Introduction to Neuroscience: Behavioral Neuroscience

Echolocation in Bats

Nachum Ulanovsky

Department of Neurobiology, Weizmann Institute of Science

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Bats comprise ~20% of mammals and are versatile foragers

Photo: Merlin Tuttle

~1,100 species of bats in total (~ 850 species of echolocating bats)

Much of the bats' success is due to echolocation (biosonar)

Most bats use Echolocation – which also shaped their ears, noses… and names

Big brown bat
Eptesicus fuscus

Grey long-eared bat
Plecotus austriacus

Greater horseshoe bat
Rhinolophus ferrumequinum

Examples of bats hunting using echolocation

Movie: bat catching moth

Movie: bat catching spider

(movies slowed down considerably)

The bat's sonar system in numbers

- Frequency range: ~ 5 kHz – 200 kHz
  (depends on species)

- Frequency resolution: 0.1 %

- Temporal resolution: 400 ns, and possibly even
  10 ns (resolution of target range in bats)

Good frequency resolution *and* good temporal resolution → the auditory system is *not* a simple Fourier analyzer

- Directional (azimuthal) accuracy as good as 1-2°
  (compared to 10-15° in passive hearing by bats
  and rodents of similar size)

- Dynamic range (for echo sound intensity): 135 dB

The bat's sonar system in numbers (Cont.)

- Dynamic range (for echo sound intensity): <u>135 dB</u>

  Bats can detect echoes from ~ 0 dB SPL (20 μPa) up to perfectly-reflected echoes of their own calls, which have an emitted power of 135 dB SPL
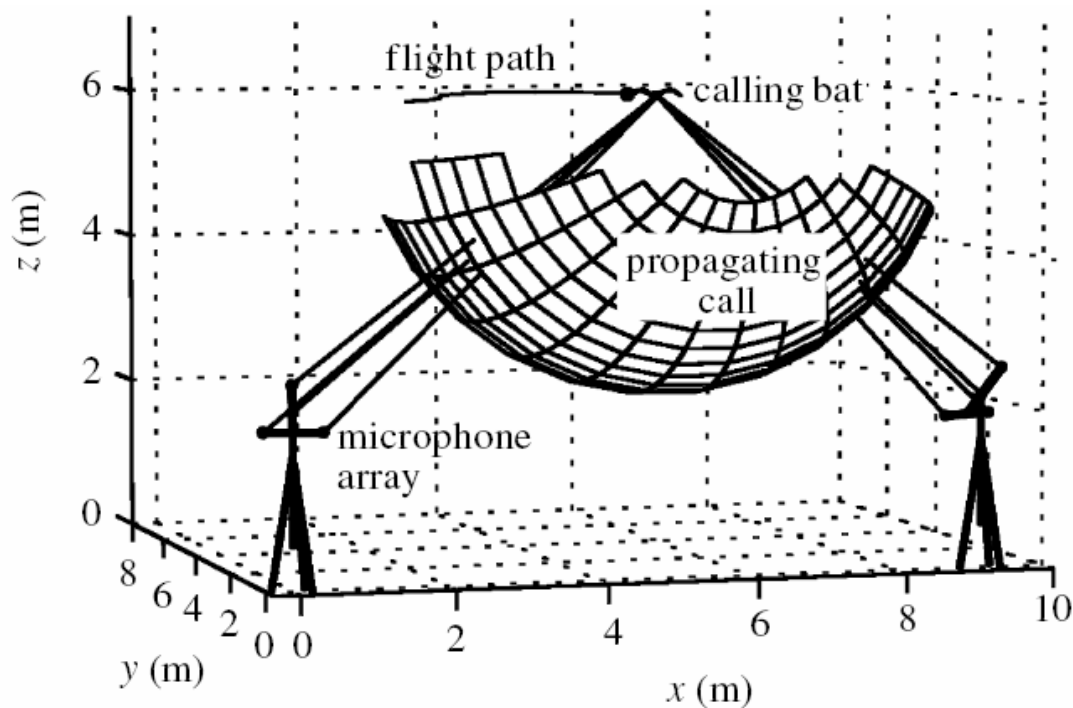

To actually measure the emitted power in free-flying bats, researchers have to reconstruct the bat's 3-D position: for this, they use arrays of microphones → Differential Time Of Arrival (DTOA) localization technique in 3-D (similar to the way GPS works).

The bat's sonar system in numbers (Cont.)

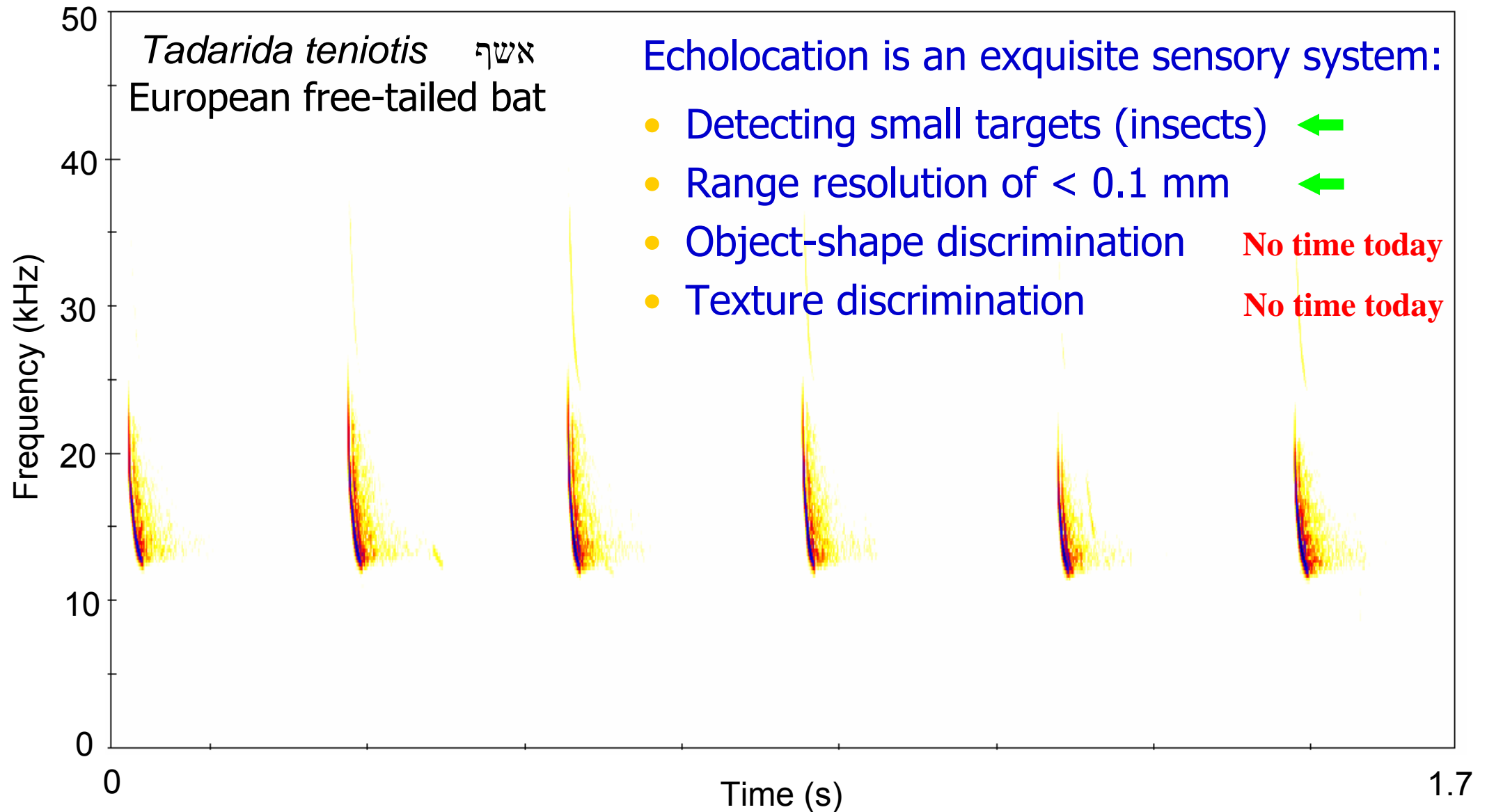- Dynamic range (for echo sound intensity): <u>135 dB</u>

Bats can detect echoes from ~ 0 dB SPL (20 µPa) up to perfectly-reflected echoes of their own calls, which have an emitted power of 135 dB SPL
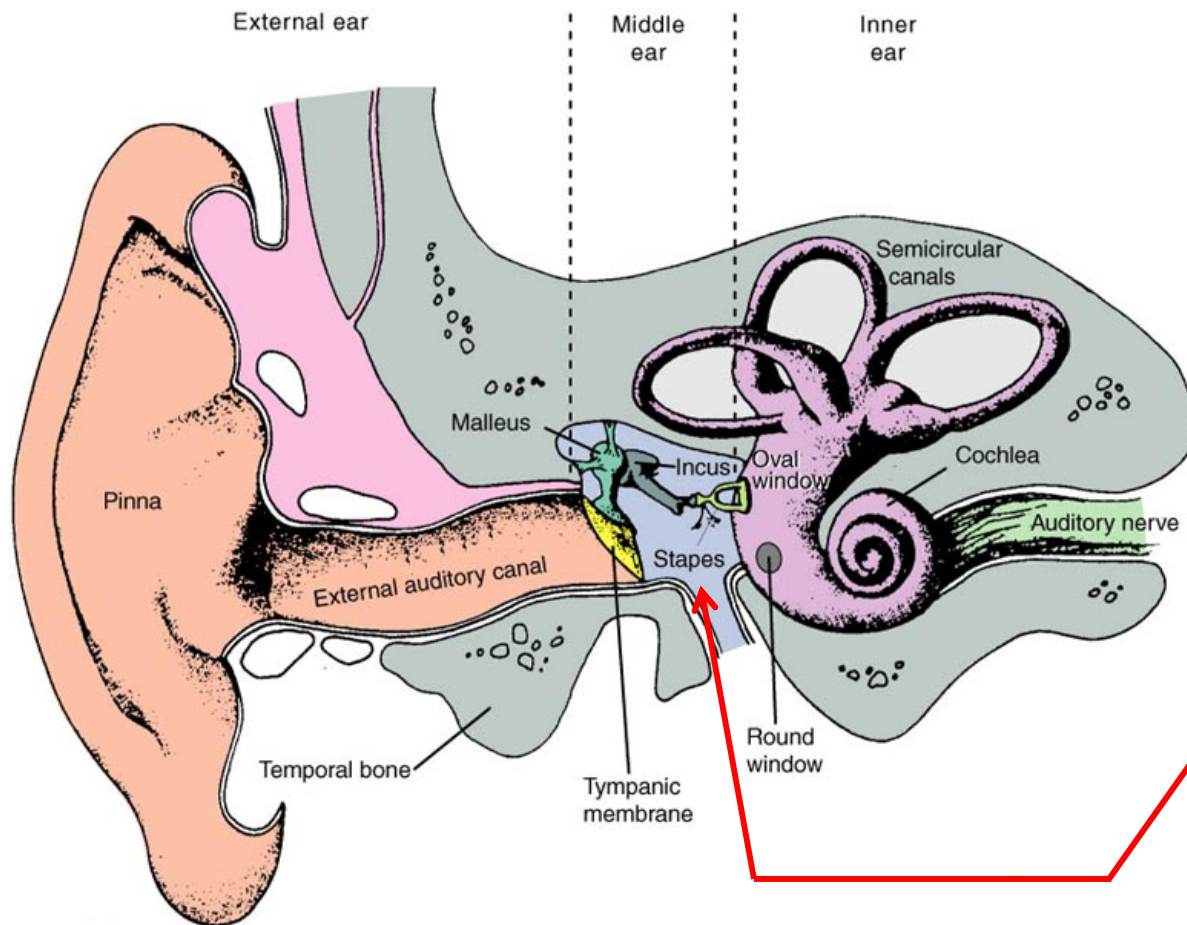
And what do bats do in order to avoid self-deafening during sound production?

- During sound production, the middle ear bones get almost fully disconnected from each other, in order to avoid self-deafening (this disconnection is partially also present in vocalizing humans).

- Brainstem mechanisms.

A sequence of echolocation calls produced by one bat

Tadarida teniotis   אשף
European free-tailed bat

Echolocation is an exquisite sensory system:

- Detecting small targets (insects) ⬅
- Range resolution of < 0.1 mm ⬅
- Object-shape discrimination   No time today
- Texture discrimination   No time today

Frequency (kHz): 0, 10, 20, 30, 40, 50

Time (s): 0 — 1.7

Talk Outline

- Echolocation (biosonar): Behavior and Sensory Ecology
- Neurobiology of Echolocation

Talk Outline

- Echolocation (biosonar): Behavior and Sensory Ecology
- Neurobiology of Echolocation

→ I will *not* have time to talk today about other echolocating animals, such as: dolphins (and other odontocete whales), shrews, swiftlets, oilbirds.

Donald Griffin: Discovered bat echolocation in 1935 as a graduate student at Harvard, while doing a Ph.D on a different topic (migration and navigation in bats).

STUDENTS: Take good example from him!

The basics of biosonar
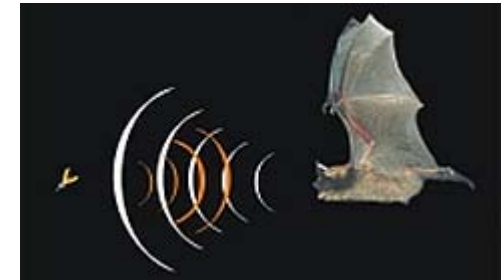
Basic sonar math:

Target range : $R = c\,T\,/\,2$

Doppler shift : $f_r = f_e\,(1 + 2\,v/c)$

The factors ½ and 2 in these equations are due to the two-way travel

Target direction: Computed based on time-difference & intensity difference between ears, and based on spectral filtering by the ears

Where:

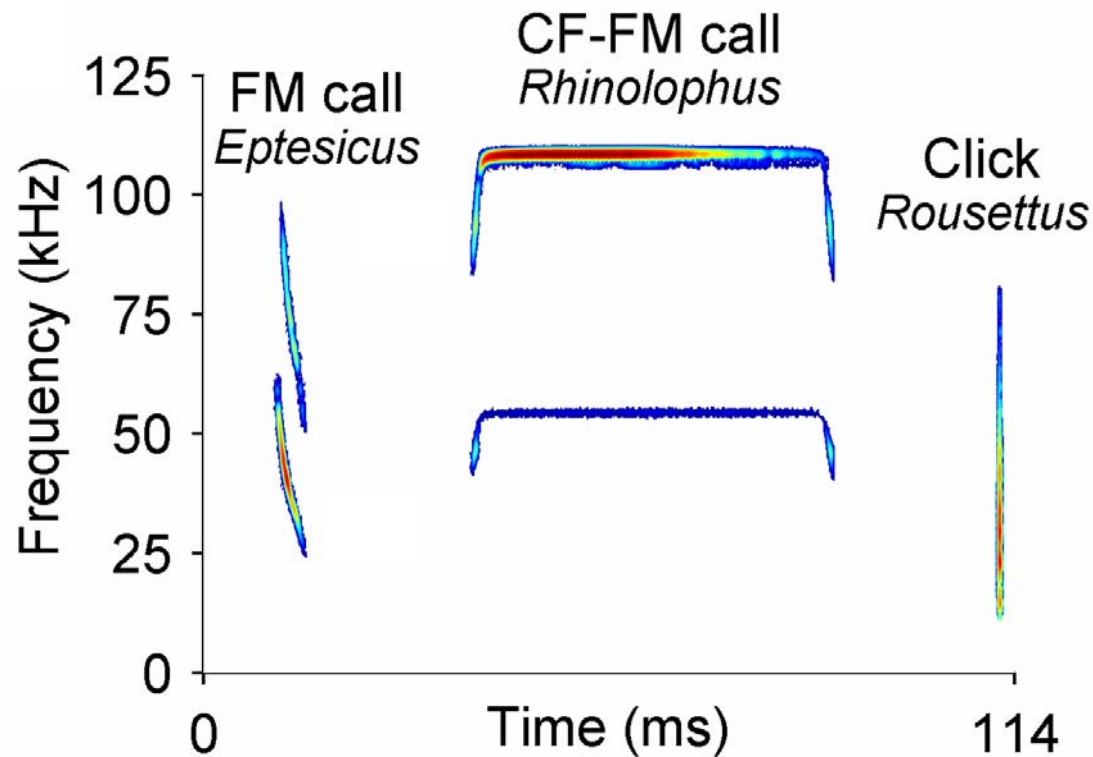R = target range

c = speed of sound in air ~ 340 m/s

T = pulse-echo delay

f_r = frequency as received in the bat's ears

f_e = frequency emitted from bat's mouth (or bat's nose)

v = bat's flight speed

Basic types of echolocation calls

FM call
Eptesicus

CF-FM call
Rhinolophus

Click
Rousettus

(Ulanovsky & Moss, *PNAS* 2008)

The most-studied bats are:

FM bats, that use frequency modulated (FM) calls with duration ~ 0.25 ms – 5 ms, and duty cycle < 10%

and

CF-FM bats, that have a long constant frequency (CF) component, ~10 ms – 40 ms in duration and with a duty cycle > 30% – these bats also have an FM chirp at the beginning and/or end of the call.

• **But why do bats use such calls?**
• **And why do they use ultrasound at all?**

The Sonar Equation ("Radar Equation") gives the answer

$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, exp(-2\alpha R)}{R^4}$$

Where:

P_{echo} = Power of echo that gets to the bat

P_{call} = Power of sonar call produced by the bat

R = target range

G_{tr} = Gain of transmitting antenna (mouth or nose)

A_{ear} = Area of receiving antenna (i.e., the size of the ear)

λ = Wavelength

σ = Sonar cross section

α = Atmospheric attenuation constant

The Sonar Equation ("Radar Equation") gives the answer

$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, exp(-2\alpha R)}{R^4}$$

Many theoretical similarities between RADAR and SONAR.

RADAR – Radio detection and ranging

SONAR – Sound detection and ranging

The Sonar Equation: intuition

$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, exp(-2\alpha R)}{R^4}$$
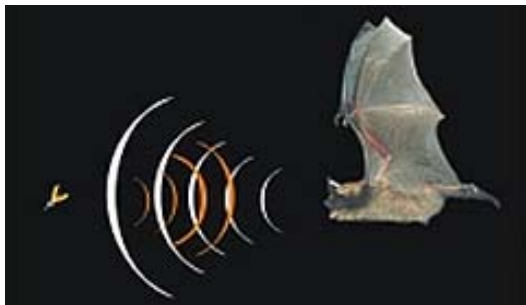
Signal of power P_{call} is:
… transmitted from antenna with gain G_{tr} (*directionality*)
… reduced $\sim 1/R^2$ via geometric spreading ("spreading loss")
… reduced also via atmospheric attenuation, $exp(-2\alpha R)$
… a fraction σ is reflected back to the bat
… reduced *again* $\sim 1/R^2$, giving a total spreading loss $\sim 1/R^4$
… received by an antenna with area A_{ear} (ear size)

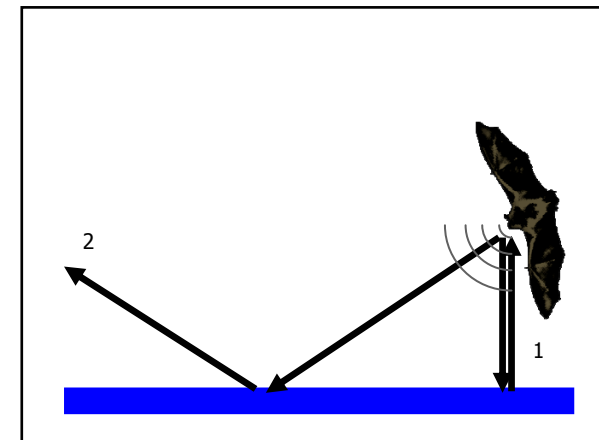# Most elements of the Sonar Equation depend on frequency

$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, \exp(-2\alpha R)}{R^4}$$

σ = **Sonar cross section** = $\sigma(f)$

Depends on:

- **Frequency:** $f^4 \sim 1/\lambda^4$
- **Target Size/Wavelength** (r/λ)
- **Geometry**
- **Materials**

Sonar cross section for sphere with radius r
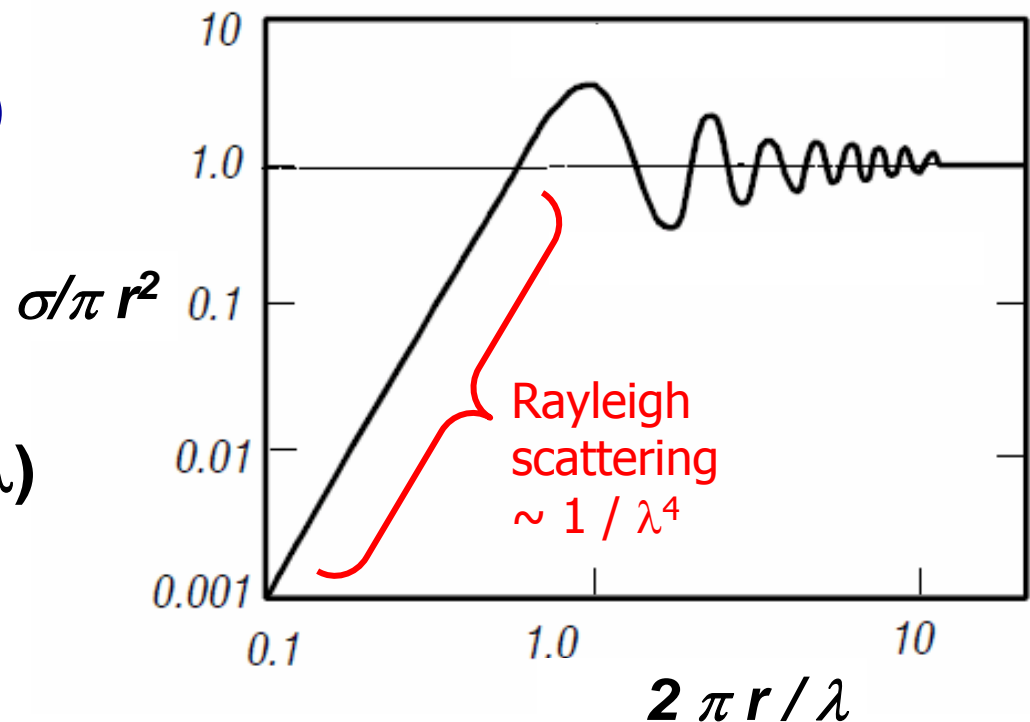
$\sigma/\pi\, r^2$

Rayleigh scattering $\sim 1/\lambda^4$

$2\,\pi\, r/\lambda$

Most elements of the Sonar Equation depend on frequency

$$P_{echo} \sim \frac{P_{call} \, G_{tr} \, A_{ear} \, \sigma \, exp(-2\alpha R)}{R^4}$$

σ = **Sonar cross section** = $\sigma(f)$

→ **Bats use ultrasound (small λ) in order to detect small targets (small r)**

Sonar cross section for sphere with radius r
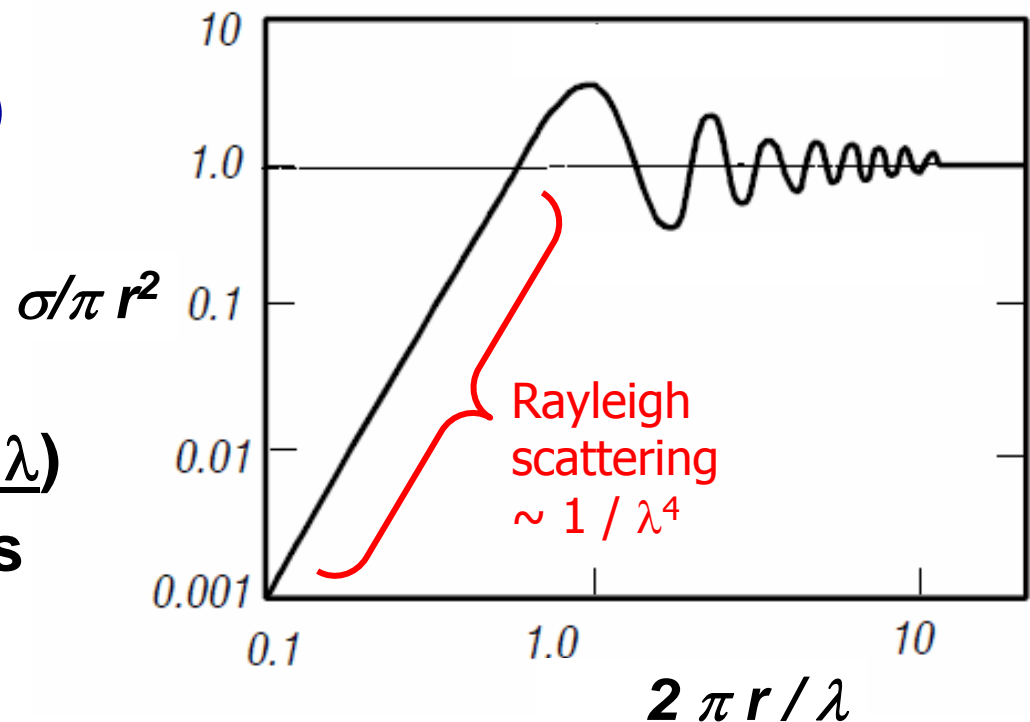
Rayleigh scattering ~ $1 / \lambda^4$

$\sigma / \pi \, r^2$

$2 \, \pi \, r / \lambda$

Most elements of the Sonar Equation depend on frequency

$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, \exp(-2\alpha R)}{R^4}$$

σ = Sonar cross section = $\sigma(f)$

Geometry and type of **Material** determine how much a sound would be *attenuated*, *scattered* or *reflected*

An extreme example of smooth material & flat geometry with *specular reflection* only: Water

Most elements of the Sonar Equation depend on frequency

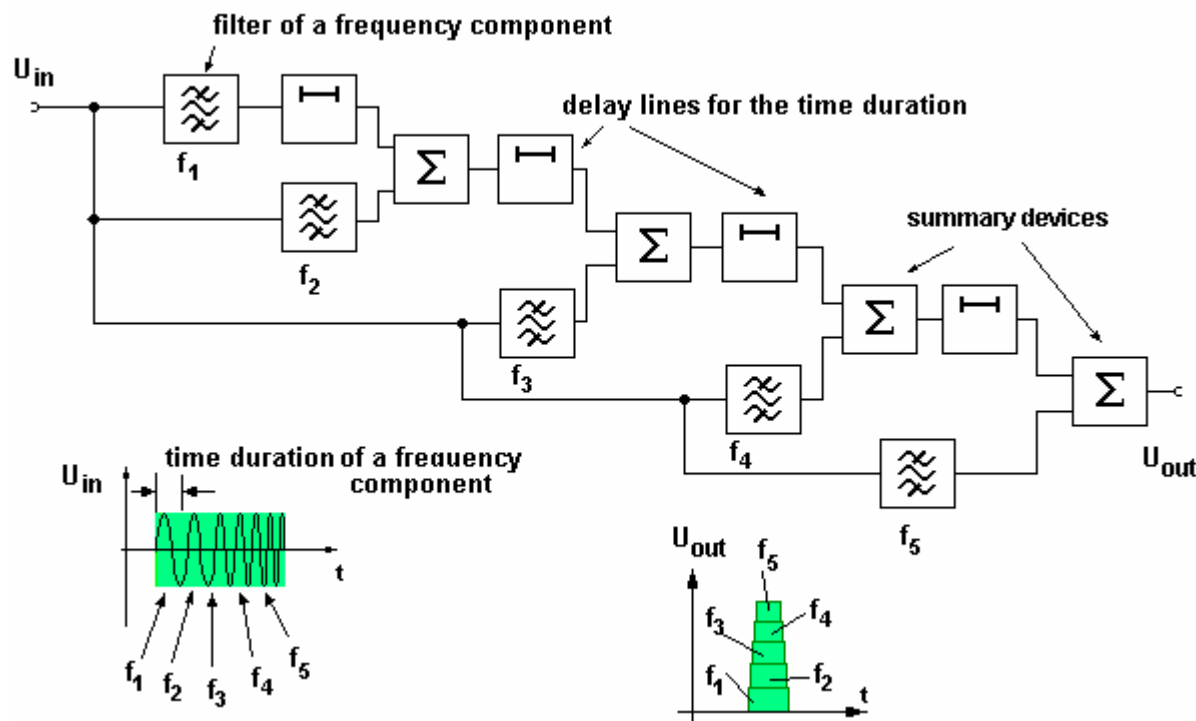$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, \exp(-2\alpha R)}{R^4}$$

Bat hunting fish by using the *non*-specular reflections caused by ripples from underwater fish
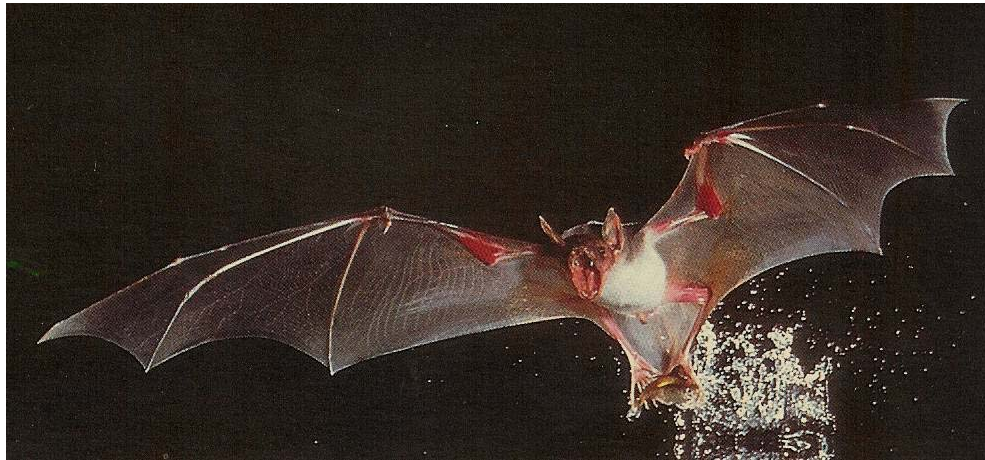
Bat drinking from water

Most elements of the Sonar Equation depend on frequency

$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, exp(-2\alpha R)}{R^4}$$

α = **Atmospheric attenuation** = $\alpha(f)$

Atmospheric attenuation constant $\alpha(f)$
strongly increases with frequency

$\downarrow$

- At low frequencies → Geometric spreading [$1/R^4$] is the dominant range-dependent factor.
- At high frequencies → Atmospheric attenuation [$exp(-2\alpha R)$] is the dominant factor, and it strongly limits the maximal possible range of echolocation at such frequencies.
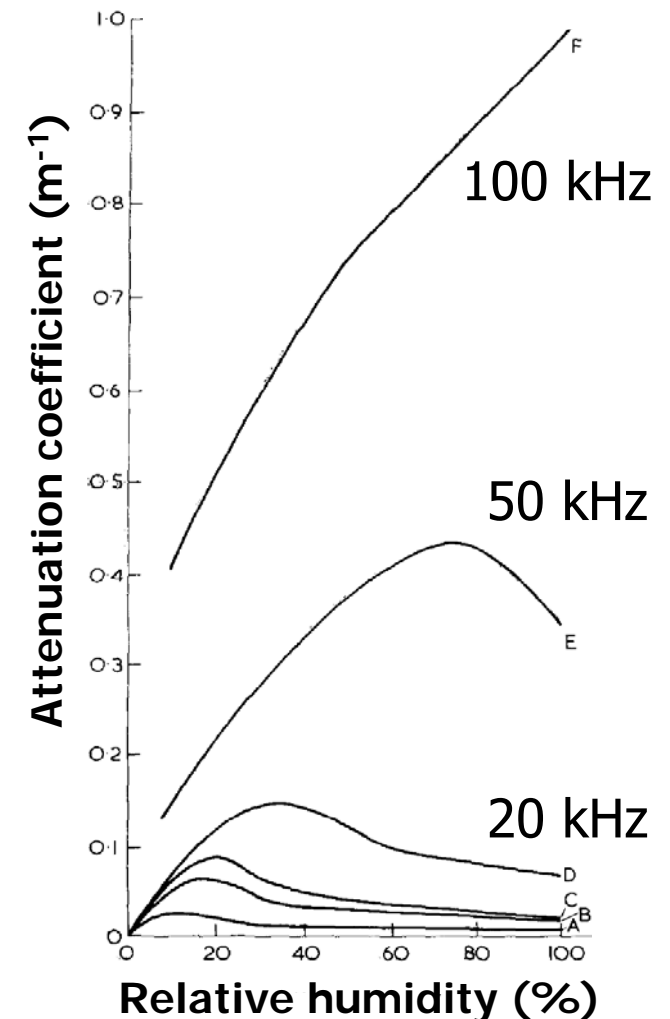
Attenuation coefficient (m^{-1})

1·0

0·9

0·8 100 kHz

0·7

0·6

0·5 50 kHz

0·4

0·3

0·2

0·1 20 kHz

0   20   40   60   80   100

Relative humidity (%)

Most elements of the Sonar Equation depend on frequency

$$P_{echo} \sim \frac{P_{call} \, G_{tr} \, A_{ear} \, \sigma \, exp(-2\alpha R)}{R^4}$$

G_{tr} = Gain of transmitting antenna = $G_{tr}(f)$

- $G_{tr} \sim f^2 \sim 1/\lambda^2$
- Beam width (angle, °) $\sim 1/f \sim \lambda$

Beam direction
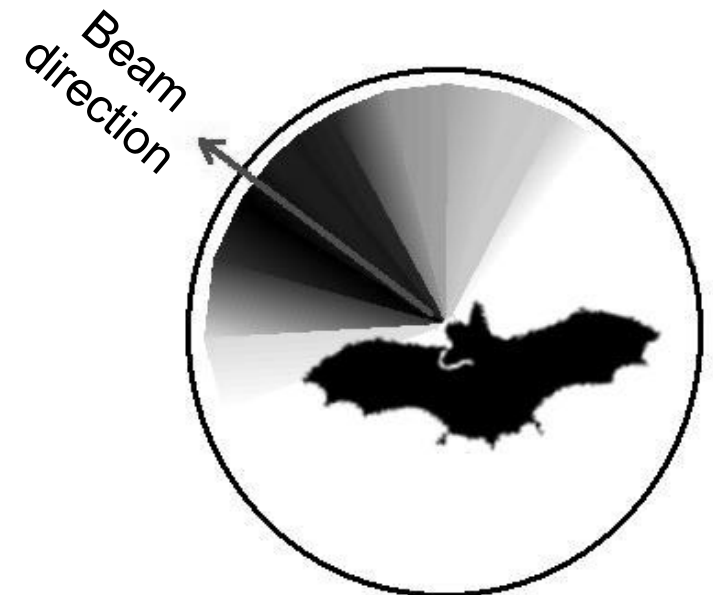
Pulse compression: Increasing P$_{echo}$ beyond the Sonar Eq.

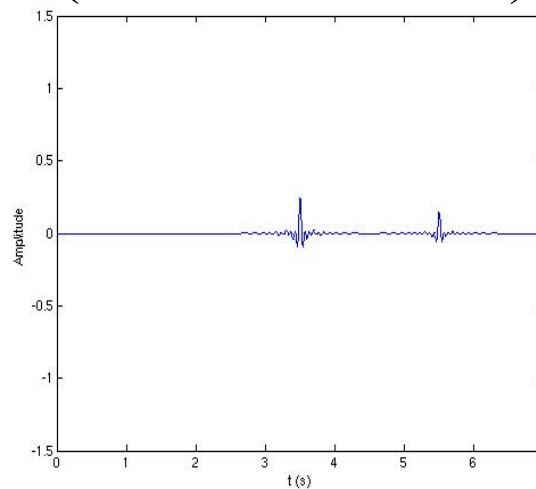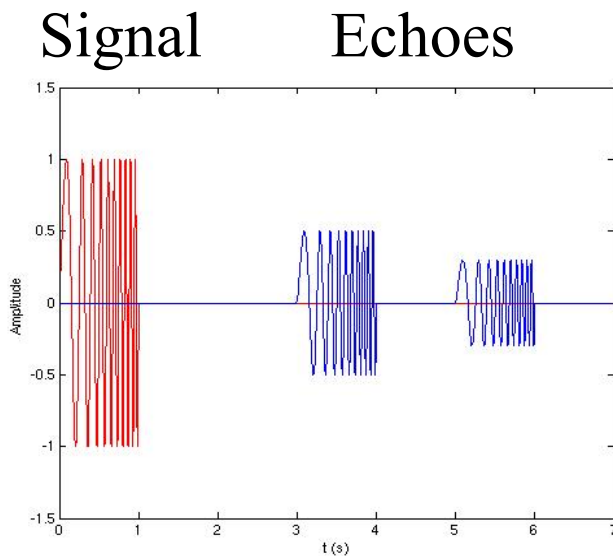$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, exp(-2\alpha R)}{R^4}$$

Pulse compression:

- Increases P_{echo} beyond what is given by the Sonar Equation.

- Improves the time resolution!

Pulse compression

$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma \, exp(-2\alpha R)}{R^4}$$

Signal   Echoes

Optimal Filter Output
(cross-correlation)

Pulse compression:

- Increases P_{echo} beyond what is given by the Sonar Equation.

- Improves the time resolution!
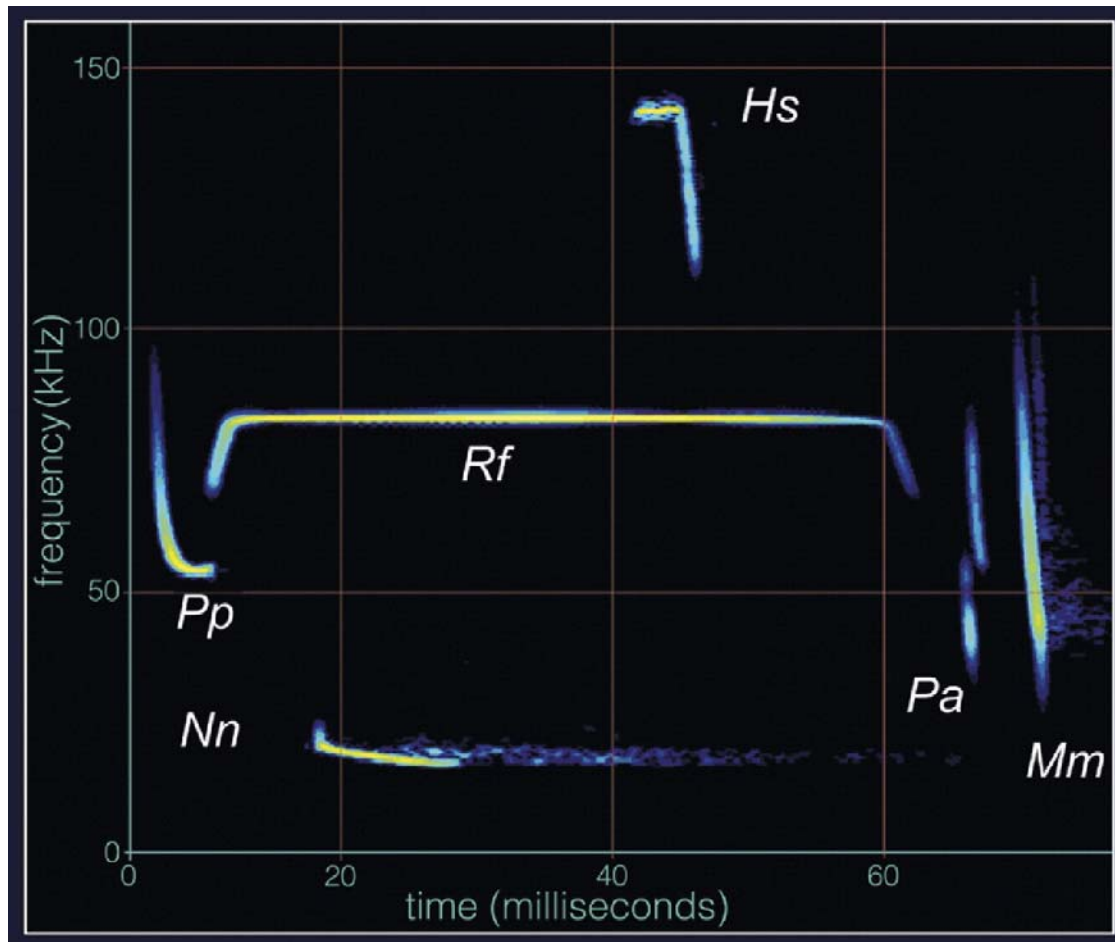
Pulse compression

Examples of biosonar calls from a variety of bat species: Almost all use some amount of Pulse Compression ("chirp" or Frequency Modulation, FM).

Pulse compression:

- Increases P_{echo} beyond what is given by the Sonar Equation.

- Improves the time resolution!

Some tradeoffs in biosonar signal design

- Call frequency:

    Frequency ↑ allows detecting <u>smaller insects</u> (min. target size ~ wavelength).

    Frequency ↓ allows <u>longer detection range</u> (less <u>atmospheric attenuation</u>).

- Call bandwidth:

    Bandwidth ↑ allows <u>more accurate range estimation</u> ($\Delta t \propto 1/\text{Bandwidth}$).

    Bandwidth ↓ allows <u>better detection</u> (more energy within neural bandwidth).

This is not just theory: Biosonar characteristics may determine the entire lifestyle of a bat

Tadarida teniotis אשף
European free-tailed bat

- Hunts <u>large insects</u> (moths, beetles) which it can detect with its sonar from <u>large distance</u> (low atmospheric attenuation, large σ)
- Fast flier (can catch up with fast insects)
- Large body (can overpower large insects)

Low frequency of sonar may be the result of large body size (basic physics of resonance) – and in turn it determines the diet.

Coming back to our original questions...

- **Why do bats use such calls?**
    - **Pulse compression (in both FM bats and CF-FM bats).**
    - **Computing Doppler shifts (by CF-FM bats: see below).**

- **Why do they use ultrasound at all?**
    - **For detecting small targets (need small λ to detect small r).**

Basic types of echolocation calls (Cont.)
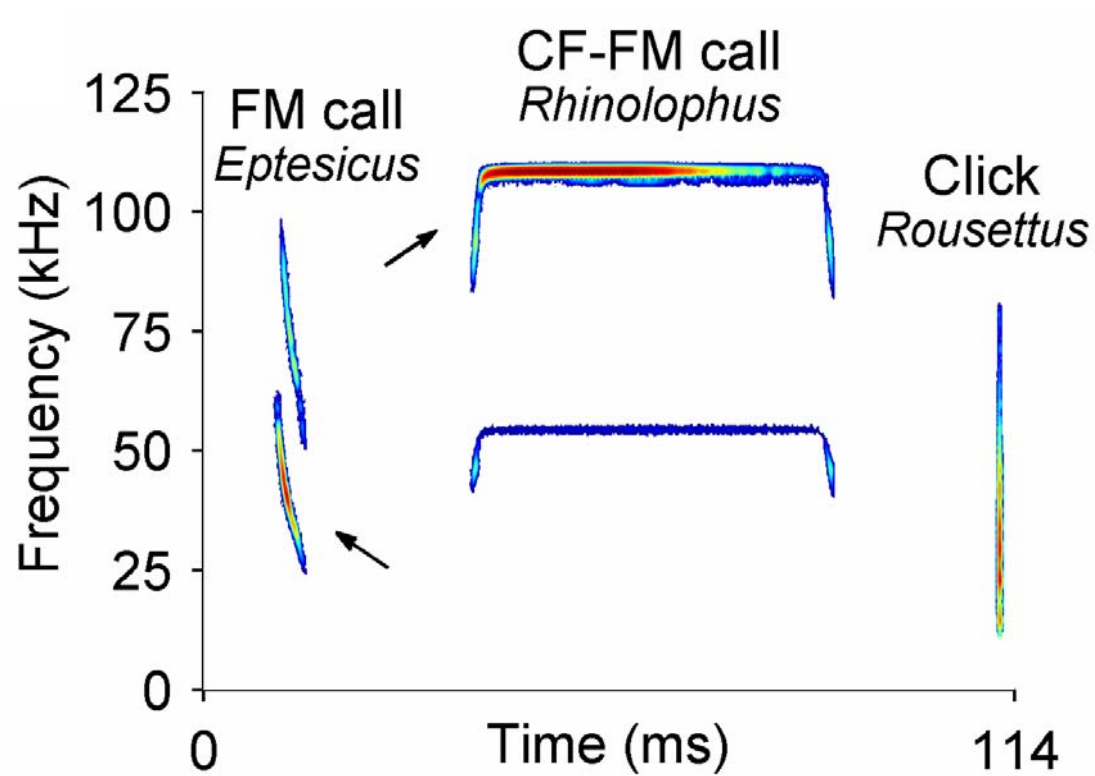
(Ulanovsky & Moss, *PNAS* 2008)

Basic types of echolocation calls (Cont.)

FM bats :

- Emit their sonar calls <u>through the larynx</u> (i.e. through the vocal cords).

- FM bats mostly use a <u>nonlinear chirp</u> (but some species use a linear chirp) $\rightarrow$ <u>pulse compression</u>.

- In behavioral experiments, FM bats were shown to discriminate jitter in <u>target range down to ~400 ns</u> (less than 0.1 mm), and possibly even 10 ns.

- FM bats can do <u>object recognition</u>, and even <u>object classification</u>.

- FM bats can do <u>texture discrimination</u> (discriminate roughness of surfaces).

Basic types of echolocation calls (Cont.)

CF–FM bats :

- Emit their sonar calls <u>through the larynx</u>.

- These bats can compute the <u>Doppler shift (target velocity)</u>.

- They can detect <u>Doppler modulations caused by the insect's wing flutter</u>.

- These bats can even <u>tell apart different insect species</u> based on their different flutter rate.

Basic types of echolocation calls (Cont.)

Clicking bats :

- Emit their sonar signals <u>via tongue-clicks.</u>

- <u>Ultra-short clicks (50-100 μs)</u> replace the mechanism of pulse compression of FM and CF-FM bats.

- Interesting strategy for <u>sonar beam-steering</u> (see below).

(Bats also have interesting communication calls)
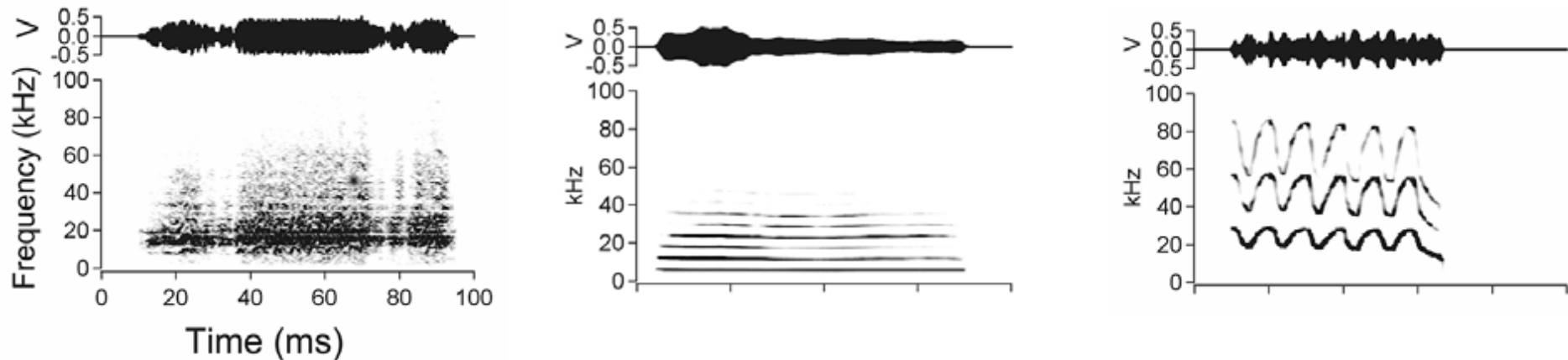
Examples of mustached bat communication calls (Kanwal & Rauschecker 2007)

Bat communication calls:

- Are very rich (among mammals, second in richness only to primates).

- Generally have a much lower frequency than the echolocation calls (so if you heard a bat, most likely you heard its communication calls, not echolocation calls – which are usually ultrasonic).

Usages of bat sonar

- Target detection + catching food   (insects, birds, frogs, fish, fruits, flowers…)

- Object recognition (based on echo spectrum); examples:

  - Flower bats: Identifying the flower species, and also the best approach direction to the flower (Sonar Cross Section is maximal at the best direction for food delivery).

  - Fish-eating bats: Identifying the water ripples produced by the fish.

- Landing

- Navigation

- Altimeter

- Collision avoidance

Movie: Swarm of bats above water-tank in Nevada (J. Simmons).

Collision avoidance – comprehending the incomprehensible
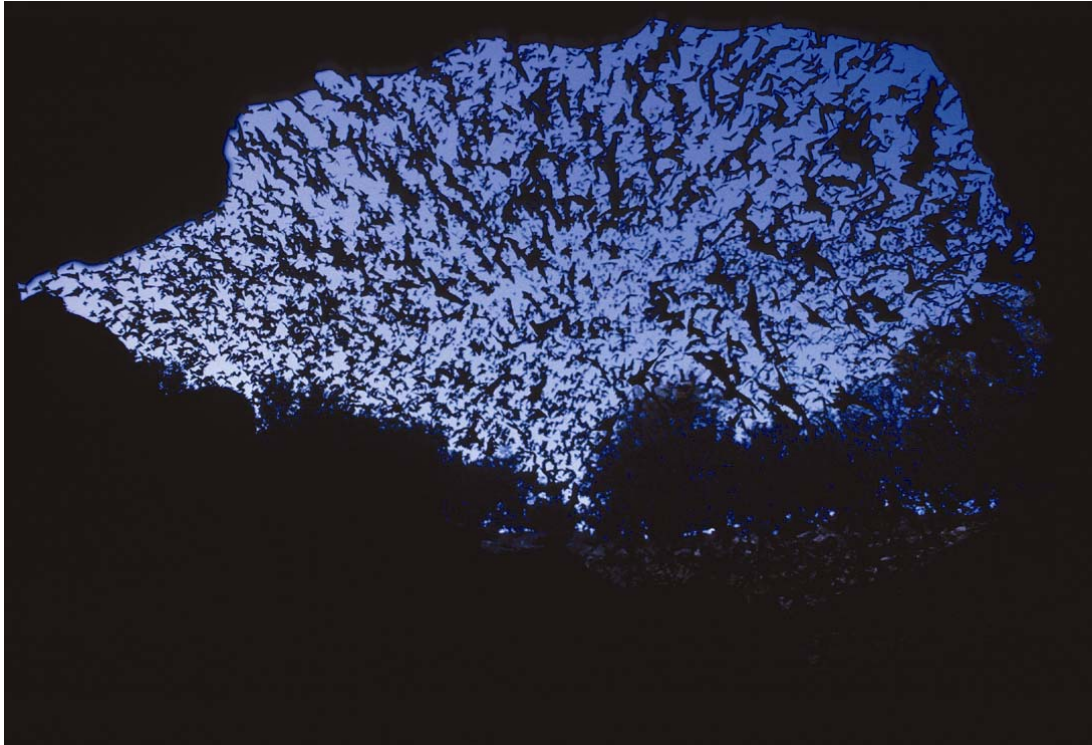
Photo: Merlin Tuttle
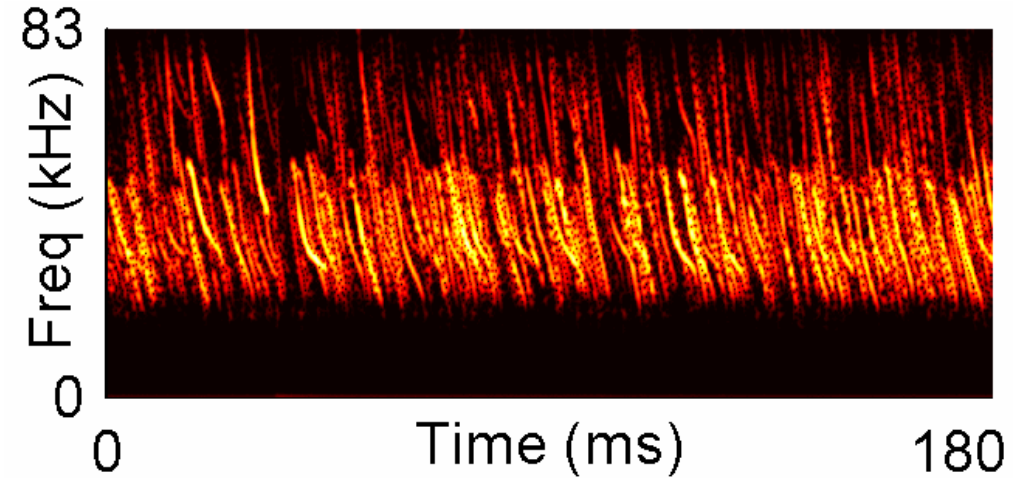
Recording: Erin Gillam

n objects $\times$ m bats =

$n \times m$ echoes (thousands)

$\downarrow$

"Cocktail-party nightmare"

Collision avoidance – comprehending the incomprehensible
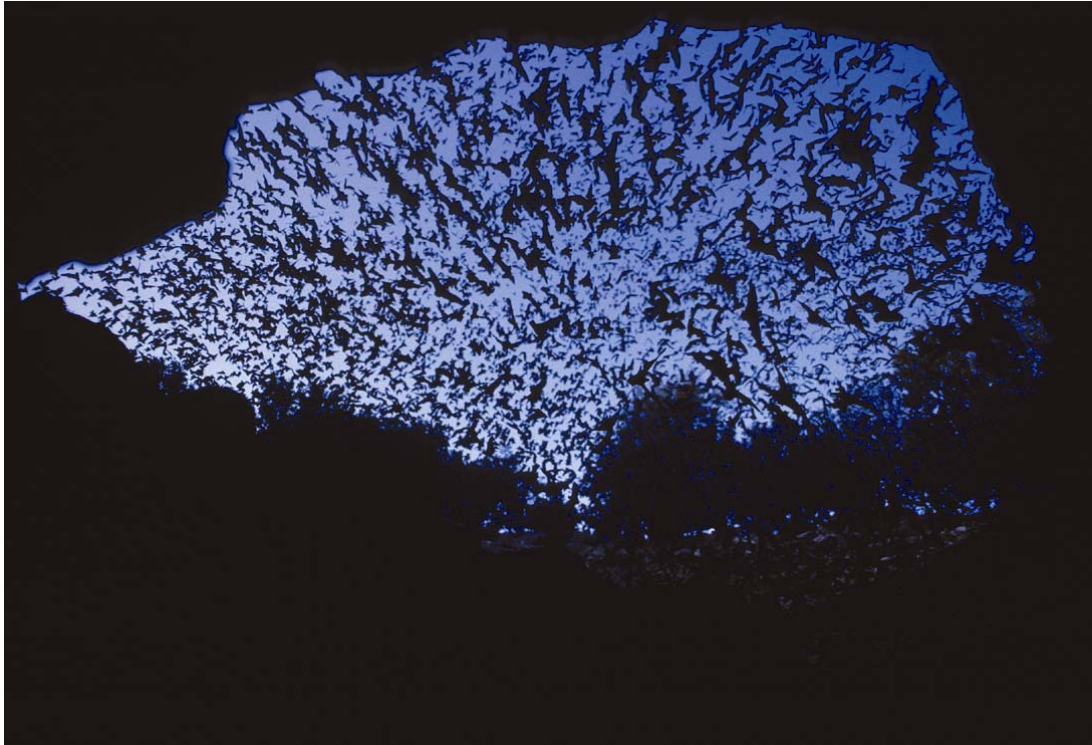
Photo: Merlin Tuttle

What are the possible solutions?

- Spatial filtering (directional hearing, moving the ears, directional emissions, sequential scanning)

- 'Tag' the timing of the bat's own calls (call 'signature', efference copy, combination-sensitive neurons)

- Integrate information across calls

- Jamming avoidance response (JAR)

- Use spatial memory – and ignore the calls (happens in some caves)

Jamming avoidance: Bats move their frequency to avoid being incidentally jammed by other bats

The stimuli
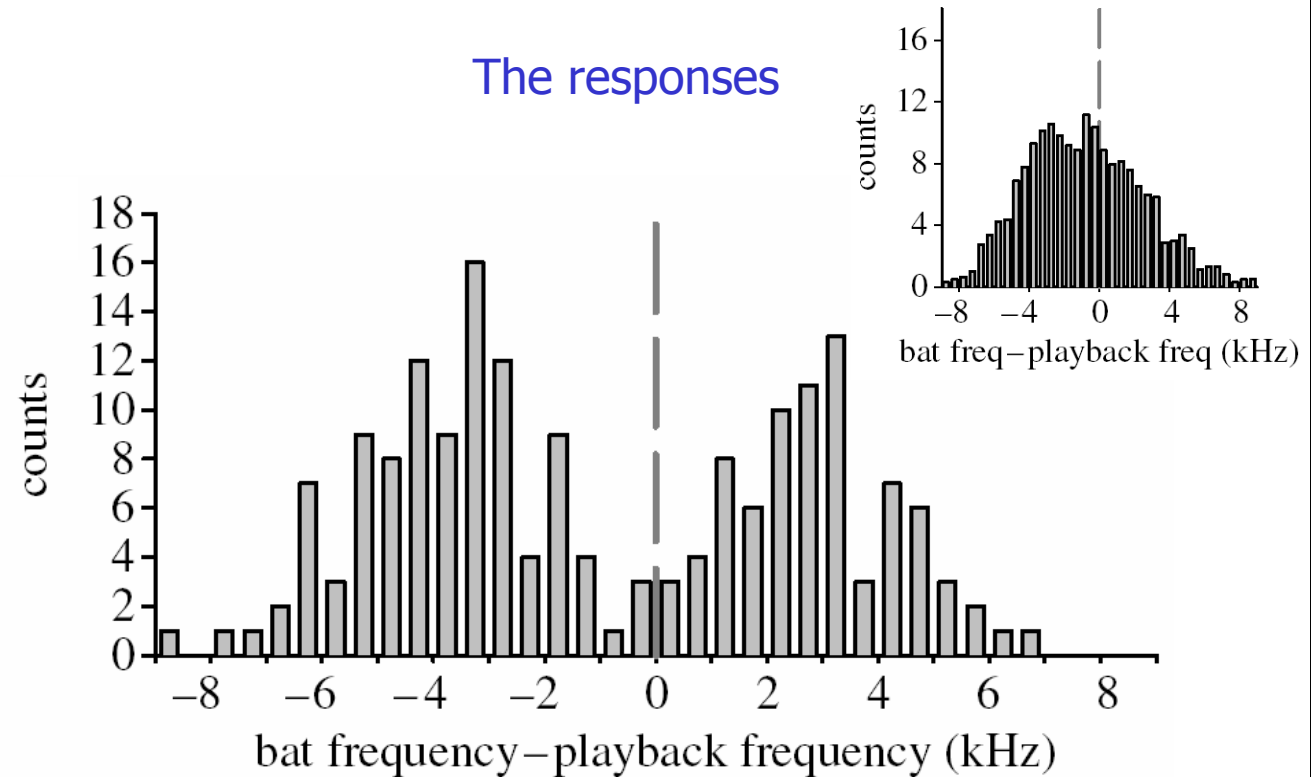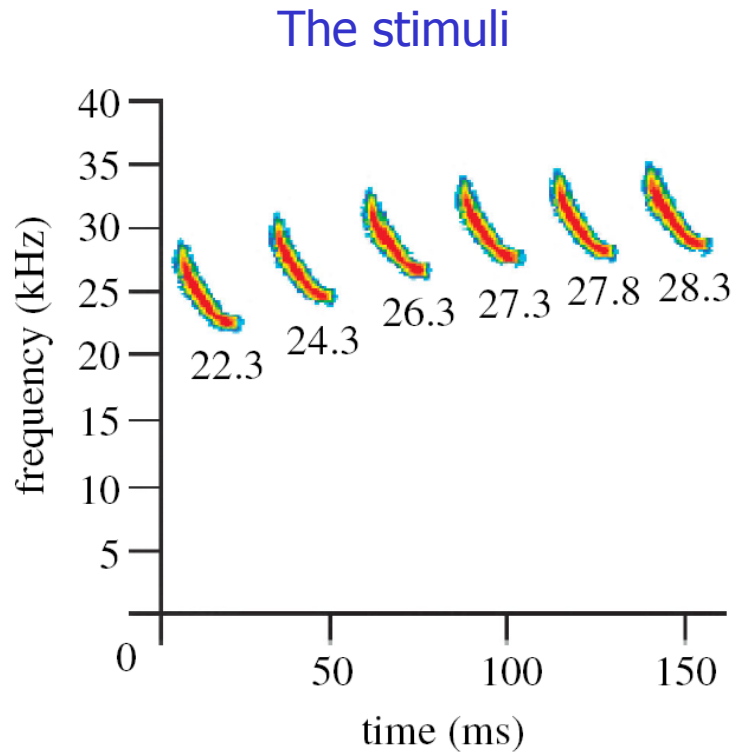
The responses

From a study by:
Ulanovsky, Gillam & McCracken (2007)

Jamming avoidance: Bats move their frequency to avoid being incidentally jammed by other bats
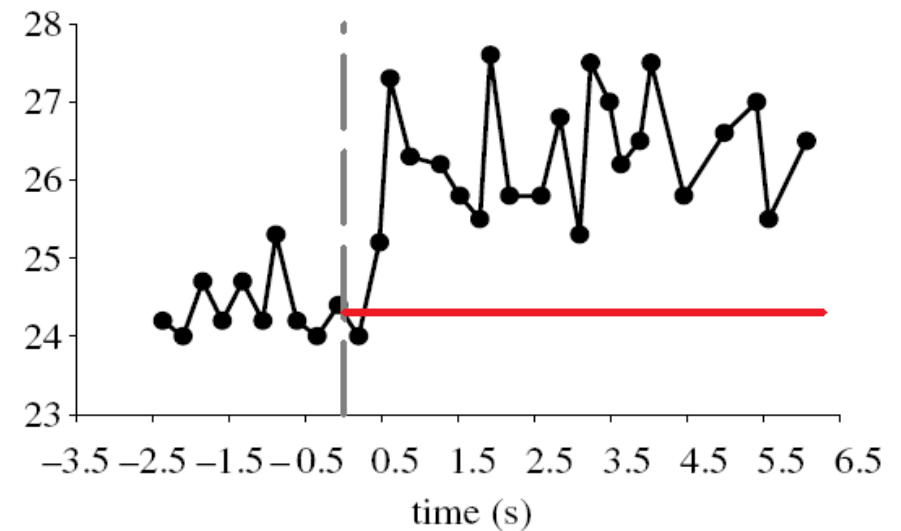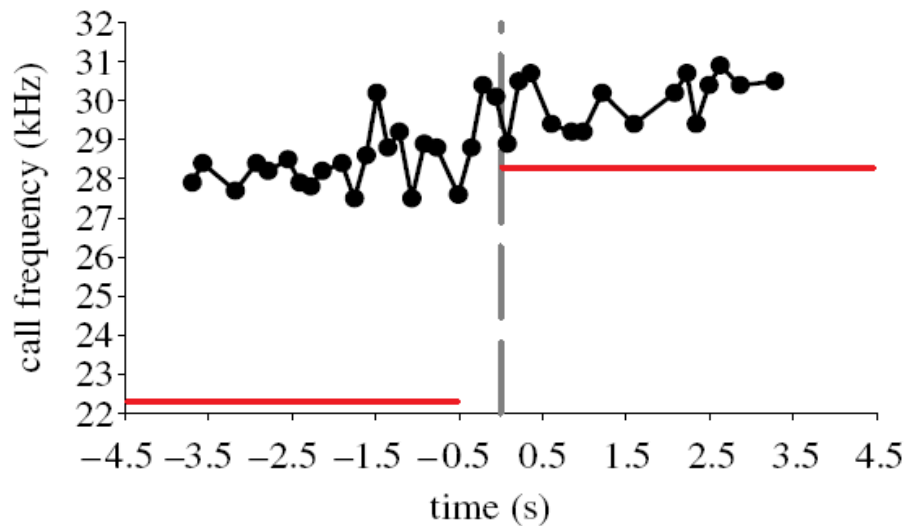
→ Jamming Avoidance Response (JAR) is but one example of the *flexibility* of bat echolocation. Biosonar is a very dynamic type of active sensing: <u>Bats can adaptively change their sonar signal design according to their needs</u>.

From a study by:
Ulanovsky, Gillam & McCracken (2007)

Bats change their signal design adaptively according to their needs. For example, insect-eating bats exhibit typical phase transitions: *Search → Approach → Tracking (Attack)*
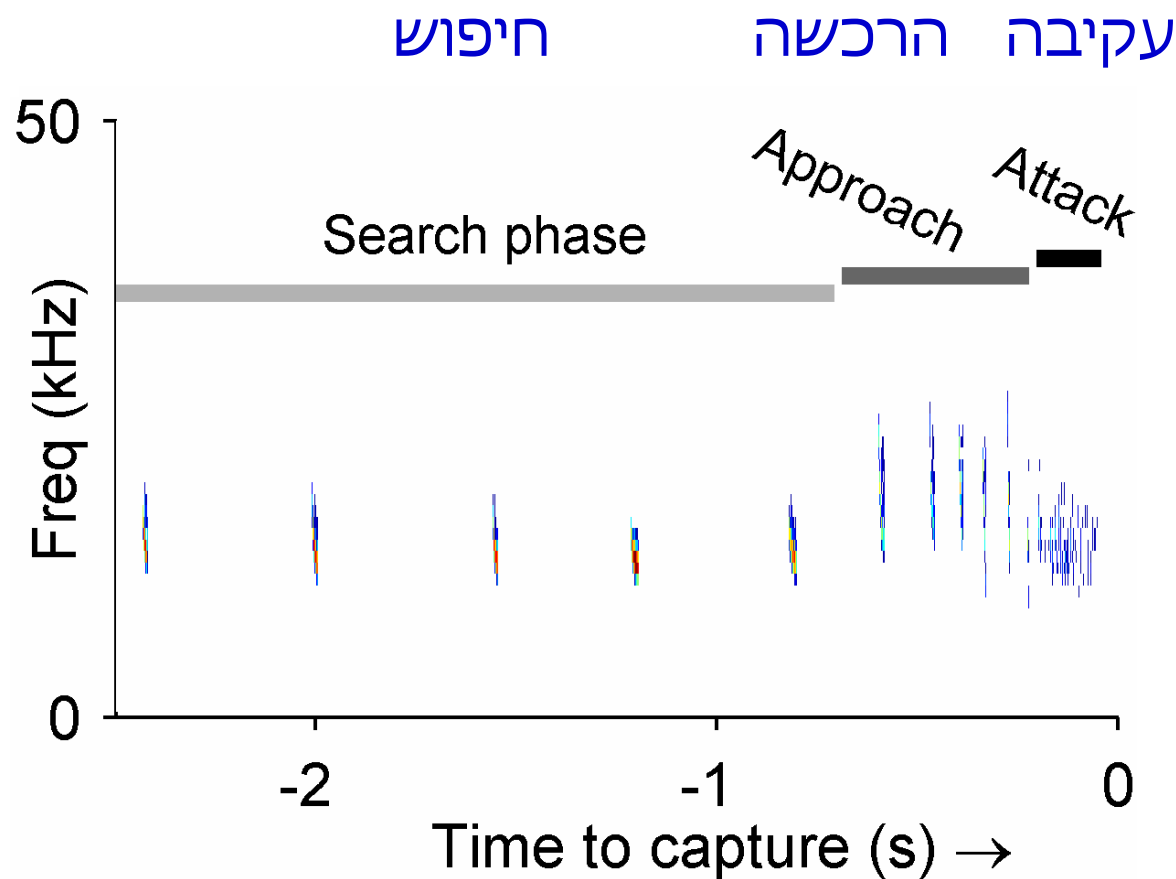
(Ulanovsky & Moss, *PNAS* 2008)

Examples of six more bat species showing sonar phase transitions: *Search → Approach → Tracking (Attack)*
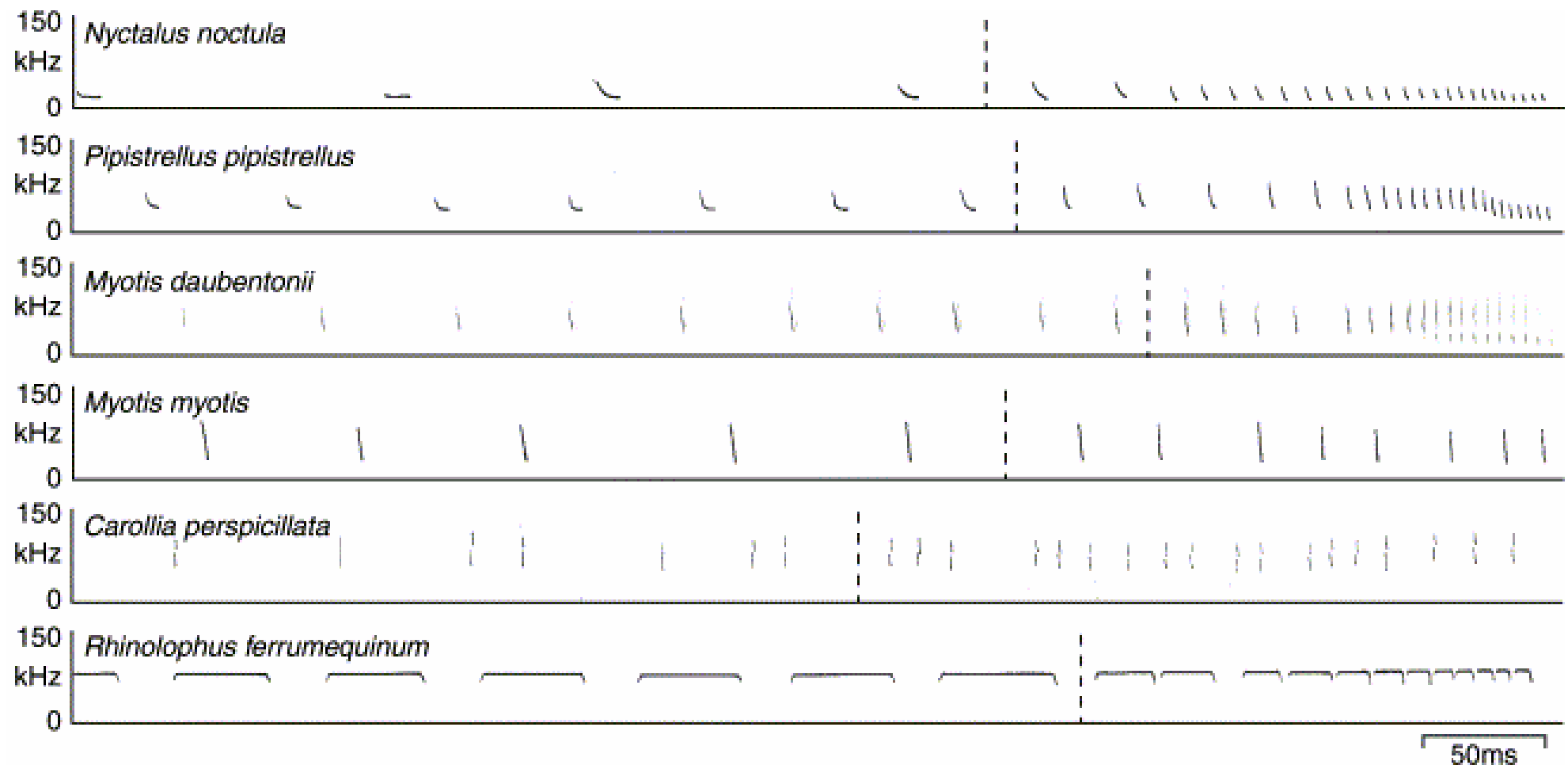
Rationale for the observed adaptive changes in signal design

Changes in echolocation calls during the closing-in on the insect:

- <u>Larger bandwidth</u> = gives better accuracy in estimating the target range (derived from basic sonar / radar theory)

- <u>Higher rate of calls</u> = higher update rate, allows better tracking of the moving target.

- <u>Shorter call duration</u> = smaller overlap between outgoing call and incoming echo, allows tracking insects at closer ranges – almost until the insect's interception.

- <u>Lower call frequency (in some species)</u> = wider emission beam, allows tracking the insect at very short ranges, without loosing the insect due to a too-narrow beam.

Emission beams used by bats

Bats emit their beam either through their mouth (e.g. big brown bat) or through their nose (e.g. horseshoe bat).

Arrays of microphones are used to measure the beam shape.
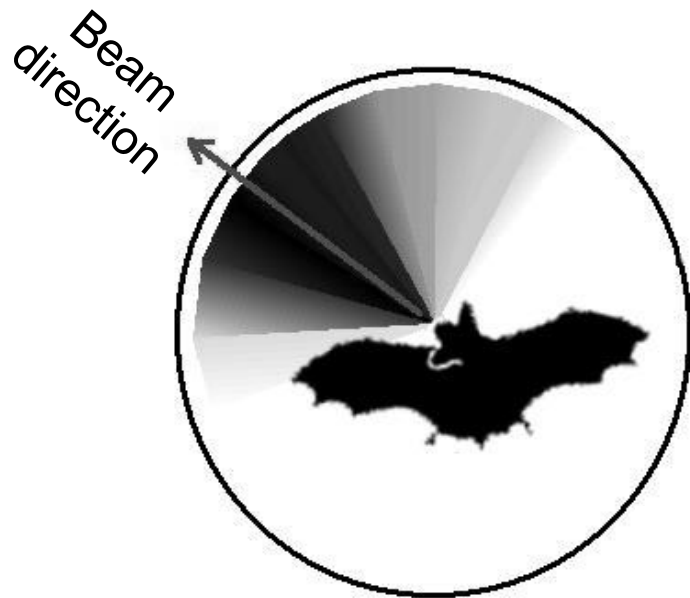
Real beam shape measured from a big brown bat
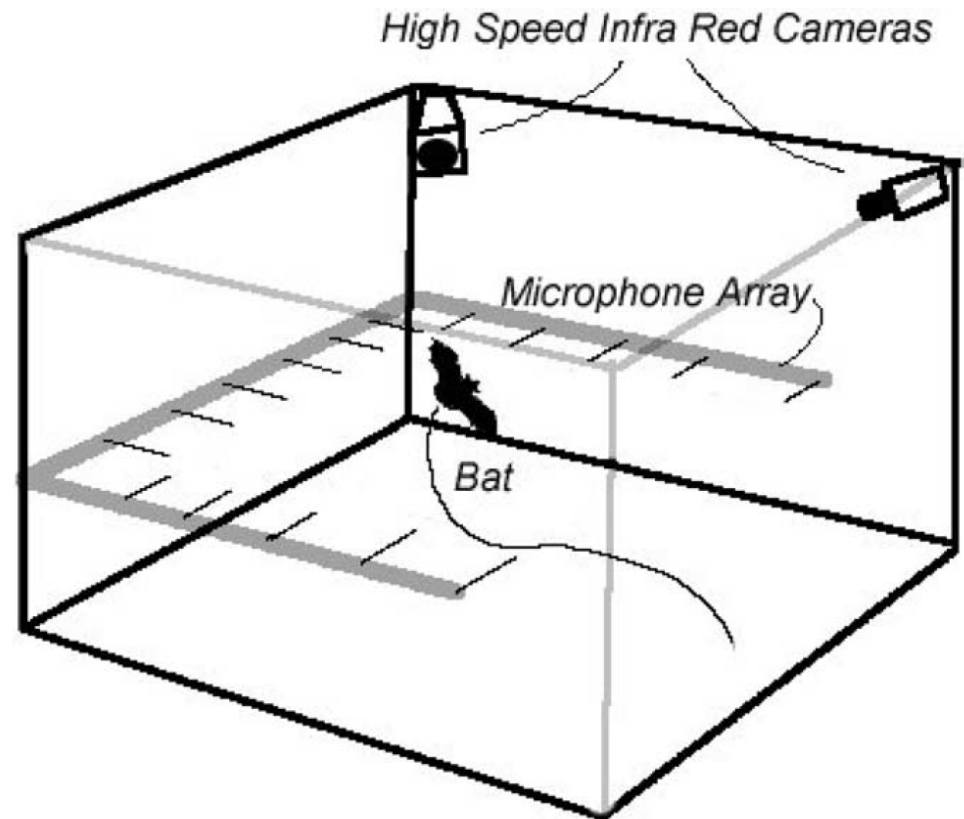
Emission beams used by bats

When switching from the search phase to the approach phase / tracking phase, the bat 'locks' its beam onto the target direction.
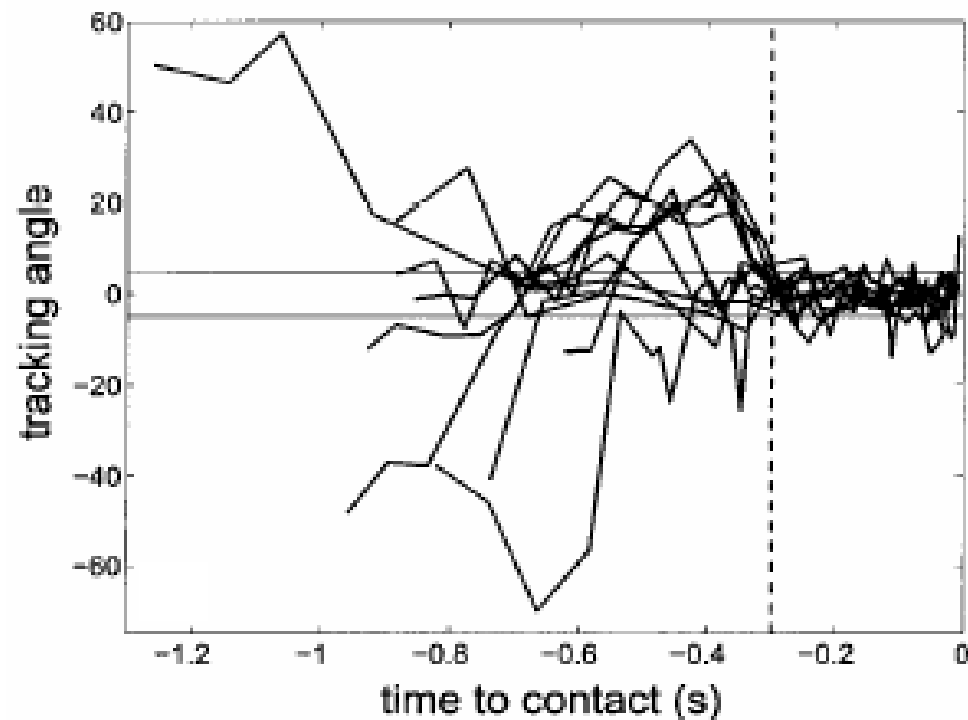
Emission beams used by bats

The 'locking' of the beam onto the target coincides with the increase in call rate.
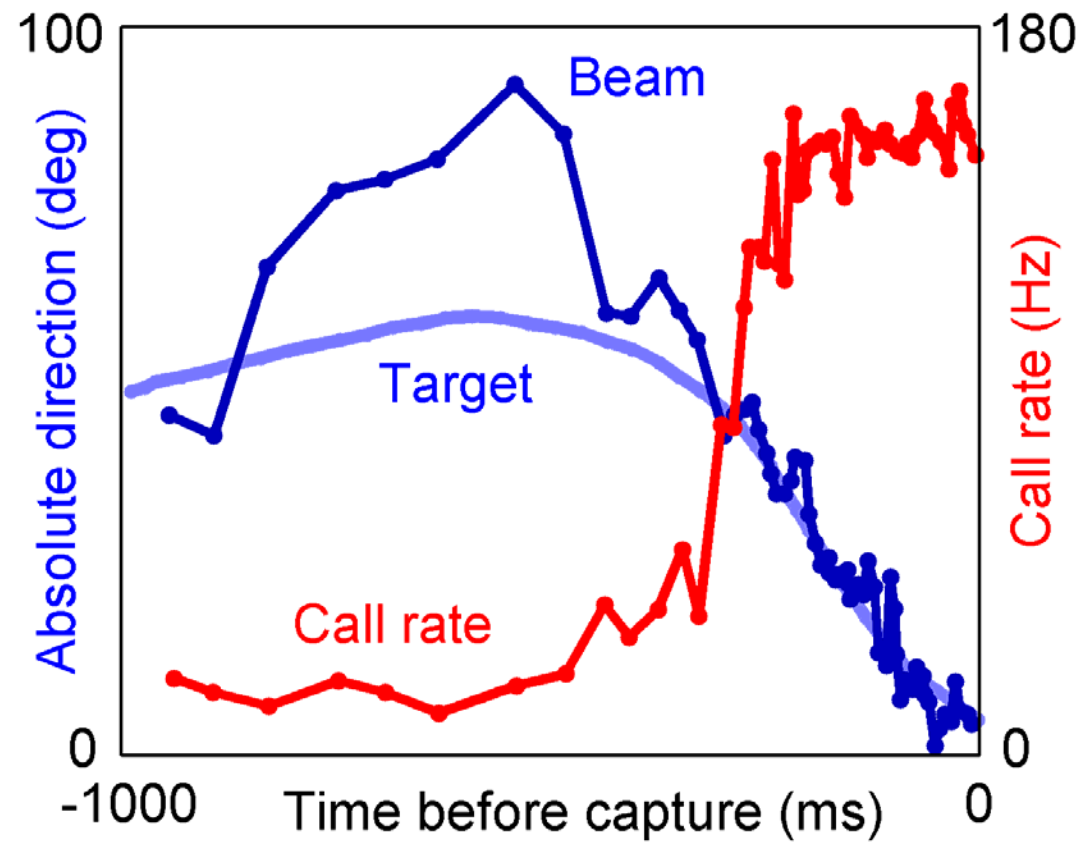
A movie showing the phase transitions in bat sonar when chasing an insect: *Search* → *Approach* → *Tracking (Attack)*

Movie: Bat catching mantis (K. Ghose).

Clicking bats (*Rousettus*) use a different beam-steering strategy: They lock the beam's maximum *slope* on target, which optimizes localization
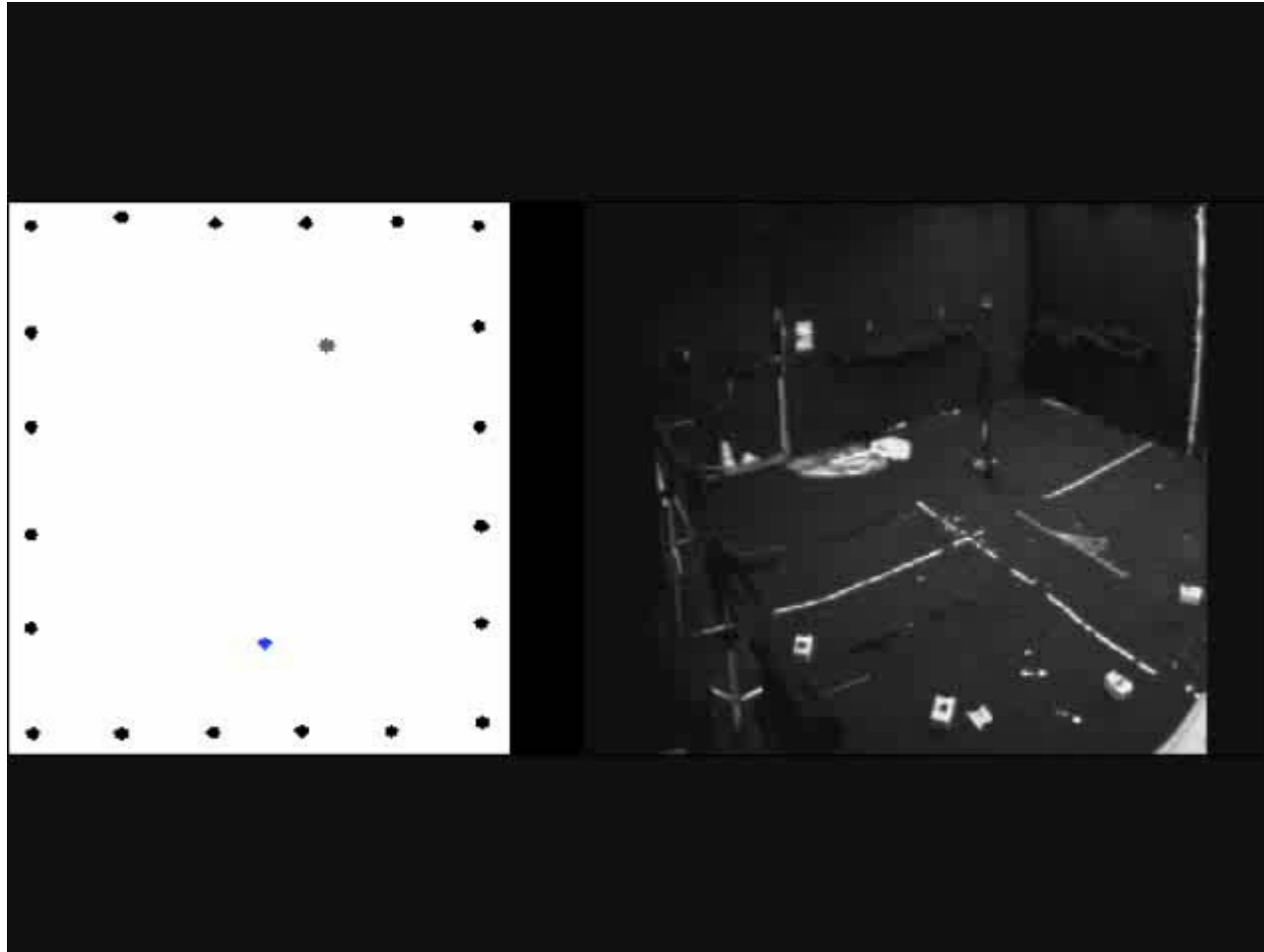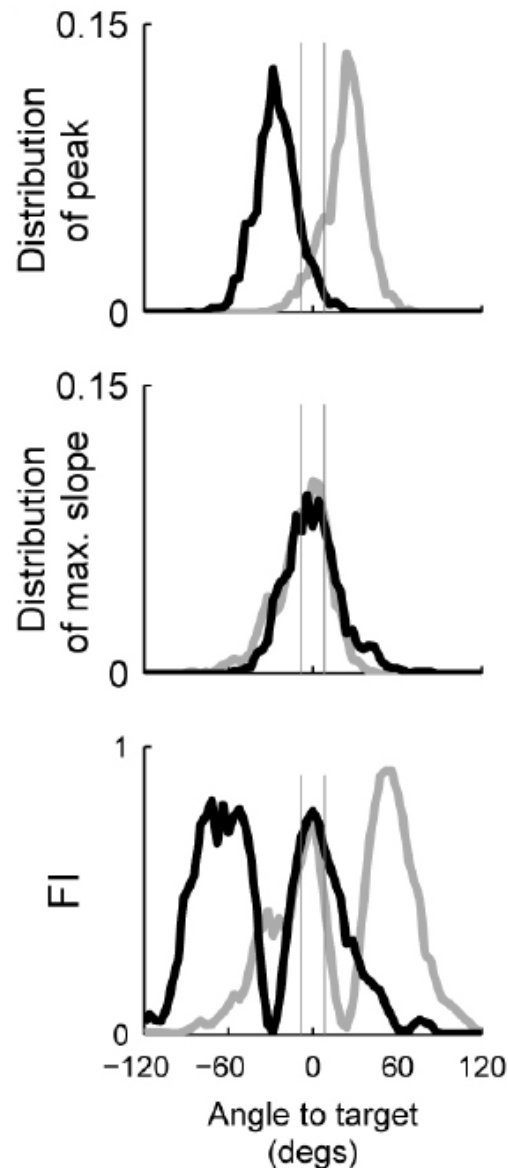

Yovel, Falk, Moss, Ulanovsky,
Science (in press)

Clicking bats (*Rousettus*) use a different beam-steering strategy: They lock the beam's maximum *slope* on target, which optimizes localization


Emission Curves
If we want *optimal SNR*

Emission
Power

Direction
to target

Azimuth
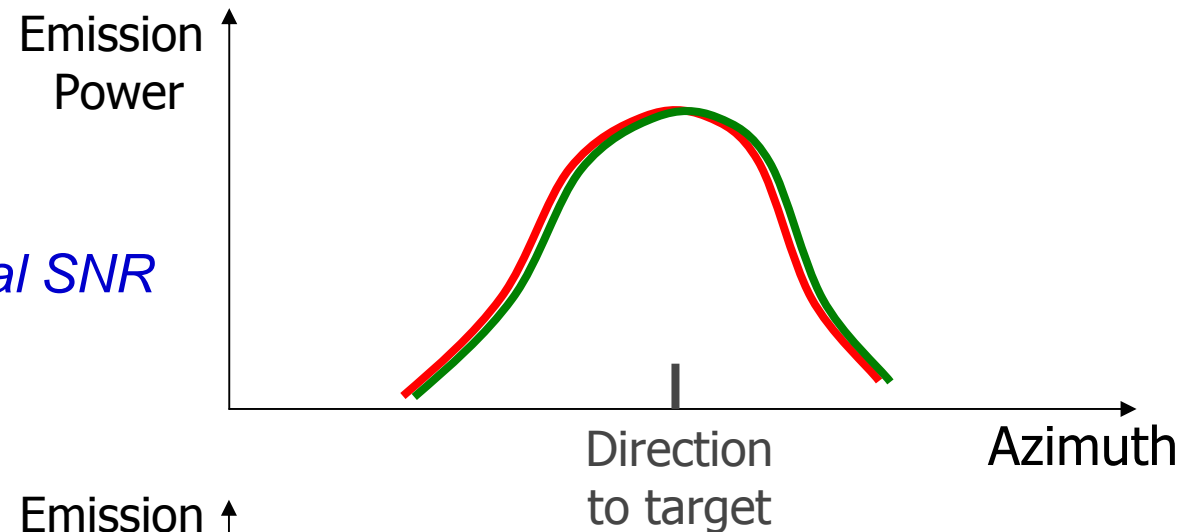
Emission Curves
if we want *optimal localization*
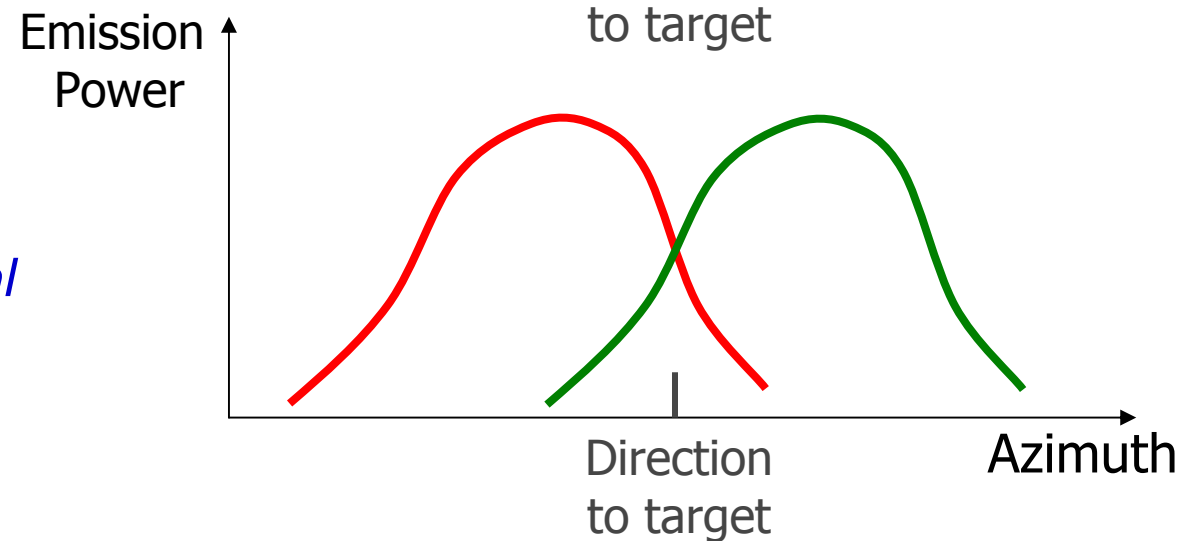
Emission
Power

Direction
to target

Azimuth

Clicking bats (*Rousettus*) use a different beam-steering strategy: They lock the beam's maximum *slope* on target, which optimizes localization

Fisher Information (FI):
Meets a theoretical optimality criterion: best possible target localization based on echo intensity

Yovel, Falk, Moss, Ulanovsky,
Science (in press)

Measuring bat's temporal resolution by the psychophysical technique of two-alternative forced choice (2-AFC)
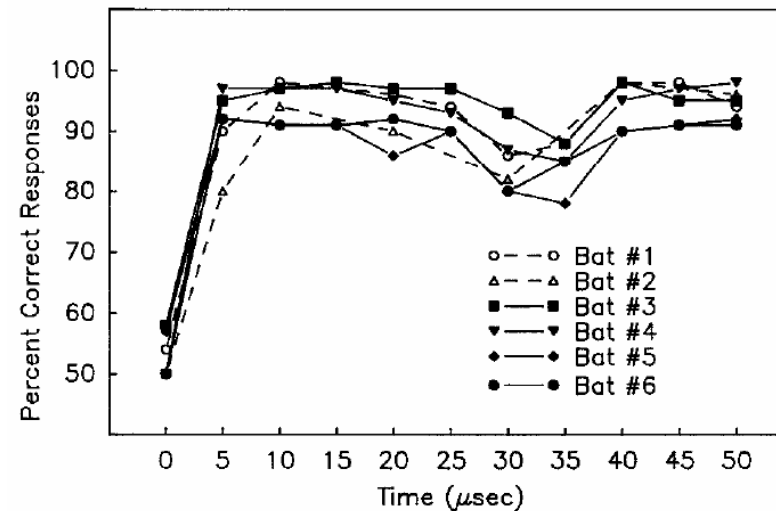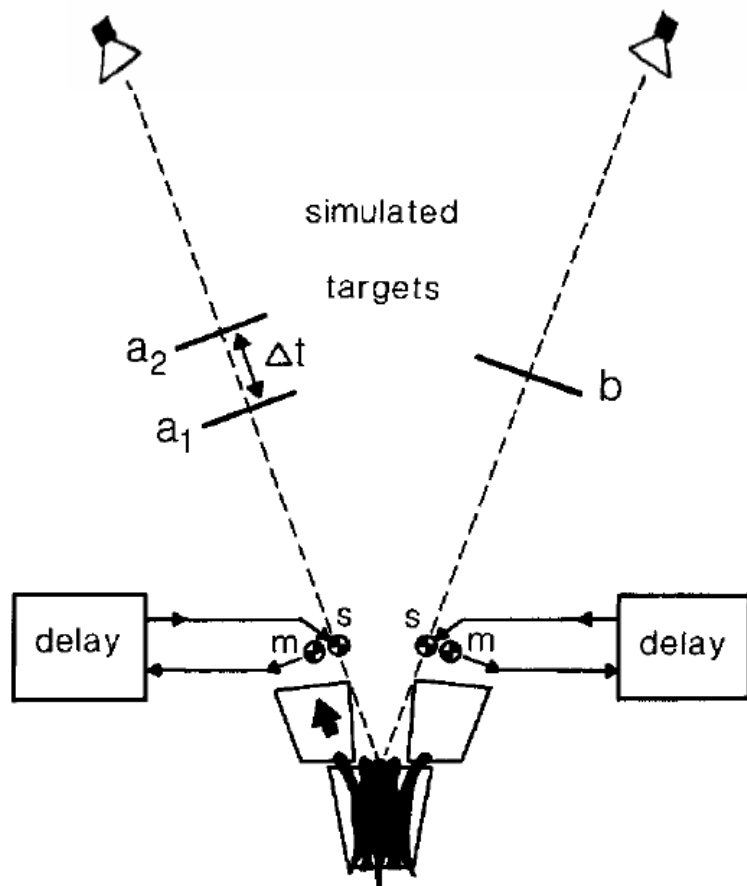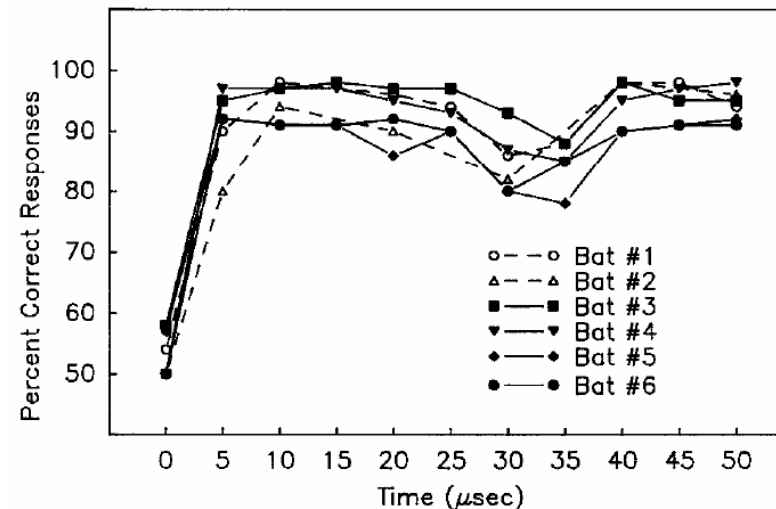

400 ns threshold
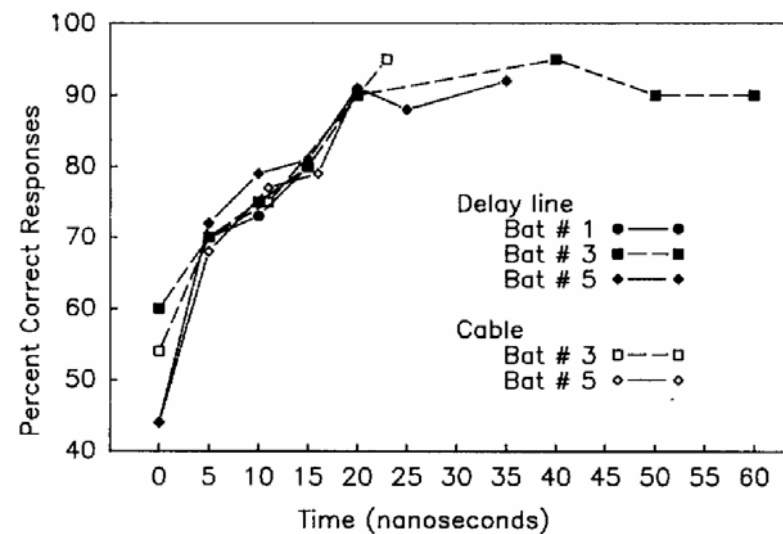
10 ns threshold?!

Measuring bat's temporal resolution by the psychophysical technique of two-alternative forced choice (2-AFC)

Big brown bats discriminate jitter in <u>target range down to ~ 400 ns</u> (less than 0.1 mm), and possibly even 10 ns. This extraordinary temporal resolution is ~3 orders of magnitude below the rise-time of action potentials in the bat's brain (which is ~ <u>400 μs</u>, or so) !

400 ns threshold

10 ns threshold?!

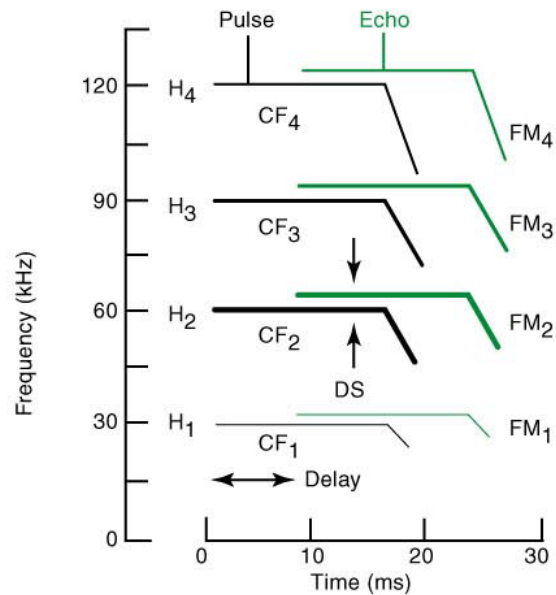**Jim Simmons**: Pioneer of the two-alternative forced choice (2-AFC) technique for behavioral studies of bats.
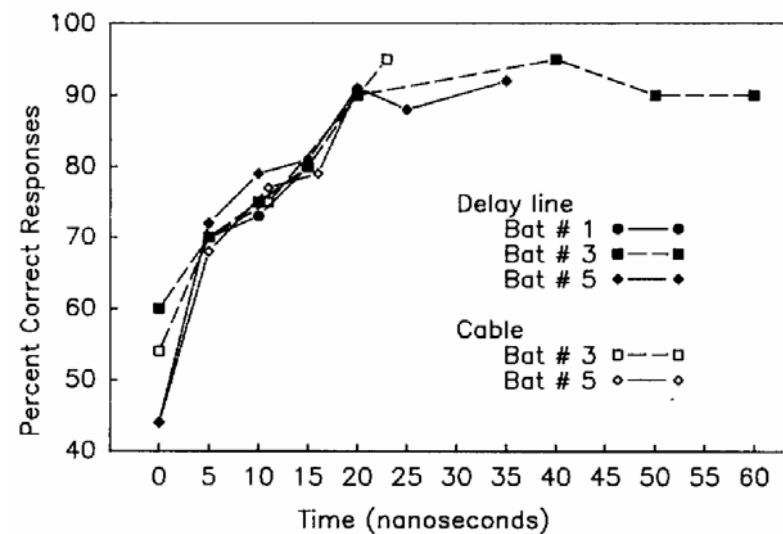
Talk Outline

- Echolocation (biosonar): Behavior and Sensory Ecology
- Neurobiology of Echolocation

Neural processing of sonar signals in the mustached bat's brain

Schematic of the CF–FM call of the mustached bat.

- The CF-FM call is ideal for overcoming the **Clutter** problems in highly cluttered environments, by doing Doppler processing.
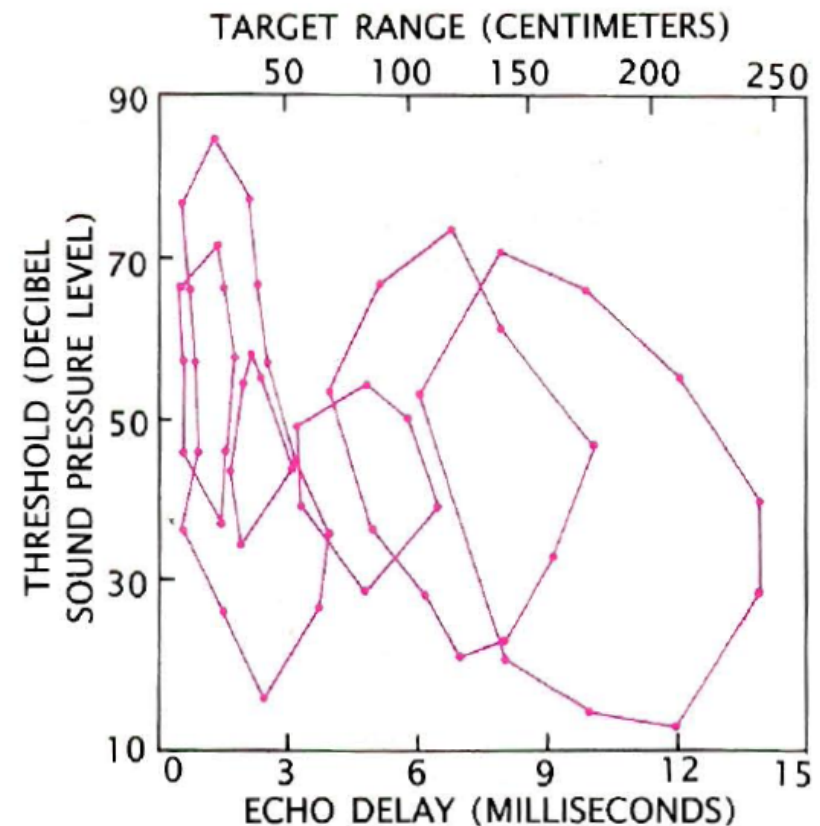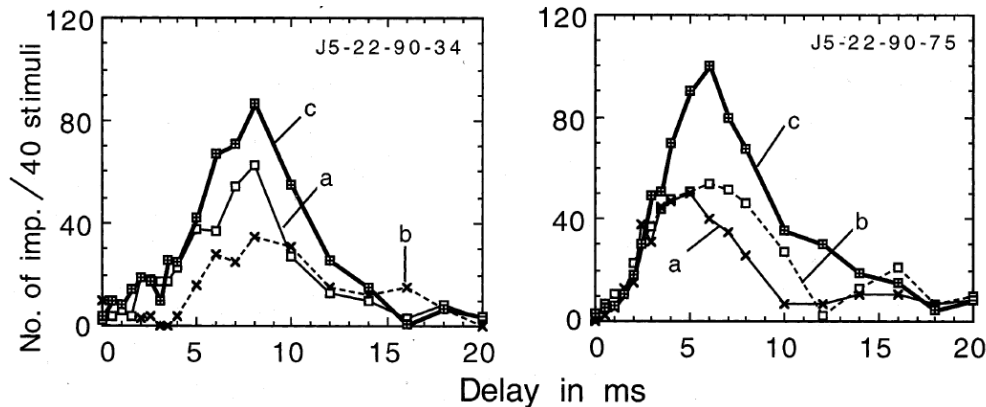

Nobuo Suga: Pioneer of bat electrophysiology research. Studied the neural basis of echolocation in the mustached bat.
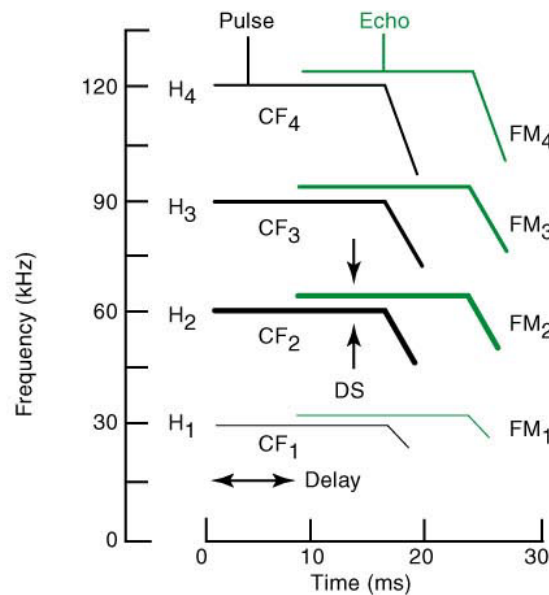
Neural processing of sonar signals in the mustached bat's brain

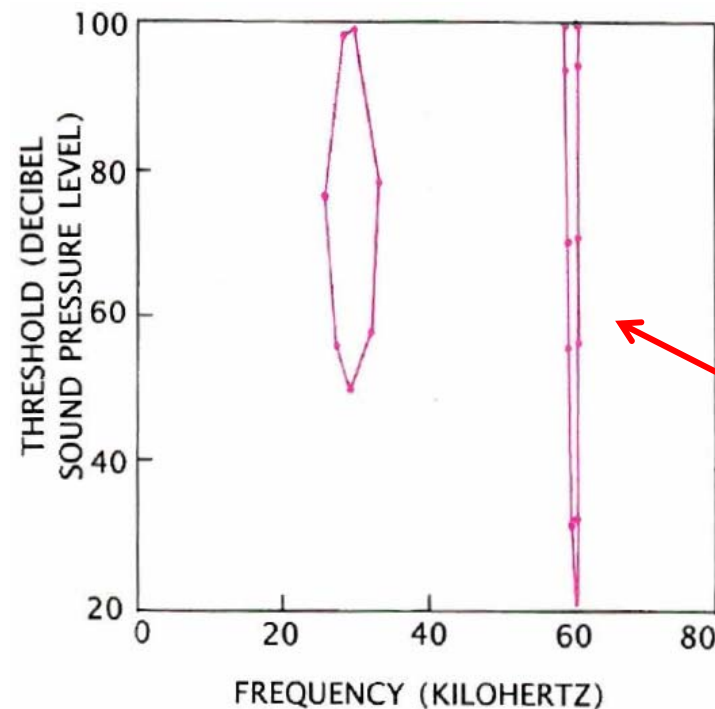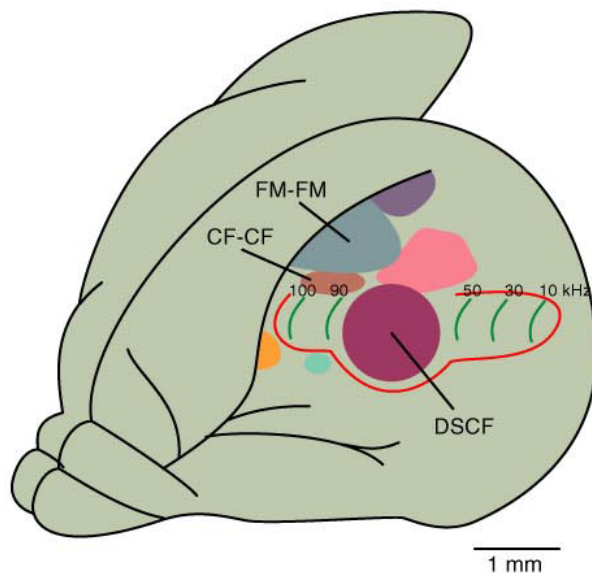Prominent characteristics of the auditory cortex of this bat:

1. Delay tuned neurons (neurons sensitive to target range) – first discovered by Nobuo Suga

# Neural processing of sonar signals in the mustached bat's brain

2. '<u>Auditory fovea</u>' (DSCF area) contains neurons with extremely narrow frequency tuning, centered around the dominant harmonic of the bat call (CF_2, the 2nd harmonic). The narrowest frequency tuning in any animal's cortex.
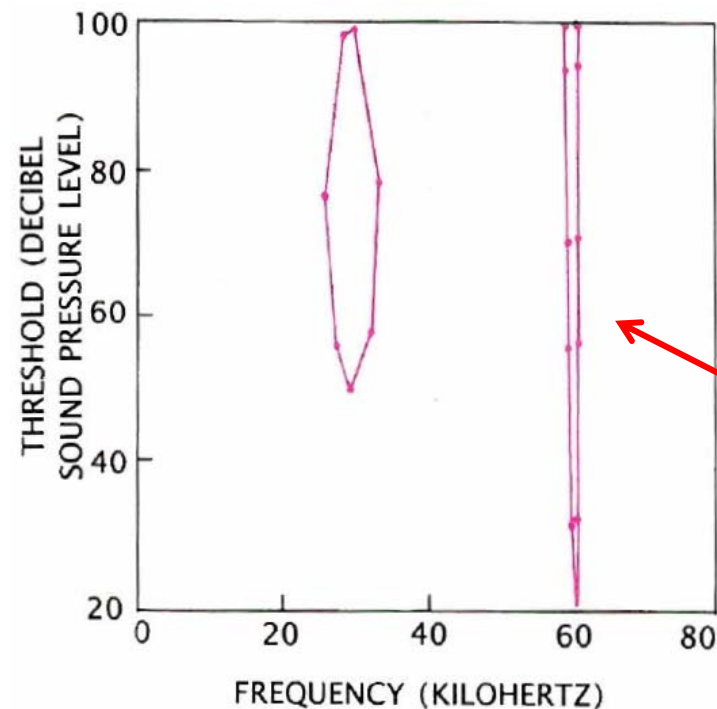

Frequency tuning of neuron from DSCF area

Neural processing of sonar signals in the mustached bat's brain

Level (dB)

88

1

0.1   Freq (kHz)   40
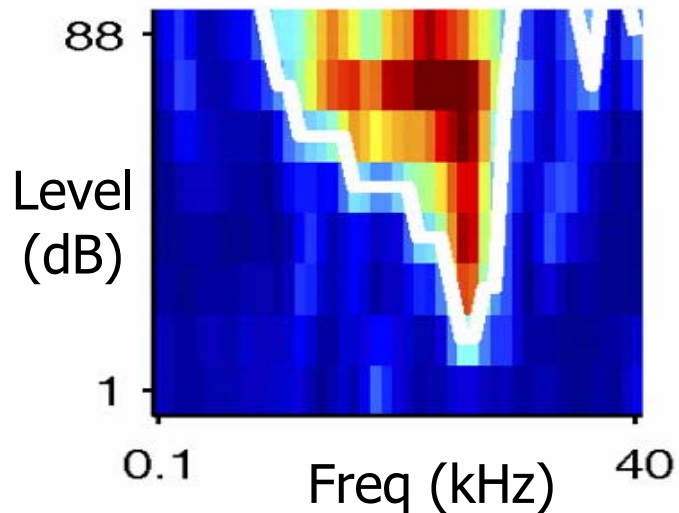
Neurons in the auditory cortex of all mammals (in this graph: the cat) serve as *filters*: They pass only signals within the frequency range of their "tuning curve" (white line).

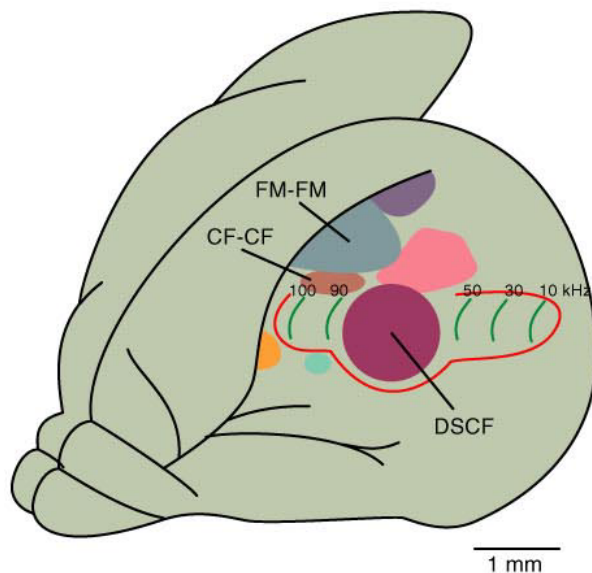But in the mustached bat (and in the CF-FM horseshoe bats) these filters are particularly sharp.

THRESHOLD (DECIBEL SOUND PRESSURE LEVEL)

100

80

60

40

20

0   20   40   60   80

FREQUENCY (KILOHERTZ)
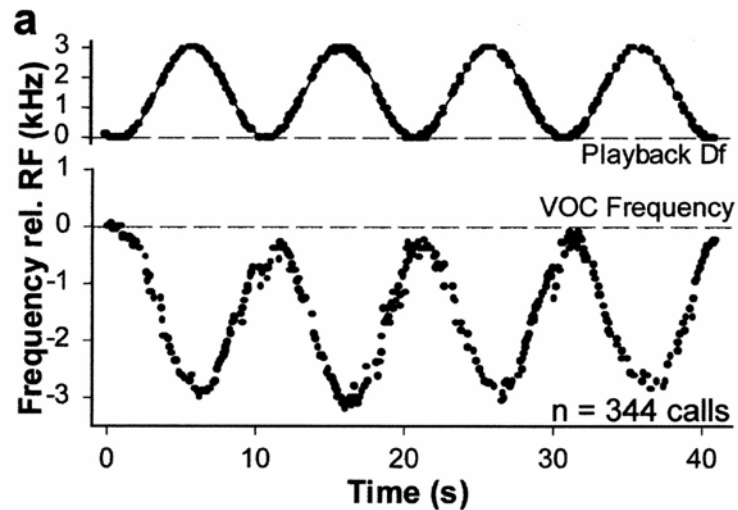
Frequency tuning of neuron from DSCF area

Neural processing of sonar signals in the mustached bat's brain
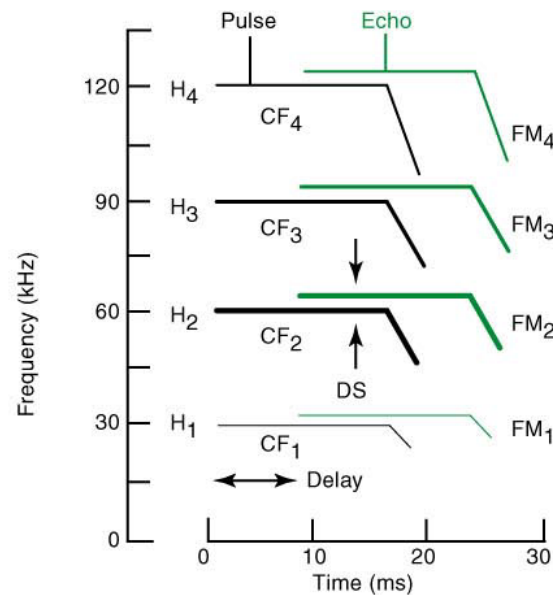
Neurons in the DSCF area specialize in detecting rapid Doppler modulations (*insect wing flutter*).

Neural processing of sonar signals in the mustached bat's brain

Doppler shift compensation in horseshoe bats
(Smotherman et al. 2003)

<u>Doppler shift compensation behavior</u>:
Mustached bat (and Horseshoe bats, other CF-FM bats) shift their frequency so as to keep the frequency of the <u>echo</u> inside the narrow frequency tuning of their neurons.
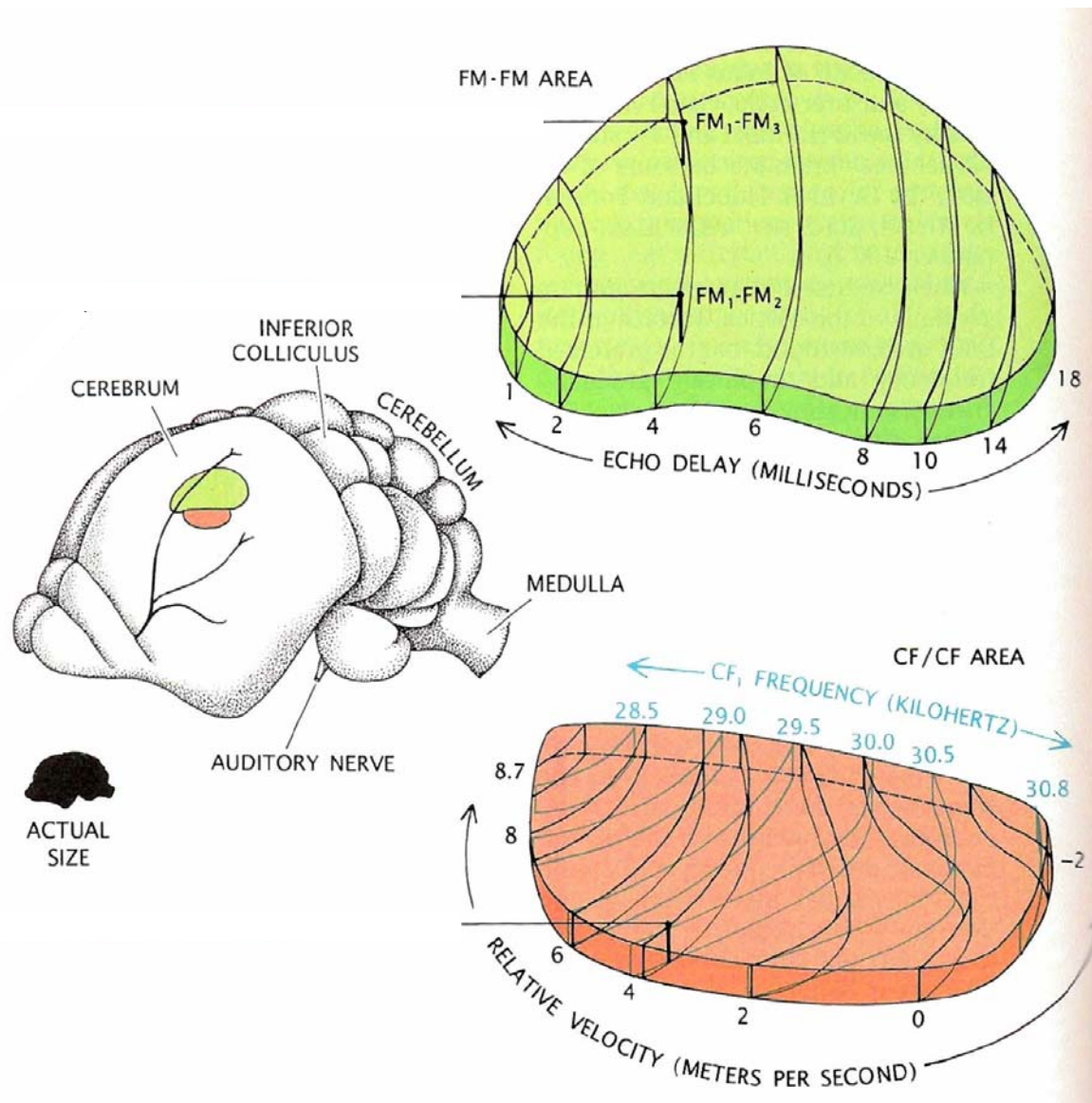
Neural processing of sonar signals in the mustached bat's brain

3. (A) <u>Modularity of auditory cortical fields</u>, and (B) <u>computational maps:</u>

<u>FM–FM areas</u>: neurons specializing in computing pulse-echo delay (*target range*).

<u>CF–CF areas</u>: neurons specializing in computing Doppler magnitude (*target velocity*).

Summary: Why study bat echolocation

- **A "top-down model" for auditory research:**

  Most auditory research (and research in sensory systems in general) is "bottom-up", where researchers are trying to guess, based on responses to simple stimuli, what the neurons are trying to do. This has led to important insights (e.g. Hubel and Wiesel) but is also very limited due to the multi-dimensionality of the stimulus space, and the nonlinearity of auditory-cortex neurons (you can't predict neural responses to complex sounds from those to simple sounds).
  IN CONTRAST: In bats, where we know sonar theory and (think that) we understand much of what the animals are doing, we can attempt top-down "intelligent guesses" about what the neurons are "trying to do".

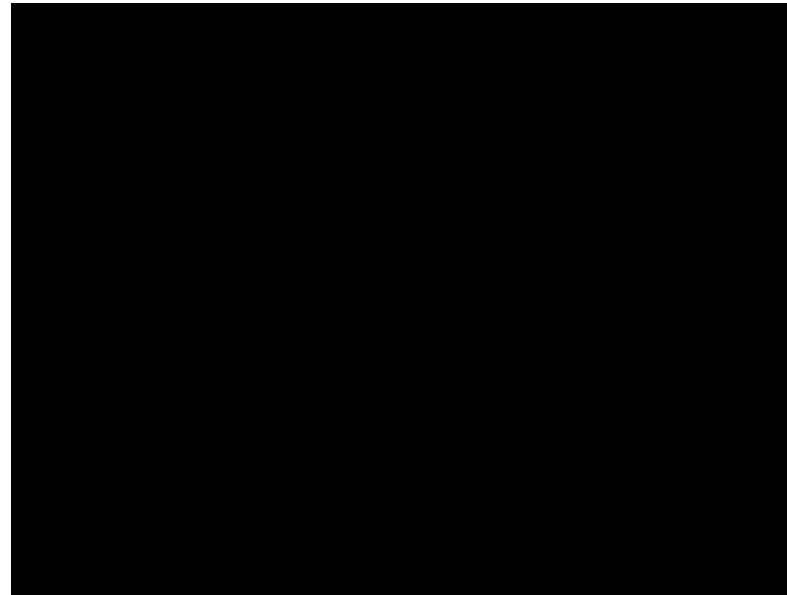- **A good animal model for active-sensing systems:**

  We can measure the sensory behavior in a freely-behaving animal, using microphone arrays (it is much more difficult to do this in other active-sensing systems, such as rat whisking system or primate vision).

Summary: Why study bat echolocation

- **The technological reasons**: The performance of bat's airborne Sonar is superior to man-made airborne Radars (or man-made underwater Sonar):

    - Bats can handle much better <u>multi-emitter and multi-target situations</u> compared to radar

    - <u>SNR</u>: ~ + 9 dB in man-made sonar, −4 dB in bat sonar.   Difference = 13 dB !

    - <u>Dynamic range</u> for echo power: 135 dB : better than radar

    - <u>Range resolution / pulse compression resolution (for 25 kHz BW)</u>
      ~ 400 ns / 40 μs = 10^{-2} : much better than radar

Summary: Why study bat echolocation

- **Lessons for use of echolocation by blind humans?**

Thank you