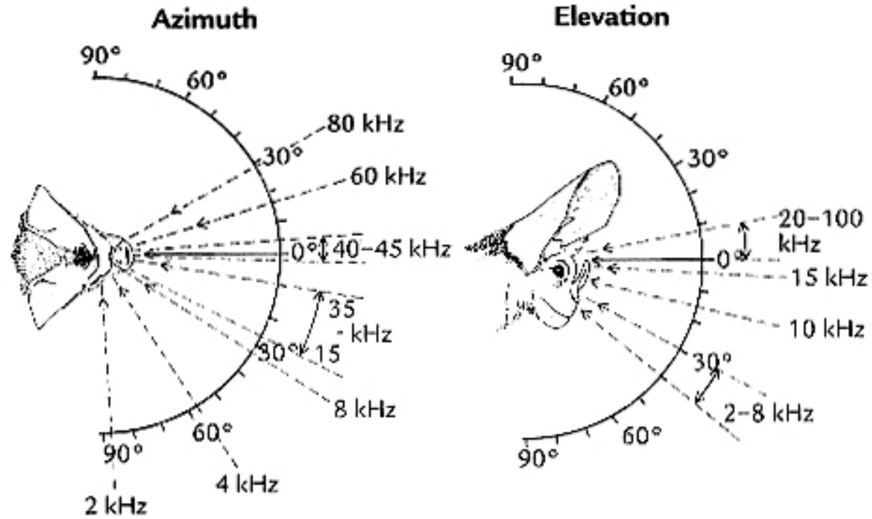
Fig. 2.21. The Indian false vampire bat, *Megaderma lyra*, a carnivorous ground gleaner.

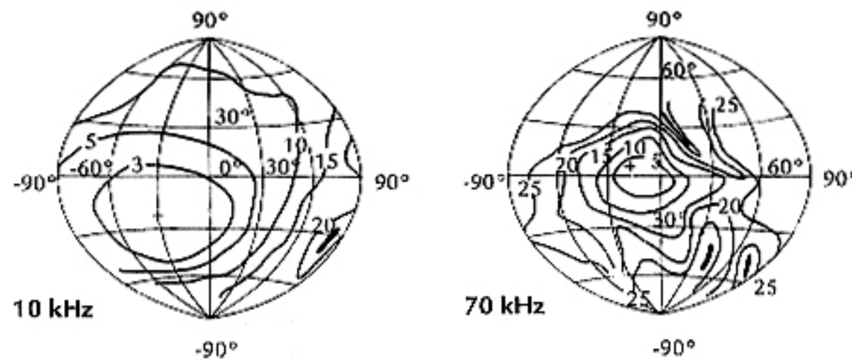
Nose leaf and ear diversity in bats



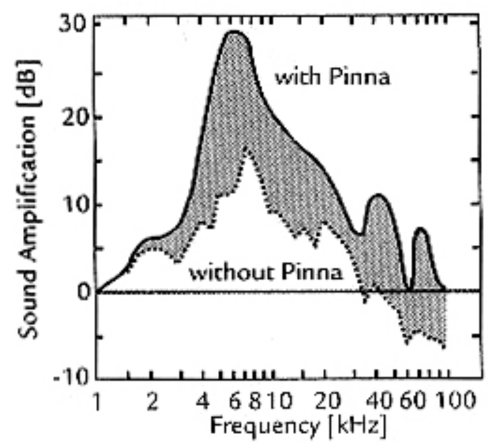
Ear pinna amplifies selected frequencies



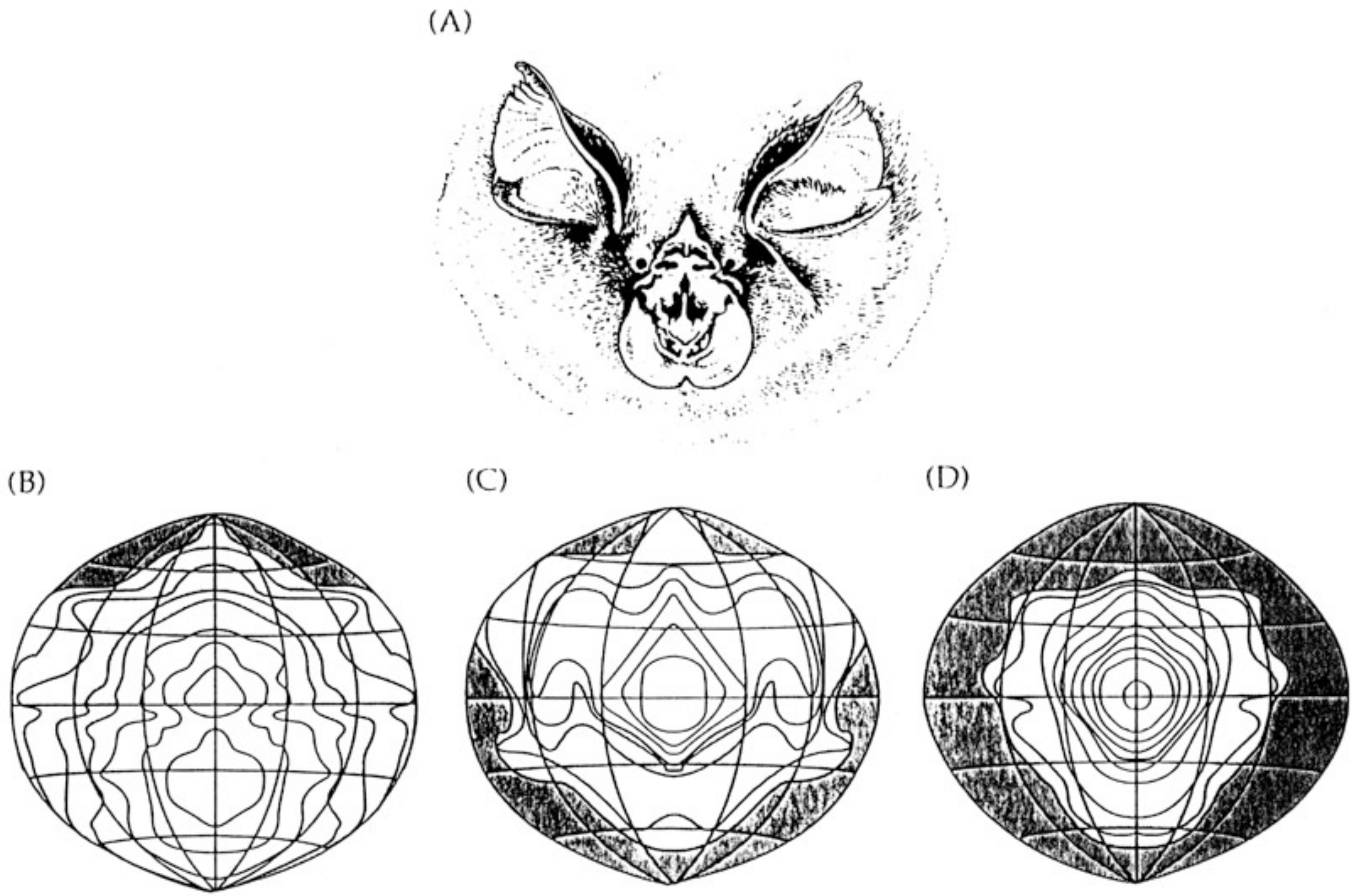




- Pinna acts as a horn
- Larger pinna transmit lower frequencies better
- Wavelength of the resonant frequency equals 4 x length of the ear canal



Ear and nose leaf focus sound



Emitted sound field　　Received sound　　Sonar beam

Information decoded from echos

Target detection

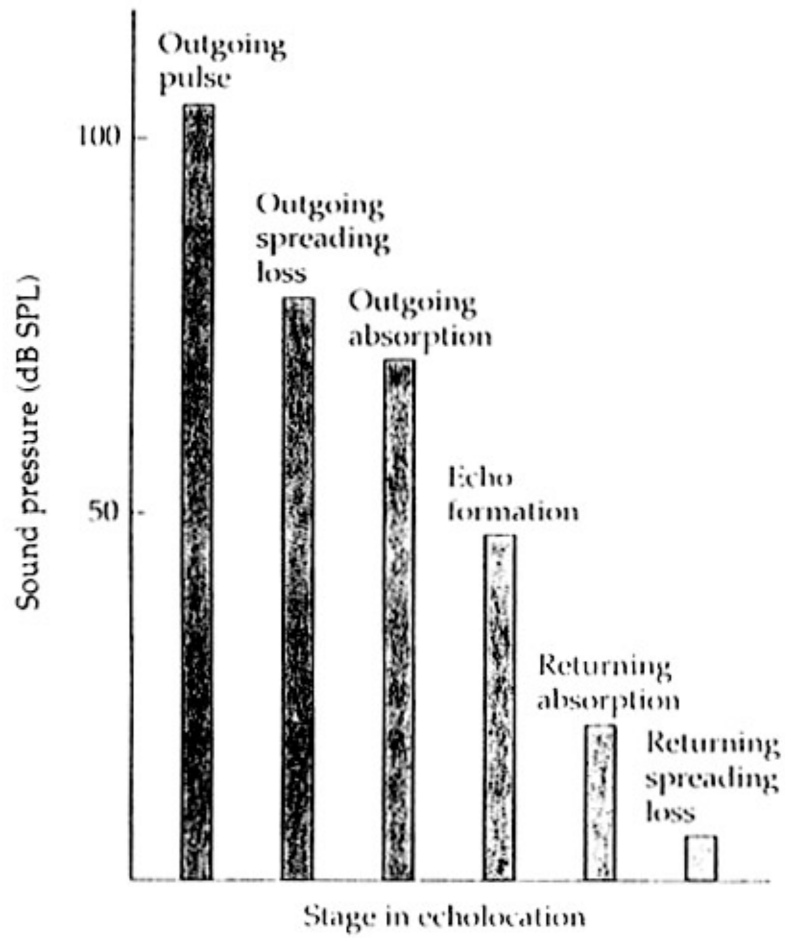
Distance

Angular direction

Velocity & trajectory

Target size & shape

Bat echolocation

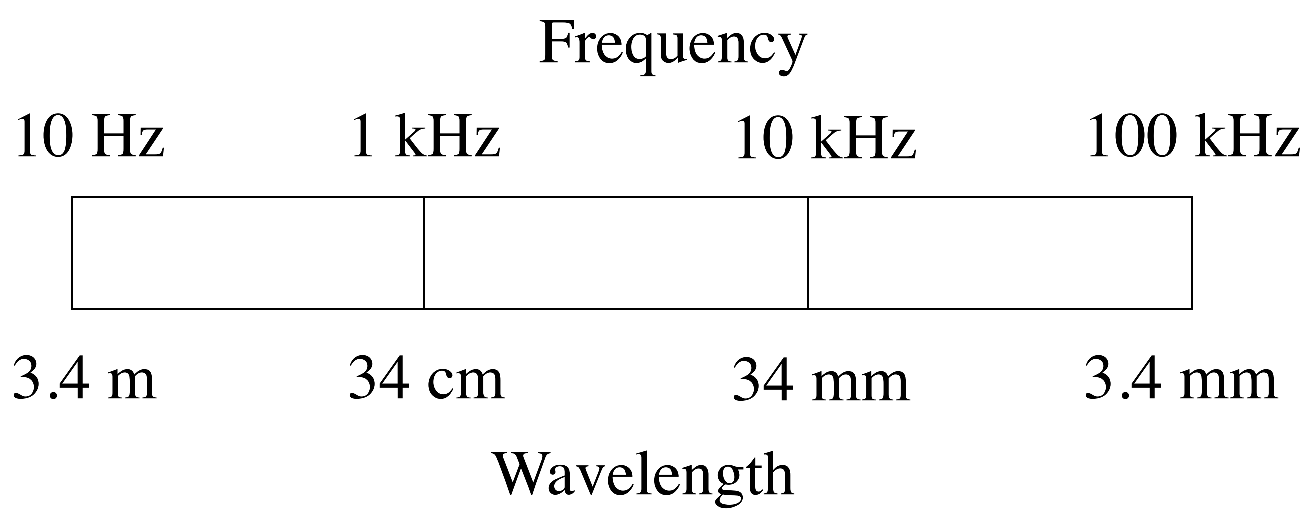


60 kHz pulse
19 mm target at 3 m

- 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

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



Attenuation is due to spherical spreading medium absorption and scattering

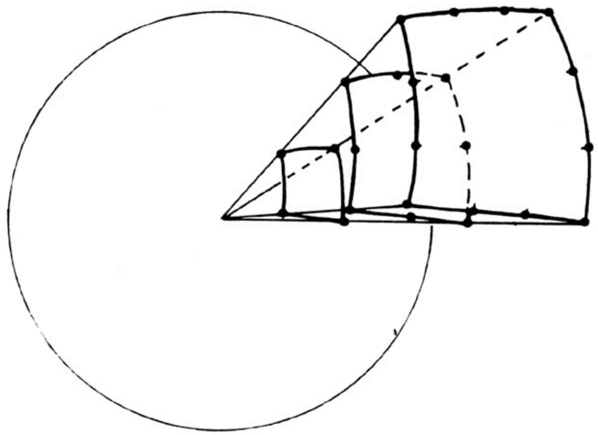
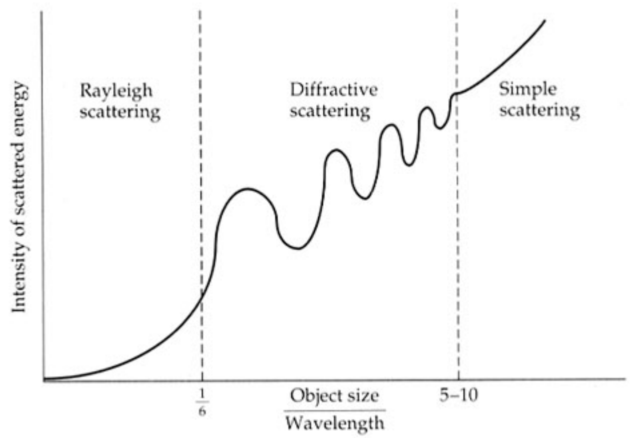
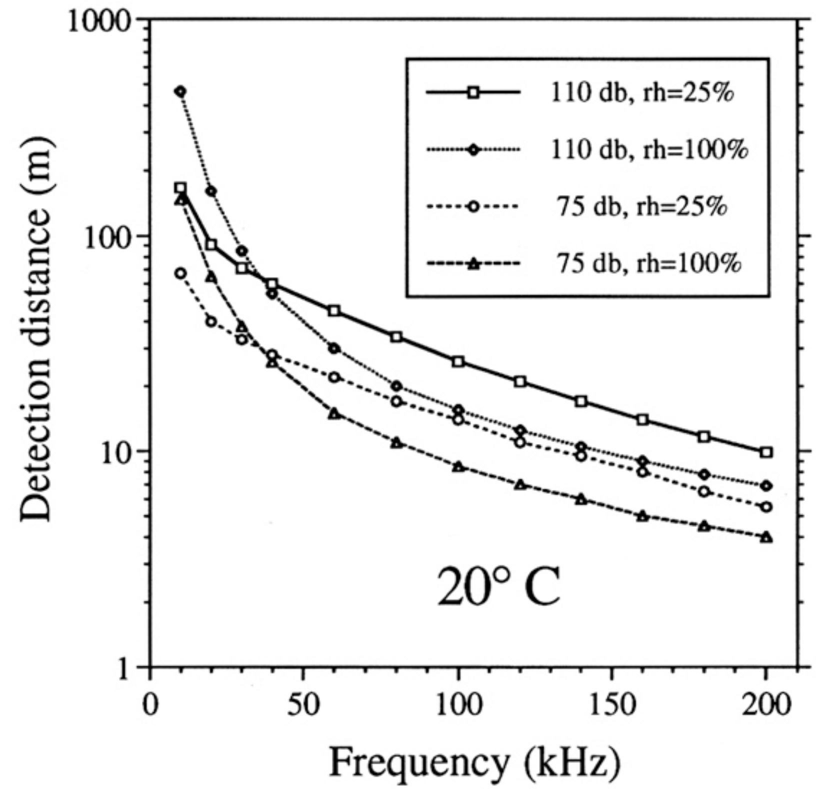
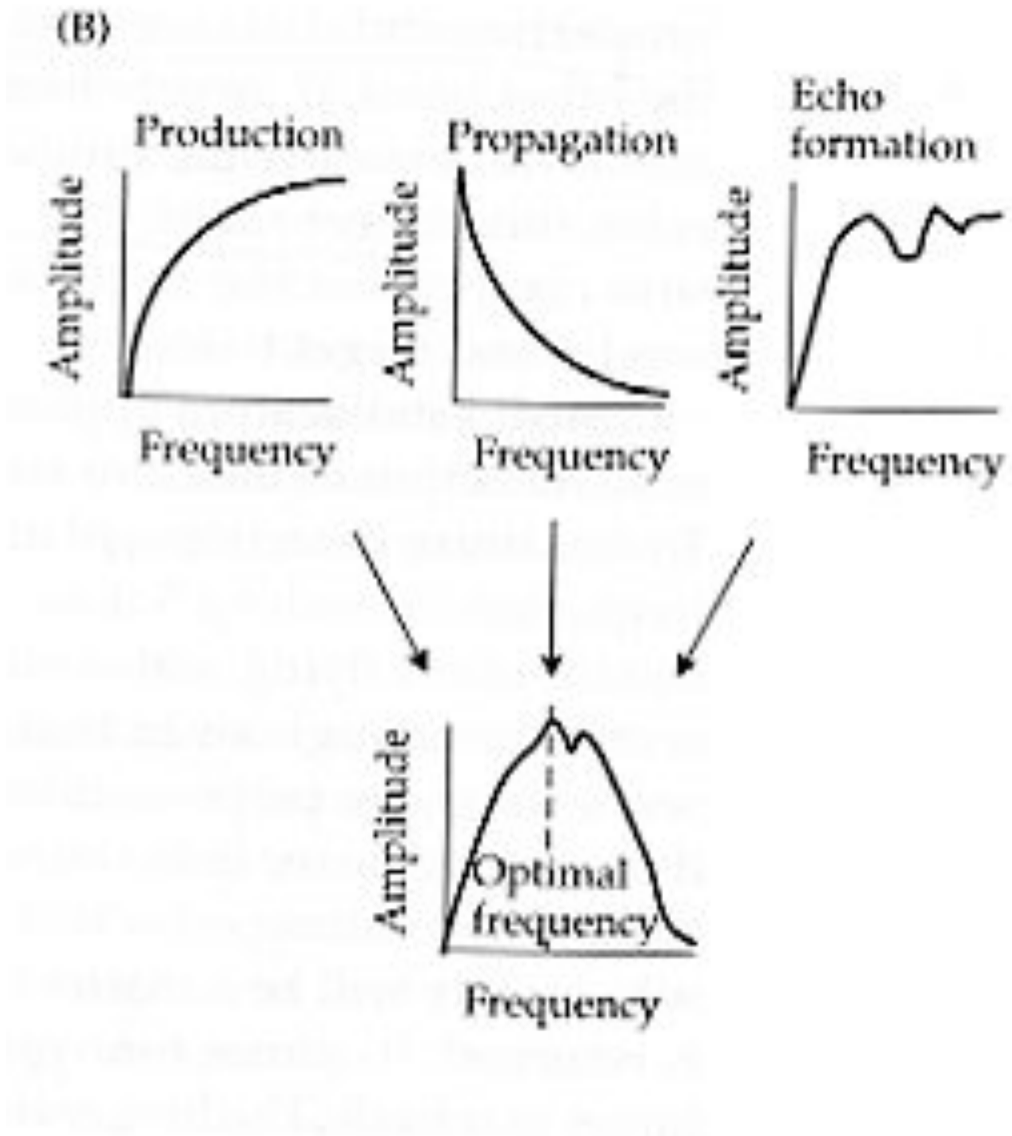


Figure 1.6. Spherical spreading of a sound wave from a point source to demonstrate why attenuation of sound pressure follows the inverse square law.



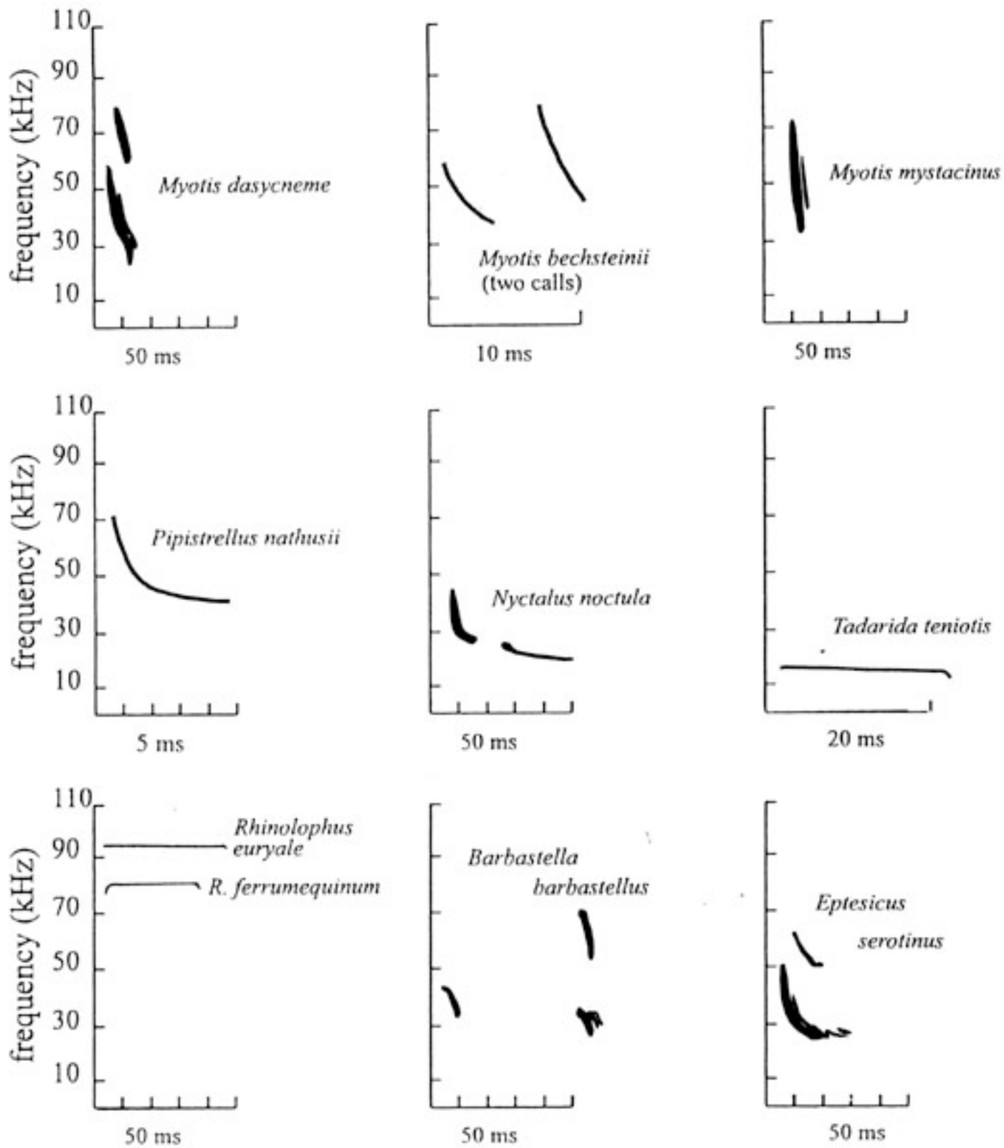


Wavelengths for echolocation



Echolocation call design

FM = frequency modulated



CF = constant frequency

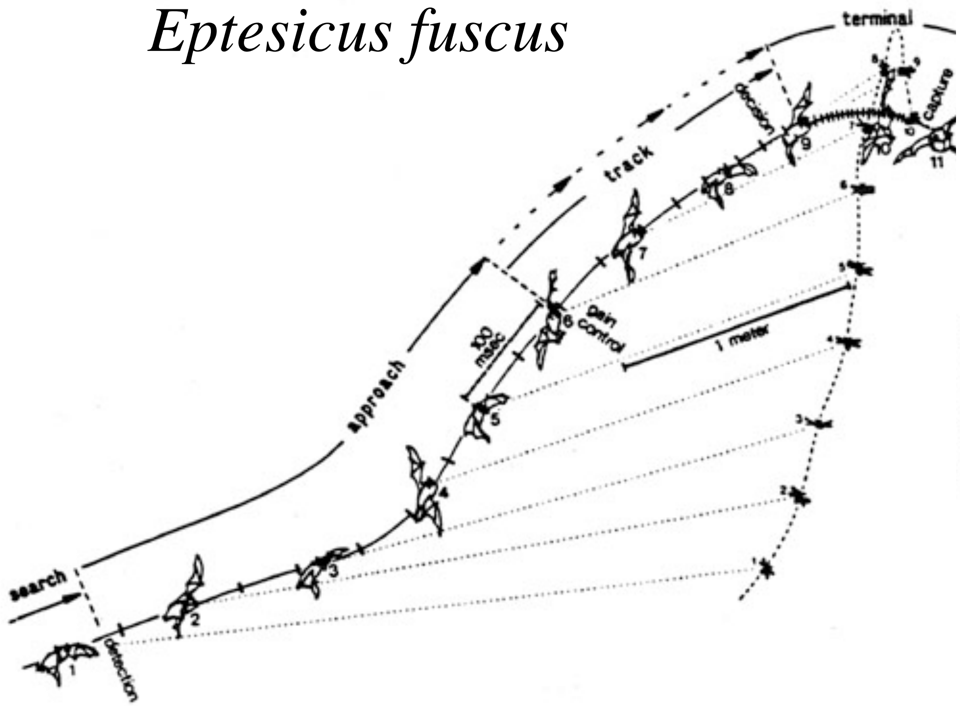
CF = constant frequency

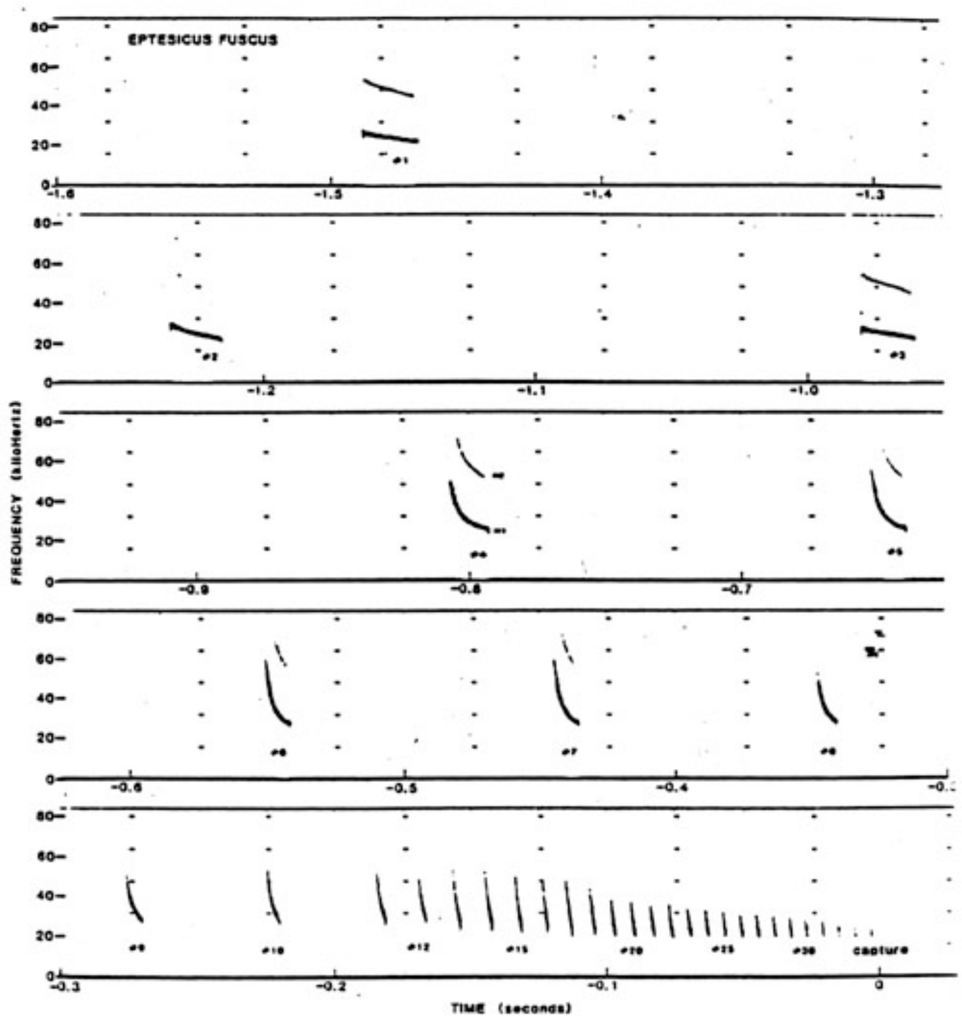
Why produce FM calls?

- 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

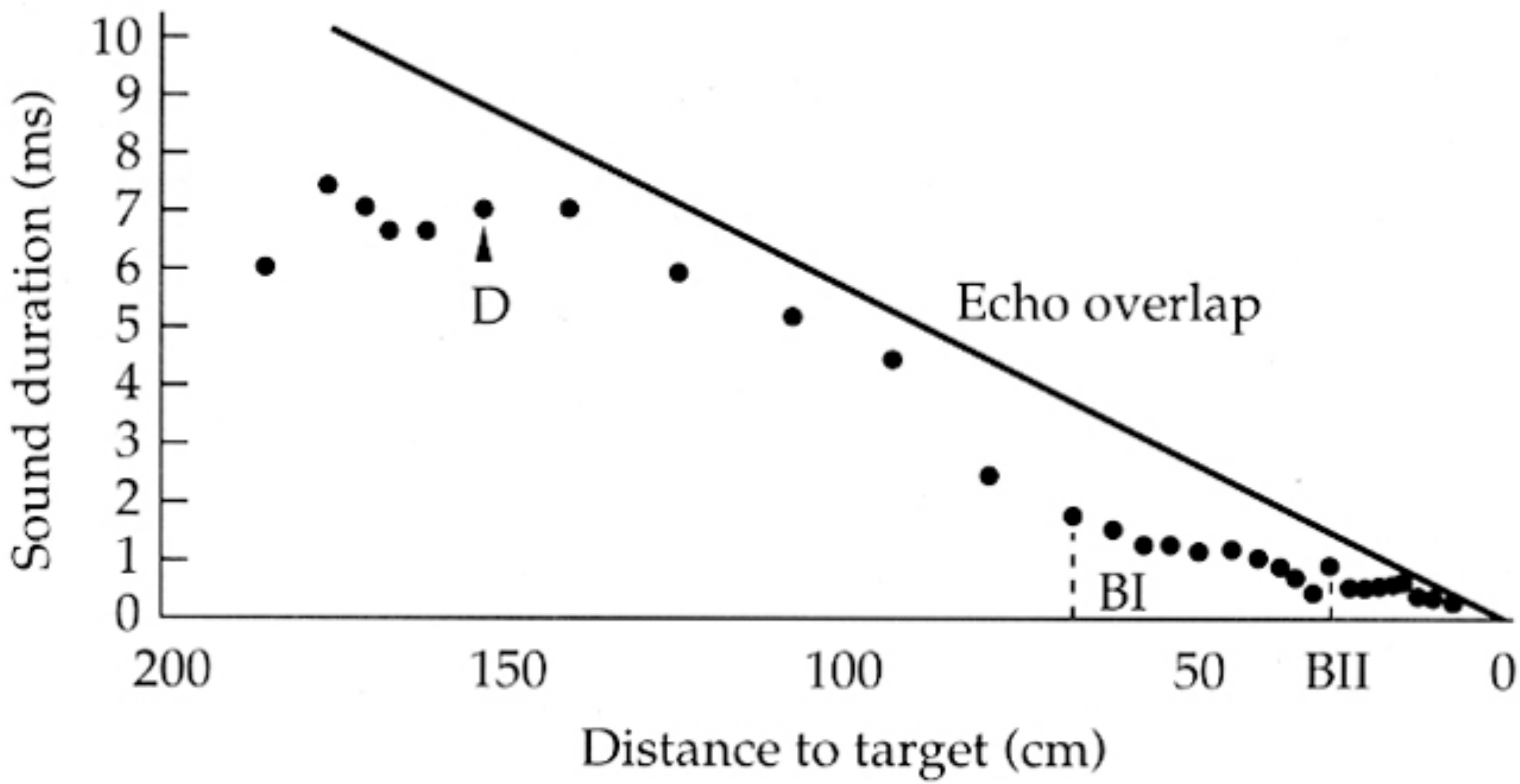
Big brown bat
Eptesicus fuscus



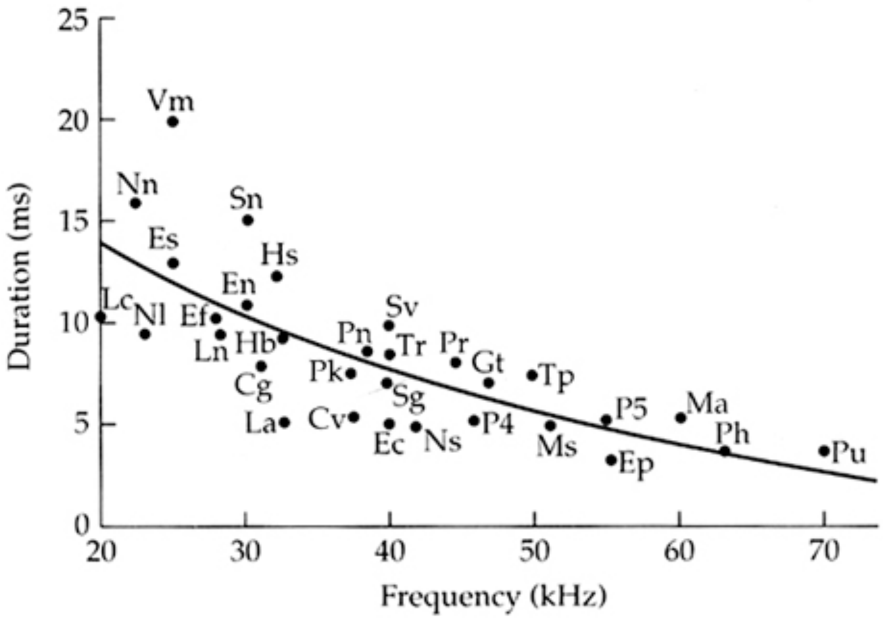


Note low duty cycle, bandwidth
increases as bat approaches prey

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



Pulse duration declines with frequency for FM bats



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 vespertilionid 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, *Hesperoptenus blandfordi*; La, *Laephotis angolensis*; Lc, *Lasiurus cinereus*; Ln, *Lasionycteris noctivagans*; Ma, *Miniopterus australis*; Ms, *Miniopterus schreibersii*; Nl, *Nyctalus leiserli*; Nn, *Nyctalus noctula*; Ns, *Nycticeinops schleffeni*; P4, *Pipistrellus sp1*; P5, *Pipistrellus sp2*; Ph, *Pipistrellus hesperus*; Pk, *Pipistrellus kuhli*; Pn, *Pipistrellus nathusii*; Pr, *Pipistrellus ruepelli*; Pu, *Pipistrellus nanus*; Sg, *Scotorepens greyii*; Sn, *Scotophilus nigrita*; Sv, *Scotophilus viridis*; Tp, *Tylonycteris pachypus*; Tr, *Tylonycteris robustula*; Vm, *Vespertilio 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

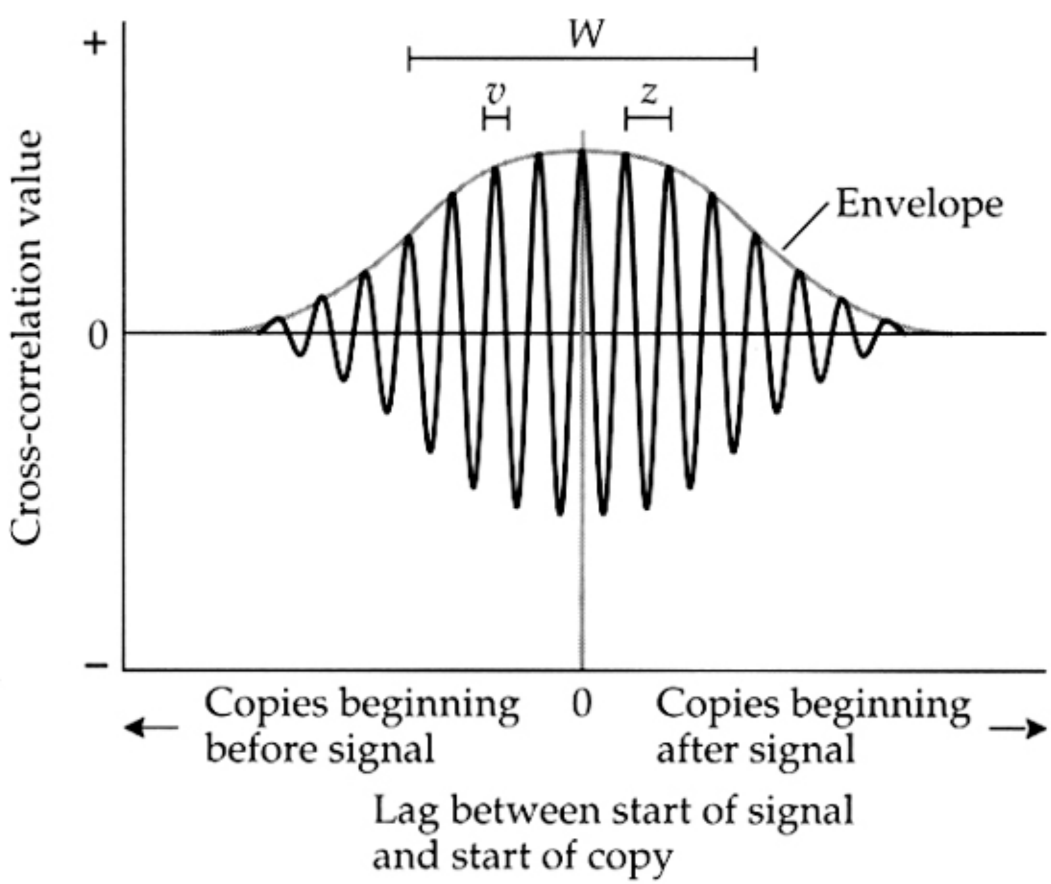
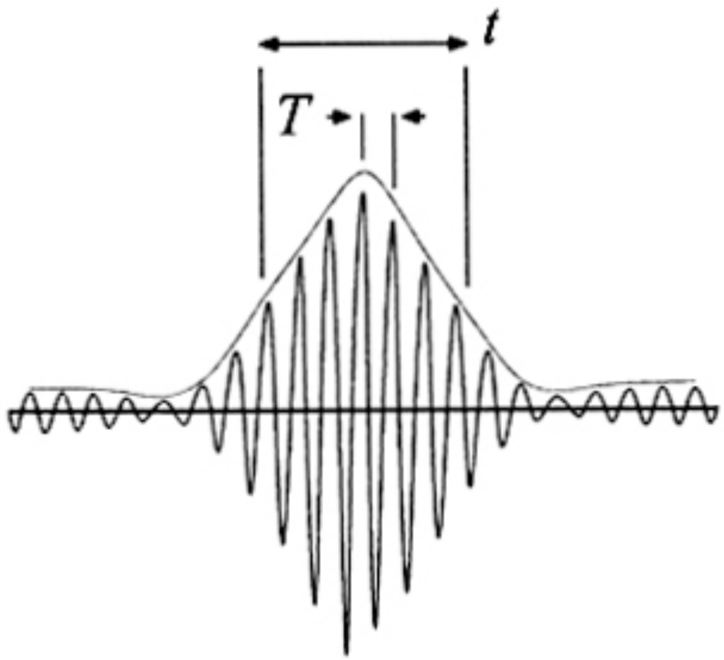


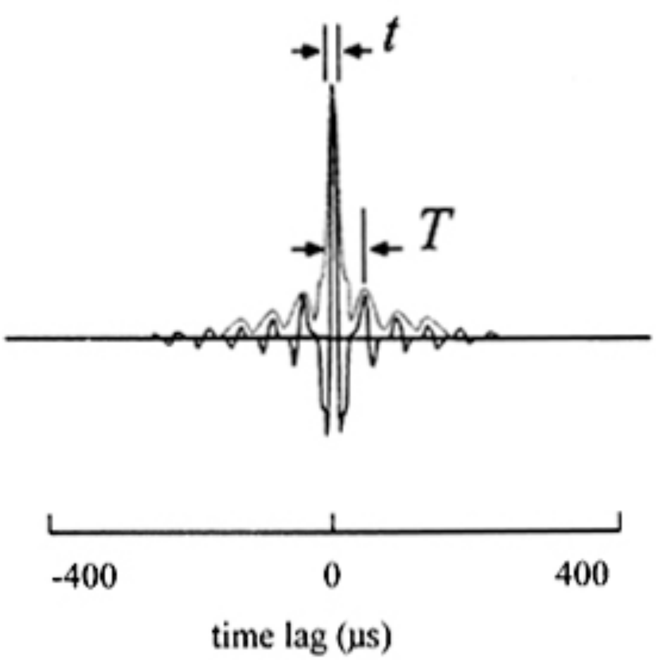
Figure A Typical autocorrelation function between a signal and a copy of itself at varying lags. Lags can be negative (copy begins before signal) or positive (copy begins after signal).

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

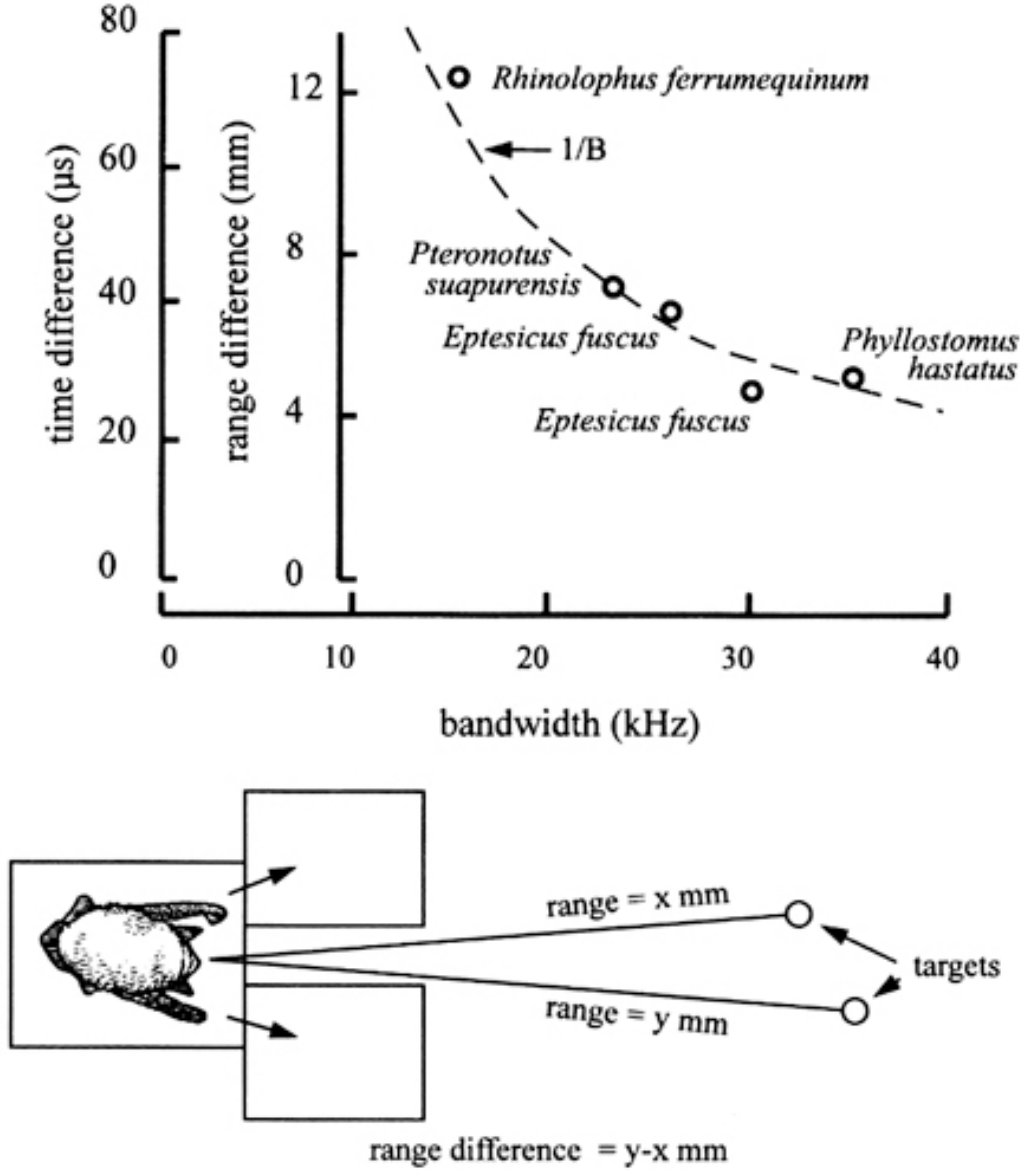


Fig. 3.10. Relationship between call bandwidth and target ranging acuity. Target ranging resolution should theoretically be equal to the reciprocal of the bandwidth, the dotted line in the figure. The 4 species studied by Simmons (1973) have target ranging abilities very close to those expected. Lower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

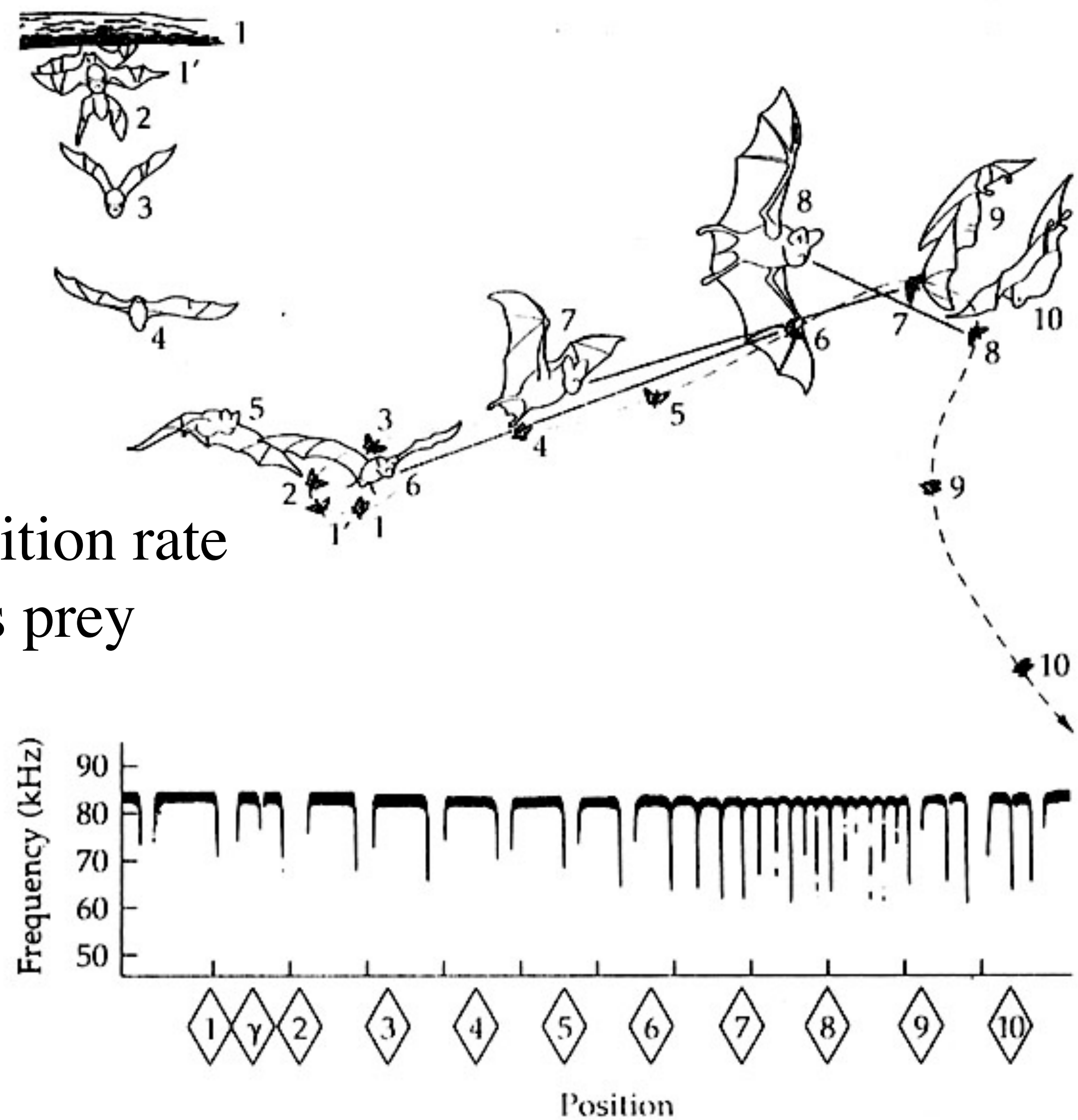
Why produce constant frequency calls?

- 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

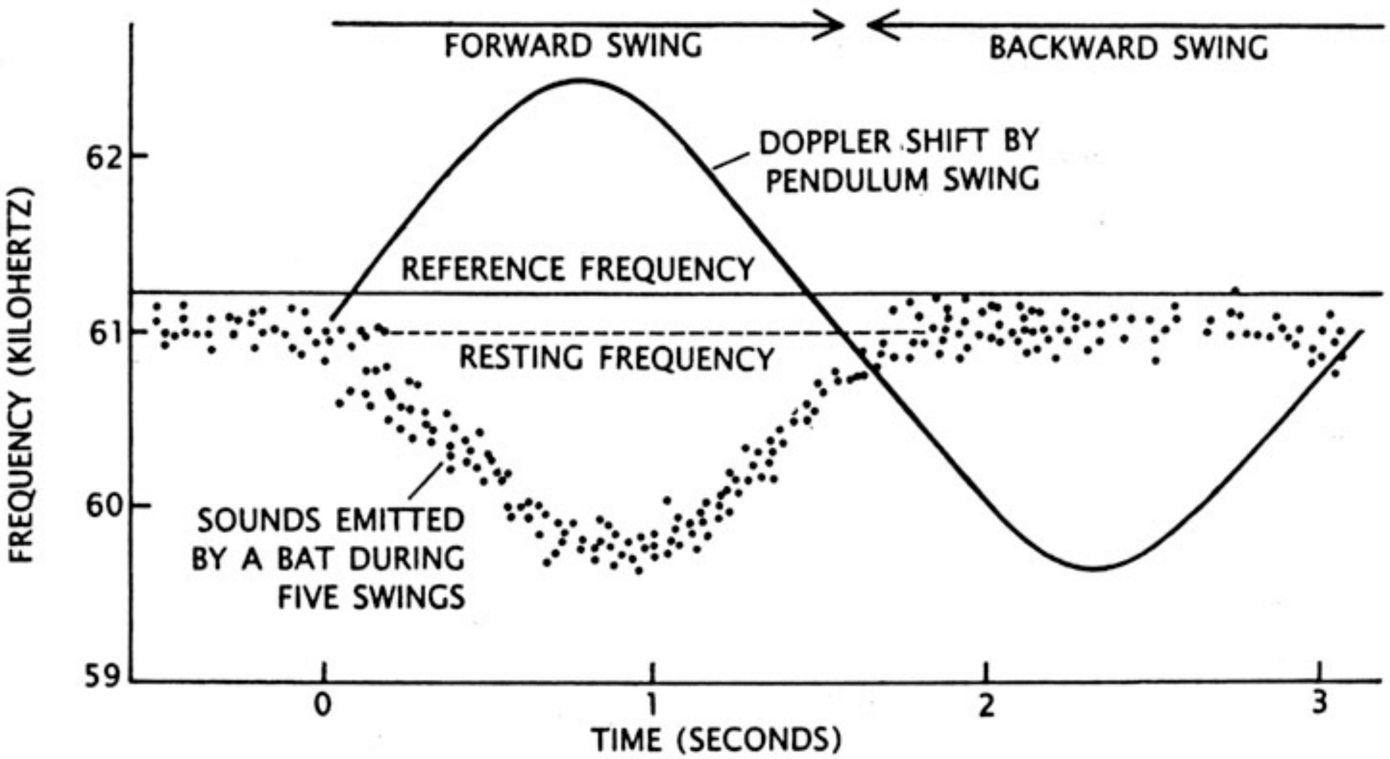
CF calls during prey capture

Greater horseshoe bat, *Rhinolophus ferrumequinum*, hunts from a perch

Note high duty cycle, repetition rate increases as bat approaches prey

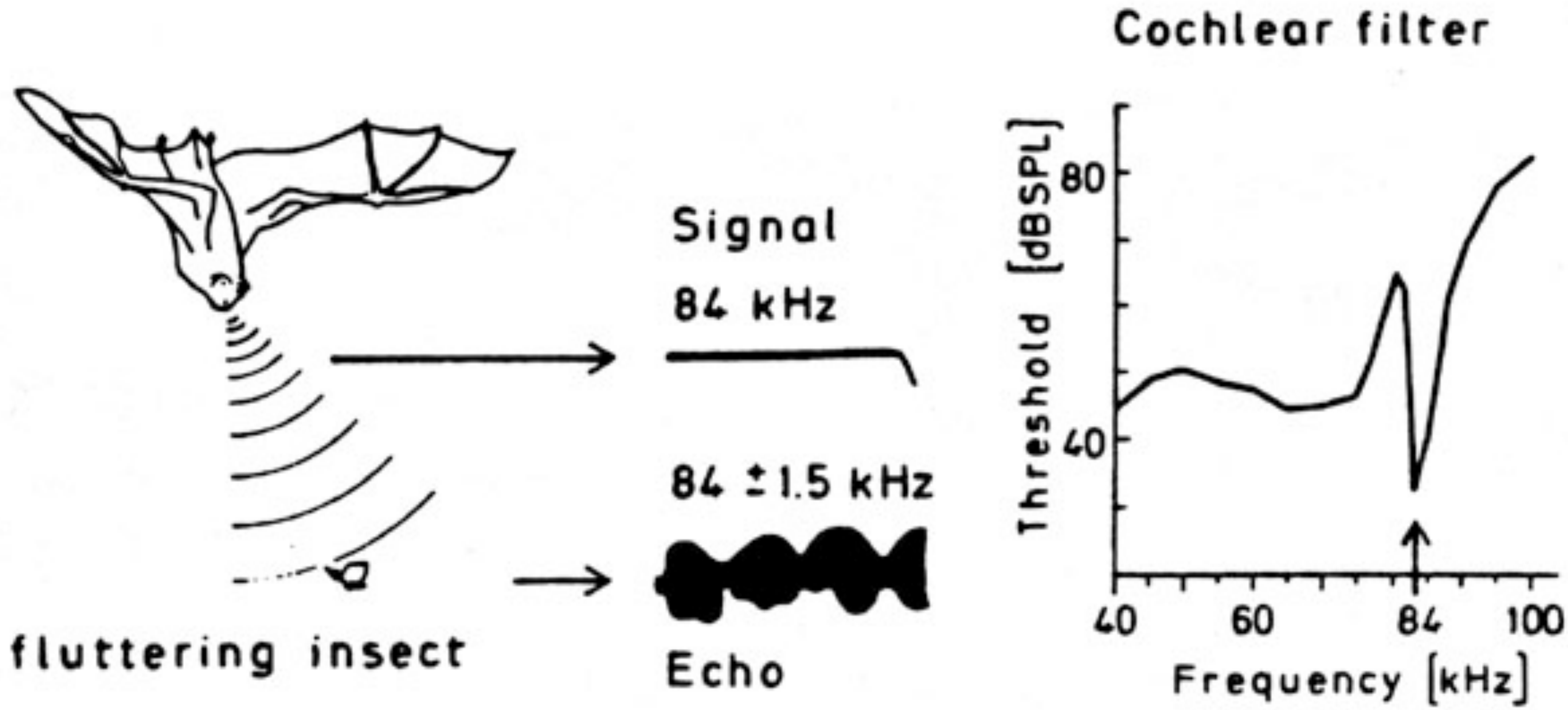


CF bats exhibit doppler-shift compensation



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.

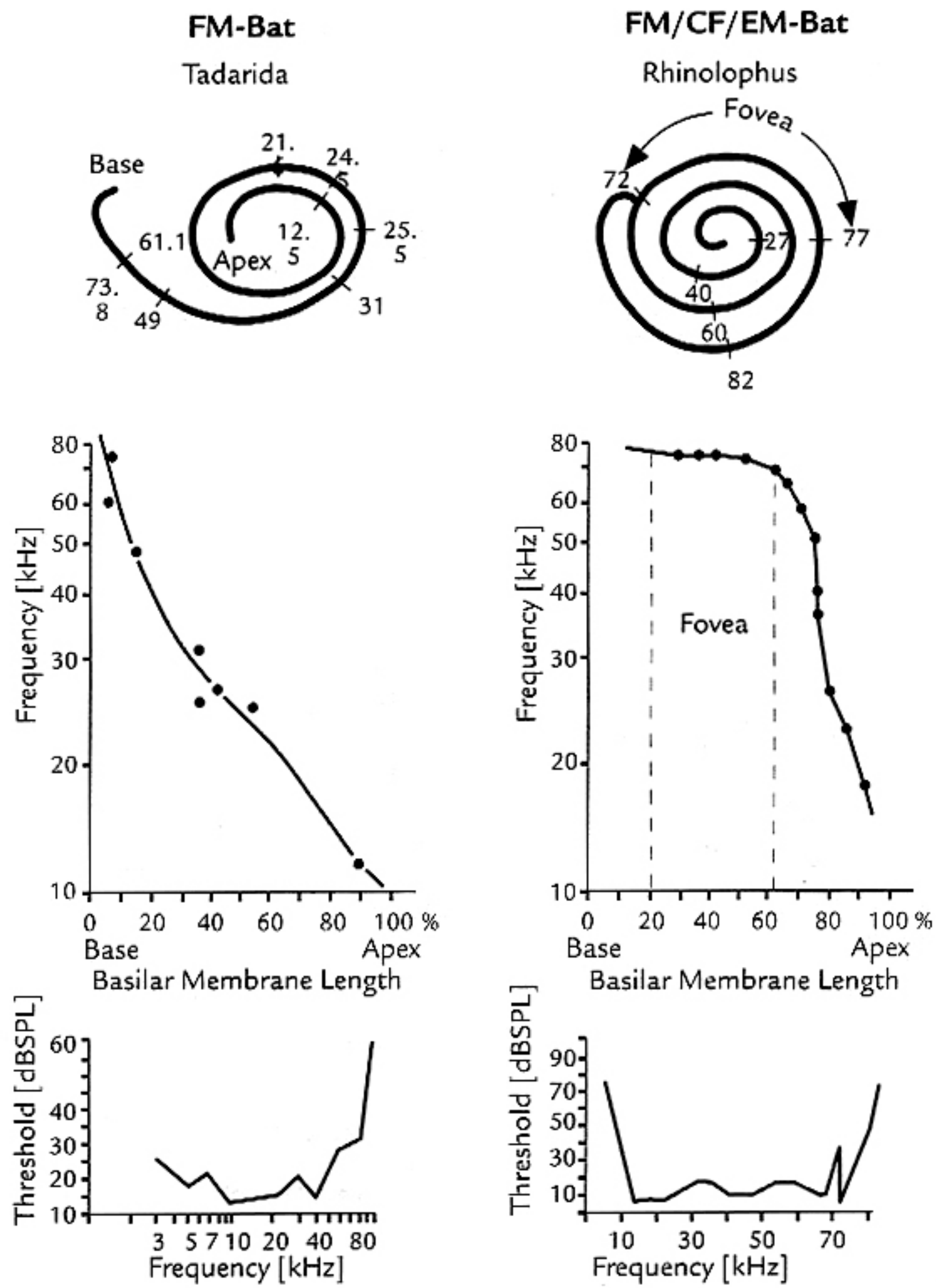
CF bats detect wing flutter as echo glints



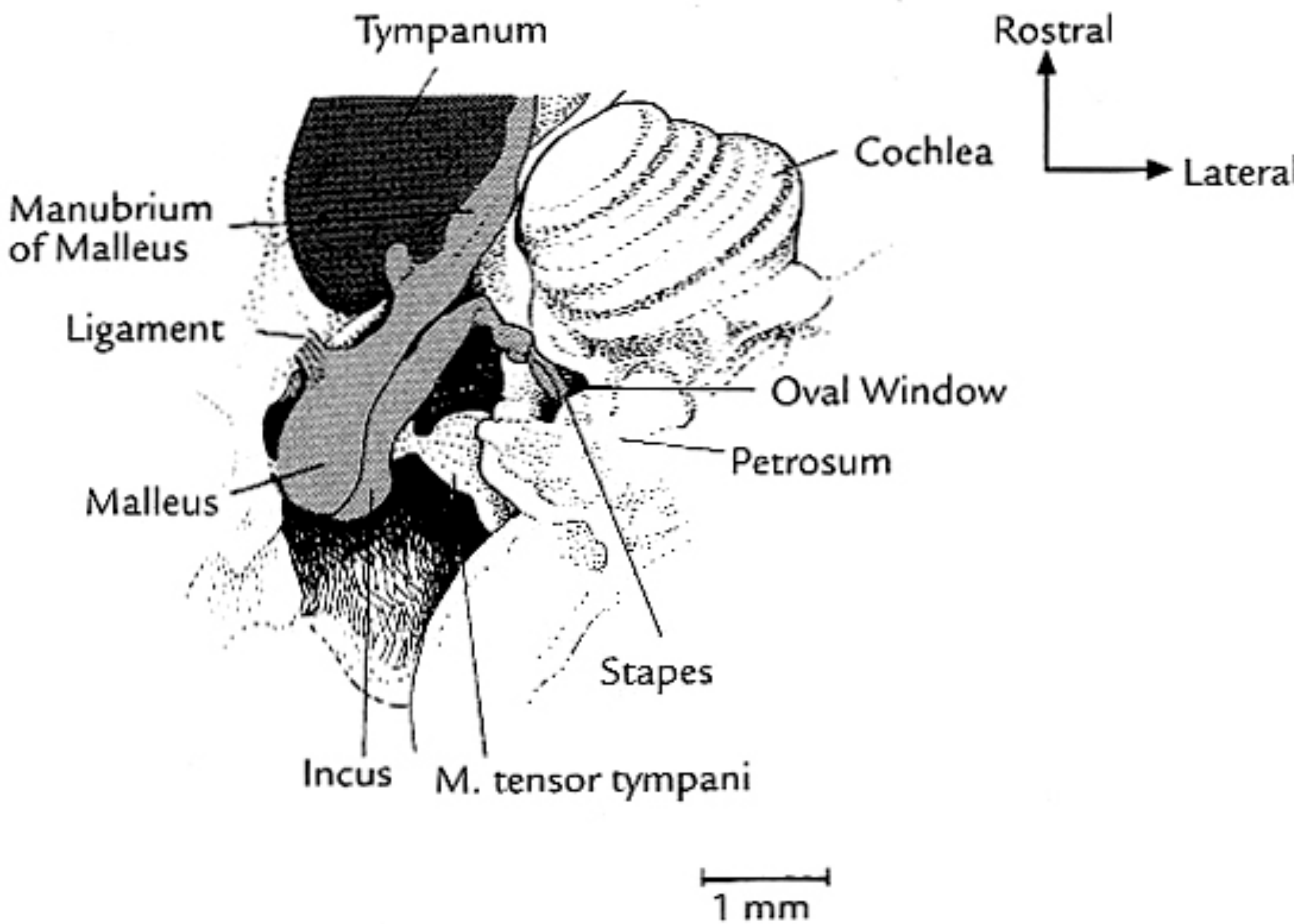
Inner ear (cochlea) adaptations

Basilar membrane is longer and thicker at base

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



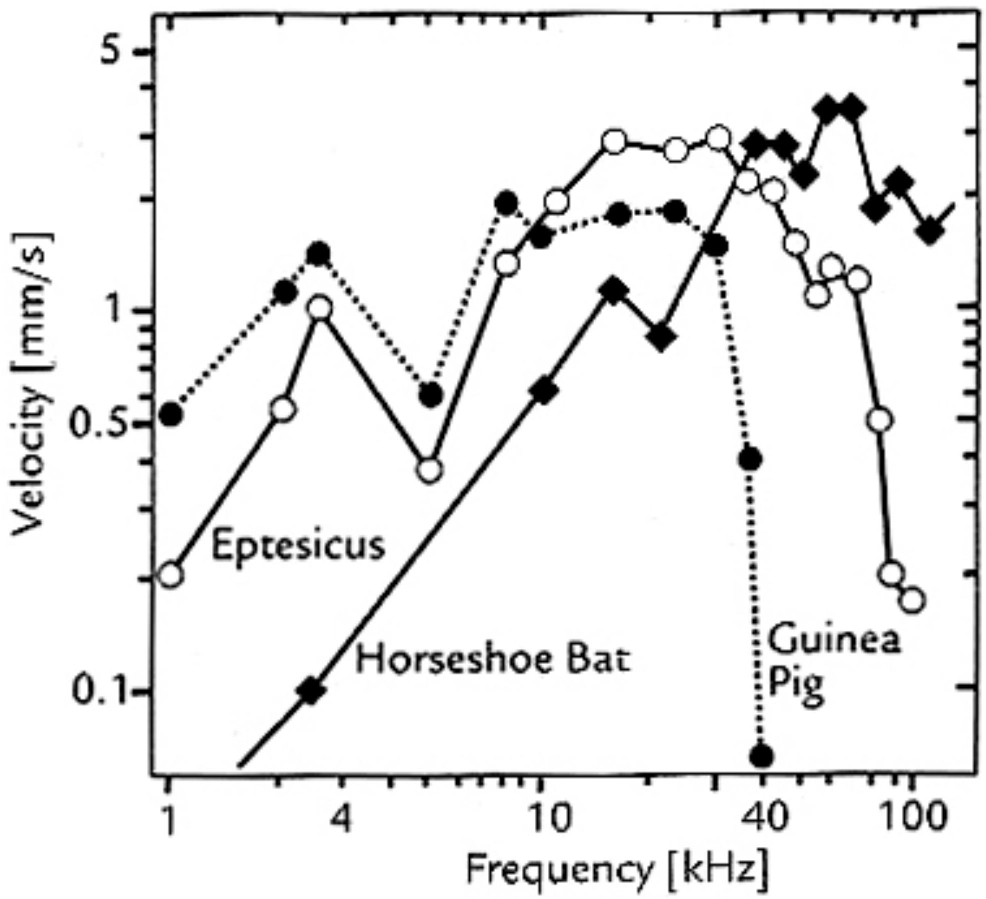
Middle ear adaptations



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

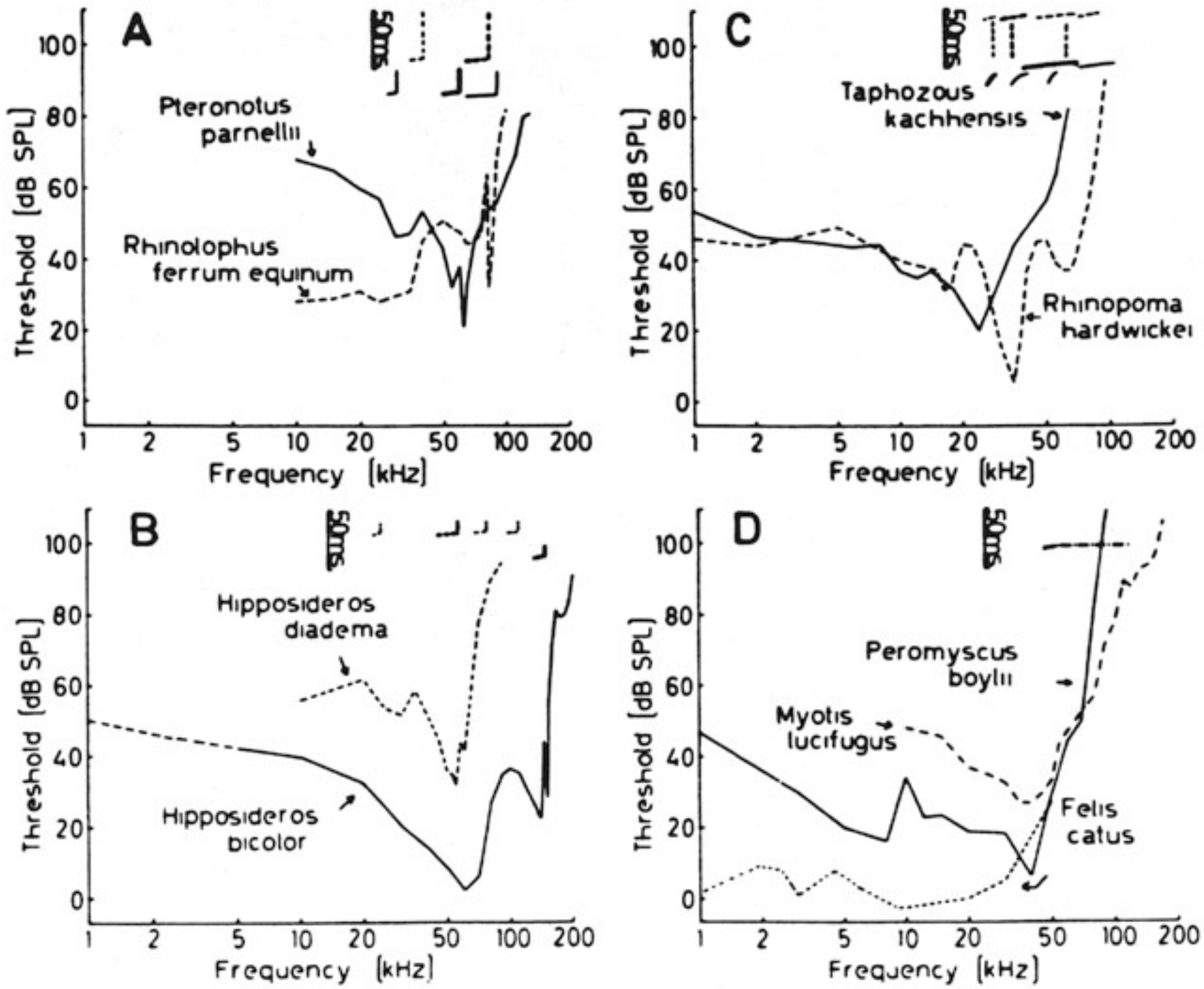


Faster at high frequencies because it is much thinner


Rhinolophus ferrumequinum

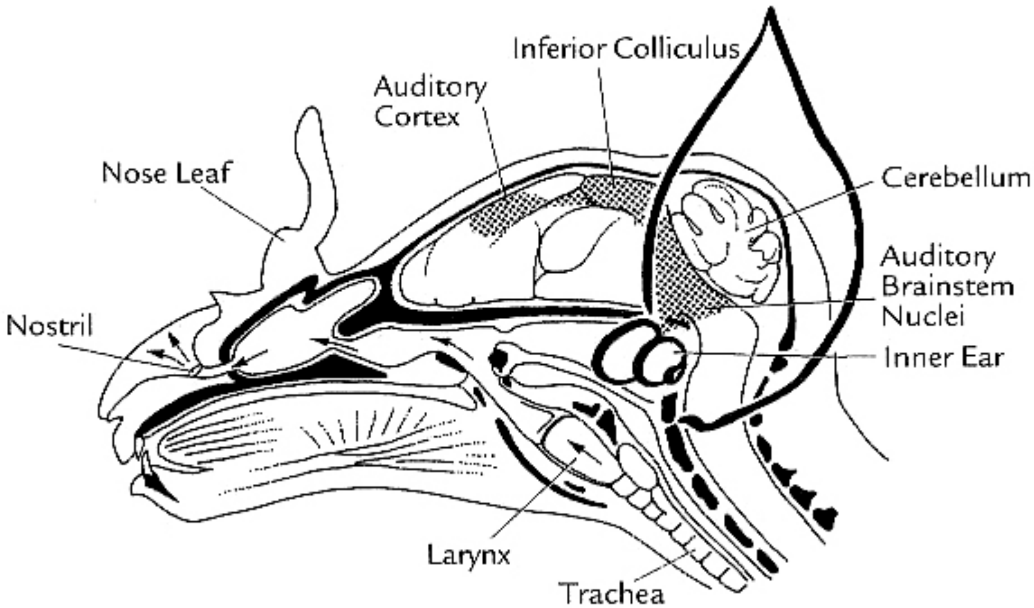
Hearing is tuned to echolocation frequency

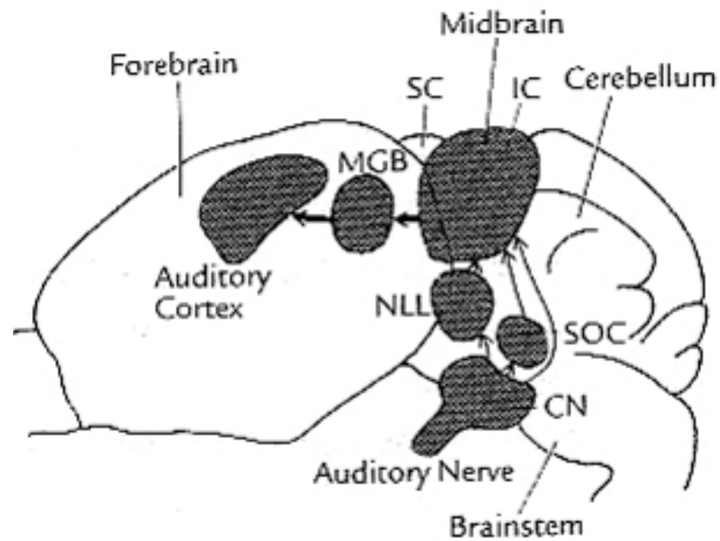
CF bats are tuned to dominant frequency



FM bats show broad frequency sensitivity

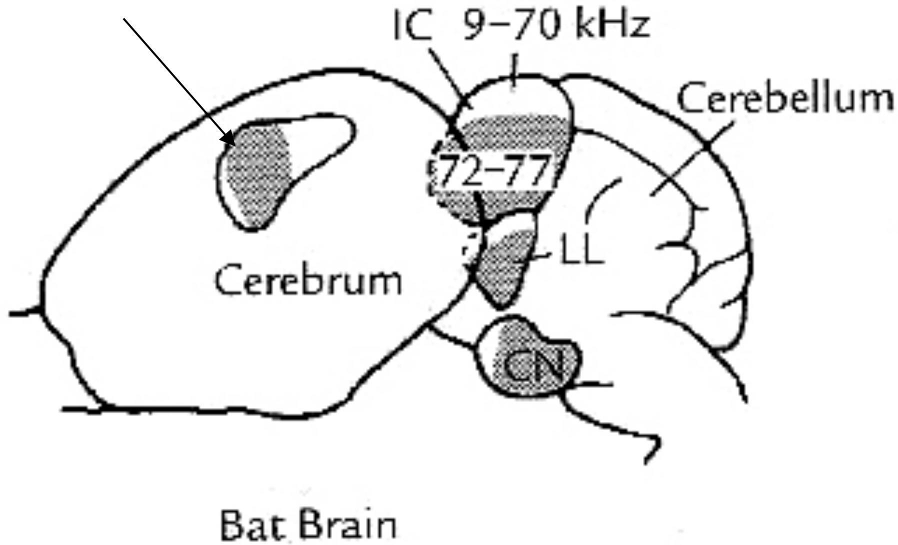
The auditory pathway

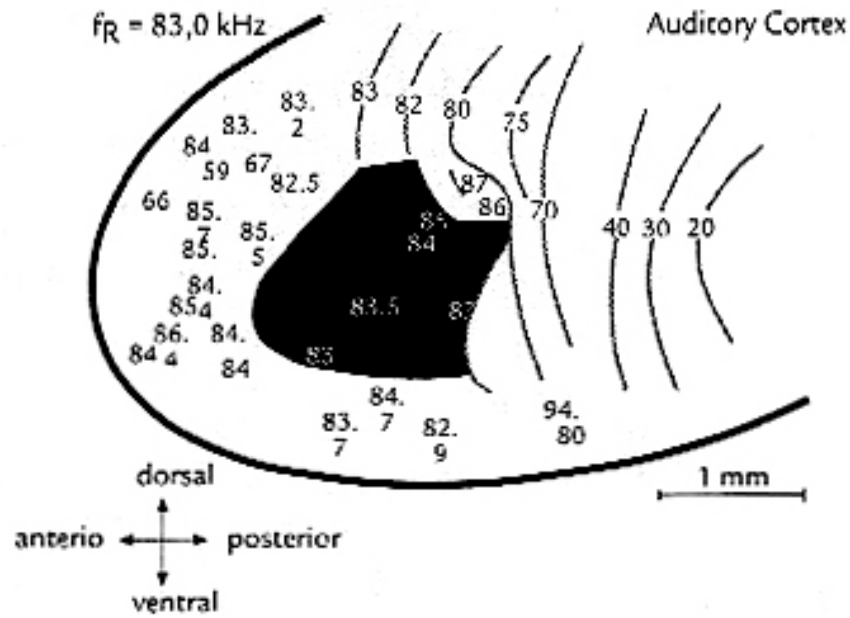




Tonotopic map in the auditory system

Auditory cortex

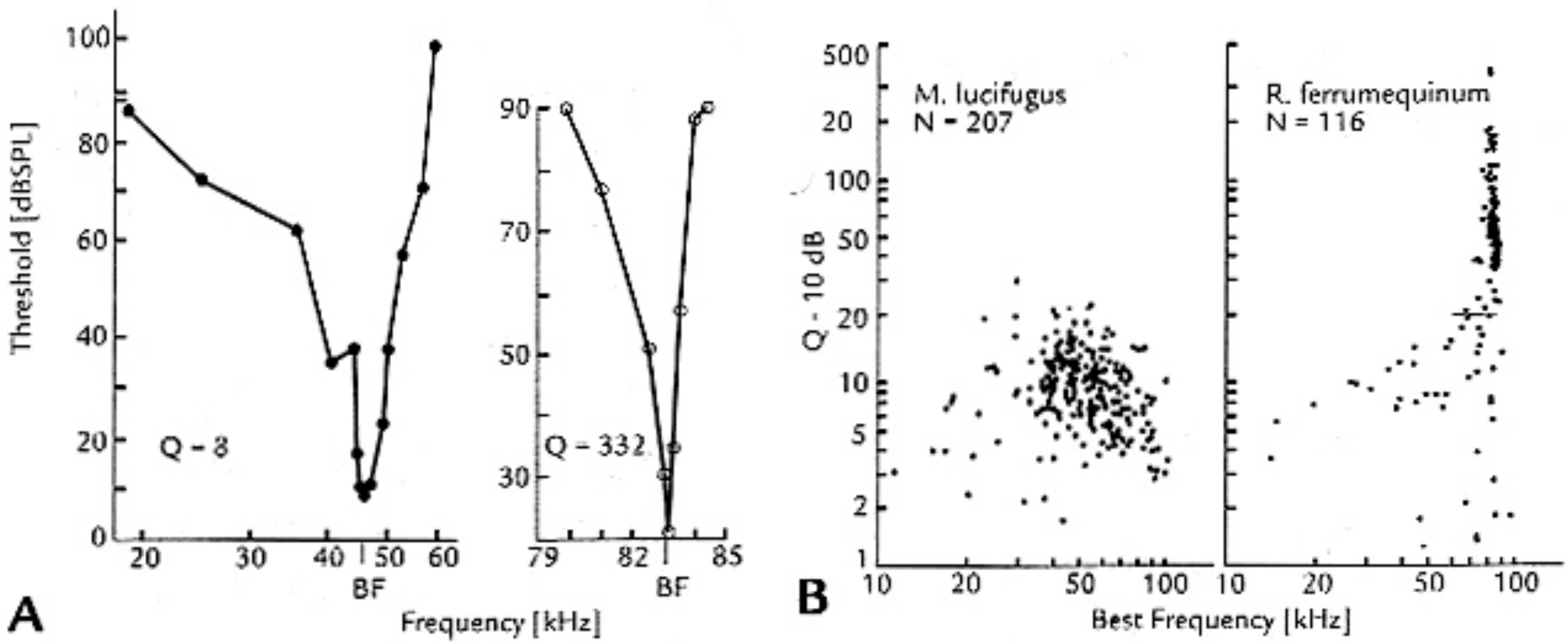




Gray areas correspond to call frequencies

Auditory cortex is expanded at frequencies associated with echolocation

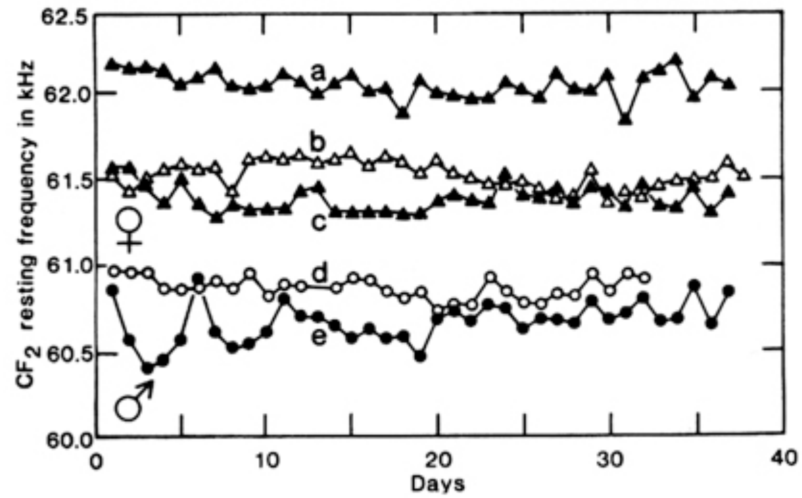
Neuronal tuning in horseshoe bats

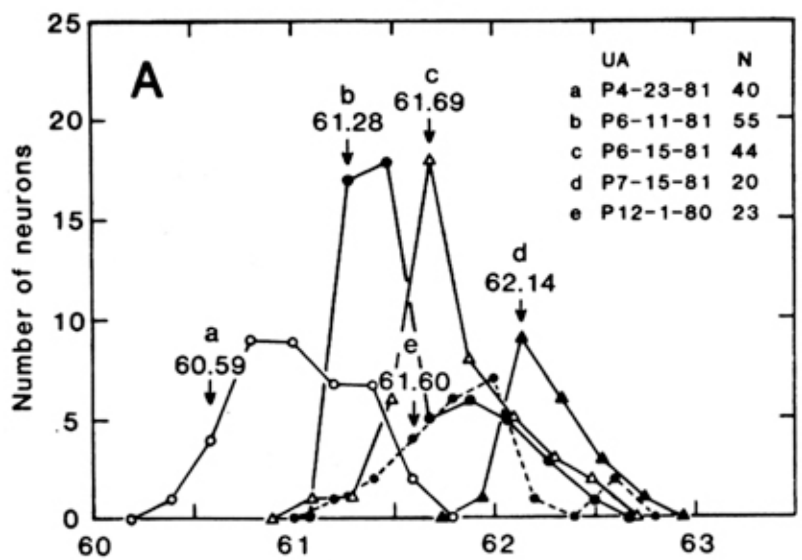


Q_{10} = best freq/ bandwidth at -10 dB


Pteronotus parnellii

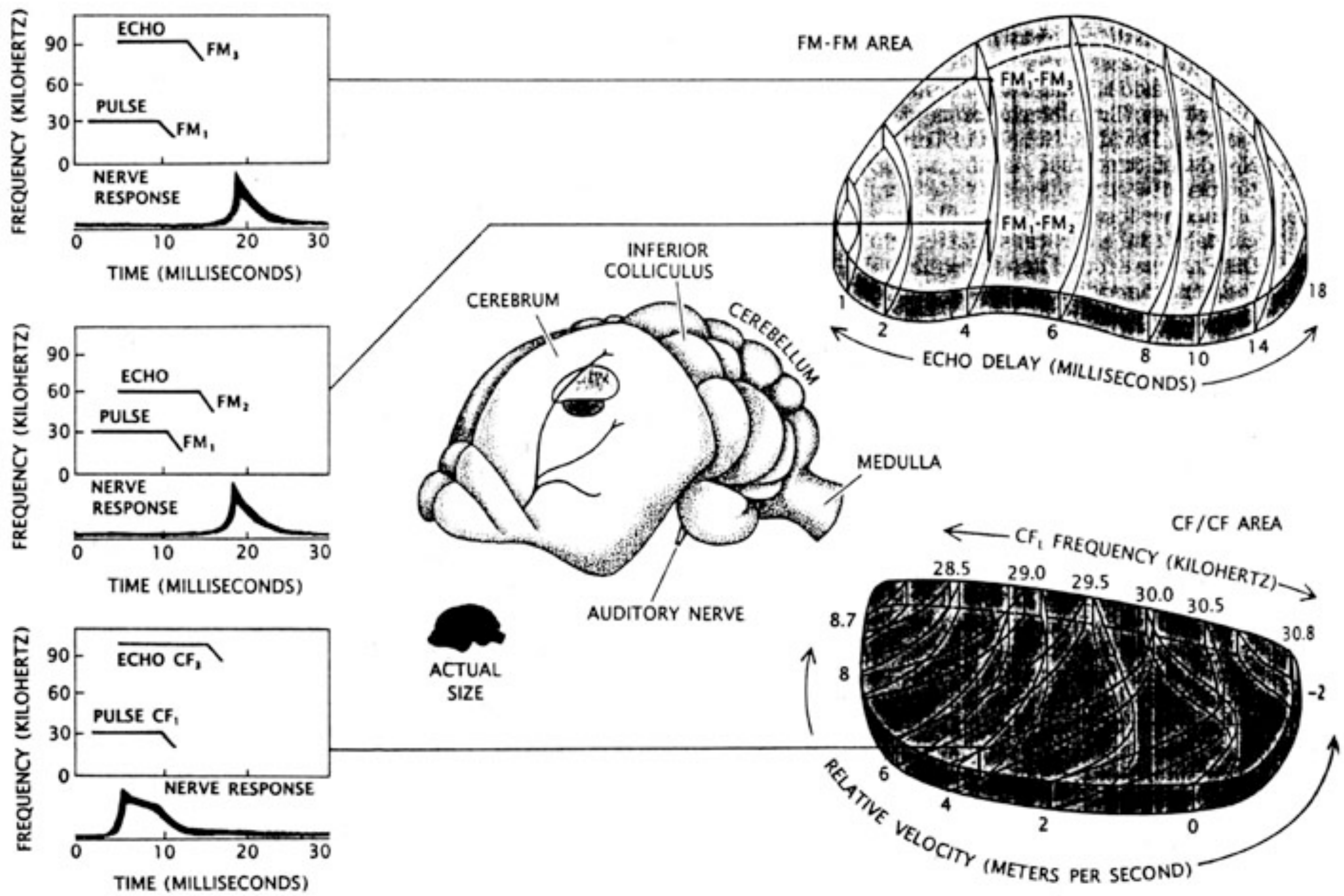
Individual *Pteronotus* bats use unique CF frequencies

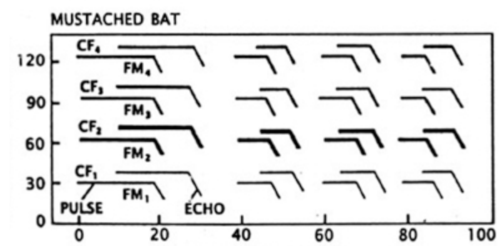




Suga, N., H. Niwa, I. Taniguchi, D. Margoliash 1987 J. Neurophys. 58:643-654

Combination-sensitive neurons encode range and velocity in CF bats



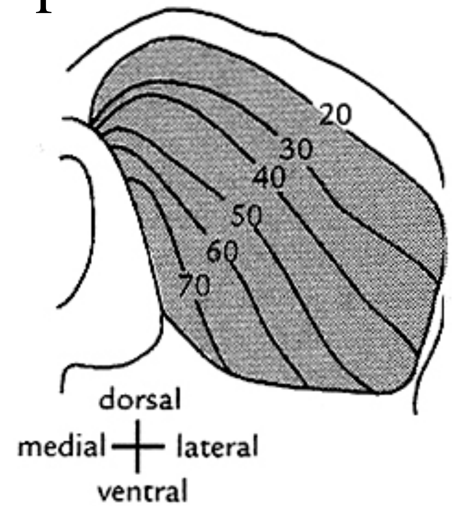


COMPUTATIONAL MAPS in the auditory cortex of mustached bats represent echo delay (or distance) and Doppler shift (or relative velocity). In the FM-FM area (*green*), neurons along each black line respond to a specific echo delay. The top graph (*right*) shows the delay-tuning curves of six FM-FM neurons;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

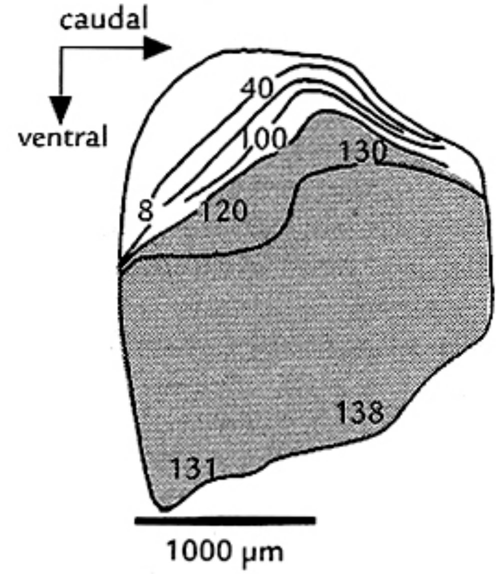
Tonotopic representation varies by species

Open space

(Eptesicus fuscus)

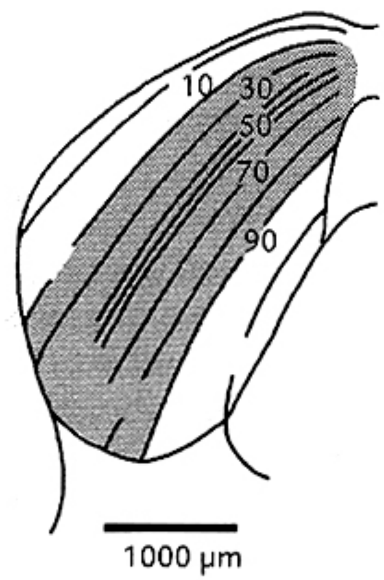


(Hipposideros speoris)



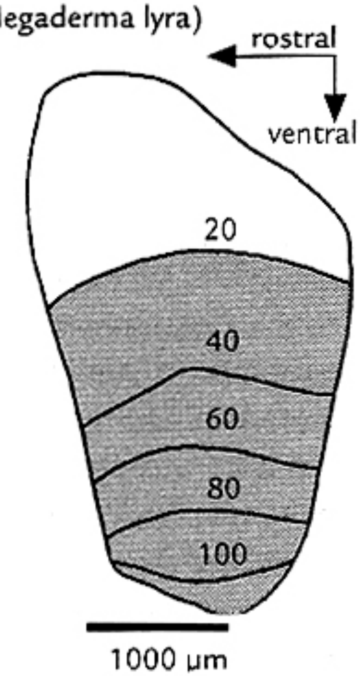
Blood feeder

(Desmodus rotundus)



Ground gleaner

(Megaderma lyra)



Inferior colliculus
frequency maps

Call design and foraging strategy

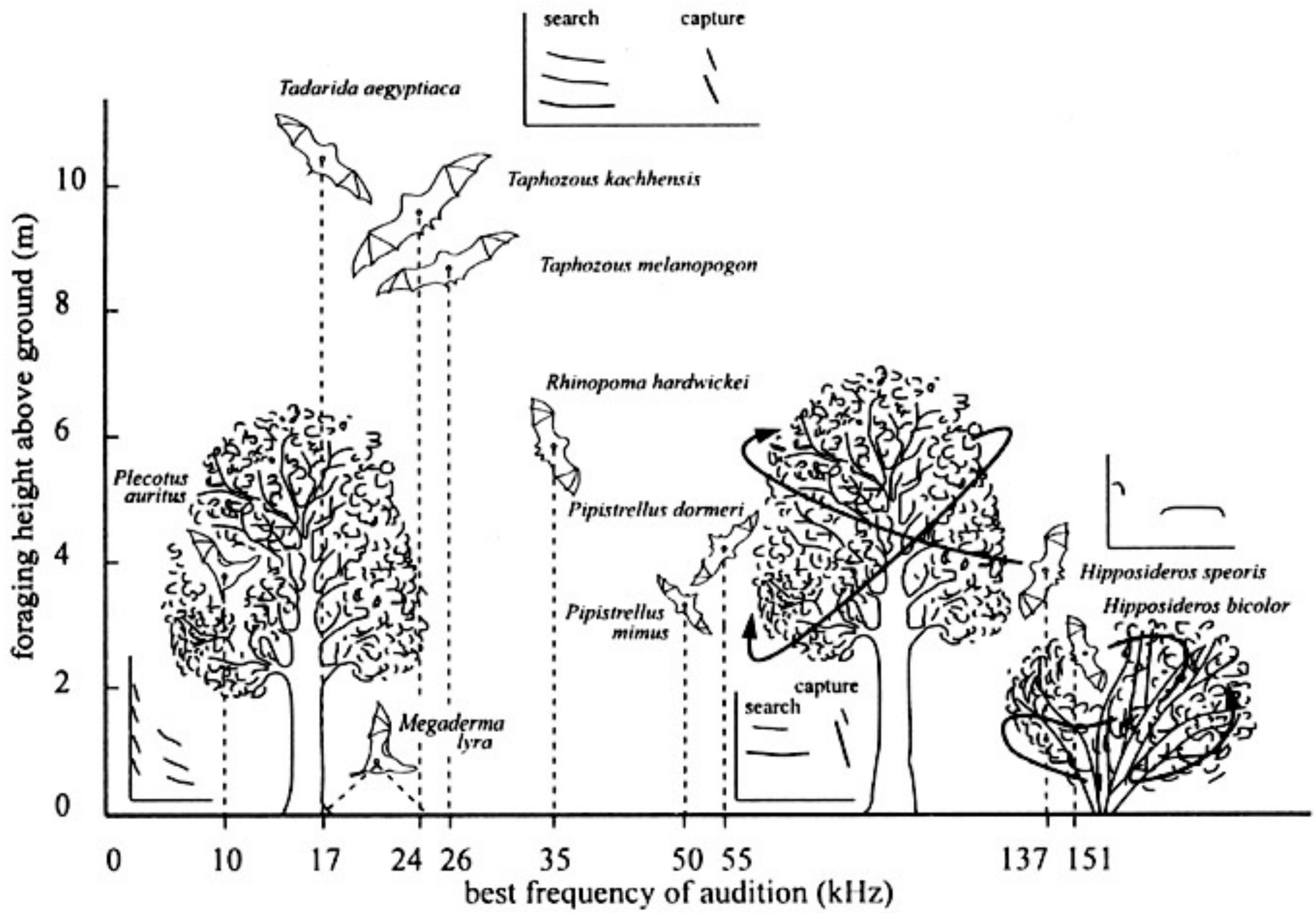
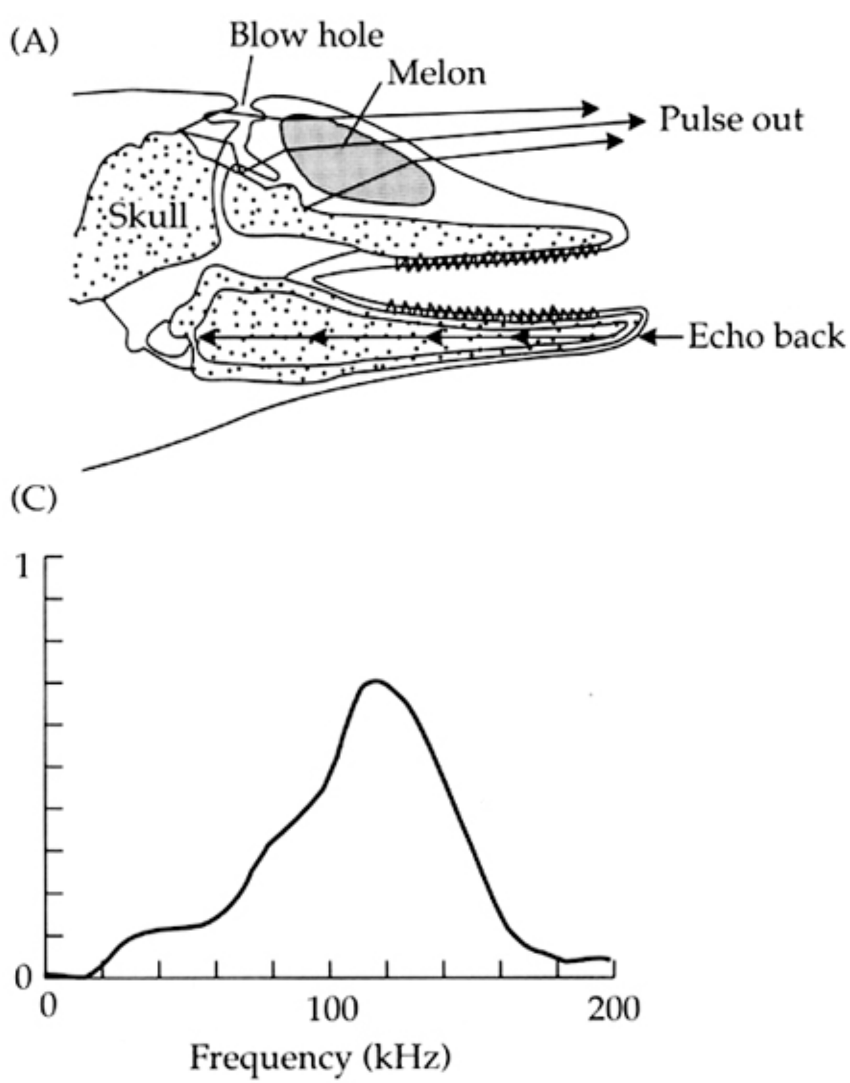


Fig. 3.24. Foraging strategy in relation to echolocation calls and auditory characteristics. Foraging height is plotted against the best frequency of audition. Bats are loosely divided into gleaners (ground and foliage), above canopy hawkers, low level open-air hawkers, and hawkers in cluttered habitats, 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	Frequency of echo
Distance	Pulse-echo time delay
Angular direction	Ear amplitude difference
Velocity & trajectory	Pulse-echo frequency change
Target size & shape	Frequency of echo