Sound Reception

- Types of ears
- Extraction of information
  - Direction
  - Frequency
  - Amplitude
- Comparative survey of animal ears

What is an ear?

- Couples sound waves traveling in environment to organism
- Converts sound to nerve impulses while retaining information present in original signal

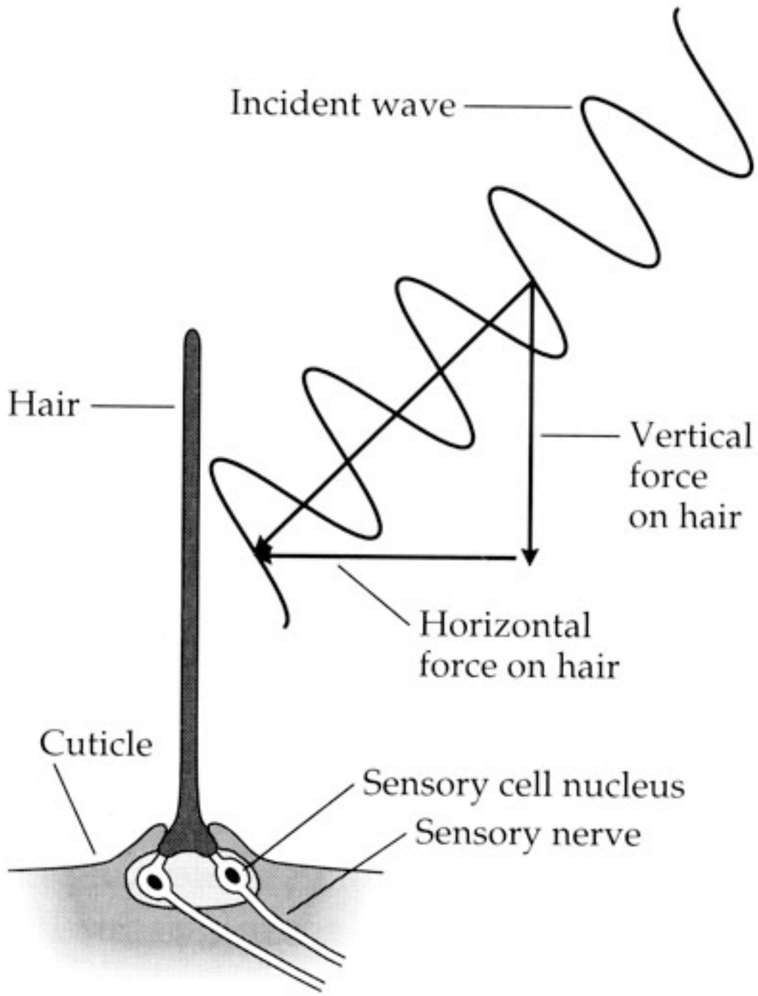
The Perfect Ear

- Wide frequency range (20 kHz)
- Wide dynamic range (100 db)
- Accurate frequency resolution
- Accurate temporal resolution
- Ability to localize sound source - direction and distance
- Good pattern recognition

Types of ears

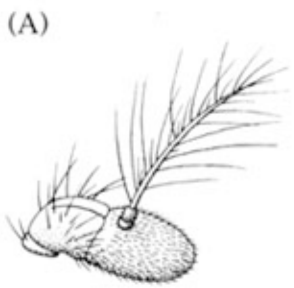
- Particle detectors
  - Near field, many insects, fish otoliths
- Pressure detectors
  - Far field, most vertebrates
- Pressure differential detectors
  - Near and far field, some insects

Particle detector



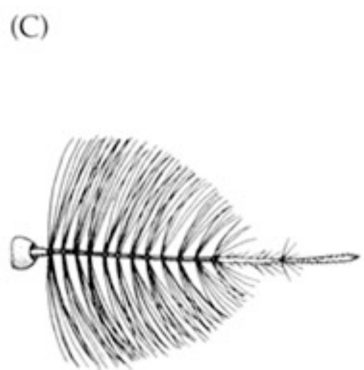
- Particle detectors are long, thin hairs
- Inherently directional
  - but amplitude confounded with direction
  - Solution: have multiple detectors with different orientation
- Found in
  - Insects: Trichoid sensilla
  - Spiders: Trichobothria
  - Aquatic arthopods

Insect particle detectors

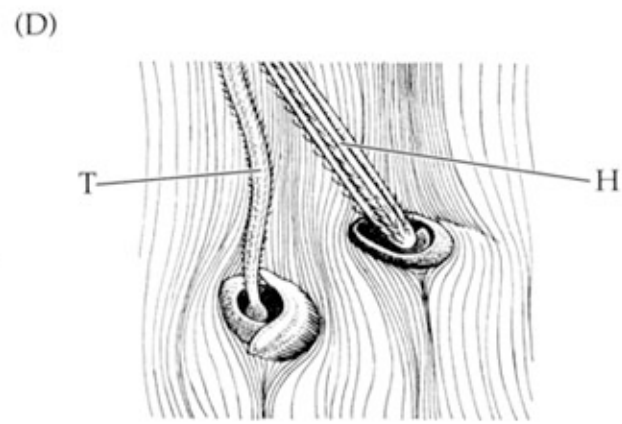


Fruit fly

Cockroach



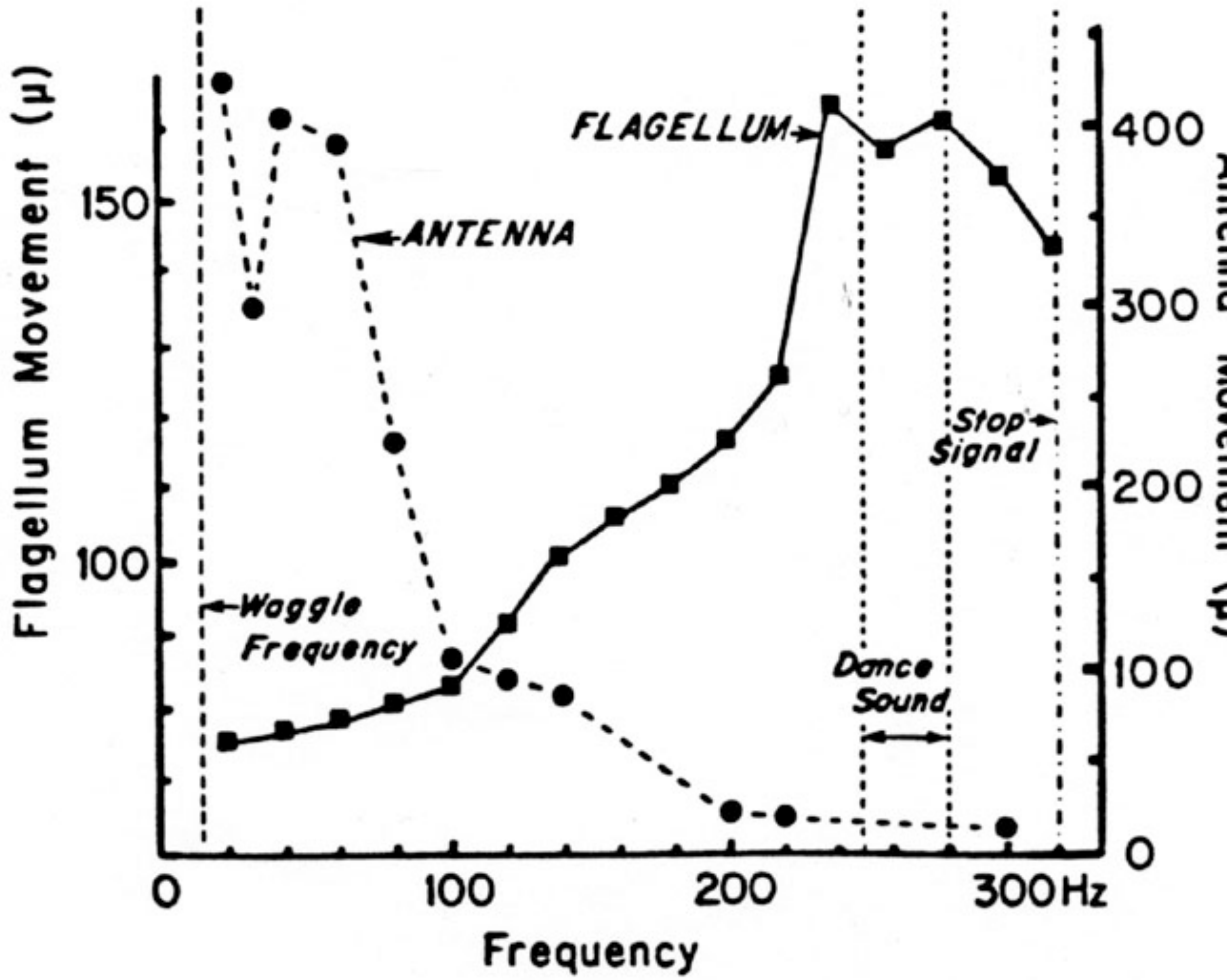
mosquito



spider

mosquito

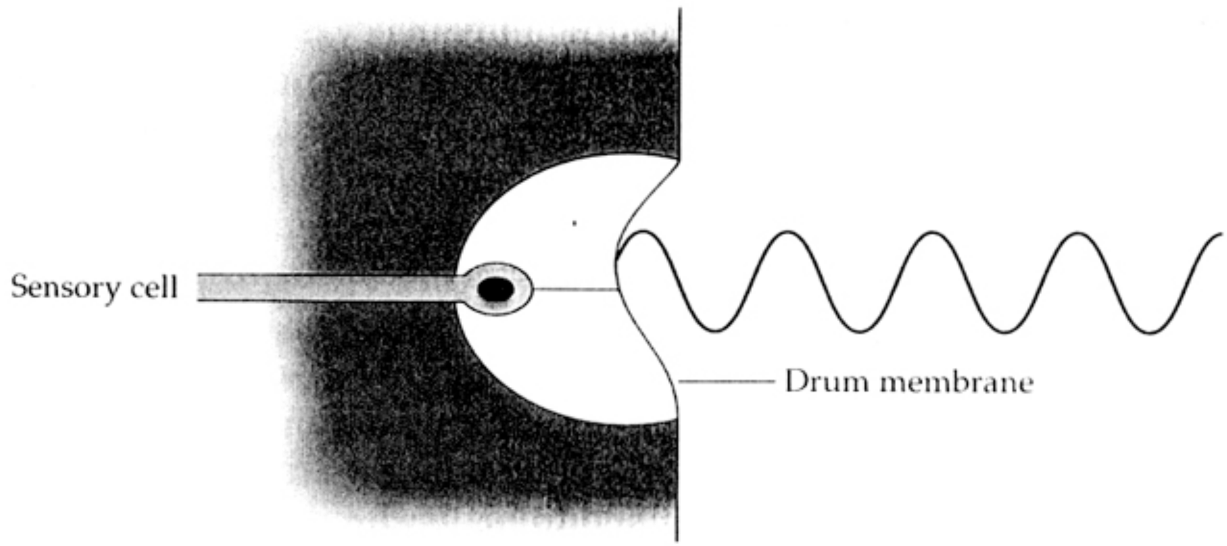
Bee antenna are tuned to the dance frequencies



Particle detector attributes

- Dynamic range is limited by mass and inertia, but with a long lever, can be very sensitive, e.g. mosquito threshold is 0 dB
- Can track slow, but not fast, waveforms. Typically, nerves phase-lock
- Limited to low frequencies (below 500 Hz) in near field
- Provide good directional information

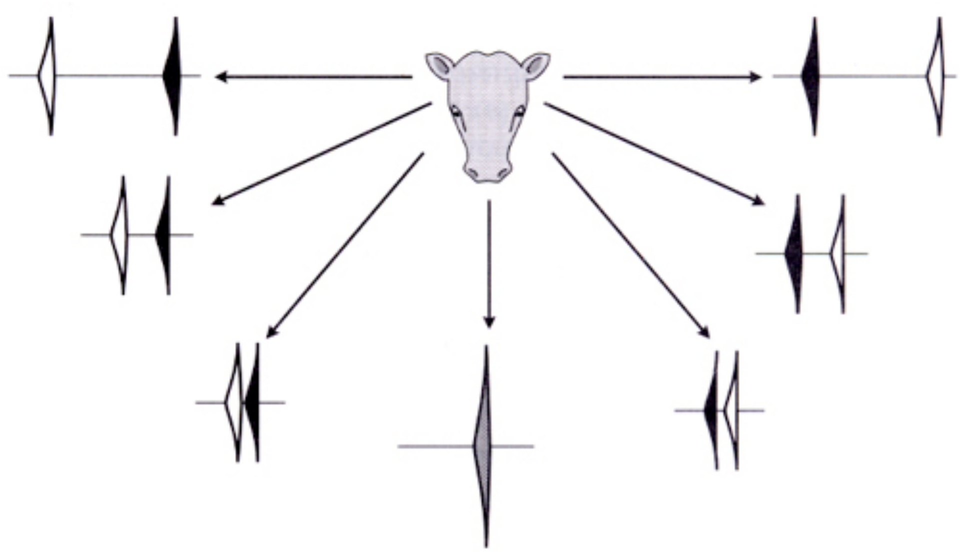
Pressure detector



- Membrane must be thin so that impedance is close to that of air
- Larger membranes can detect smaller pressure differences

Direction information

- Pressure detectors are nondirectional, need to add pinna and/or use two ears to measure
  - difference in time of arrival
  - difference in phase
  - diffractive fields around the head

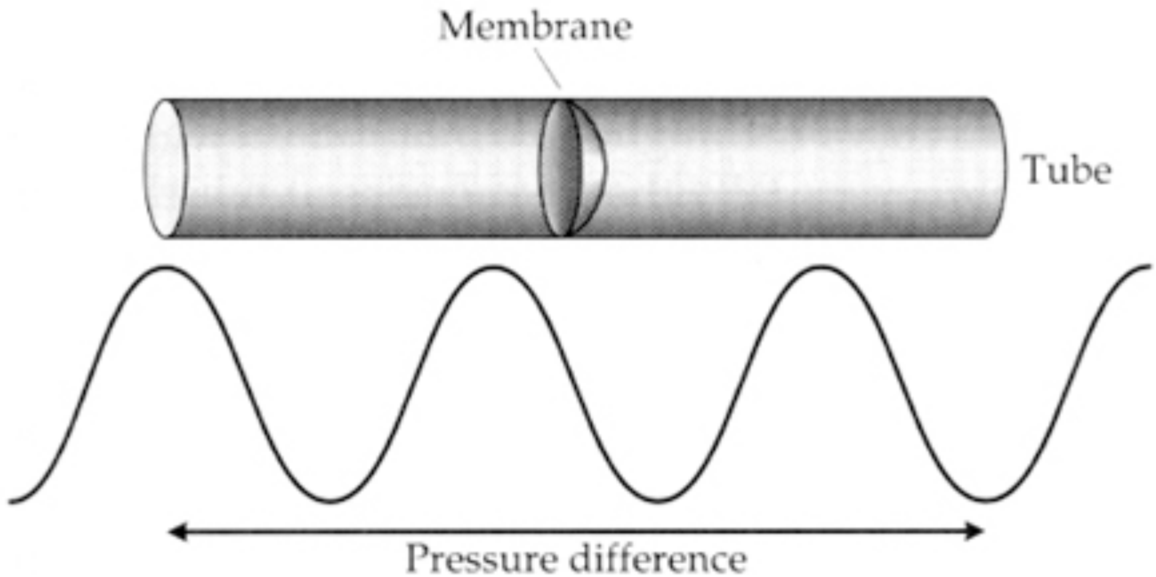


Direction detection depends on head size

- Interaural time delay is a function of head width
  - Human = 0.5 msec
  - Mouse (1 cm head width) = 0.03 msec
  - Smaller animals can't do this
  - Can be improved using neuronal delay lines (CECarr)
- Phase difference is maximum when wavelength = 2 x distance between the ears
  - Mouse could respond to 12-20 kHz
  - Humans could respond to 1 kHz
- Diffraction effect is greatest with wavelengths 2-5x head width

Pressure differential detector

$F = (2\pi AP\Delta L \cos\theta)/\lambda$ where
A = the surface area of the membrane
P = sound pressure
ΔL = the extra distance the pressure waves must travel
λ = the wavelength
θ = angle of sound incidence



Is force higher when sound wave travels parallel to tube or perpendicular?
Parallel (cos $\theta = 1$)

As wavelength of sound increases, what happens to force on membrane?
Becomes smaller

Pressure differential detectors are

- Good at high frequencies, poor at low frequencies, but low frequency can be improved by extending tube (legs)
- More sensitive than pressure detectors in near field, worse in far field
- More directional than pressure detectors

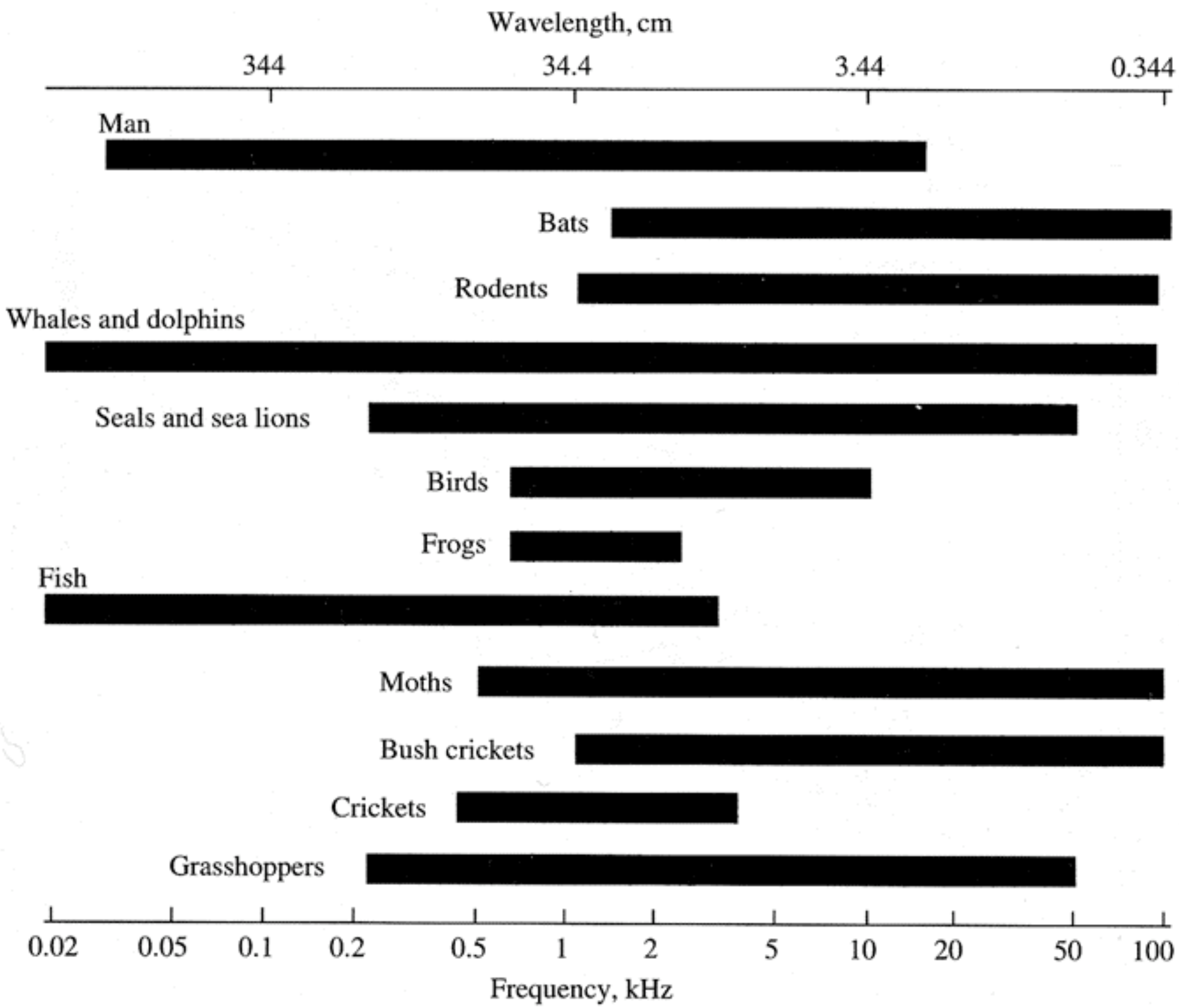
Amplitude extraction

- Signal intensity is encoded by sensory nerve firing rates
- Dynamic range is increased by having nerves with different minimum threshold sensitivities
- Creates logarithmic scale
- Insect ear cells have 20-30 dB range
- Vertebrate cells have 40-50 dB range

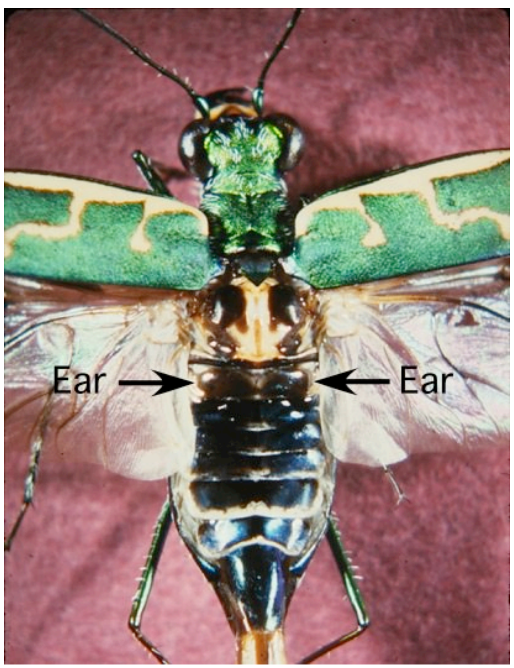
Frequency extraction

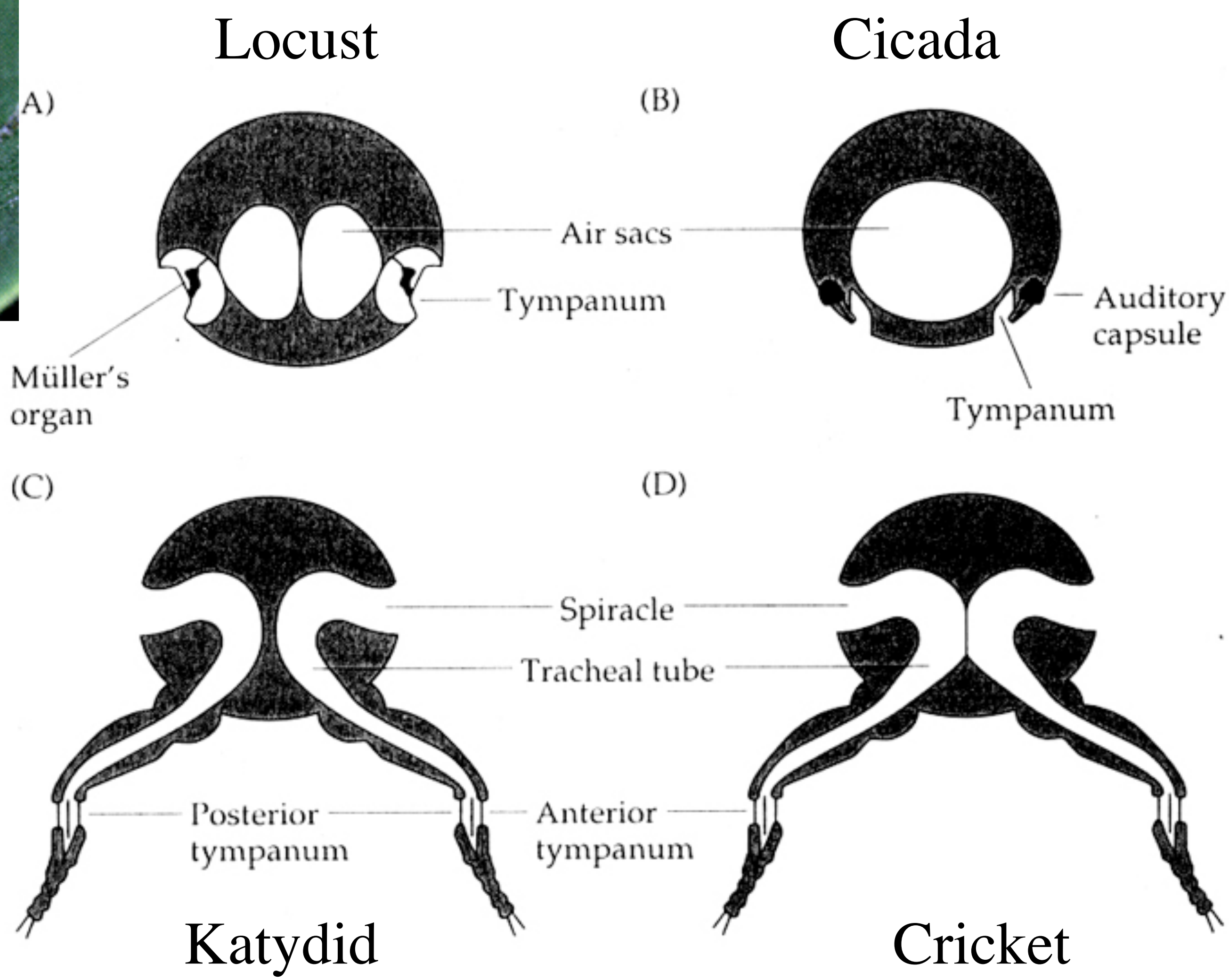
- Particle detectors limited by phase-locking
- Pressure detectors use frequency maps
  - By connecting hairs cells to a tuned tympanum (locusts and mole crickets)
  - By connecting hair cells in a separate auditory organ (e.g. cochlea) to separate detection from frequency extraction (cicadas, katydids, crickets, vertebrates)

Comparative hearing ranges

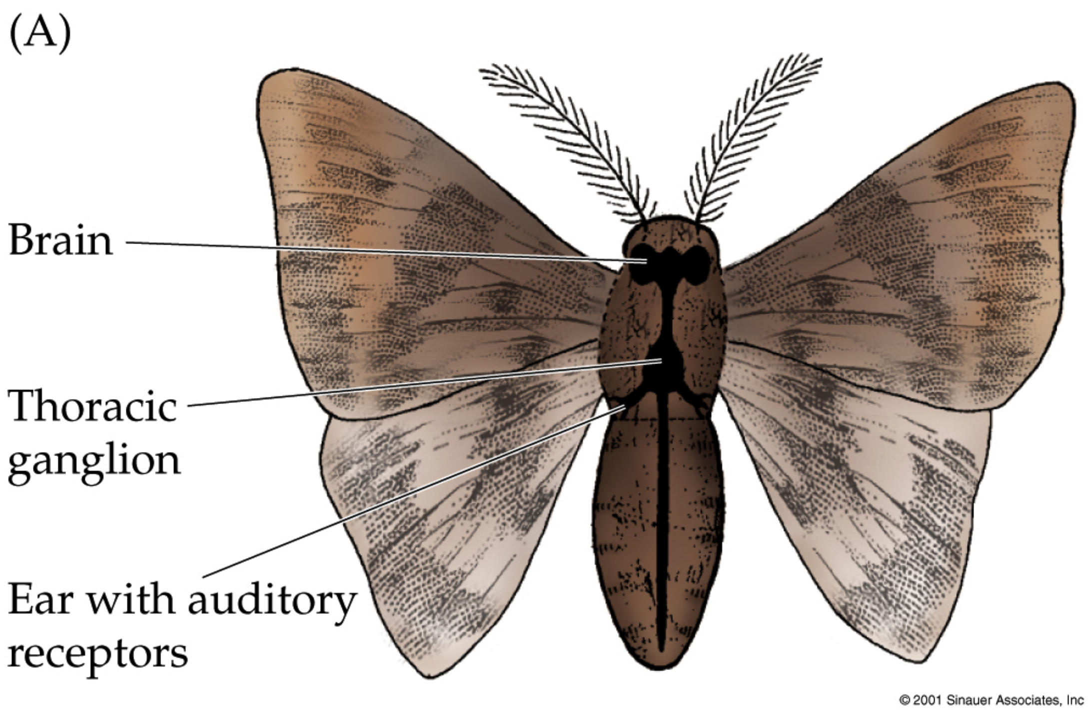


Pressure sensitive insect ears





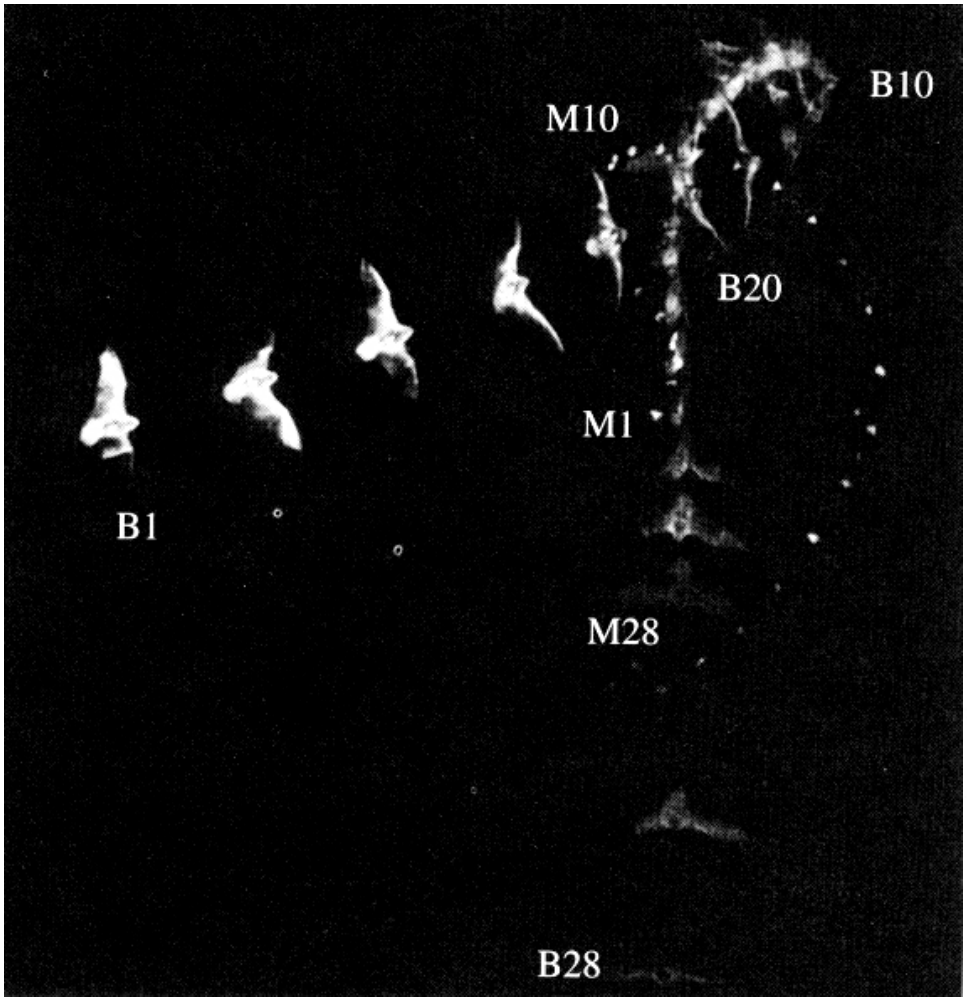
Insects with ultrasonic hearing



Noctuid moth

- Moths
  - Occurs in 7 superfamilies
- Beetles
  - Tiger beetles, scarab beetles
- Lacewings
- Preying mantis
- Locusts, crickets and katydids
  - Use for mate attraction
- Parasitoid diptera
  - Use it to find hosts

Moth evasive behavior



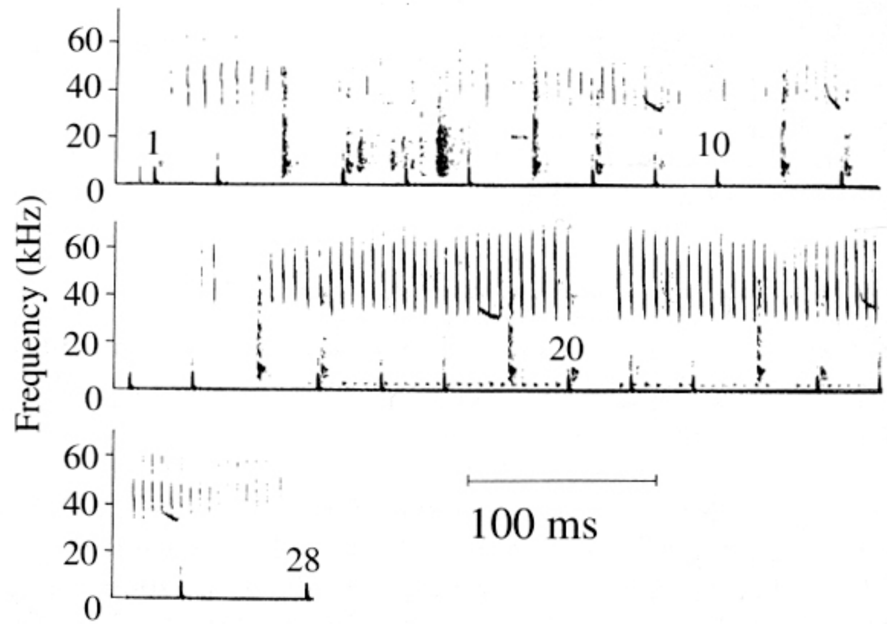


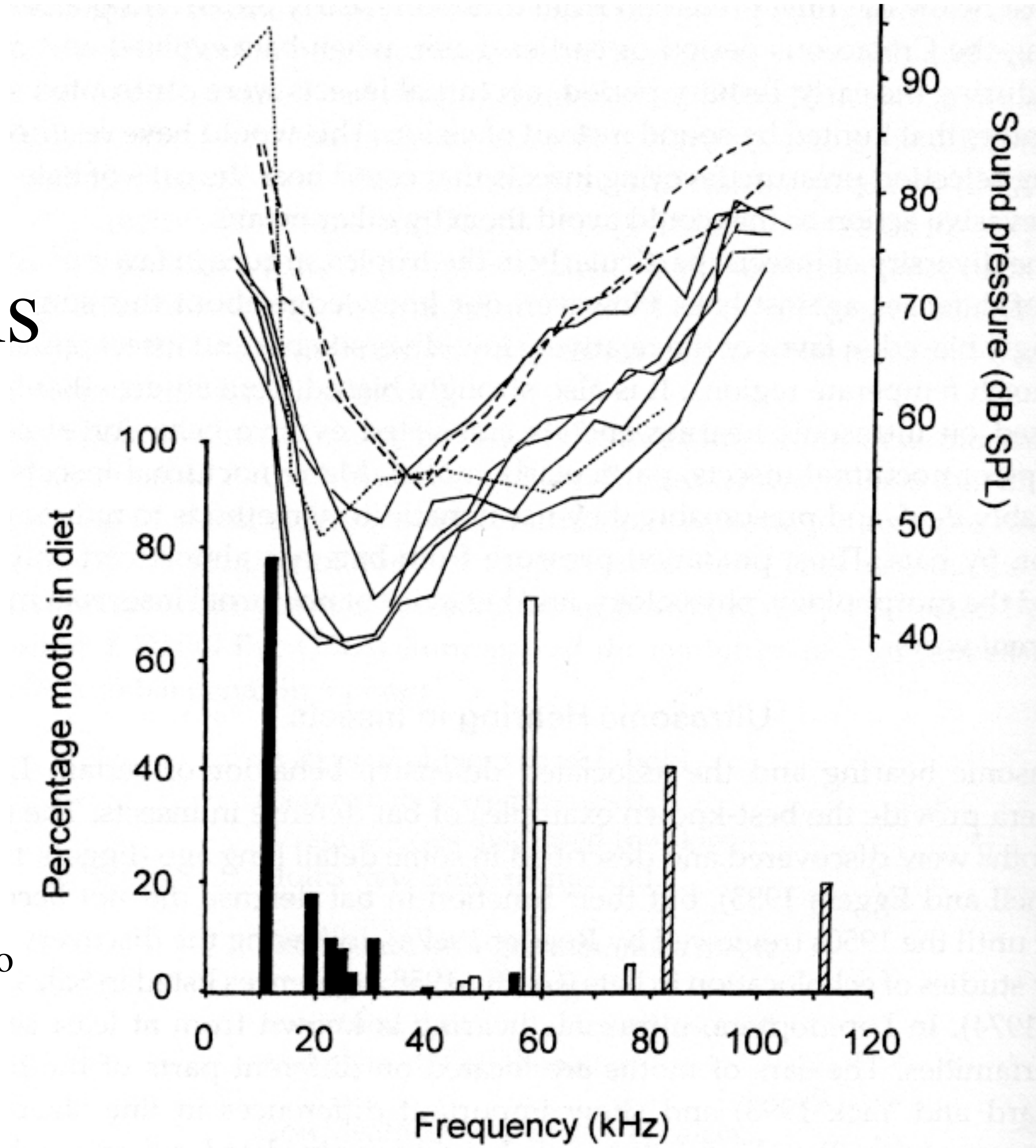
Figure 7.8. Photo of evasive response of a moth pursued by a red bat *Lasiurus borealis* in the field. The bat flies toward the moth, overshoots it, and by *B10* loops back toward the moth. At about *M12* (not shown in figure), the moth enters a power dive, and although it heads toward the bat's descending flight path, the bat again overshoots it and fails to capture the moth. Throughout the pursuit, the bat emits a prolonged terminal buzz (sonogram) in an attempt to track the moth. Images of the bat (*B*) and moth (*M*) are labeled chronologically, so the bat was at *B10* when the moth was at *M10*, 333 ms into the sequence. Flash rate was 30 Hz. The low frequency clicks on the sonogram are flash synchronization pulses. The search phase echolocation calls of a second bat can sometimes be seen in the background on the sonogram.

Moth audiograms

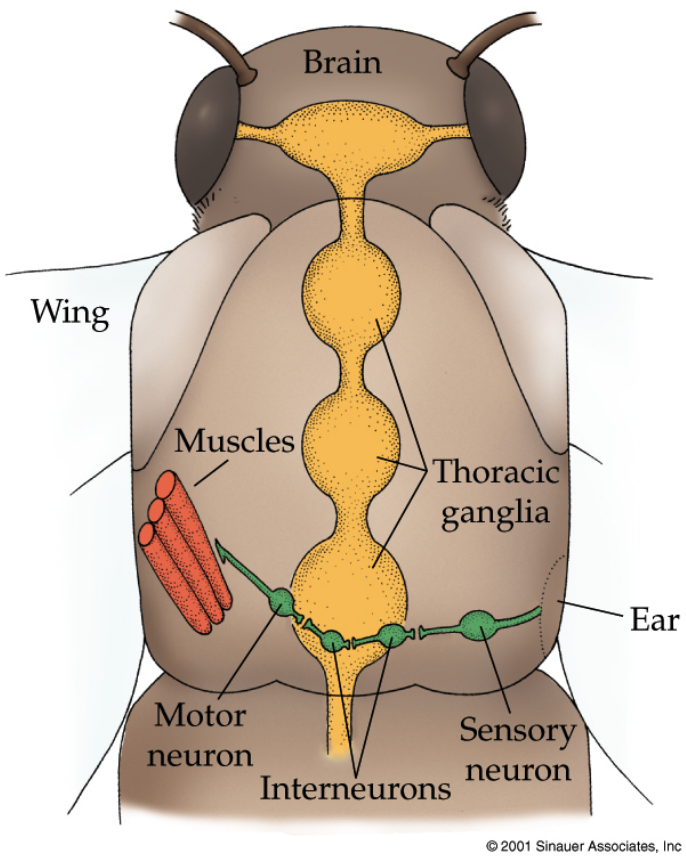
Best frequency of hearing by moths extends from 20-50 kHz

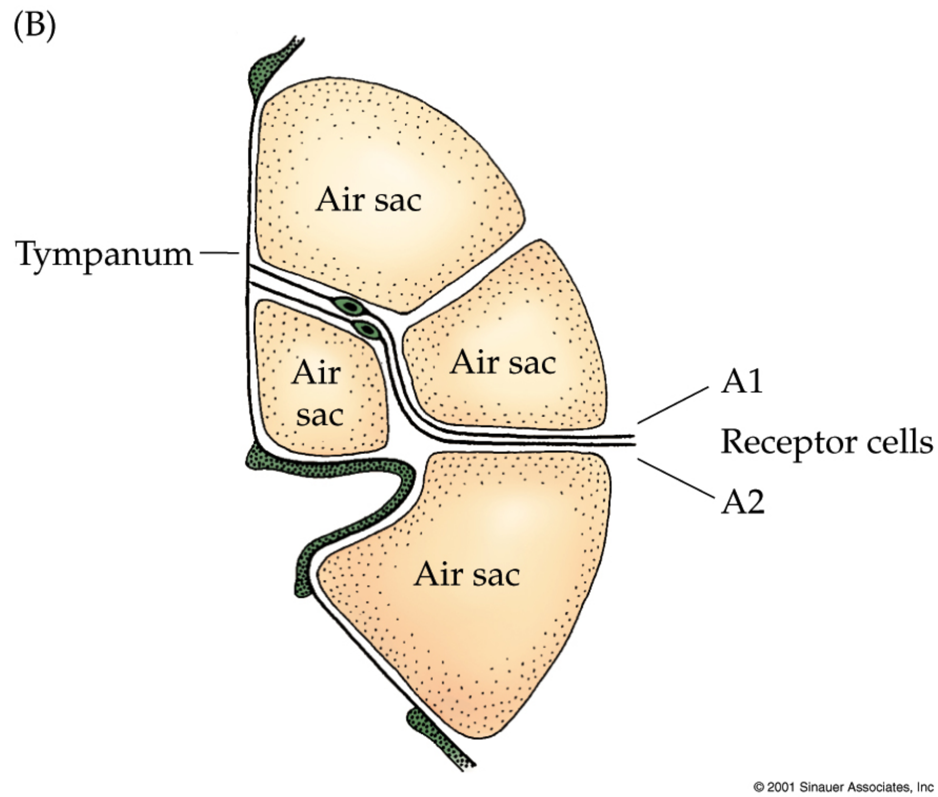
Moths are primary component of diet in bats that use calls below 20 or above 50 kHz.

High frequencies in some bats may be an adaptation to avoid detection by moths.



Noctuid moth ears





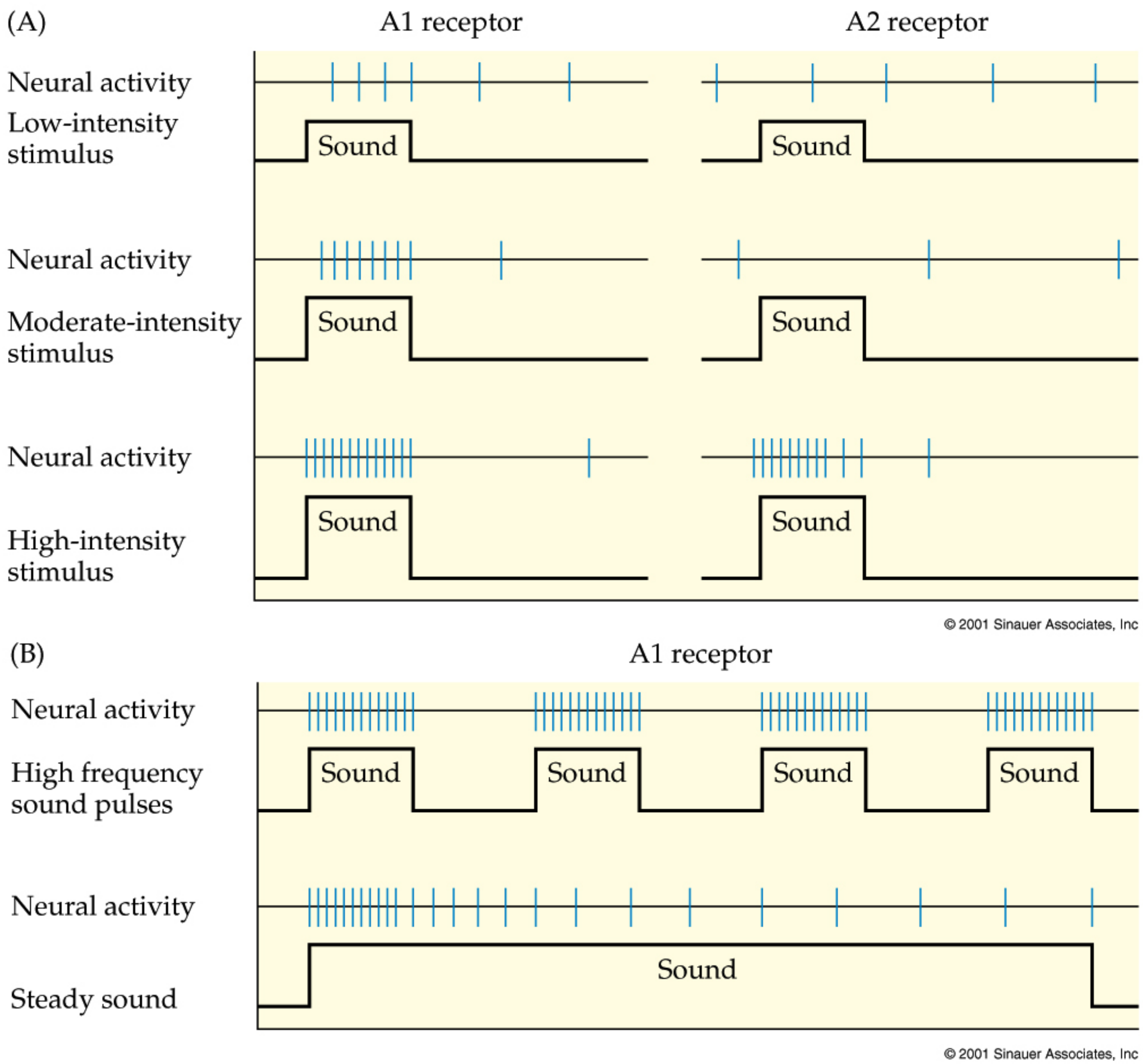
Muscle response is hard-wired.

Responses of A1, A2 receptors

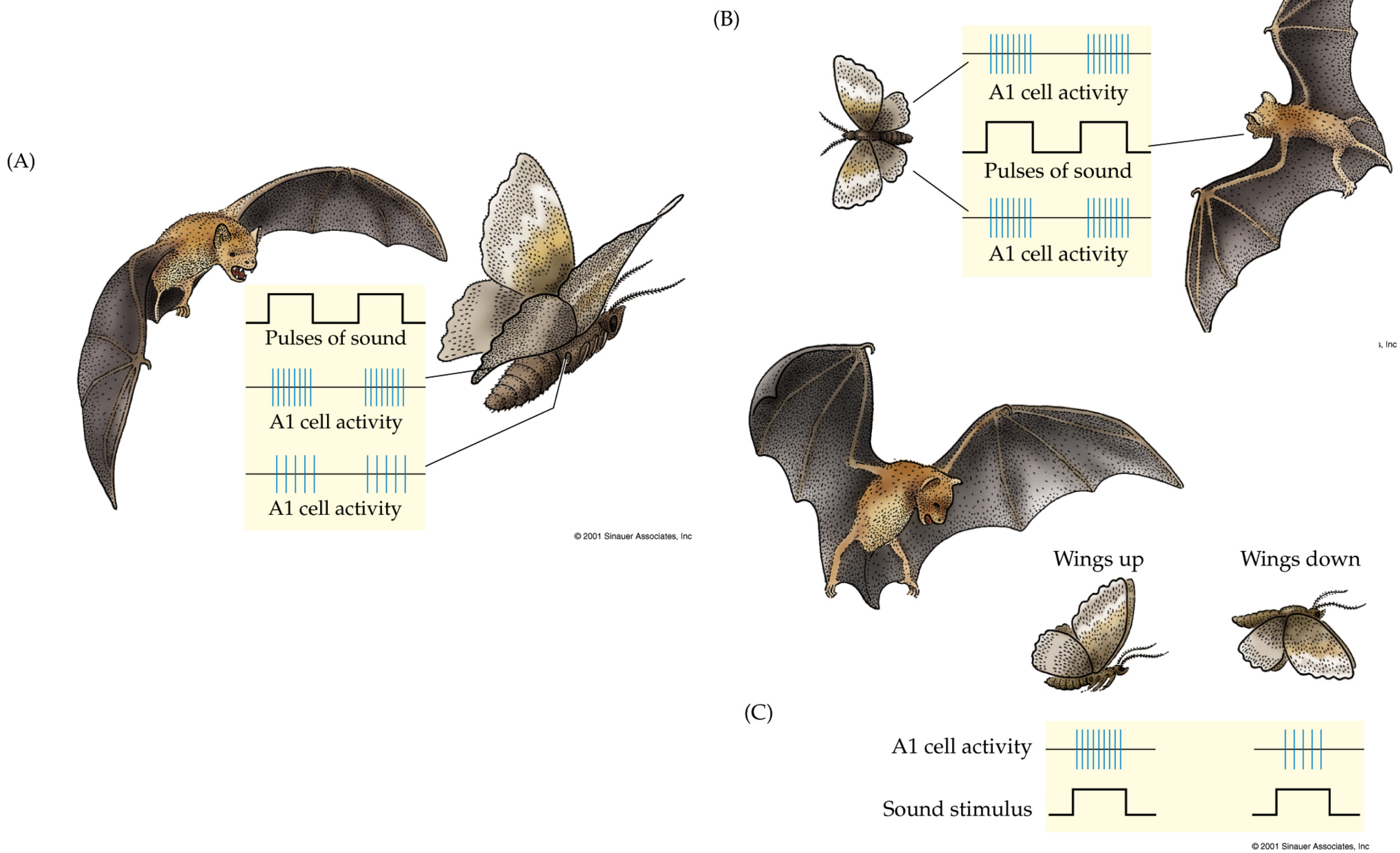
A1 receptor exhibits response to low intensity sounds. Causes moth to veer away from sound. Can detect little brown bat at 30 m. Pulse rate increases with amplitude.

A2 receptor only fires to loud sound. Causes moth to go into powerdive.

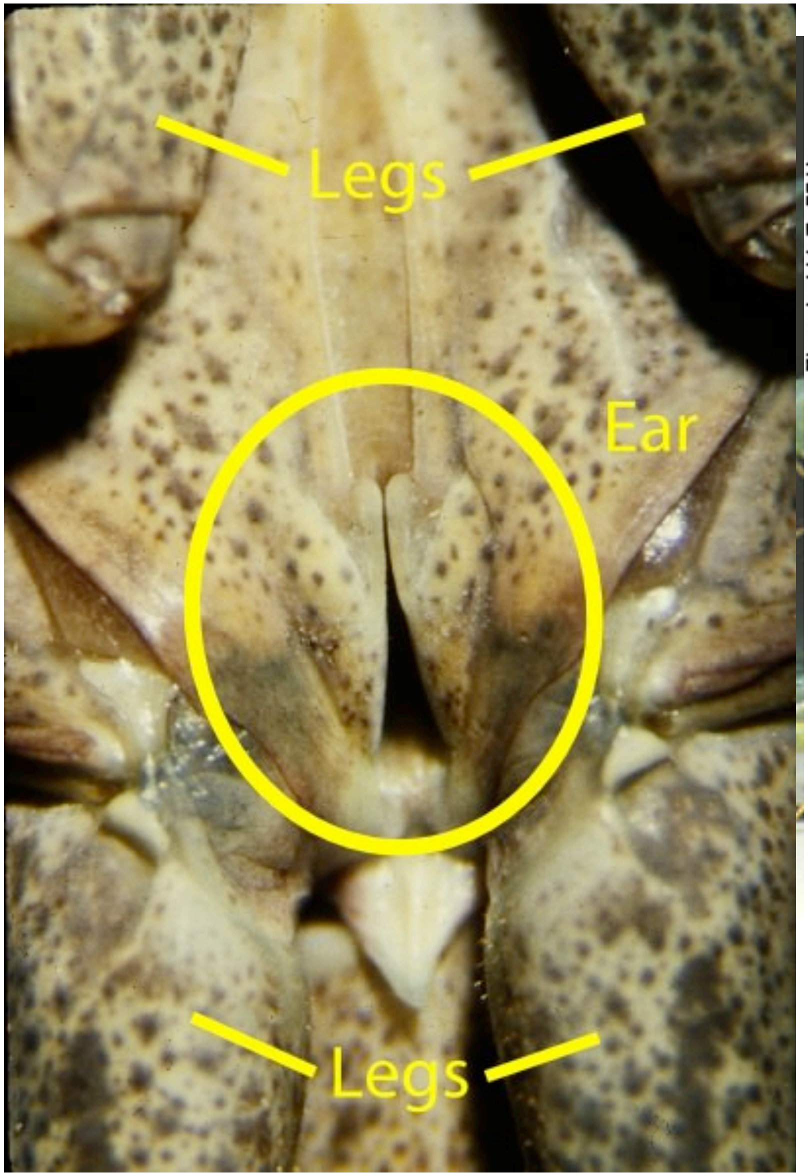
A1 receptor habituates to constant sound

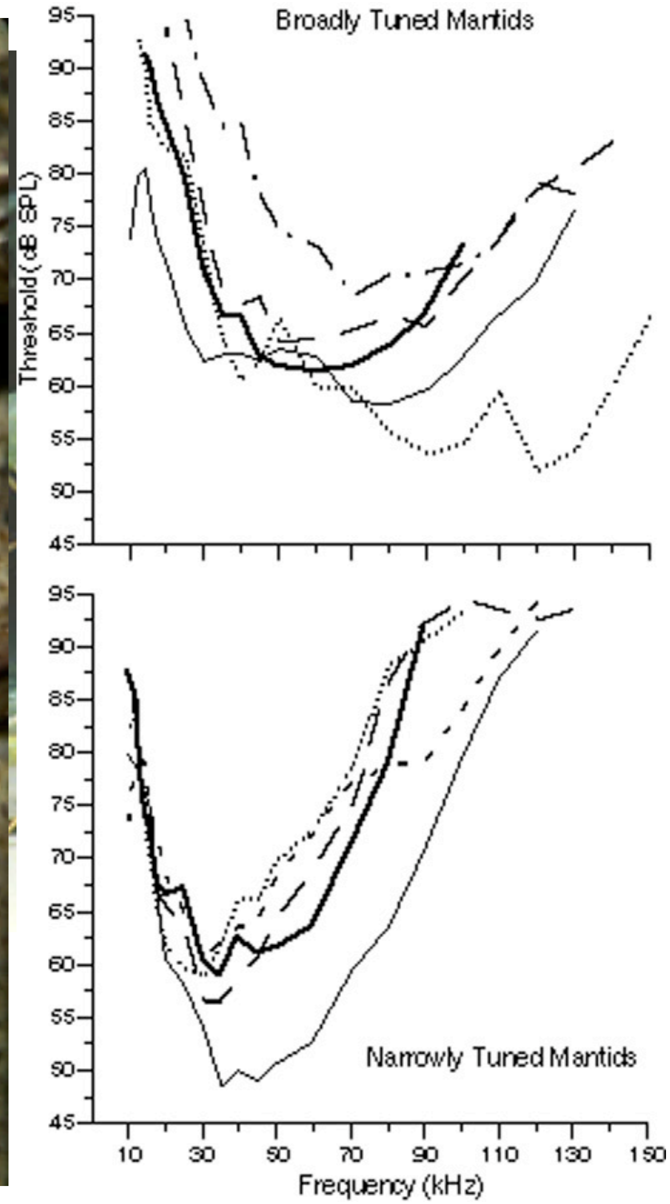


A1 response asymmetry indicates predator direction

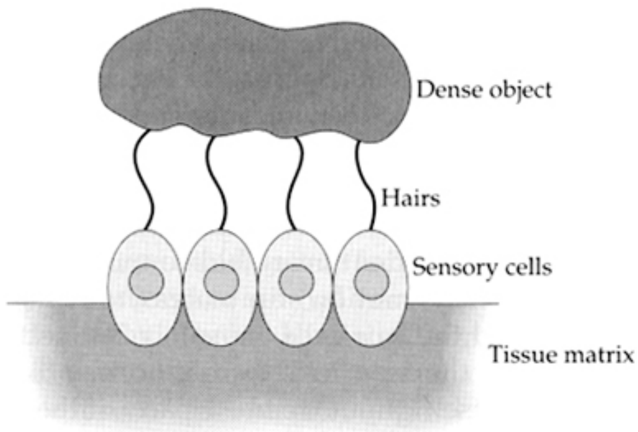


Flying mantids hear ultrasound





Fish hearing



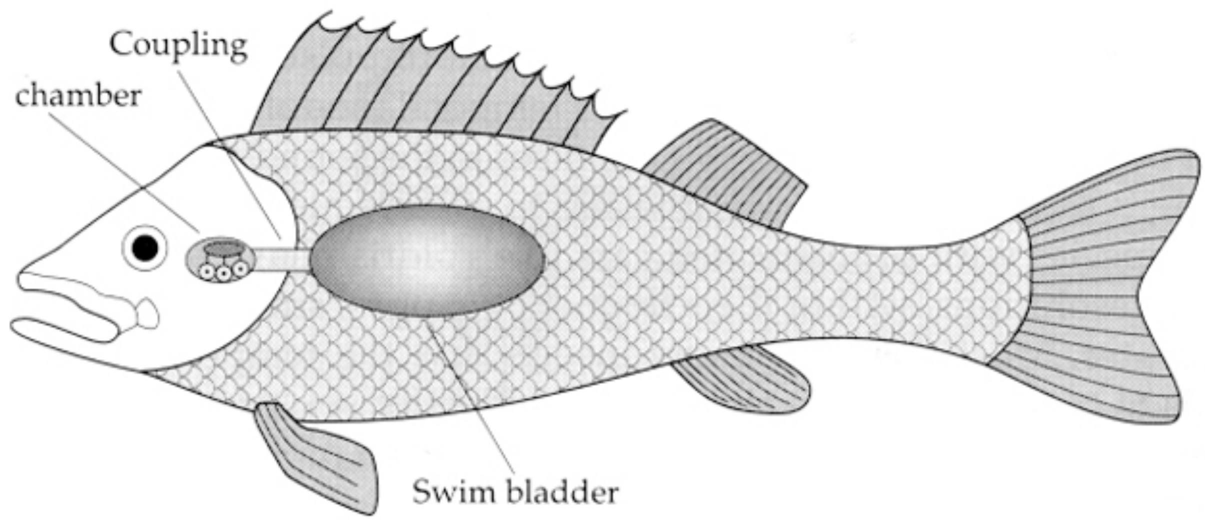
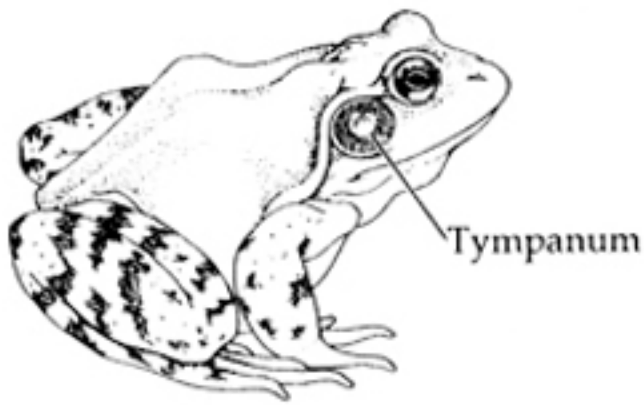


Figure 6.10 Far field sound detection by fish. The swim bladder traps pressure variations in the sound field and converts these to movements of its wall. These movements are coupled to the ear chambers by surrounding tissues, by extensions of the air bladder, and/or by small bones.

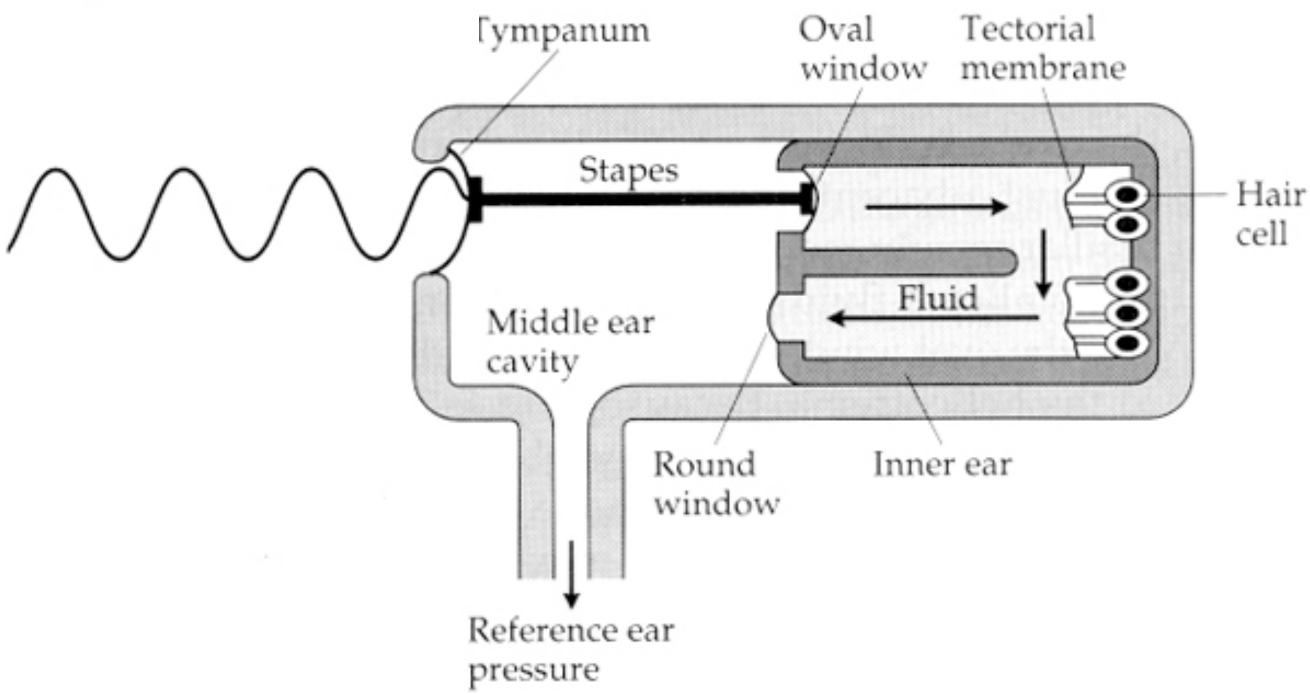
- Particle motion causes movements of otoliths in the ear chamber, which detect low frequency sounds
- Swim bladder acts as a pressure detector and can detect high frequency sound

Pressure detector: amphibian ear

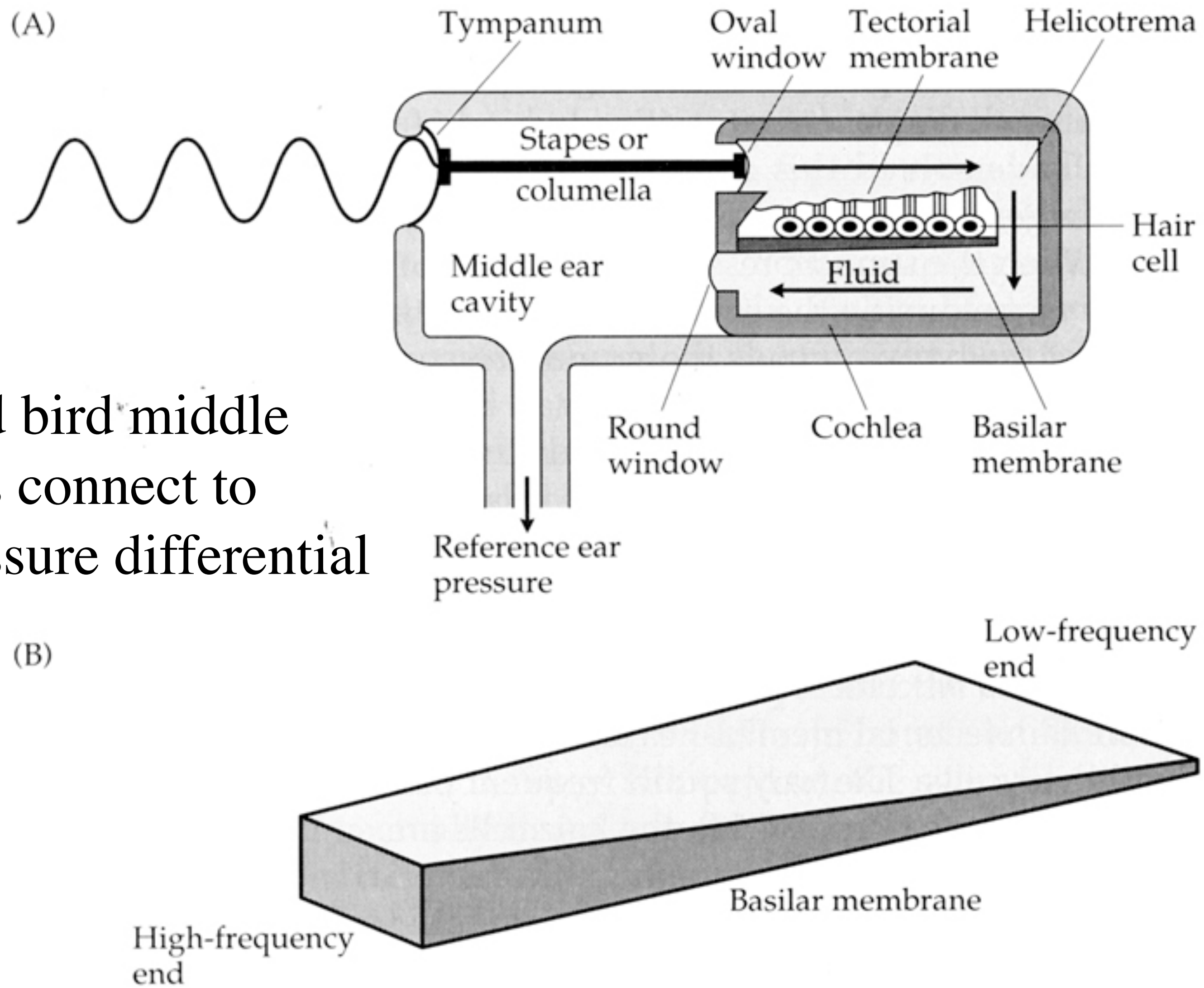


Because tissue has higher impedance than air, must have mechanism to detect pressure changes by sensory cells

Frequency is extracted by selective vibration of the tectorial membrane

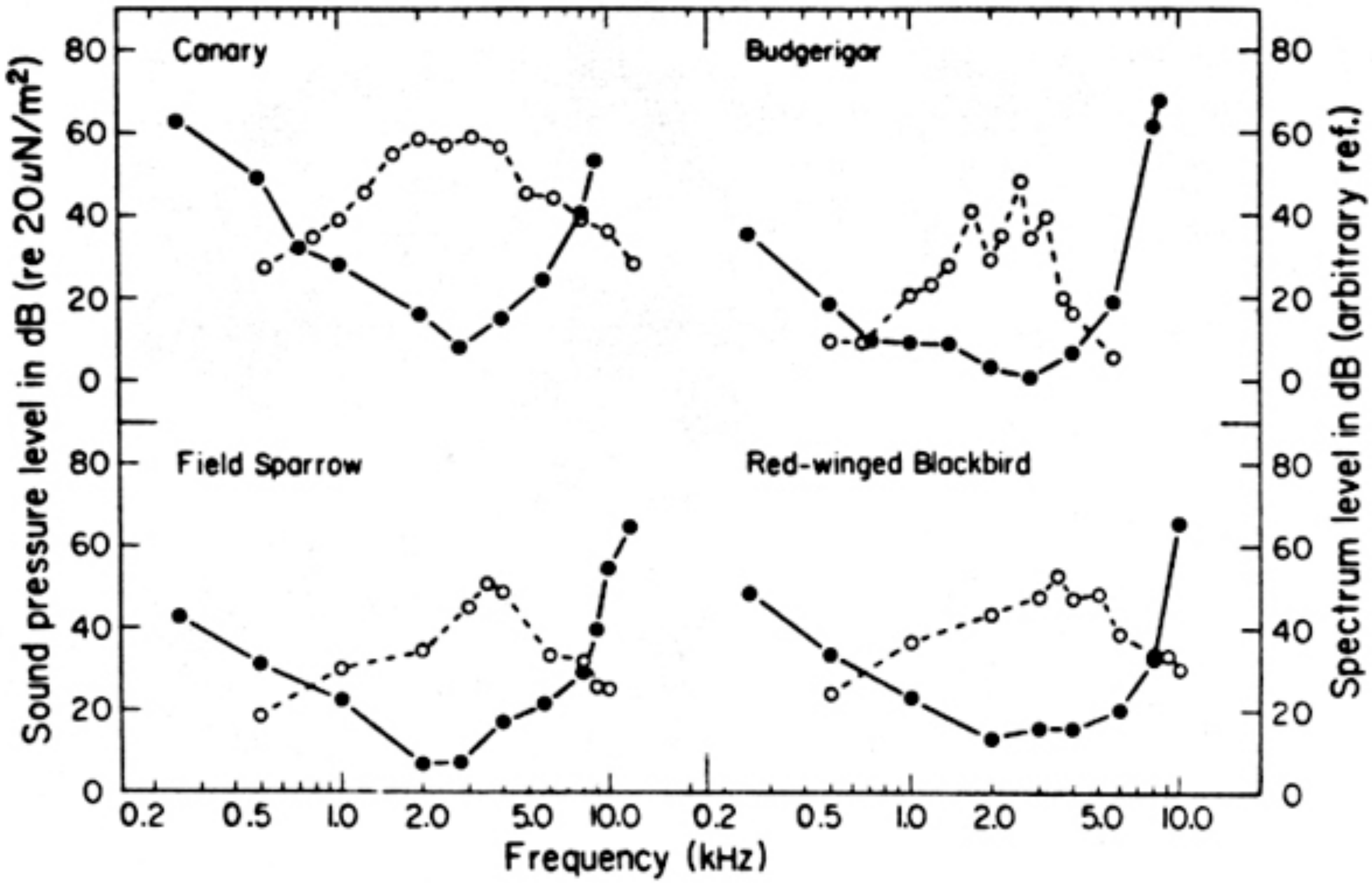


Pressure detector: reptile, bird or mammal ear



Reptile and bird middle ear cavities connect to permit pressure differential detection

Bird hearing

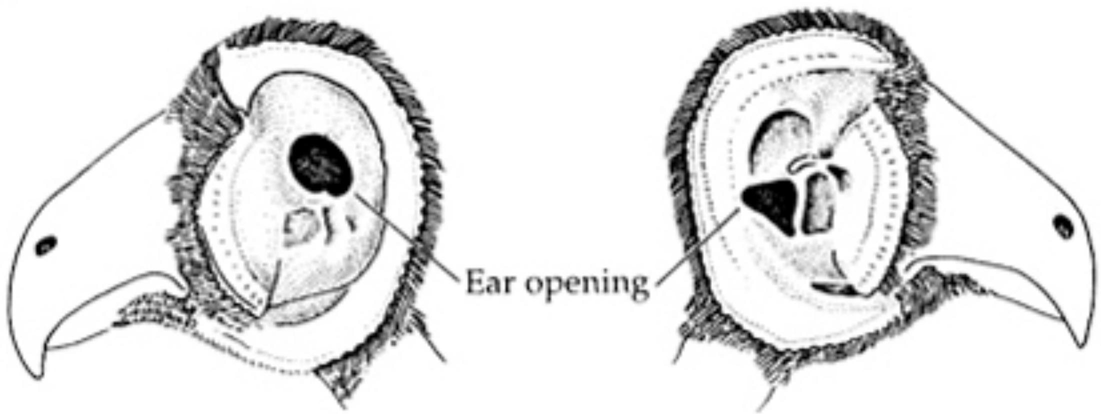


Frequency resolution: 1-2%

Temporal resolution (jitter detection): 1.2 msec

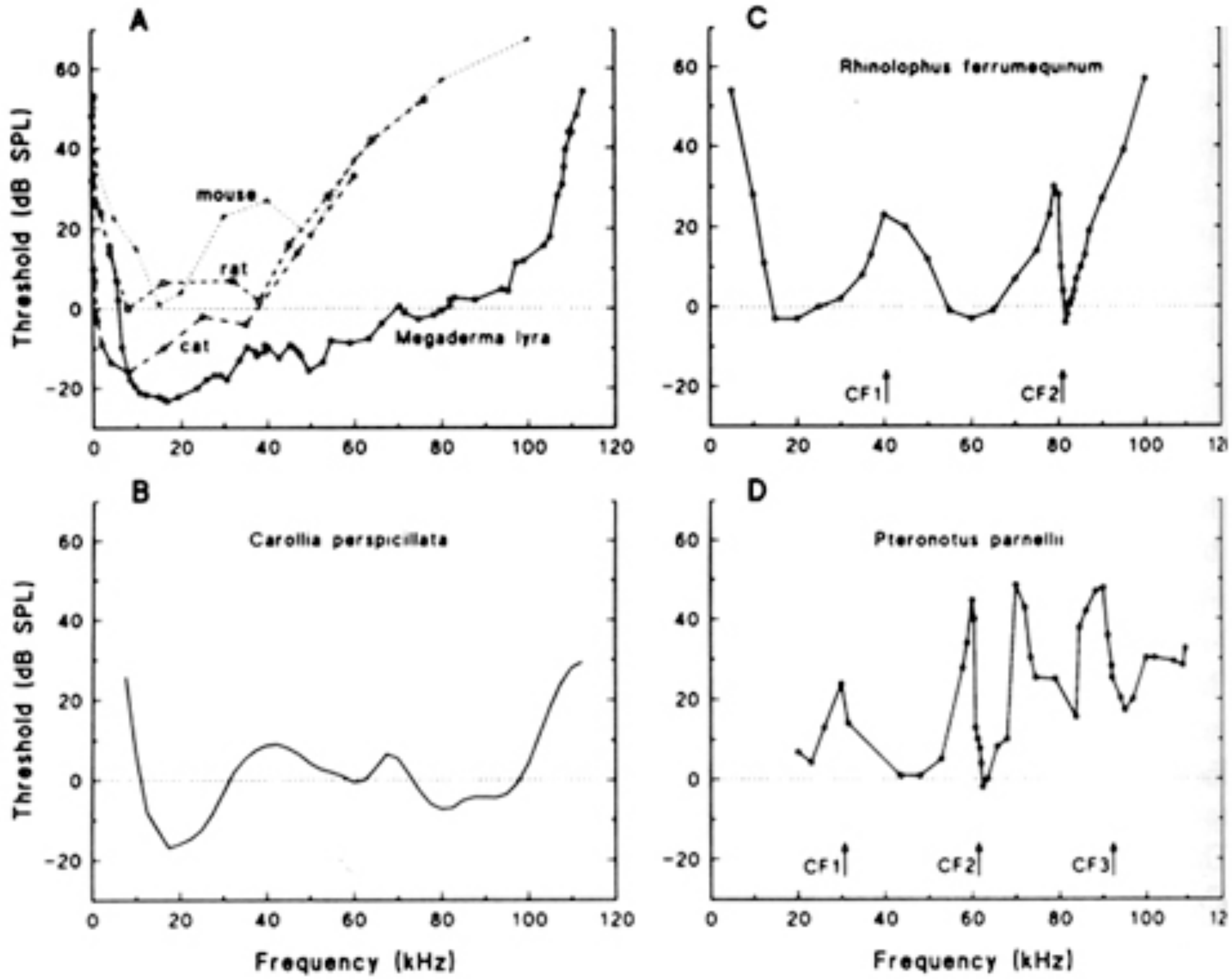
Bird ear asymmetry

Facial discs of owls act as a parabola and amplify sound by reflection



Asymmetric placement provides information on vertical direction

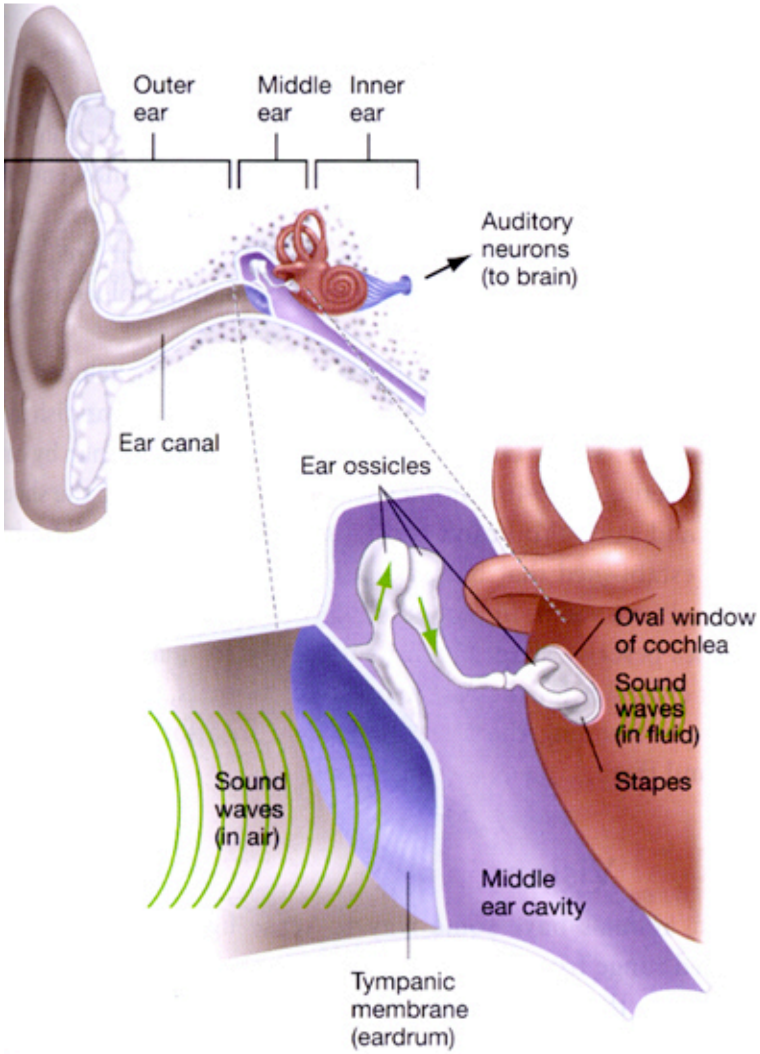
Mammal hearing

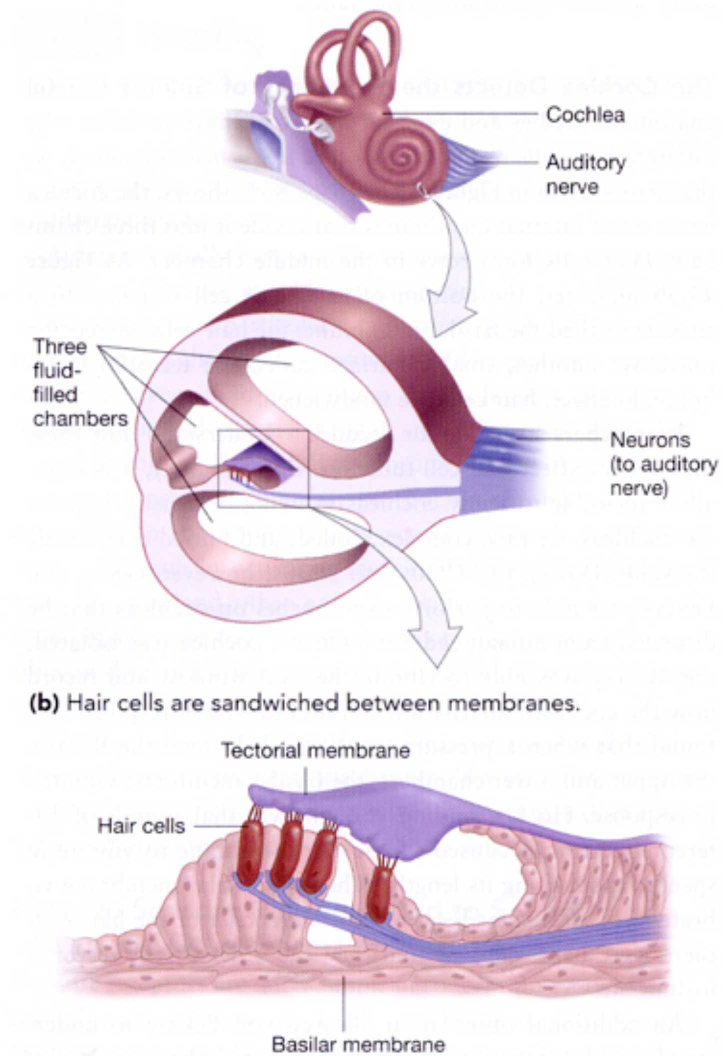


Frequency resolution: 0.2%

Temporal resolution (jitter detection): 5.9 msec

Mammalian ear

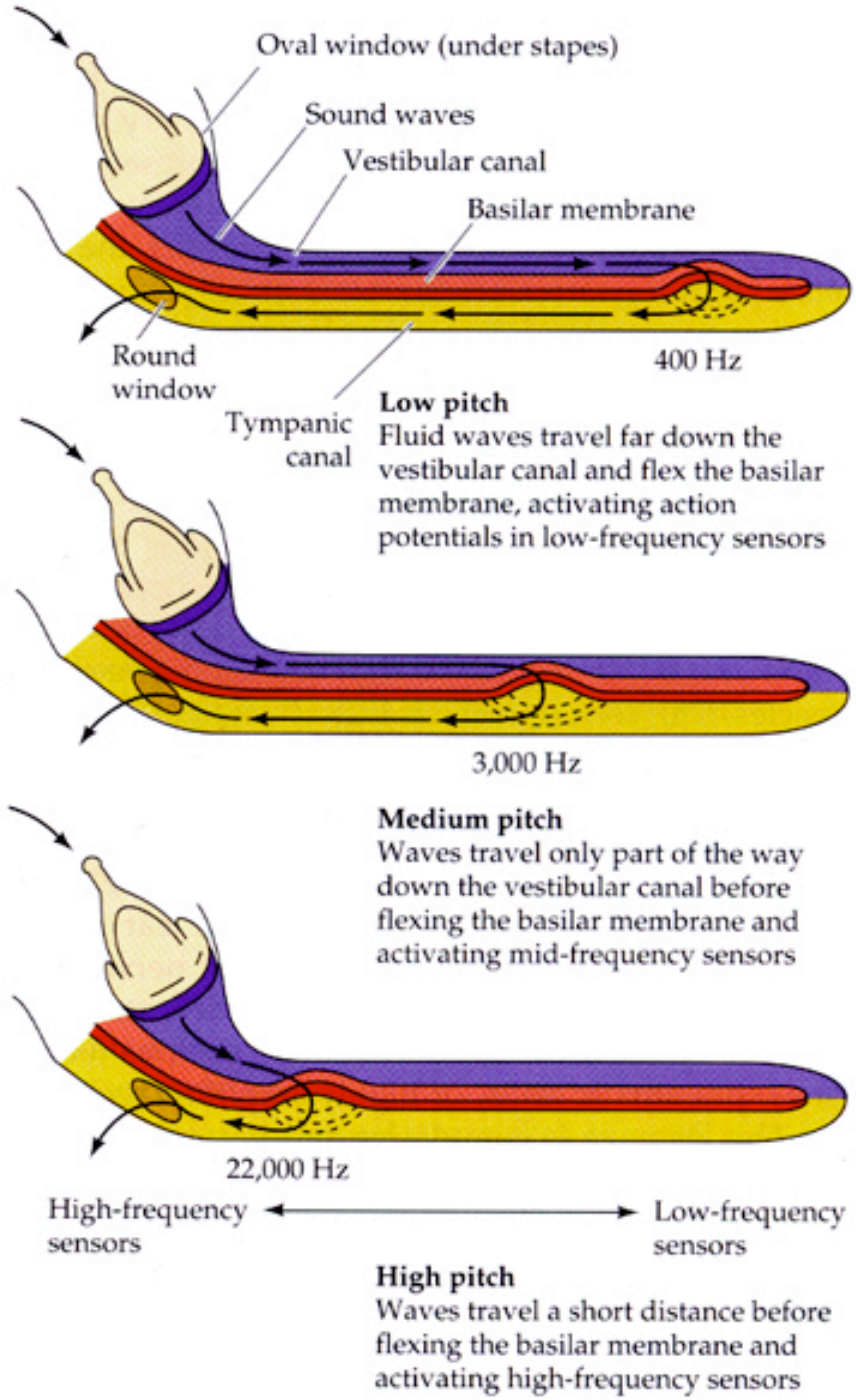




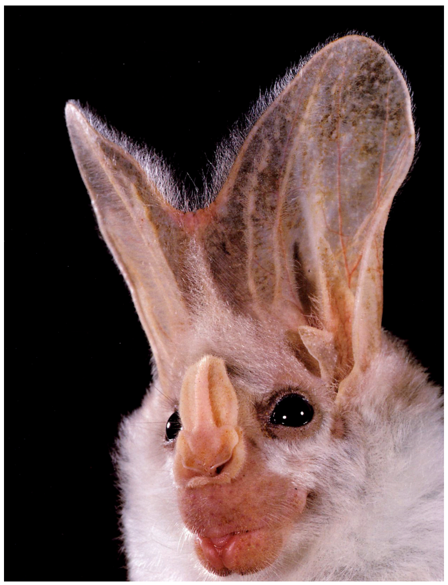
Middle ear amplifes sound 20x because tympanum >> oval window

Cochlear frequency tuning

Evolved from amphibian basilar papilla. Mammal cochlea is 2-3x longer than birds.

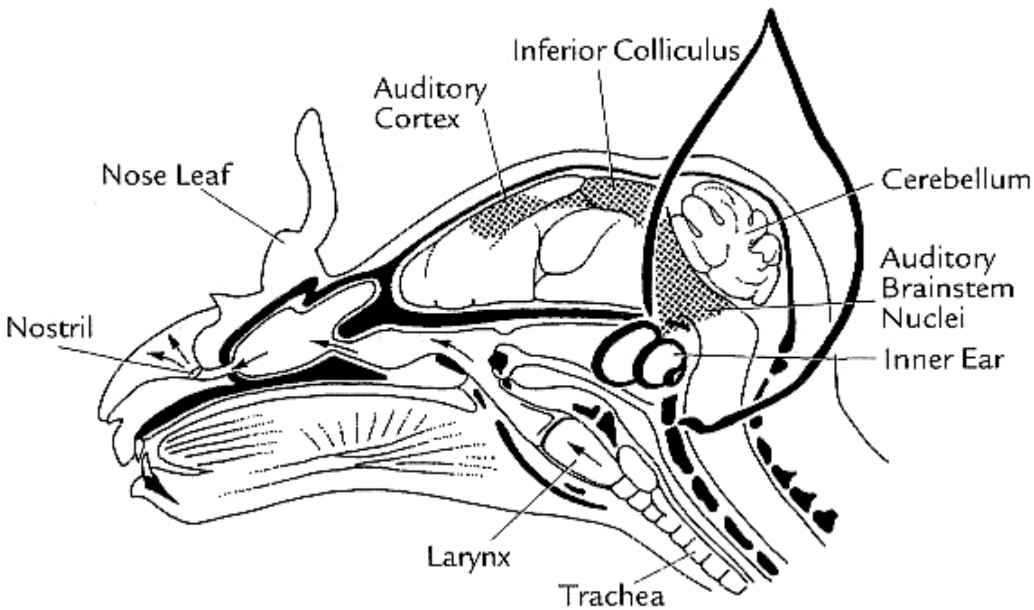


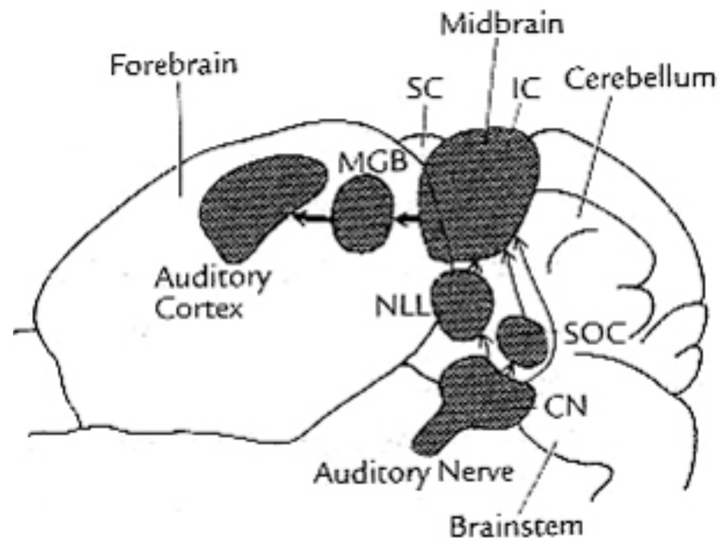
Pinnae amplify and filter frequencies



Pinnae can amplify some frequencies up to 30 dB.
High frequency sensitivity allows directional hearing using interaural intensity and frequency differences.

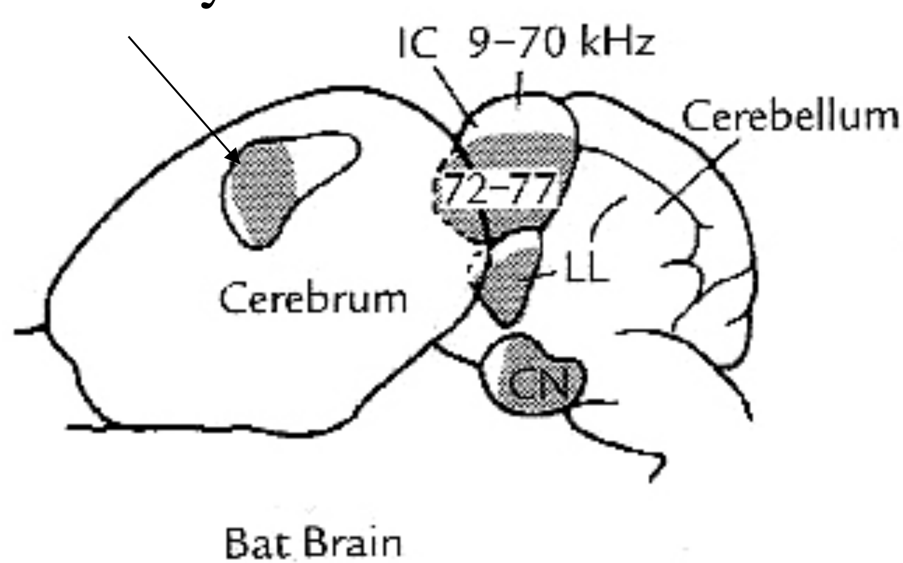
The auditory pathway

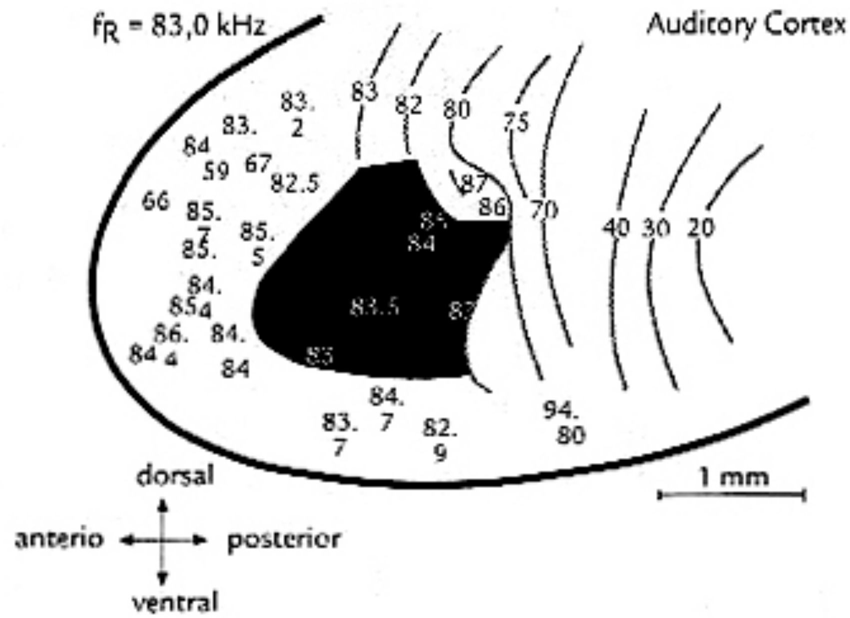




Tonotopic maps in the auditory system

Auditory cortex





Gray areas correspond to call frequencies

Auditory cortex is expanded at frequencies associated with echolocation