Introduction to Neuroscience: Behavioral Neuroscience

Echolocation in Bats

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Bats comprise ~22% of mammals and are versatile foragers

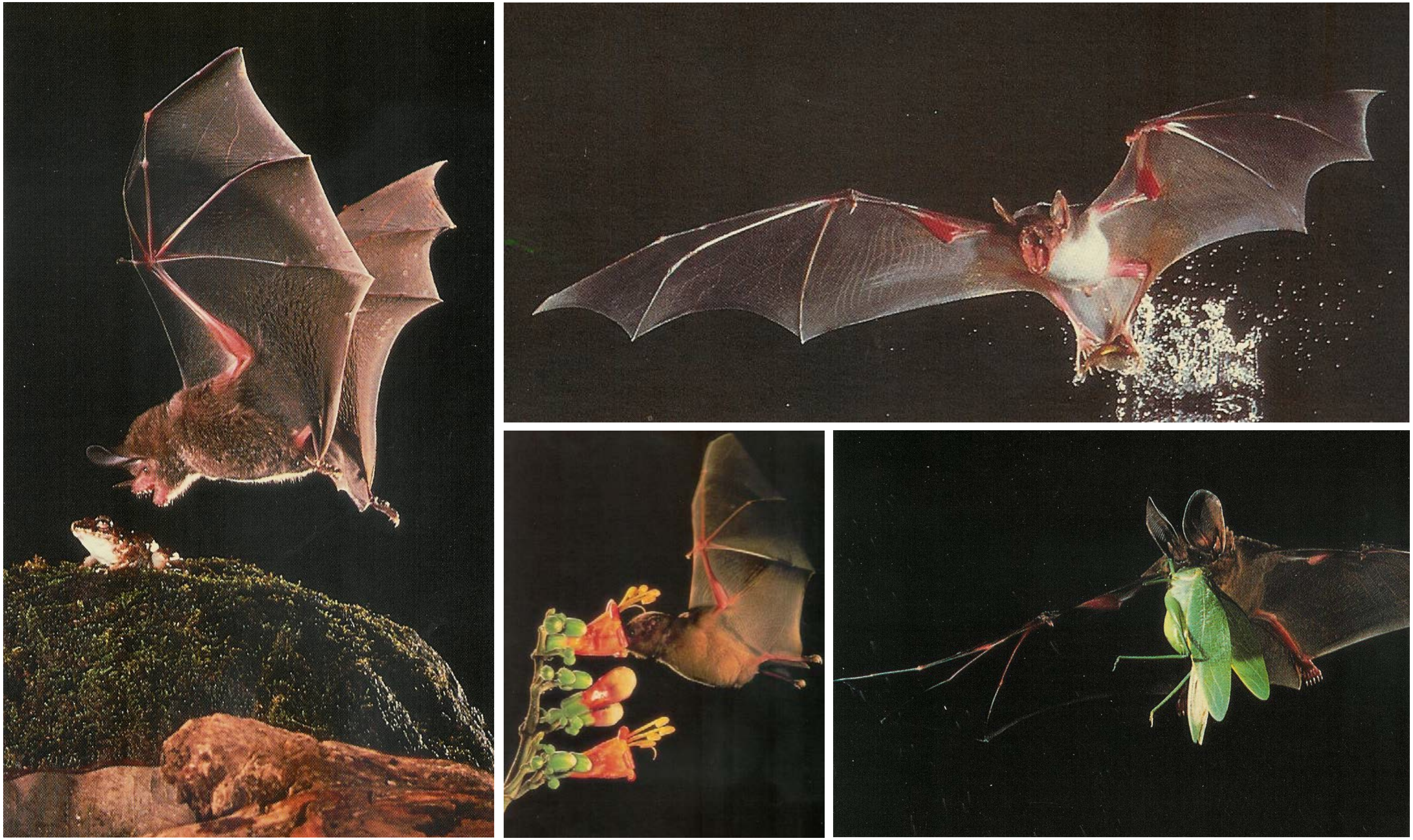


Photo: Merlin Tuttle

~1,250 species of bats in total (~ 950 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

Grey long-eared bat

Plecotus austriacus

Greater horseshoe bat

Rhinolophus ferrumequinum

Big brown bat

Eptesicus fuscus

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

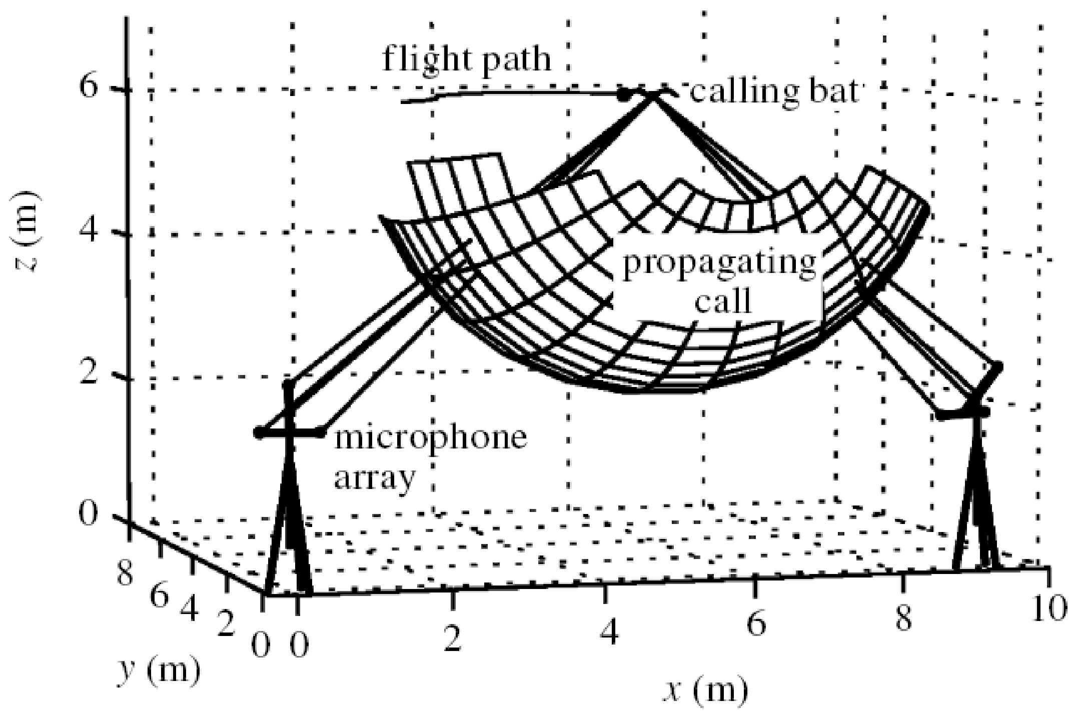
- Frequency range: ~ 5 kHz – 200 kHz (depends on species)
- Frequency resolution: 0.1 %
- Temporal resolution: 400 ns, and possibly even 10 ns (resolution of target range in bats)
- Directional (azimuthal) accuracy as good as 1-2° (compared to 10-15° in passive hearing by bats and rodents of similar size)
- Dynamic range (for echo sound intensity): 140 dB

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

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

- Dynamic range (for echo sound intensity): 140 dB

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 140 dB SPL

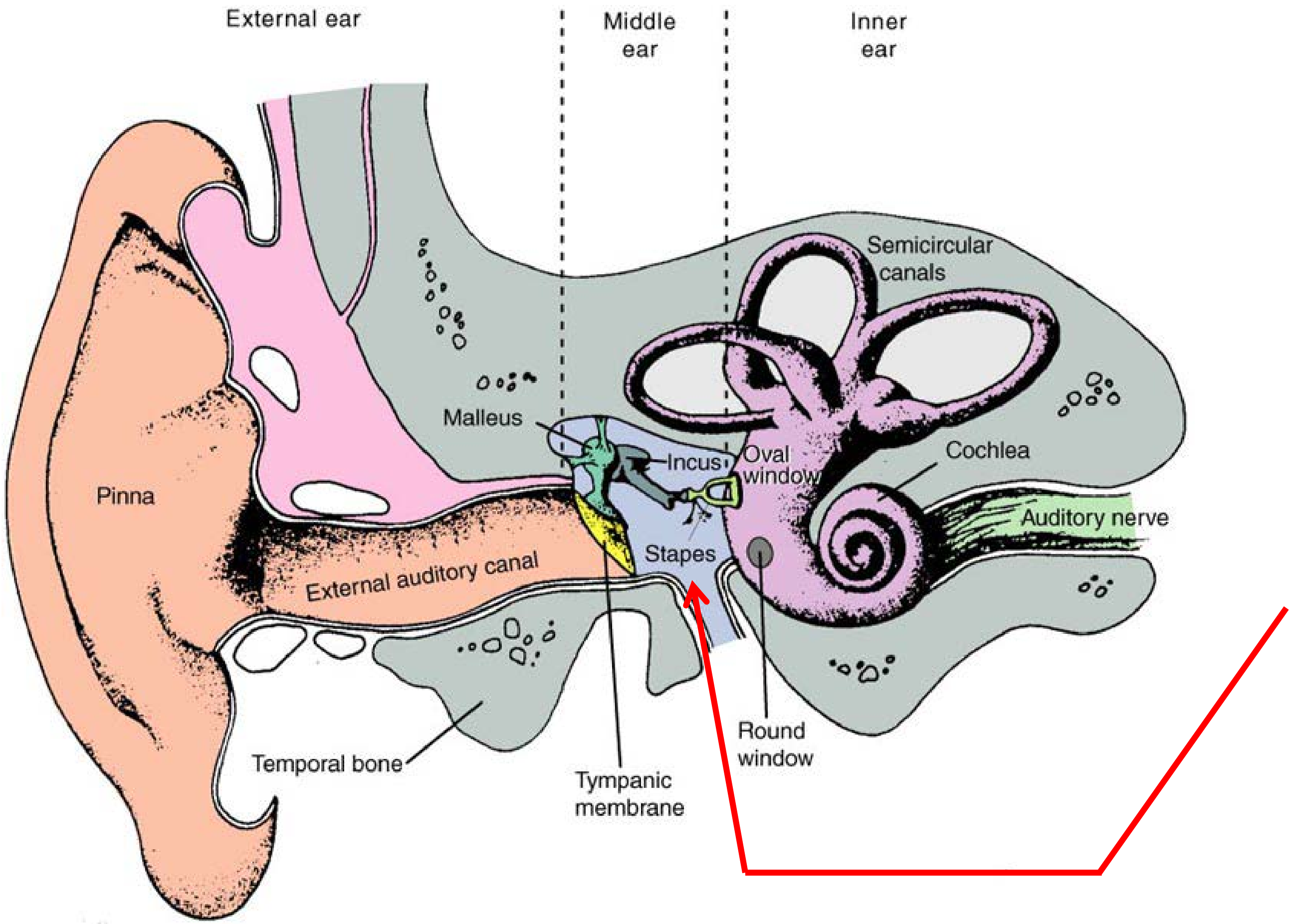


To actually measure the emitted power in free-flying bats, researchers have to reconstruct the bat's 3-D position: for this, they use arrays of microphones → Differential Time Of Arrival (DTOA) localization technique in 3-D (similar to the way GPS works).

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

- Dynamic range (for echo sound intensity): <u>140 dB</u>

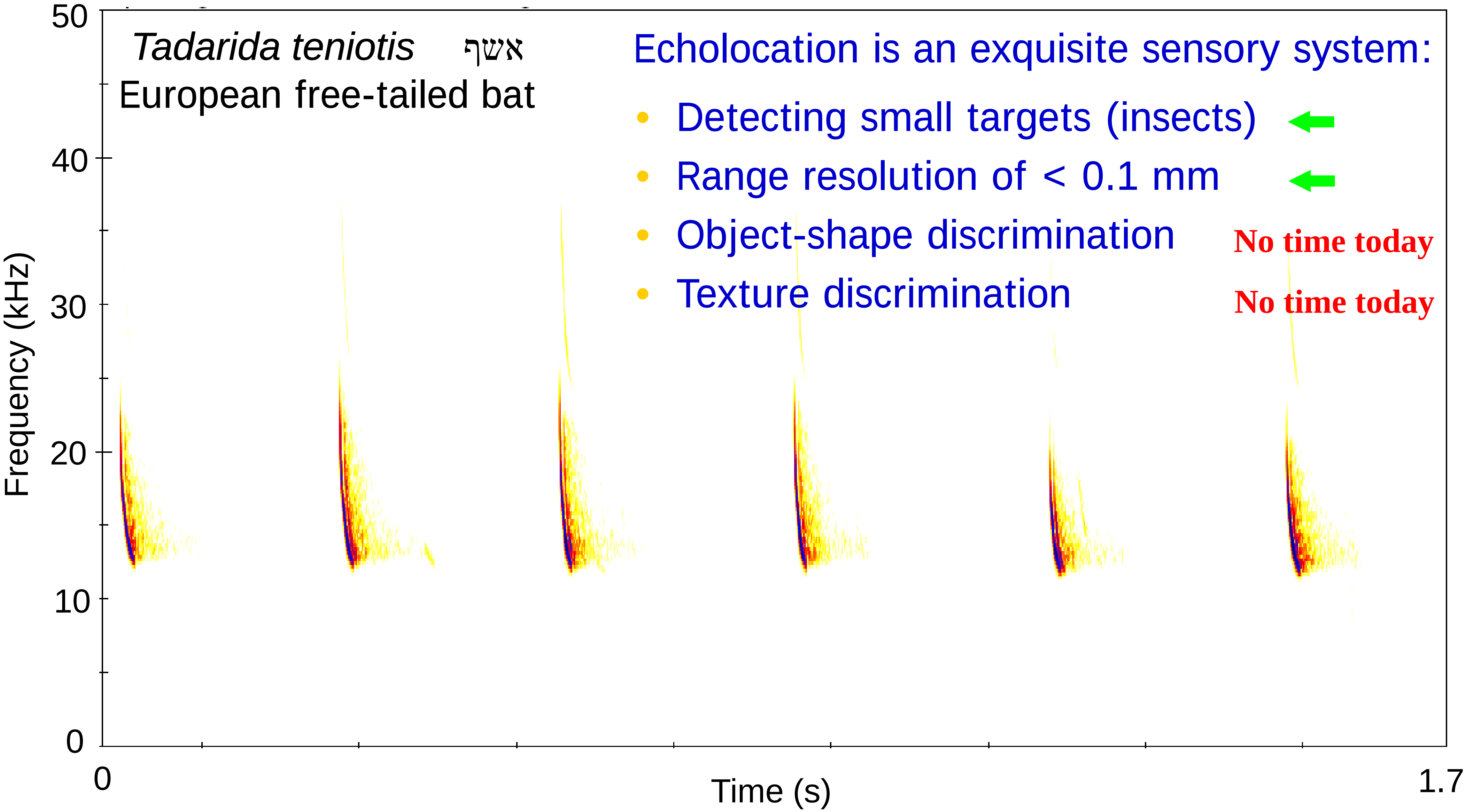
  Bats can detect echoes from ~ 0 dB SPL (20 μPa) up to perfectly-reflected echoes of their own calls, which have an emitted power of 140 dB SPL



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



Talk Outline

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

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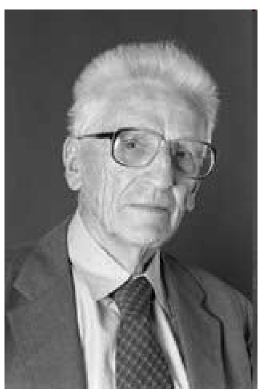
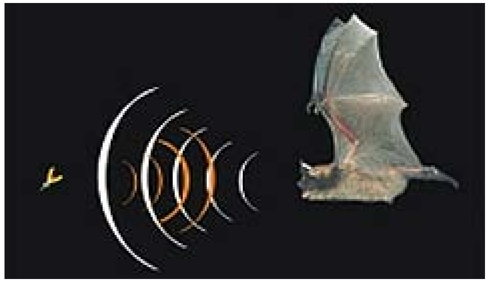
→ I will *not* have time to talk today about other echolocating animals, such as: dolphins (and other odontocete whales), shrews, swiftlets, oilbirds.



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

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

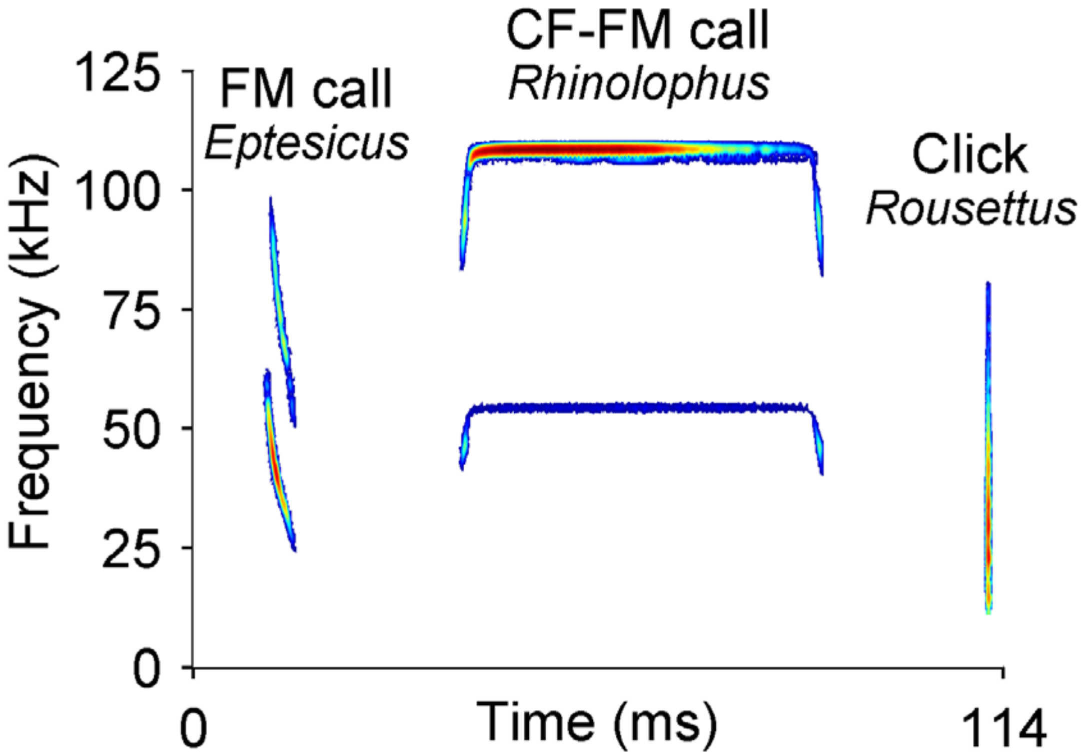
T = pulse-echo delay

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



(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

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

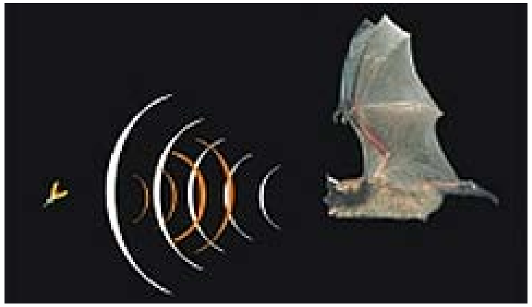
Many theoretical similarities between RADAR and SONAR.

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 ~$1/R^2$ via geometric spreading ("spreading loss")

… reduced also via atmospheric attenuation, $\exp(-2\alpha R)$

… a fraction σ is reflected back to the bat

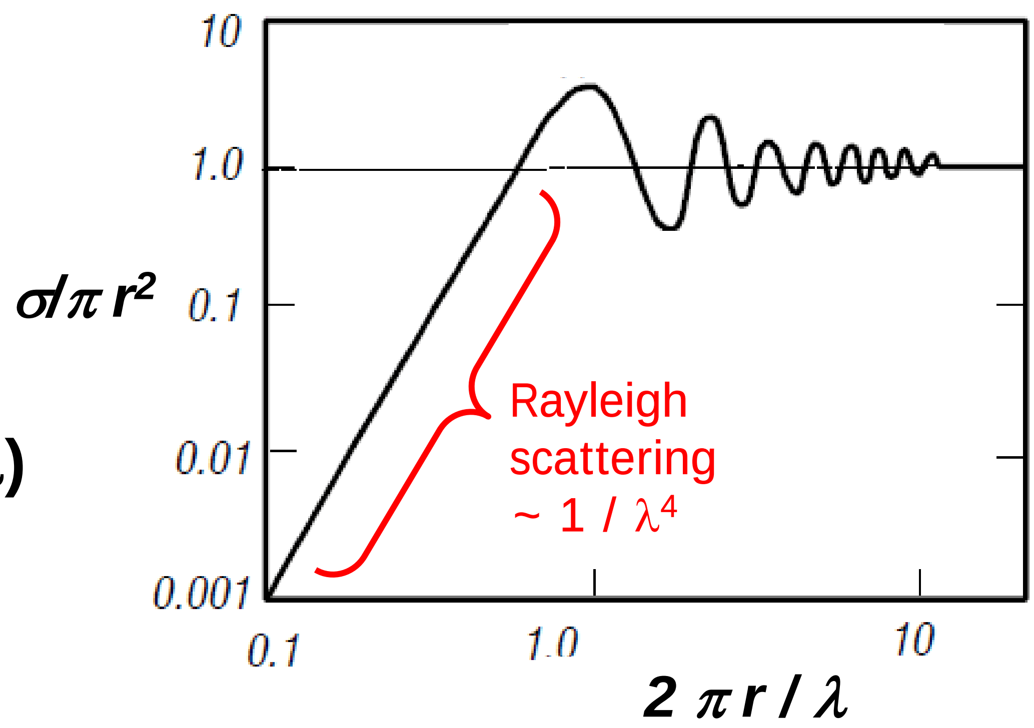
… reduced *again* ~$1/R^2$, giving a total spreading loss ~$1/R^4$

… received by an antenna with area A_{ear} (ear size)

Most elements of the Sonar Equation depend on frequency

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

Sonar cross section for sphere with radius r



σ = Sonar cross section = $\sigma(f)$

Depends on:

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

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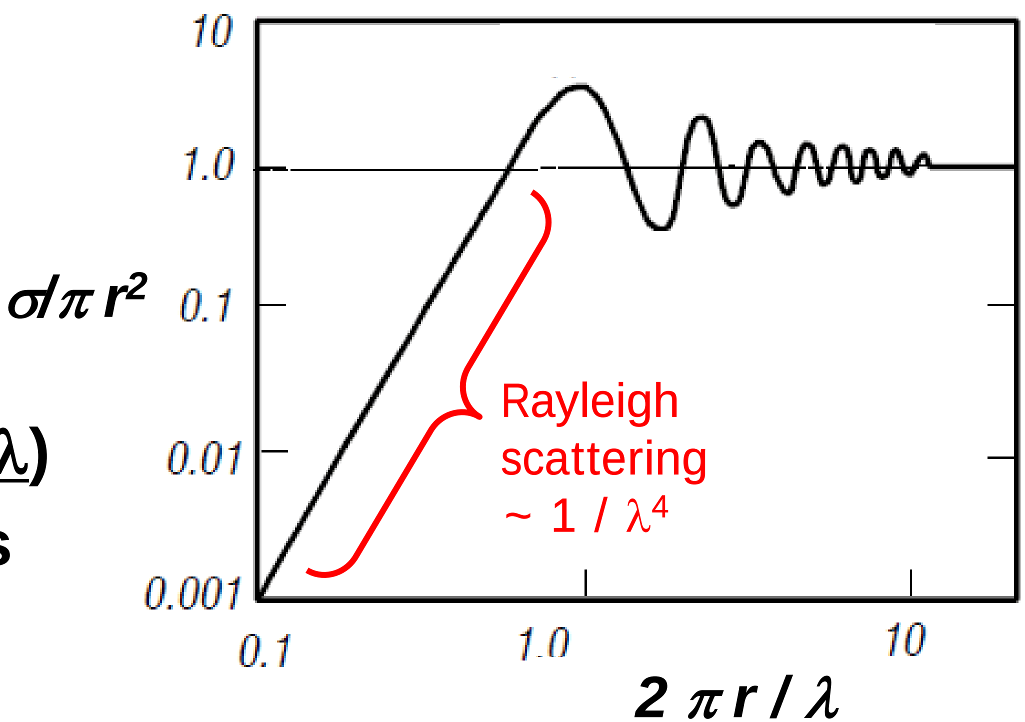


→ Bats use ultrasound (<u>small λ</u>) in order to detect small targets (<u>small r</u>)

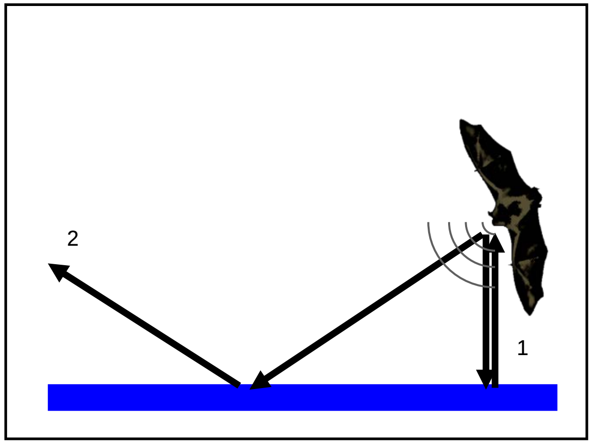
Most elements of the Sonar Equation depend on frequency

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

σ = Sonar cross section = $\sigma(f)$

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

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



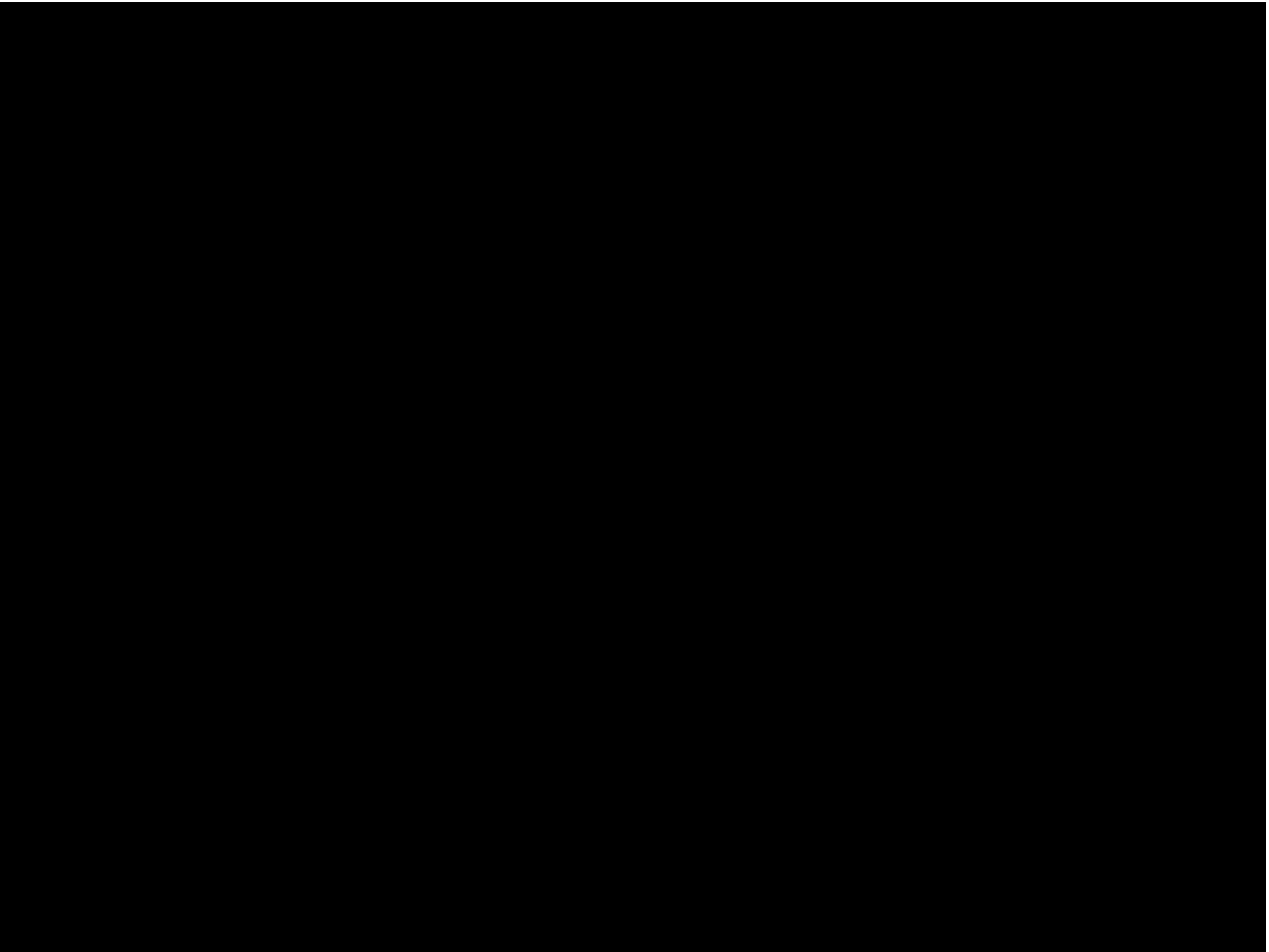
Most elements of the Sonar Equation depend on frequency

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

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

Bat drinking from water

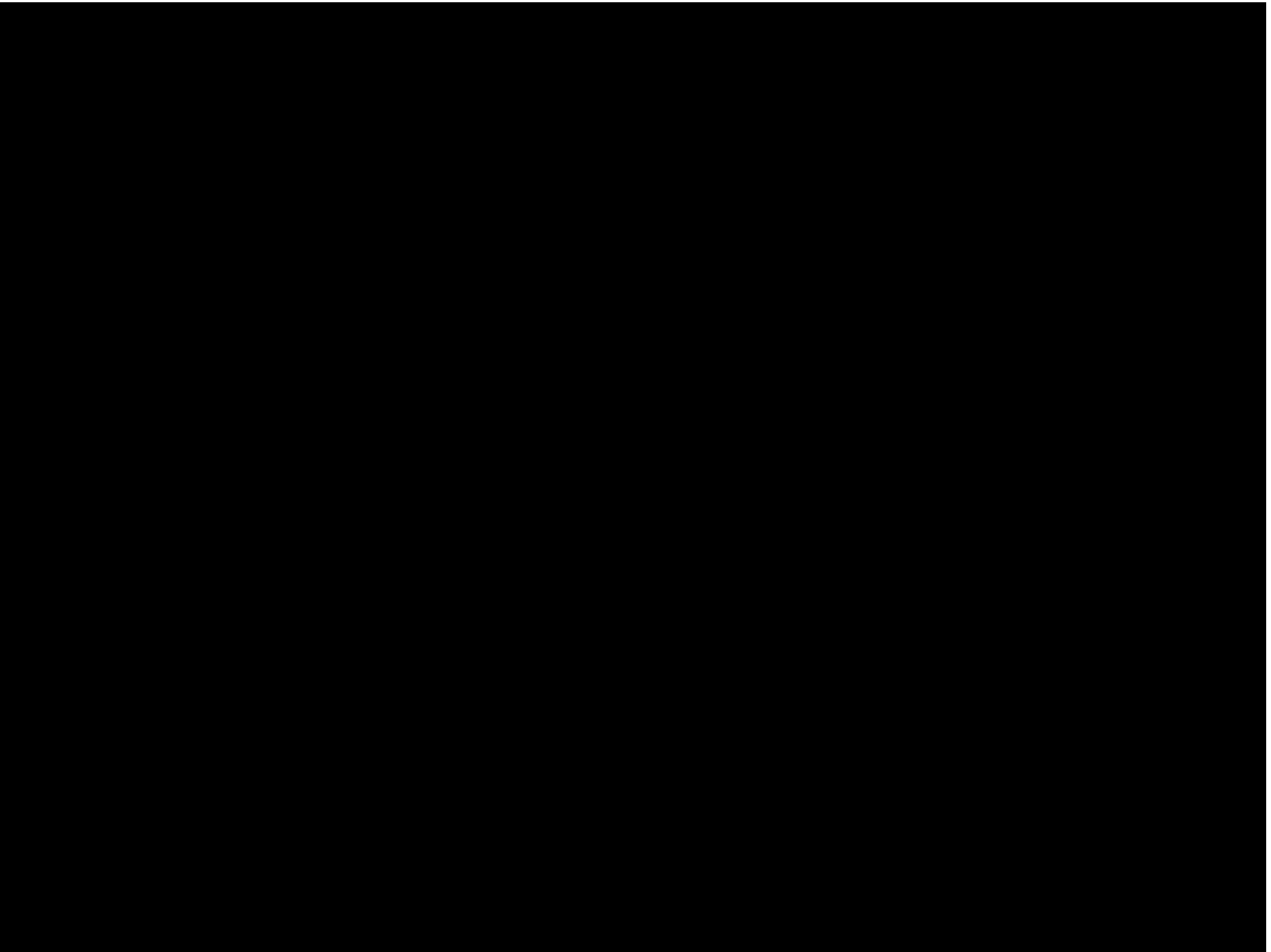
Most elements of the Sonar Equation depend on frequency



Bat drinking from smooth water

Greif et al, 2010

Most elements of the Sonar Equation depend on frequency



Bat attempts drinking from a smooth metal plate – indicating that the sonar smoothness of the surface is the indicator of "water" for bats.

Play directly from file

Most elements of the Sonar Equation depend on frequency

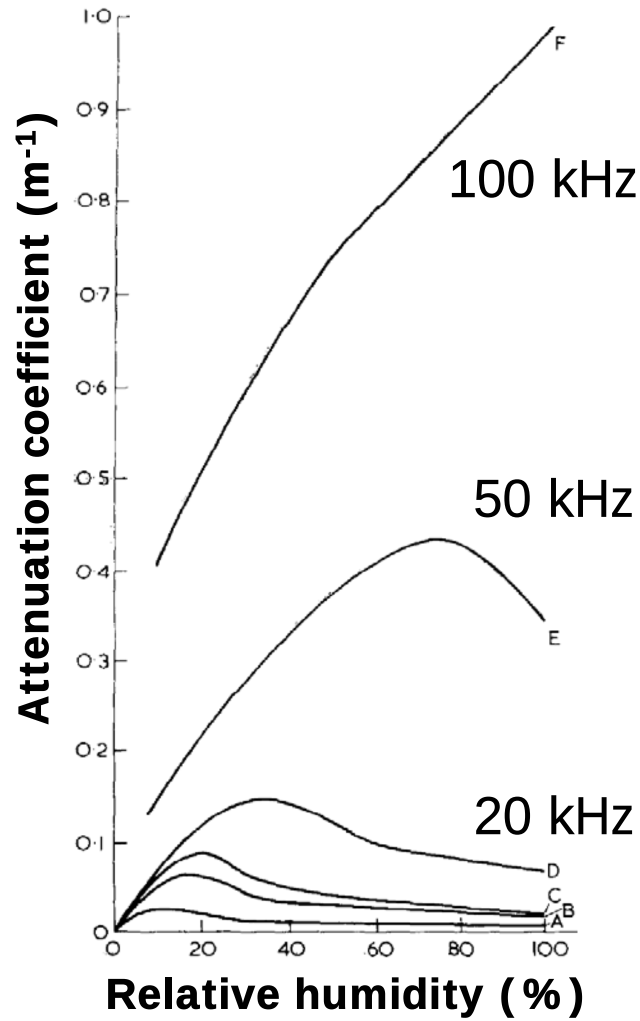
$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, \exp(-2\alpha R)}{R^4}$$

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

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

↓

- 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.

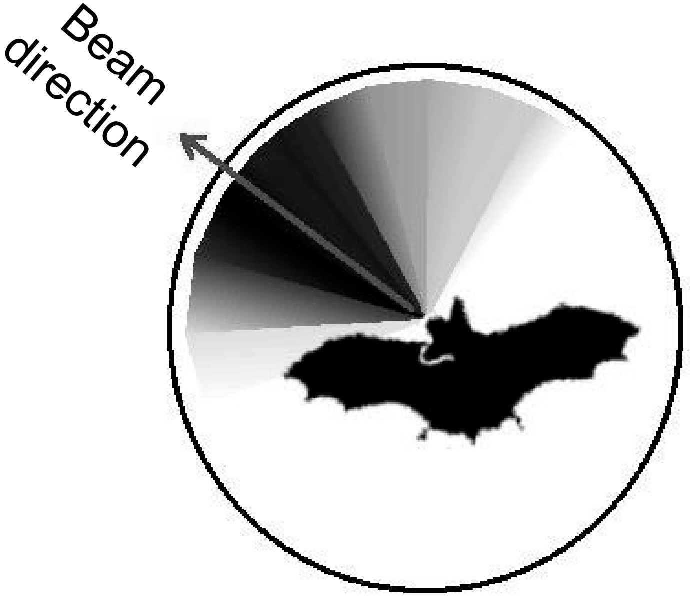


Most elements of the Sonar Equation depend on frequency

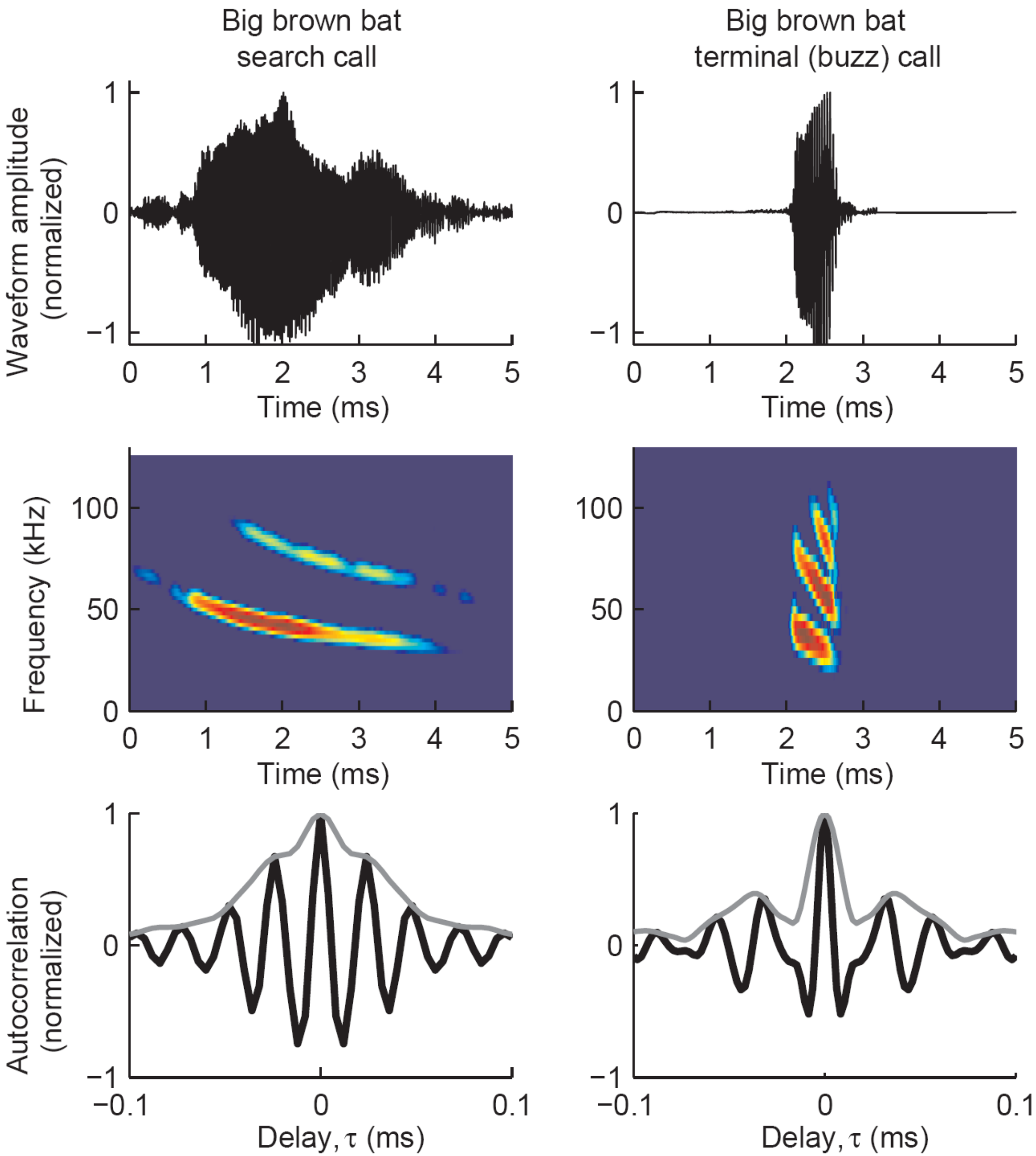
$$P_{echo} \sim \frac{P_{call}\, G_{tr}\, A_{ear}\, \sigma\, exp(-2\alpha R)}{R^4}$$

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

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



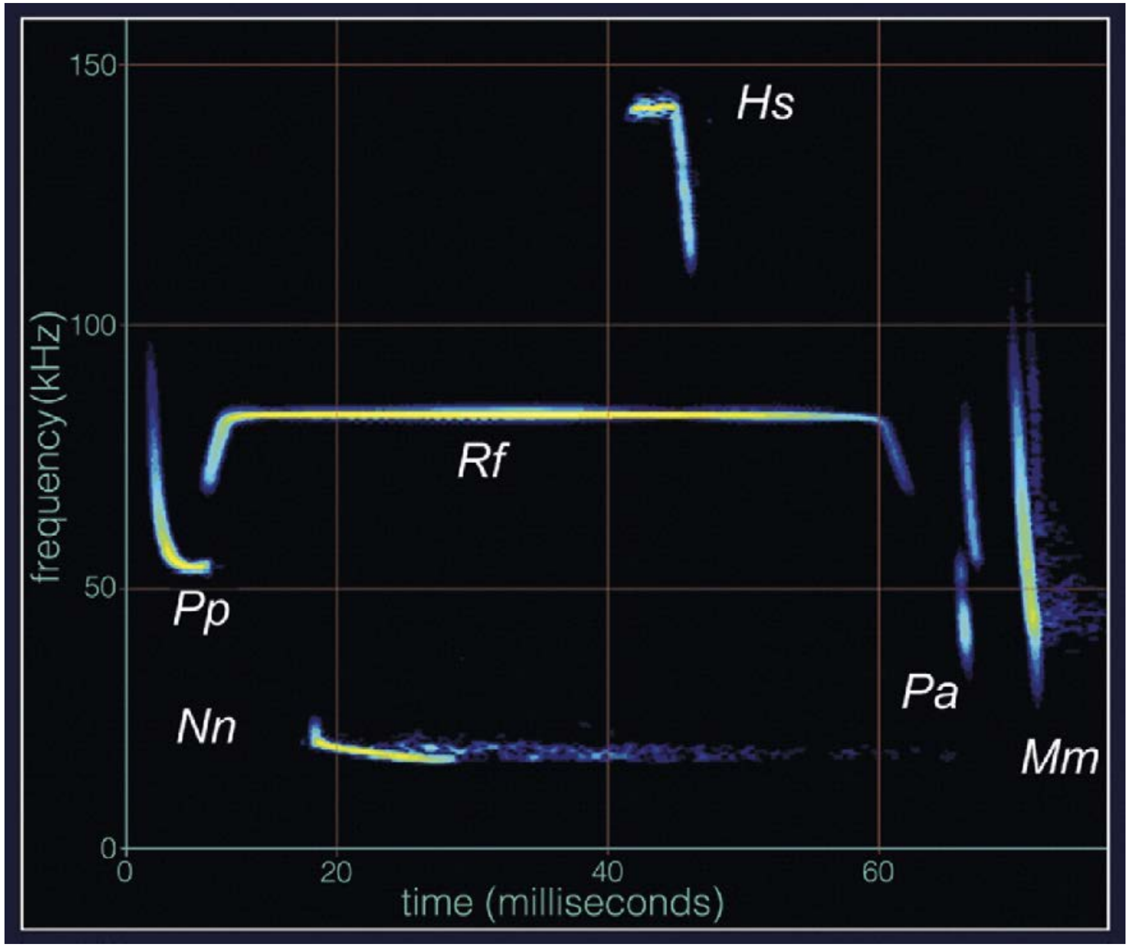
Pulse compression: Increasing P_{echo} beyond the Sonar Eq.



Pulse compression:

- Increases P_{echo} beyond what is given by the Sonar Equation.
- Improves the time resolution!

Pulse compression: Increasing P_{echo} beyond the Sonar Eq.



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:

- Time resolution is inversely proportional to chirp bandwidth: $\Delta t \sim 1 / \Delta f$

Some tradeoffs in biosonar signal design

- Call frequency:

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

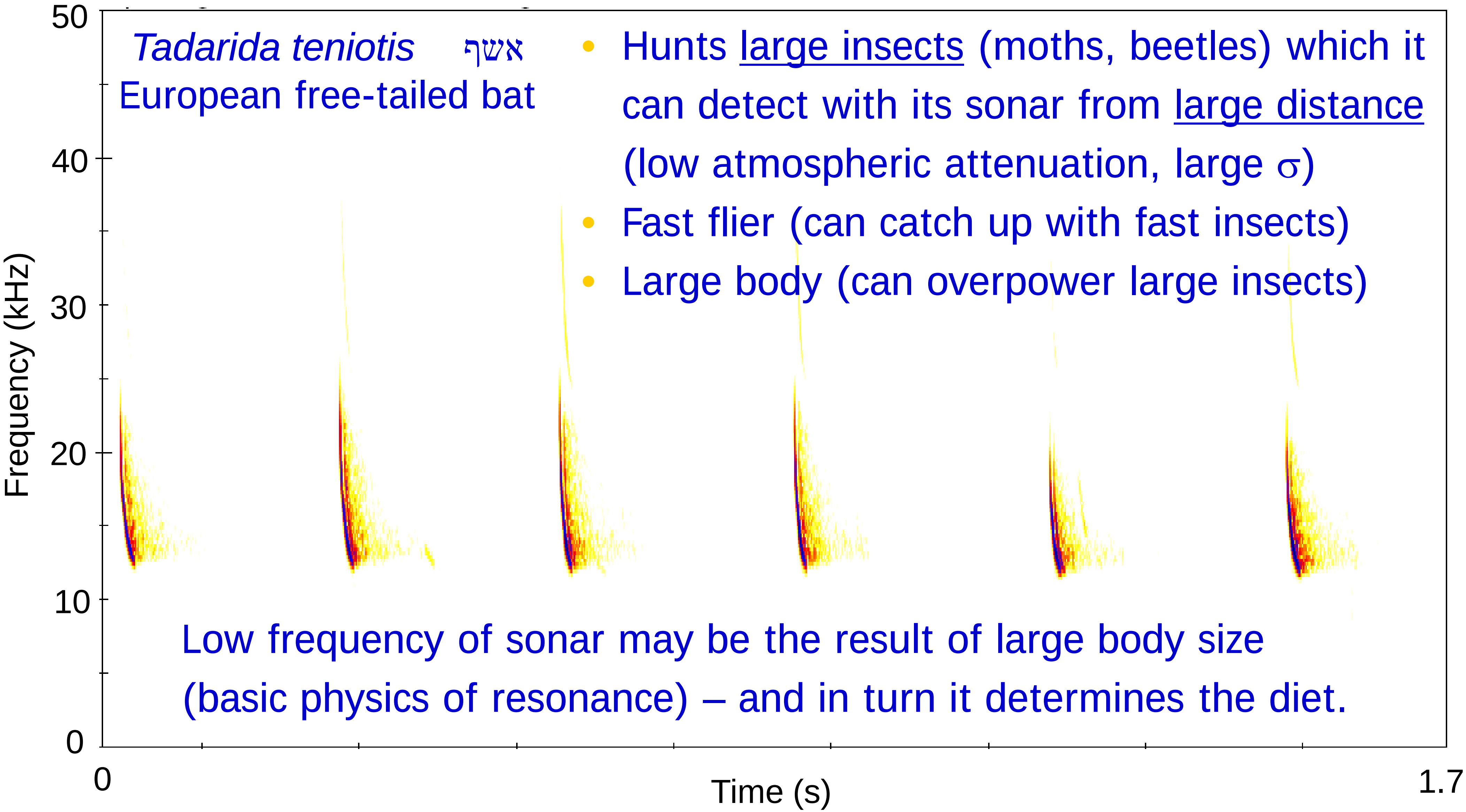
  Frequency ↓ allows <u>longer detection range</u> (less <u>atmospheric attenuation</u>).

- 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



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).**

What signal parameters should we expect bats to change adaptively according to needs / task ?

- Frequency
- Bandwidth
- Intensity (“automatic gain control” for keeping fixed echo intensity)
- Inter-pulse interval (sets the “update rate” of incoming information)
- Pulse duration (determines the duration of the bat’s “deaf times”)

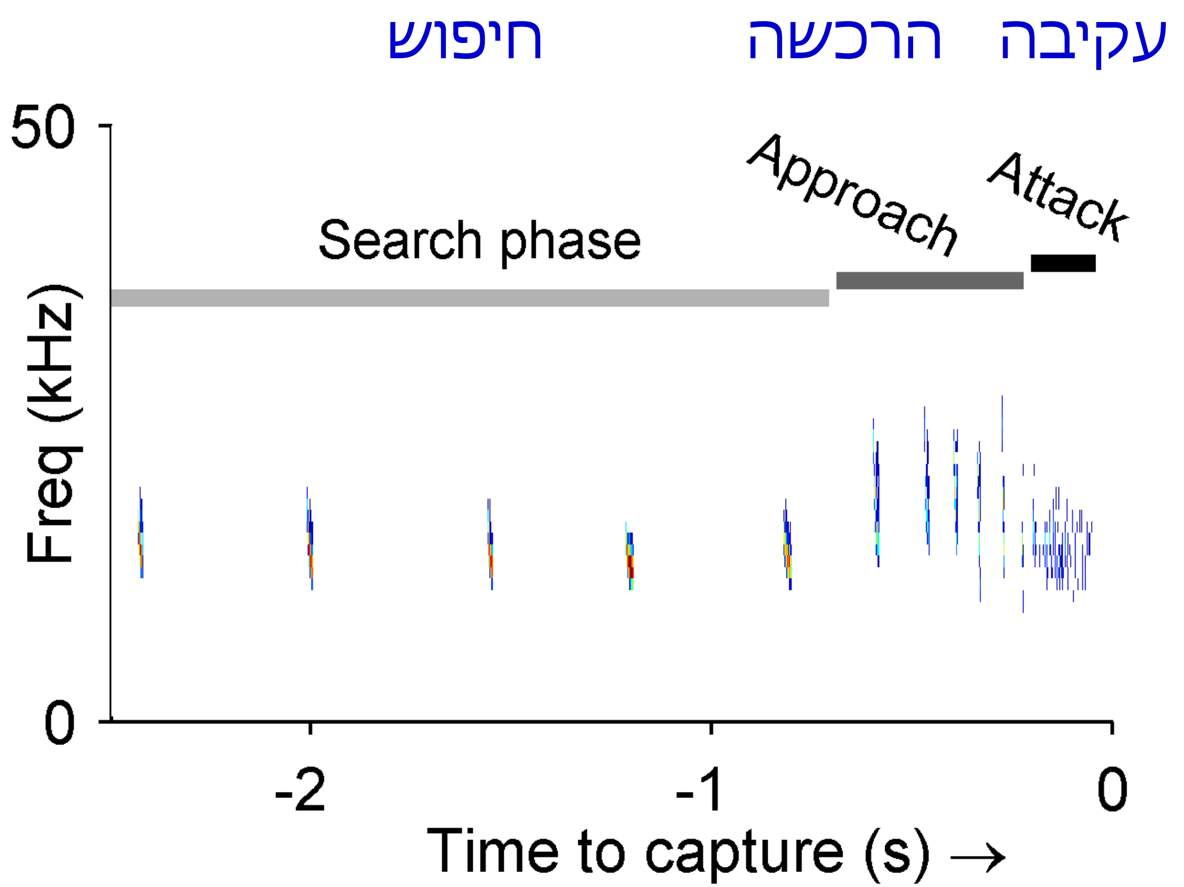
- Direction of emission beam in space (affects echo strength)
- Angular width of emission beam (affects “field of view”)

Let’s now look at examples demonstrating that bats indeed can adaptively change each of these parameters.

Bats change their signal design adaptively when attacking an insect.

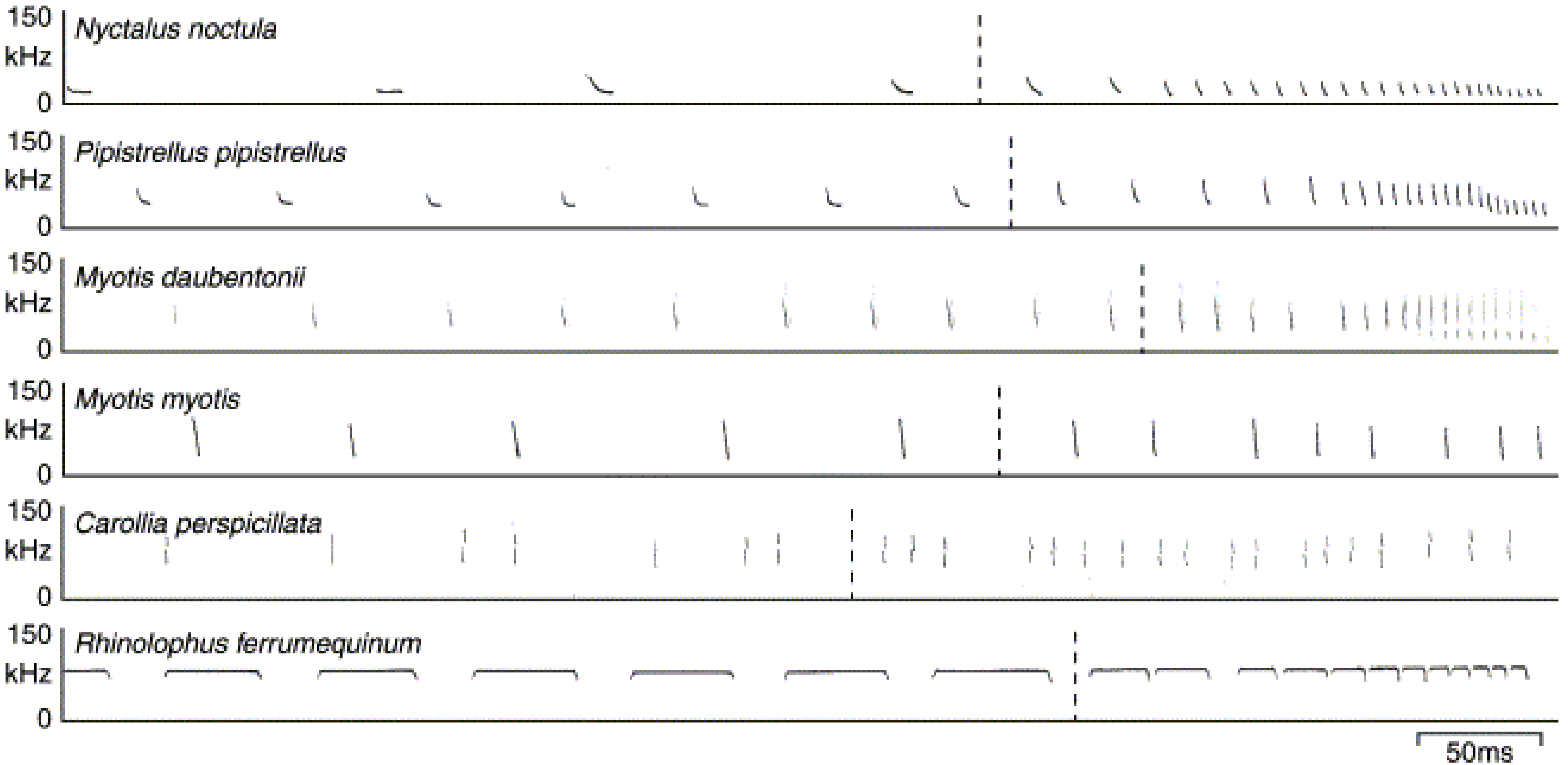
Insect-eating bats exhibit typical phase transitions:

Search → Approach → Tracking (Attack)

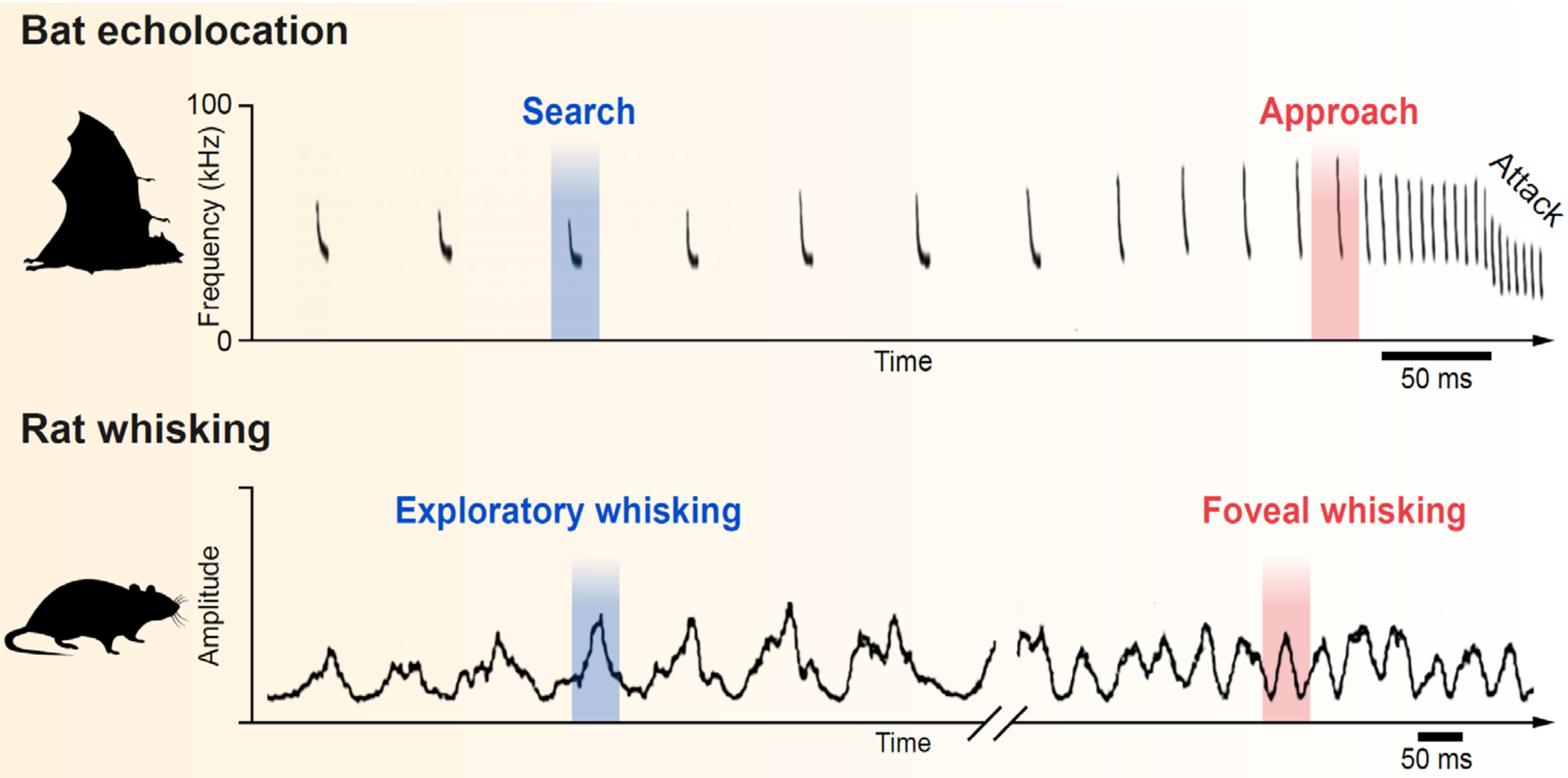


(Ulanovsky & Moss, *PNAS* 2008)

Examples of six more bat species showing sonar phase transitions: *Search → Approach → Tracking (Attack)*



Increase in sensory acquisition rate when approaching targets: A common theme across active-sensing systems ?

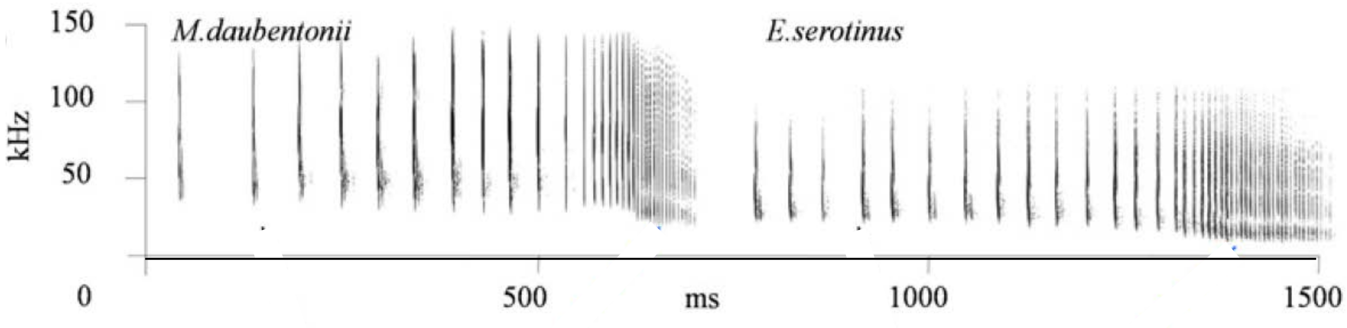


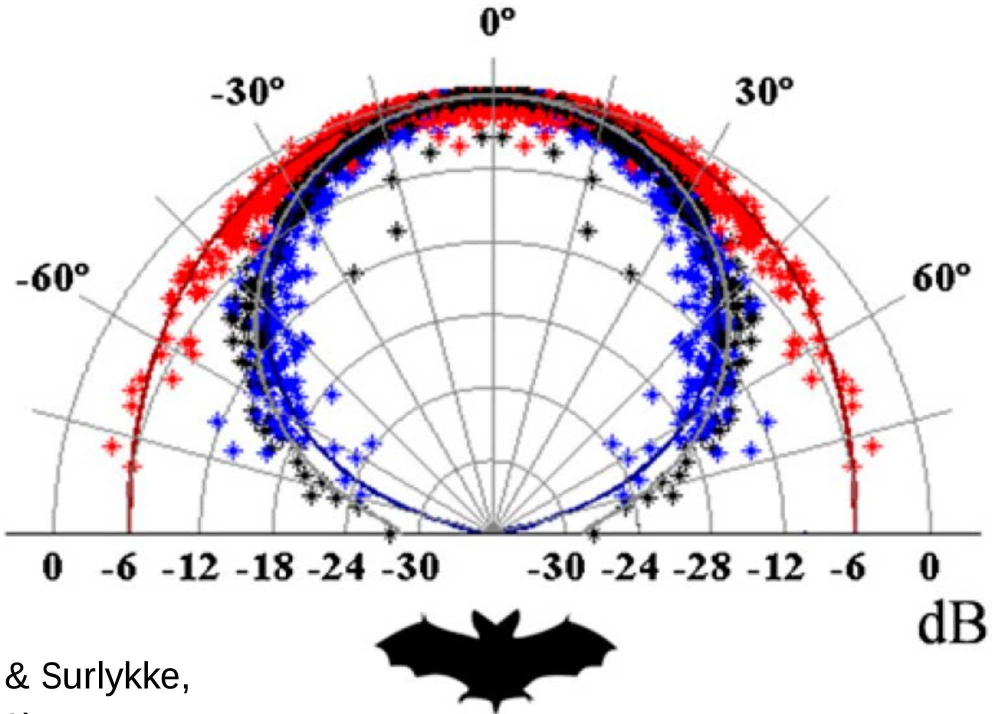
Rationale for the observed adaptive changes in signal design

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 the outgoing call (when the bat almost cannot hear anything) and incoming echo, allows tracking insects at closer ranges – almost until the insect’s interception.
- <u>Lower intensity</u> = “automatic gain control” for keeping fixed echo intensity.
- <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.

Lower call frequency means wider sonar beams: Theory and experiments





Eptesicus serotinus:

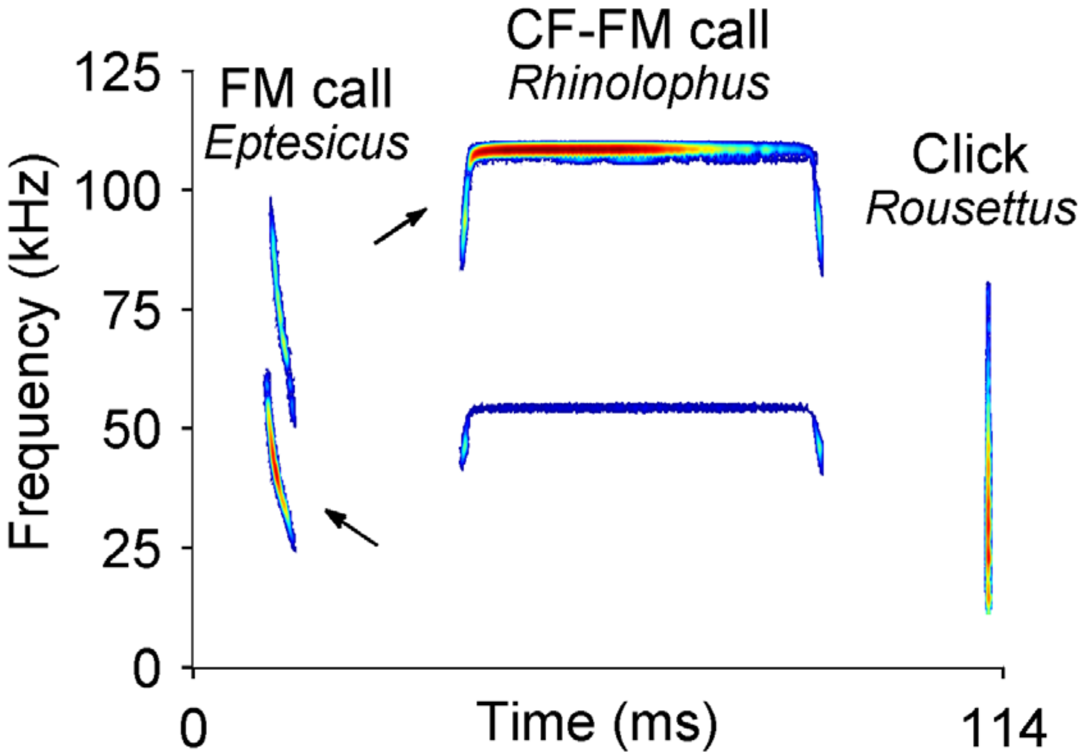
Red – 17.5 kHz

Blue – 35 kHz

Black line – theory (piston model)

(Jakobsen & Surlykke, *PNAS* 2010)

Basic types of echolocation calls (REVISITED)



(Ulanovsky & Moss, *PNAS* 2008)

Basic types of echolocation calls (Cont.)

FM bats :

- Emit their sonar calls through the larynx (i.e. through the vocal cords).
- FM bats mostly use a nonlinear chirp (but some species use a linear chirp) $\rightarrow$ pulse compression.
- In behavioral experiments, FM bats were shown to discriminate jitter in target range down to ~400 ns (less than 0.1 mm), and possibly even 10 ns.
- FM bats can do object recognition, and even object classification.
- FM bats can do texture discrimination (discriminate roughness of surfaces).

Basic types of echolocation calls (Cont.)

CF–FM bats :

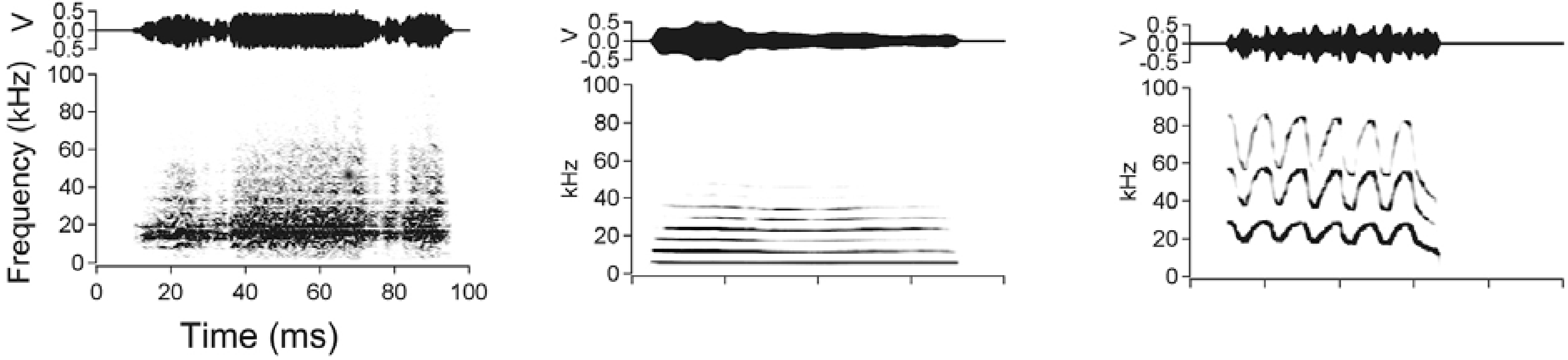
- Emit their sonar calls through the larynx.
- These bats can compute the Doppler shift (target velocity).
- They can detect Doppler modulations caused by the insect’s wing flutter.
- These bats can even tell apart different insect species based on their different flutter rate.

Basic types of echolocation calls (Cont.)

Clicking bats :

- Emit their sonar signals via tongue-clicks.
- Ultra-short clicks (50-100 μs) replace the mechanism of pulse compression of FM and CF-FM bats.
- Interesting strategy for sonar beam-steering (see below).

(Bats also have interesting communication calls)



Examples of mustached bat <u>communication calls</u> (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* its echolocation calls – which are usually ultrasonic).

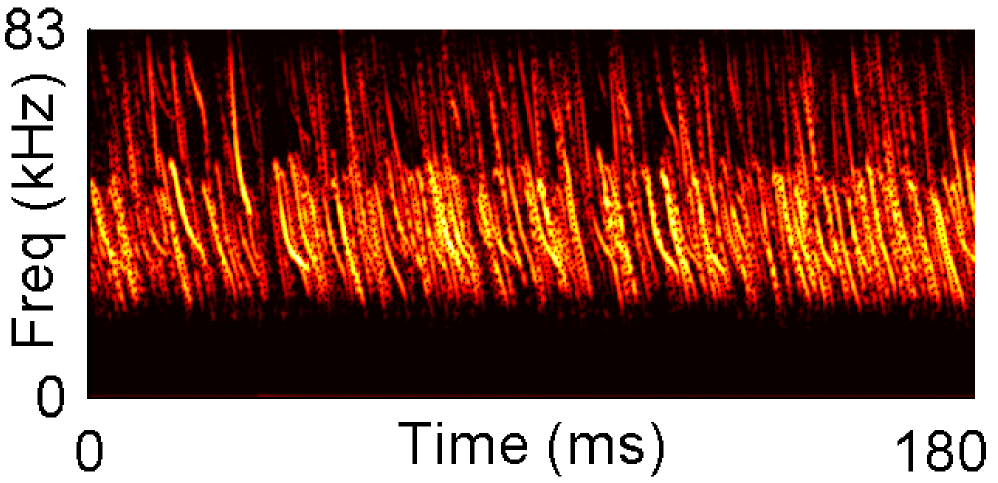
Usages of bat sonar

- 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)

↓

"Cocktail-party nightmare"

Collision avoidance – comprehending the incomprehensible

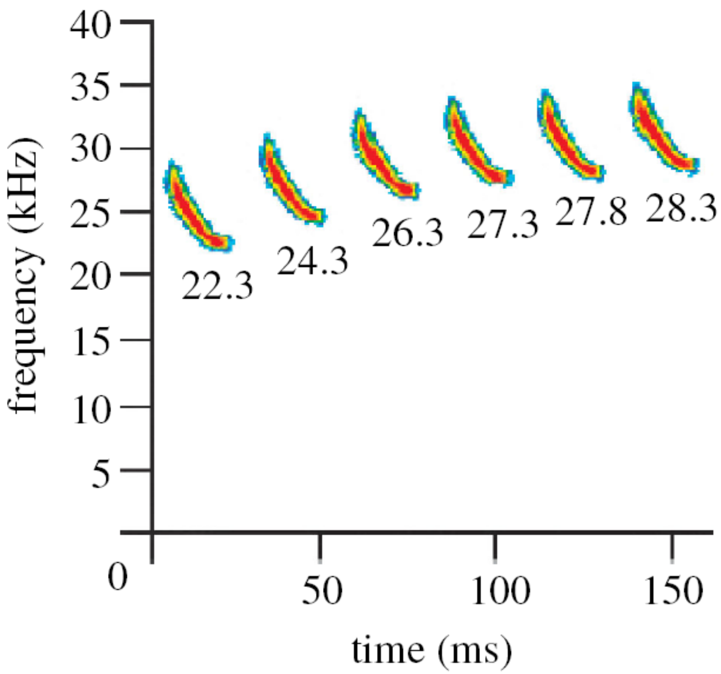
Photo: Merlin Tuttle

What are the possible solutions?

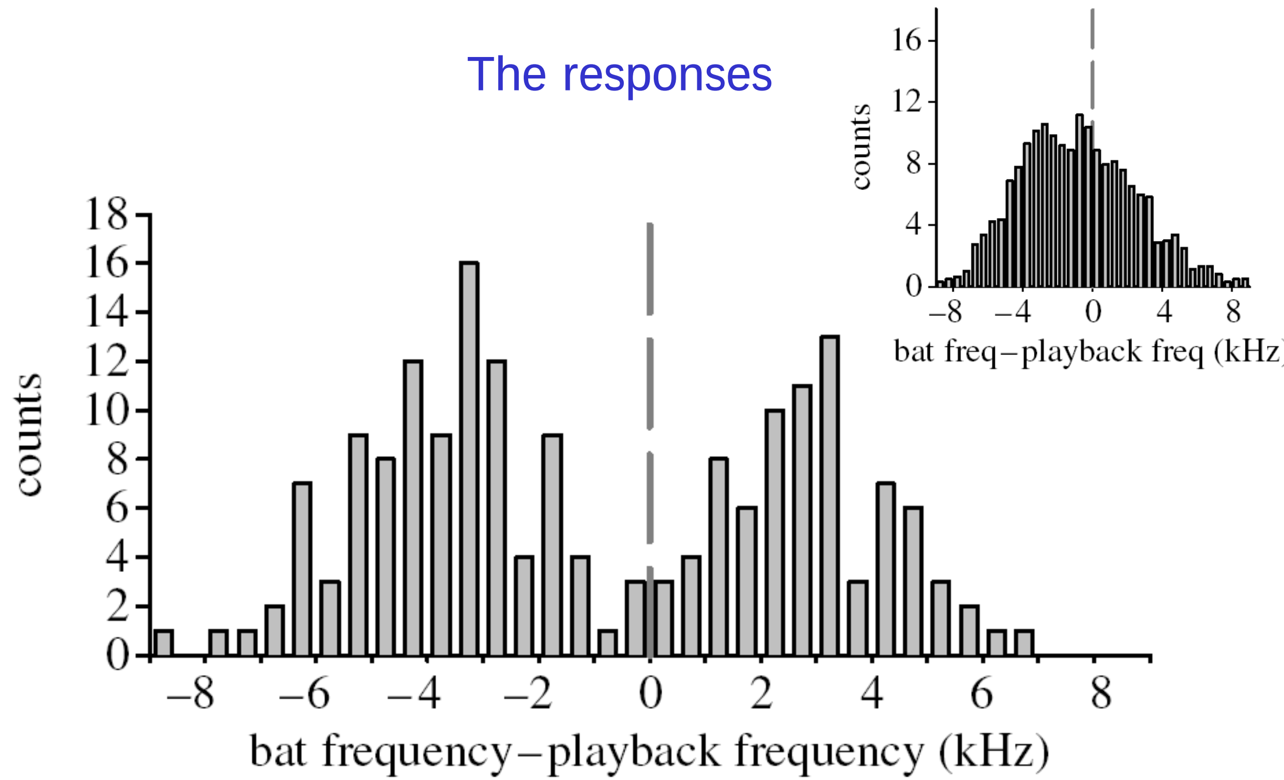
- Spatial filtering (directional hearing, moving the ears, directional emissions, sequential scanning)
- 'Tag' the timing of the bat's own calls (call 'signature', efference copy, combination-sensitive neurons)
- Integrate information across calls
- Jamming avoidance response (JAR)
- Use spatial memory – and ignore the calls (happens in some caves)

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

The stimuli

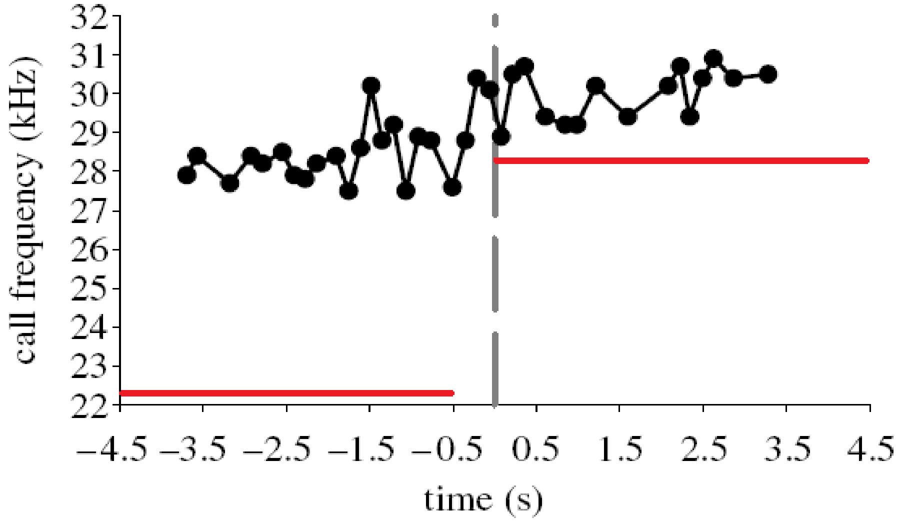


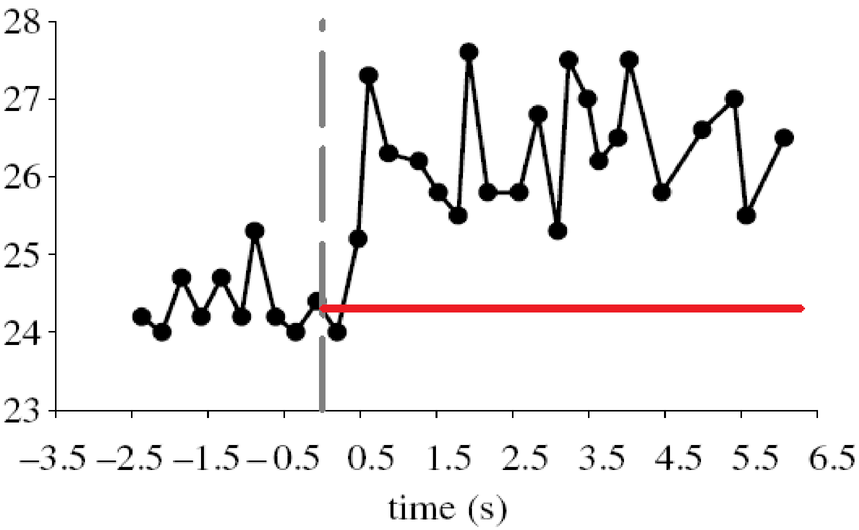
The responses



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: Bats can adaptively change their sonar signal design according to their needs.

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

Some tradeoffs in biosonar signal design: Revisiting the complexities of choosing the call FREQUENCY

- 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>).

  Frequency ↓ allows <u>wider "field of view</u>" (broader spatial emission beam).

  Frequency ↑↓ allows <u>jamming avoidance response</u>.

  Frequency ↑↓ allows <u>stabilizing the *echo* frequency</u> (see below).

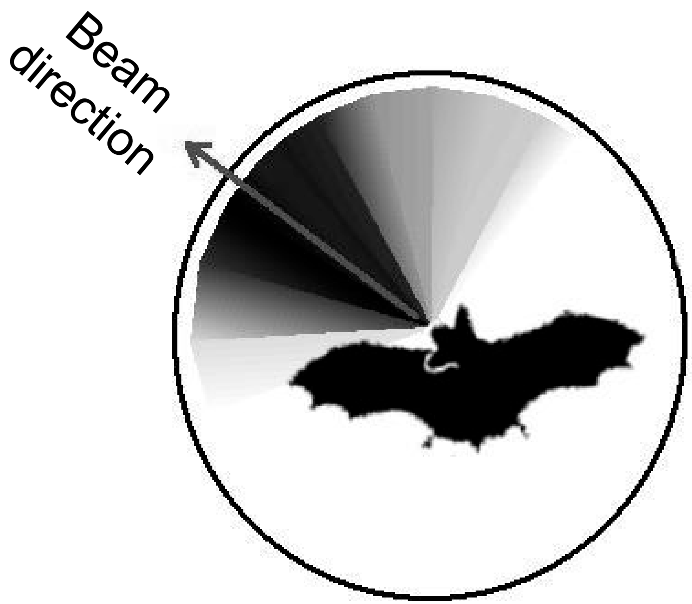
Conclusions:

- Bats dynamically change the frequency of their echolocation calls, under various situations – but they do it for a number of *different* reasons → A Complex system!

- BUT: Many of these tradeoffs can be <u>quantified</u>, based on the mathematical equations of sonar theory: There is a governing <u>theory</u> that can serve as benchmark.

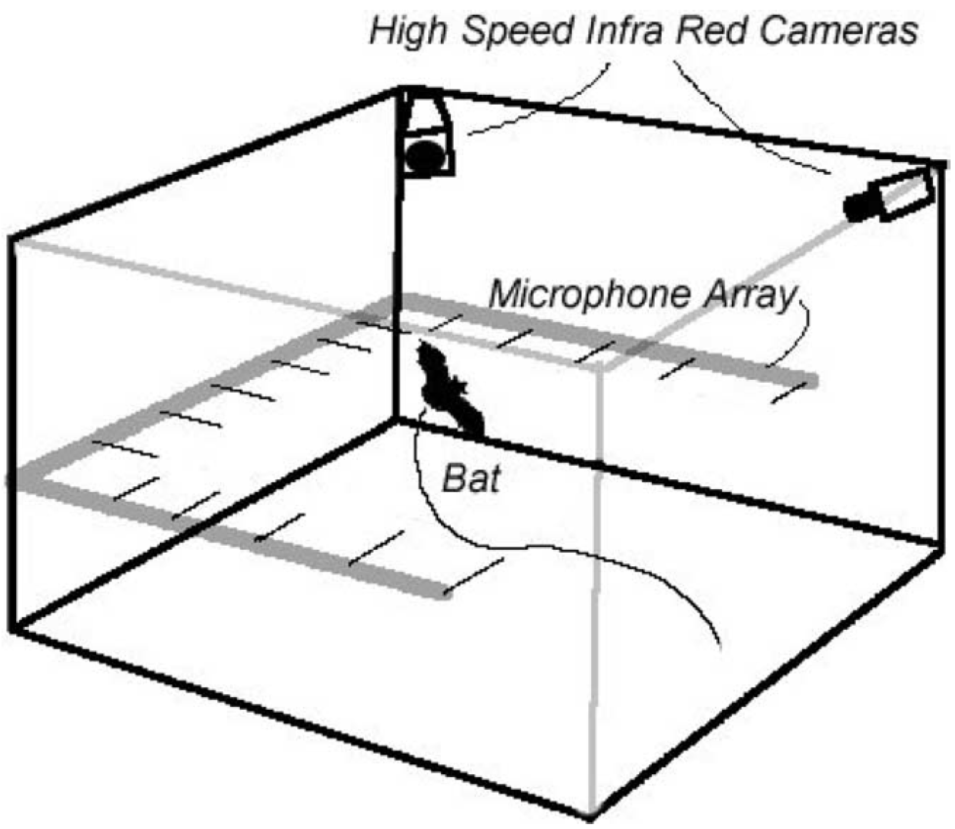
Emission beams used by bats

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



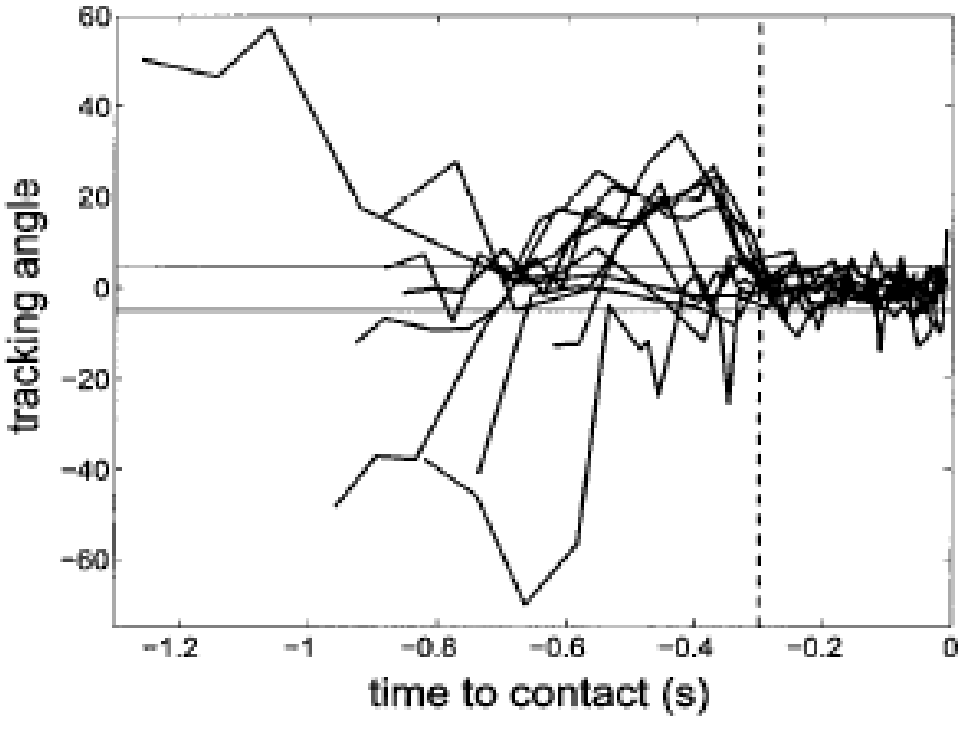
Real beam shape measured from a big brown bat

Arrays of microphones are used to measure the beam shape.



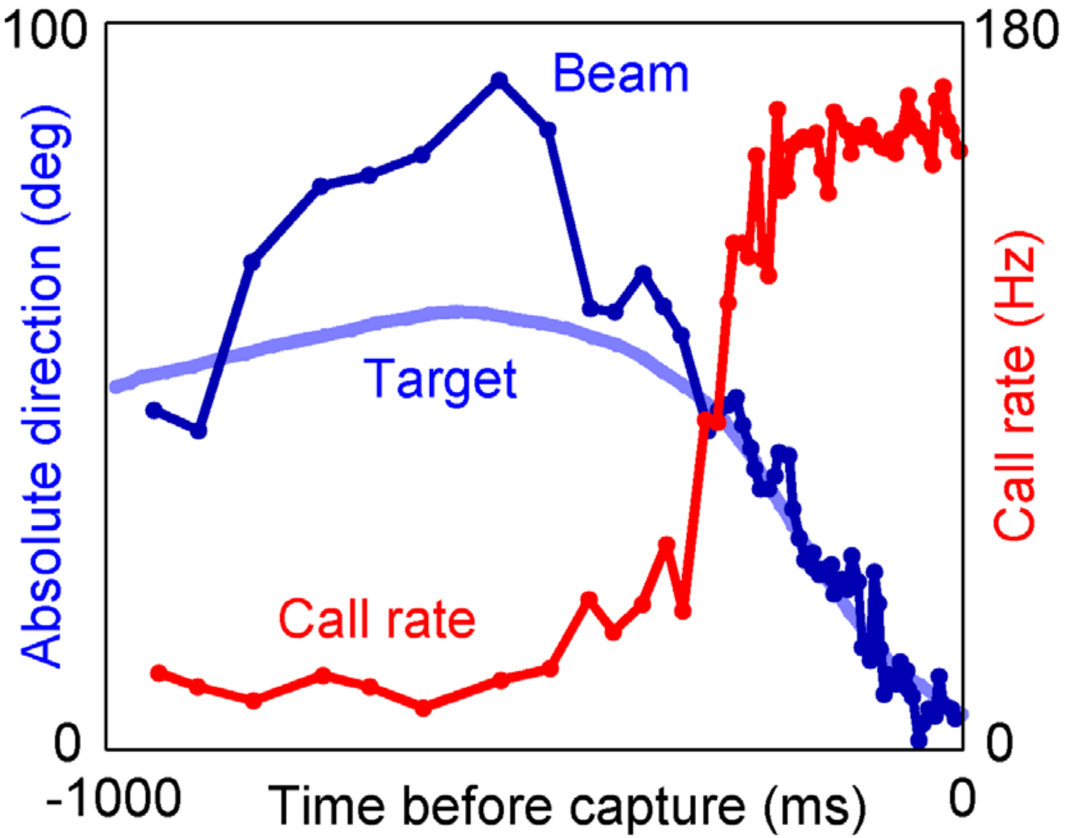
Emission beams used by bats

When switching from the search phase to the approach phase / tracking phase, the big brown bat ‘locks’ its beam onto the target direction.



Emission beams used by bats

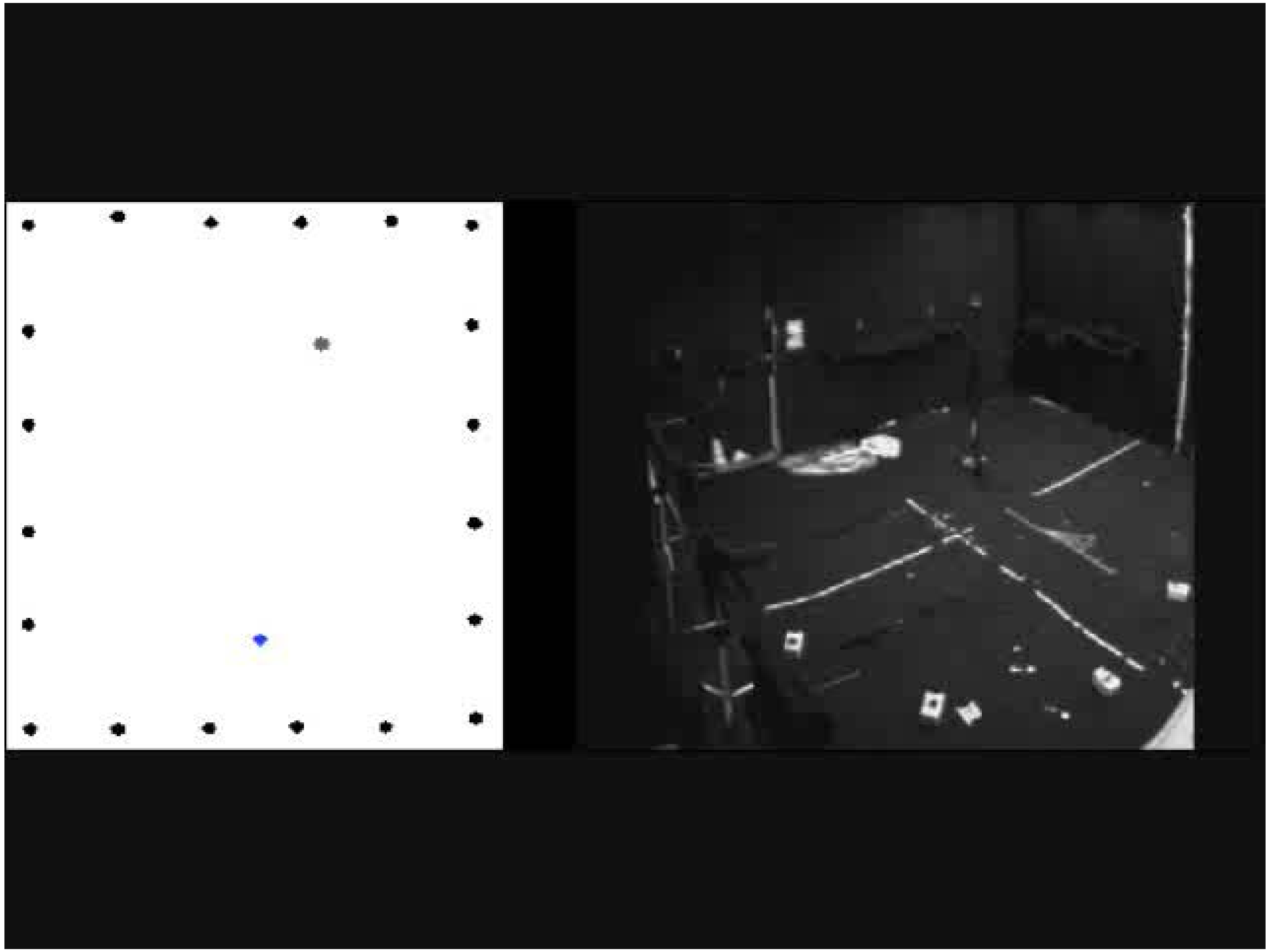
The ‘locking’ of the beam onto the target coincides with the increase in call rate.



A movie showing the phase transitions in bat sonar when chasing an insect: *Search → Approach → Tracking (Attack)*

Movie: Bat catching mantis (K. Ghose).

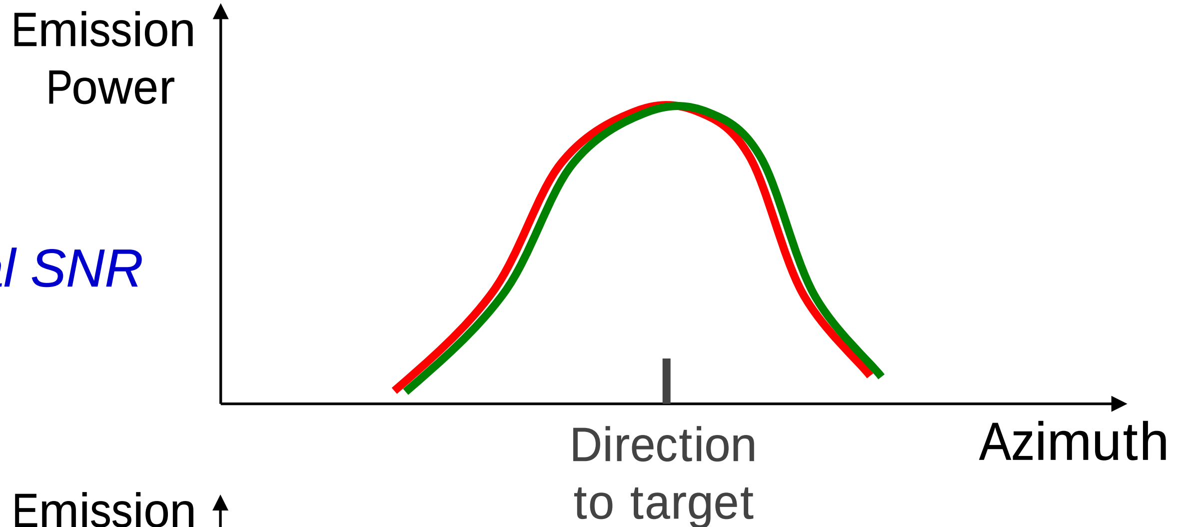
Clicking bats (*Rousettus*) use a different beam-steering strategy: They lock the beam's maximum *slope* on target, which optimizes localization



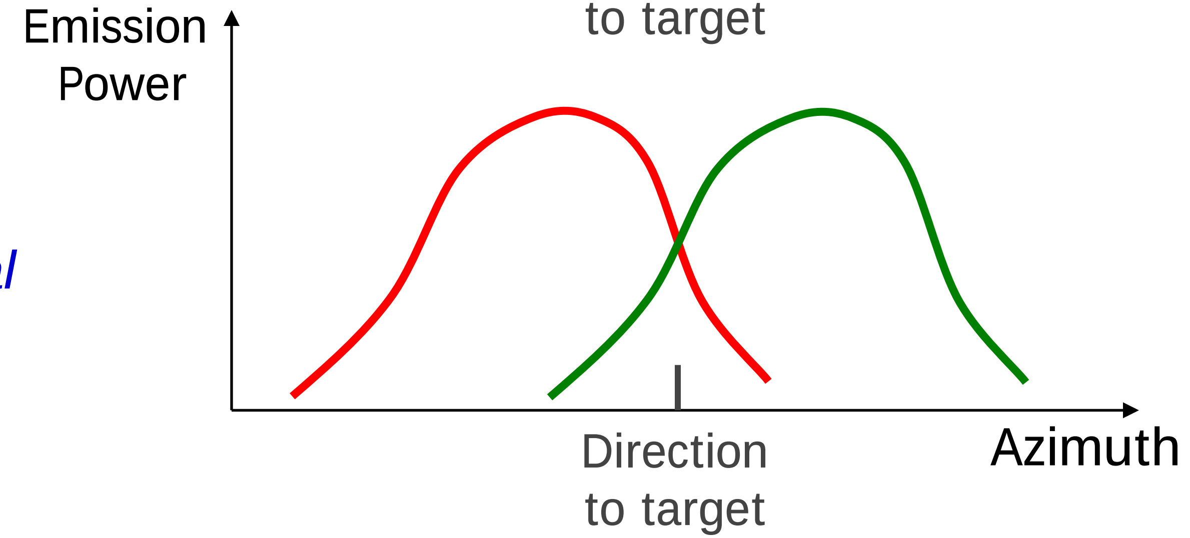
Yovel, Falk, Moss, Ulanovsky,
Science (2010)

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

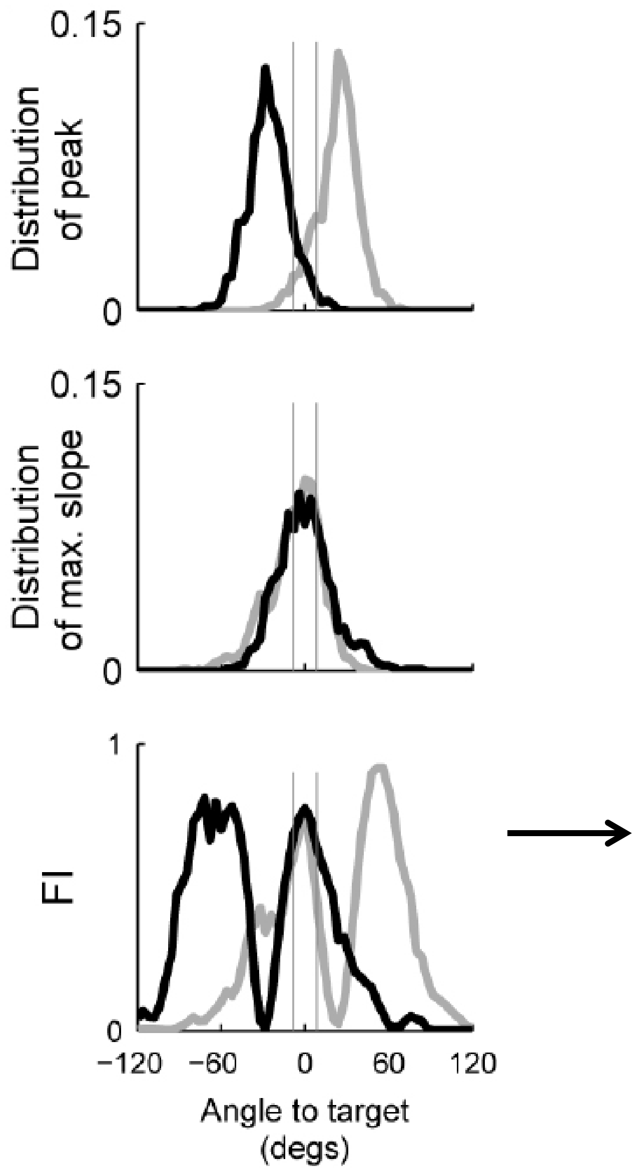
Emission Curves
If we want *optimal SNR*



Emission Curves
if we want *optimal localization*



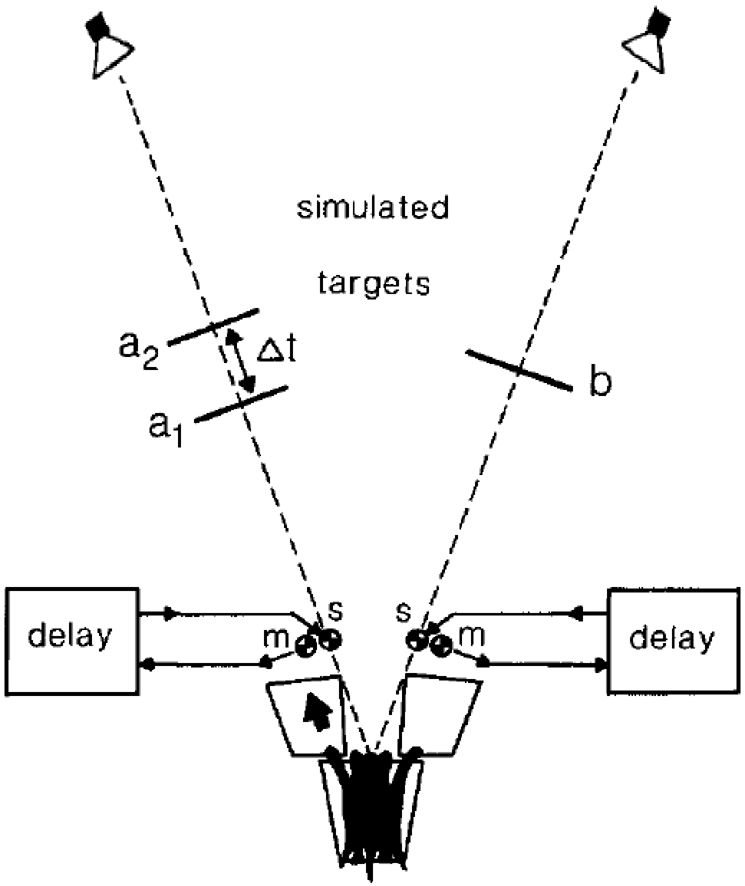
Clicking bats (*Rousettus*) use a different beam-steering strategy: They lock the beam's maximum *slope* on target, which optimizes localization

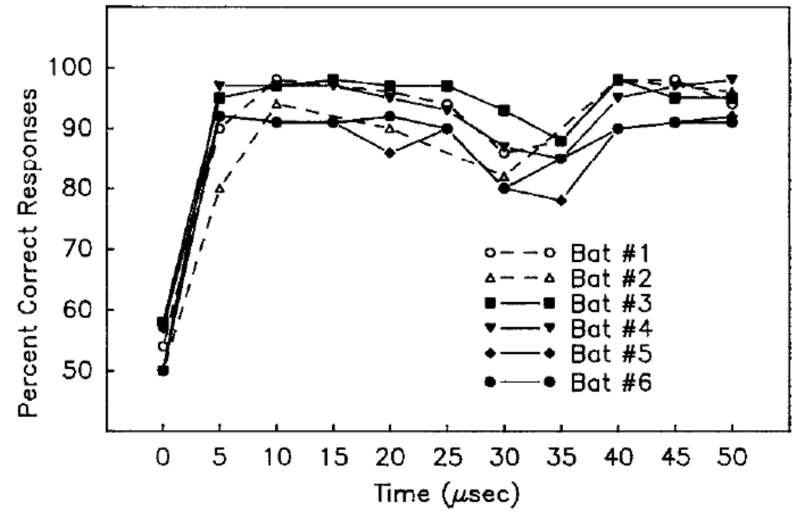


Fisher Information (FI):
Meets a theoretical optimality criterion: best possible target localization based on echo intensity

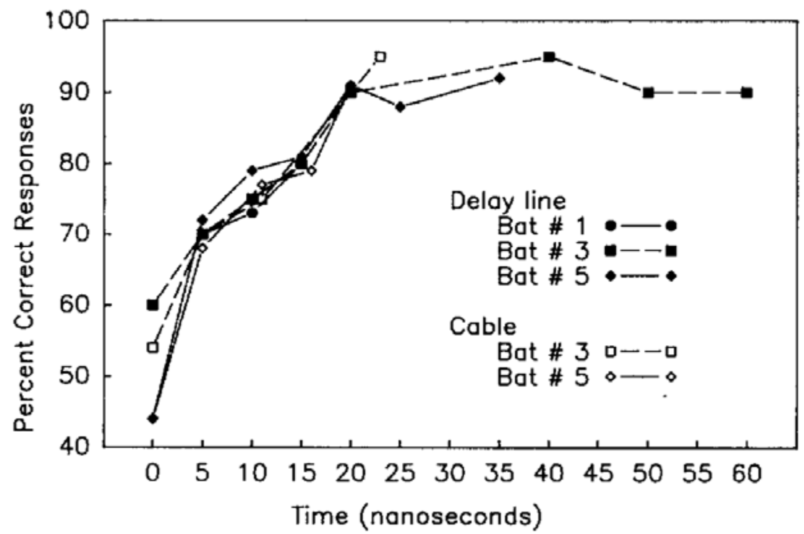
Yovel, Falk, Moss, Ulanovsky, *Science* (2011)

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





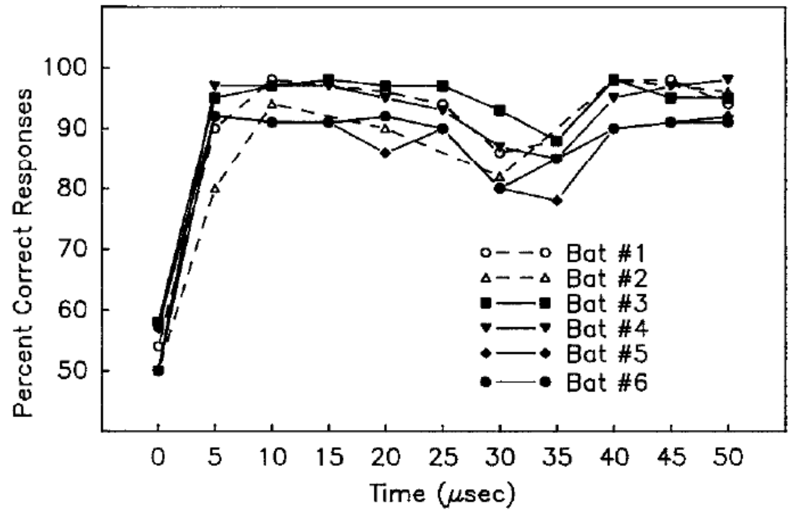
400 ns threshold



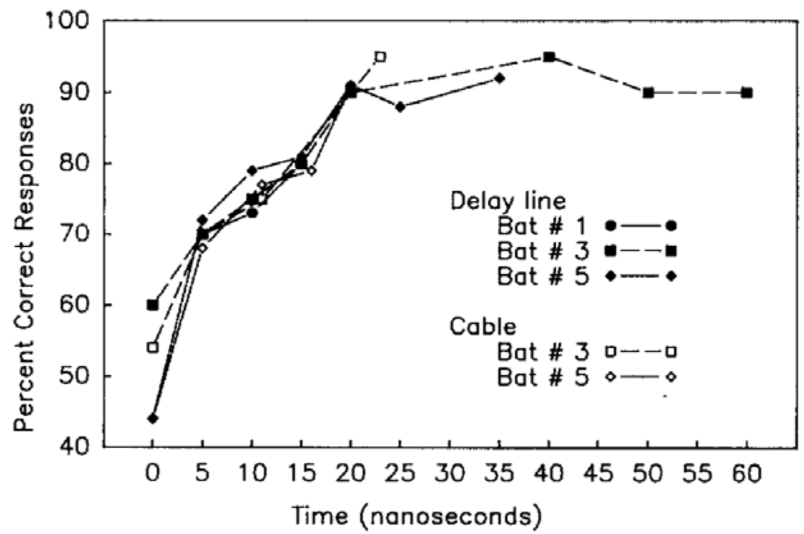
10 ns threshold?!

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

Big brown bats discriminate jitter in target range down to ~ 400 ns (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 ~ 400 μs, or so) !



400 ns threshold



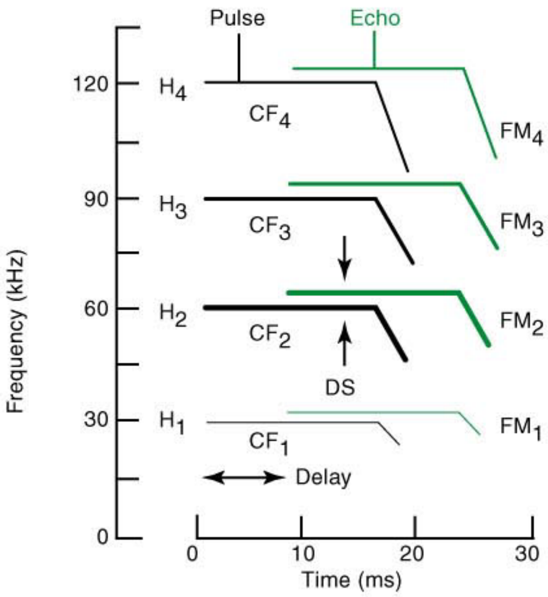
10 ns threshold?!

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

Talk Outline

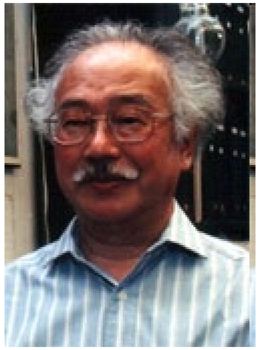
- Echolocation (biosonar): Behavior and Sensory Ecology
- Neurobiology of Echolocation

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.

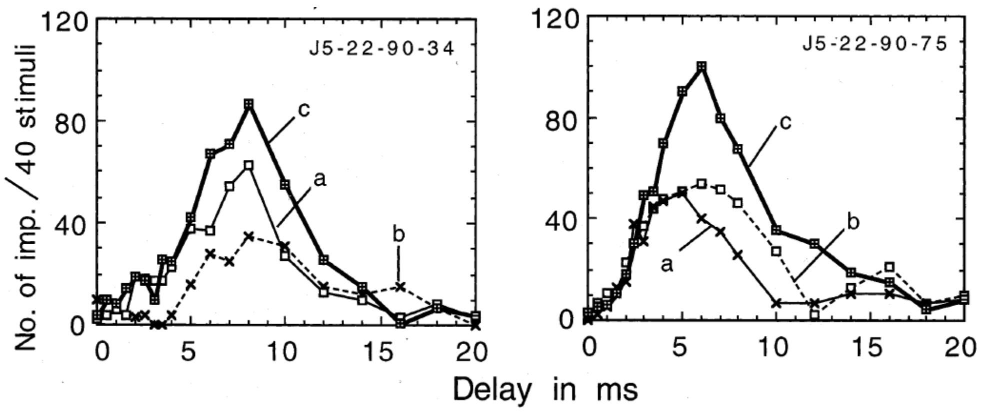


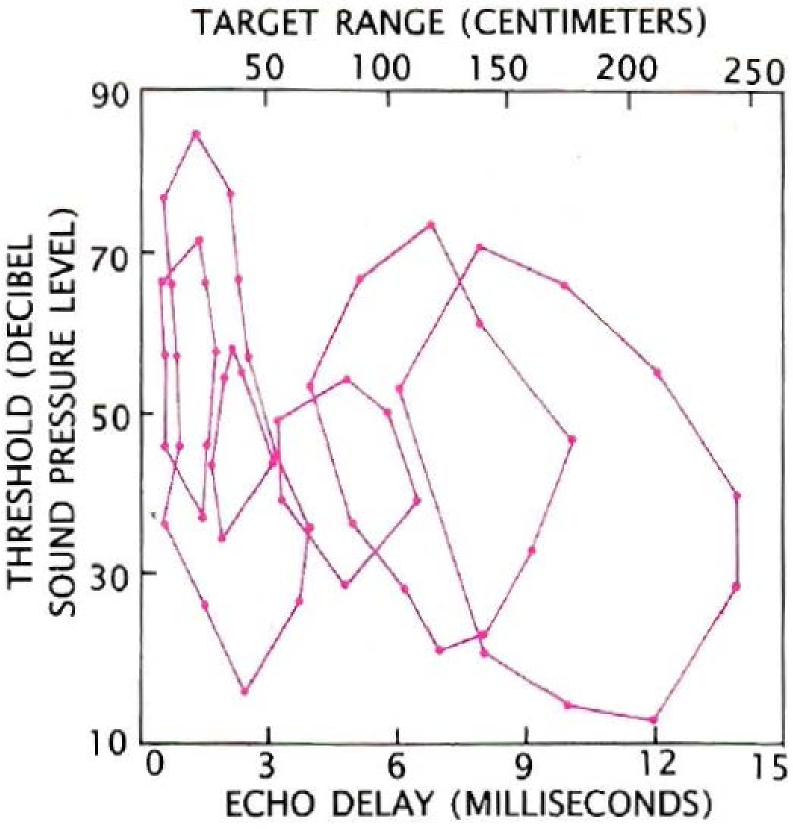
Nobuo Suga: Pioneer of bat electrophysiology research. Studied the neural basis of echolocation in the mustached bat.

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

Prominent characteristics of the auditory cortex of this bat:

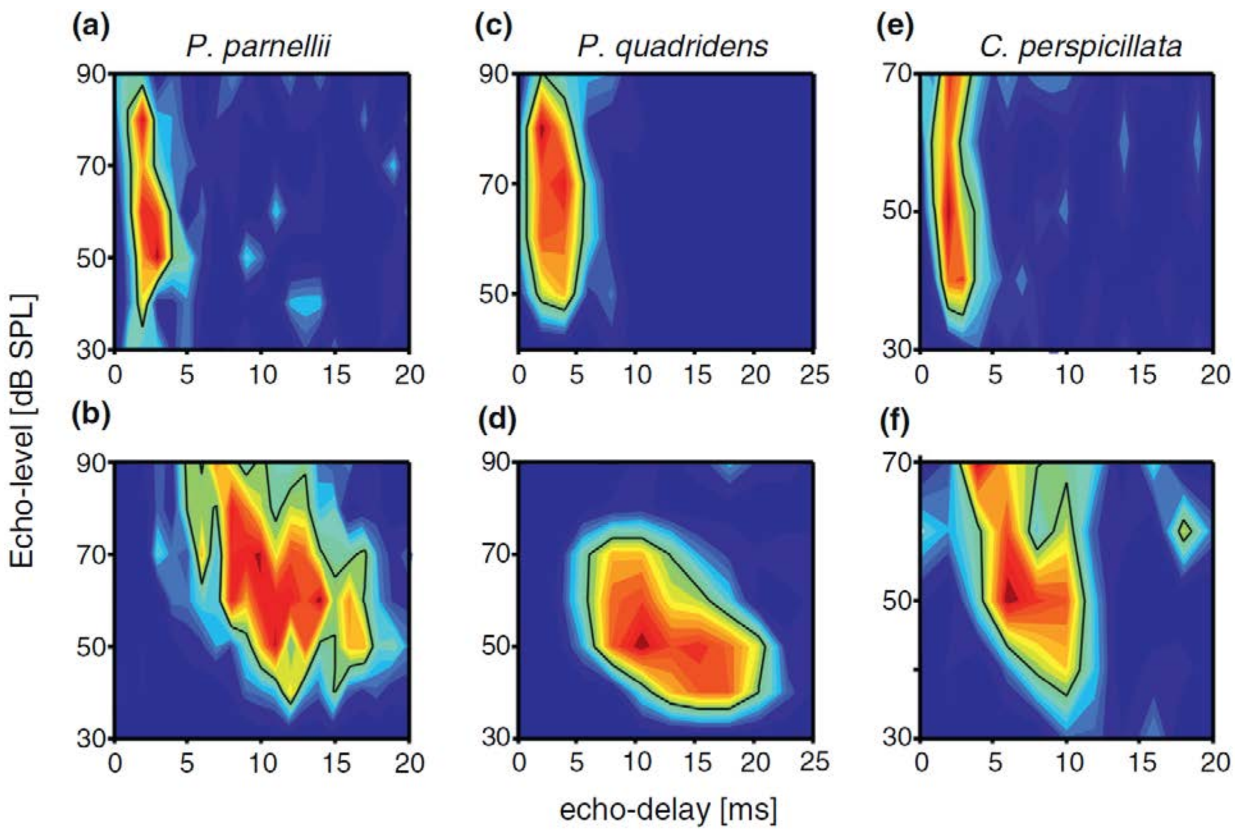
1. <u>Delay tuned neurons</u> (neurons sensitive to target range) – first discovered by Nobuo Suga





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

"Tracking neurons": Some delay-tuned neurons have *diagonal* response fields when plotting their response as function of echo-amplitude and pulse-echo delay – matching the increase of echo amplitude as the bat approaches the target. These neurons were termed "tracking neurons", because they optimally track the target. *(this is relevant for bat species that do NOT reduce their pulse intensity as they approach the target: some species do this [see below], but others do not)*

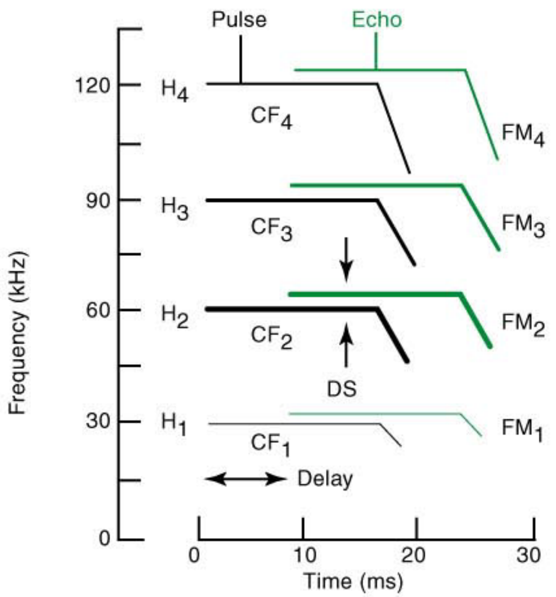


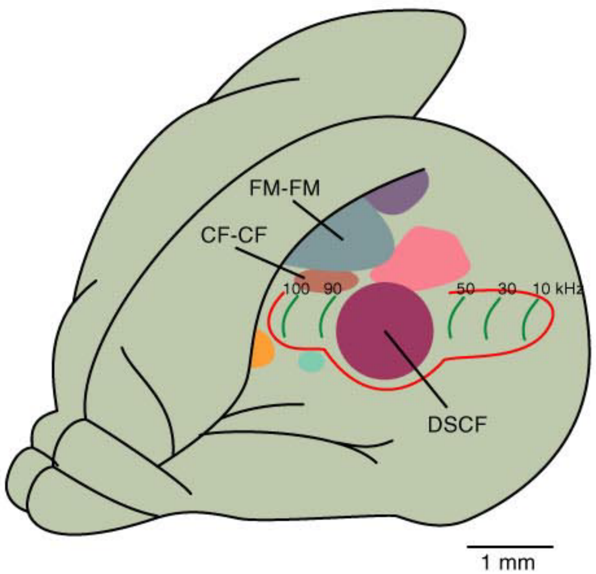
"Standard" delay-tuned neurons

"Tracking neurons" *(a subset of delay-tuned neurons)*

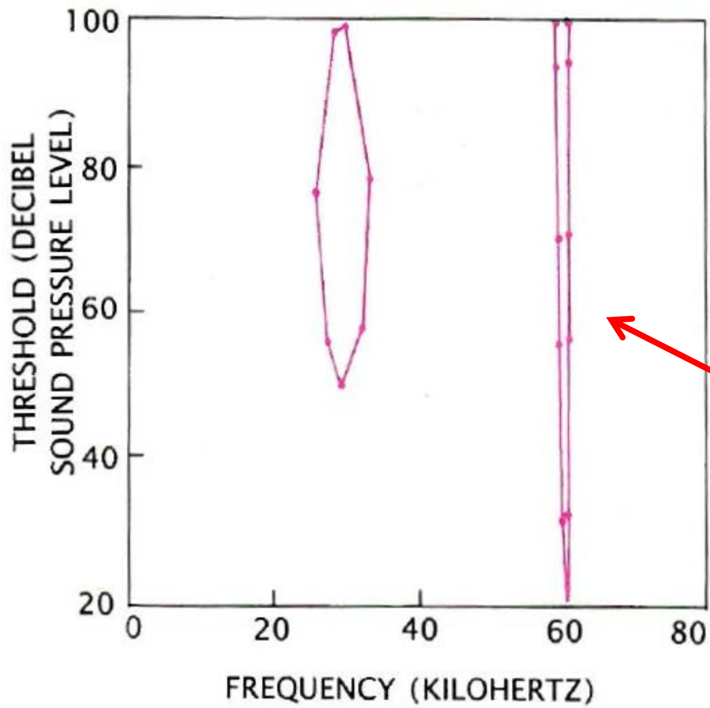
Kössl et al, 2014

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



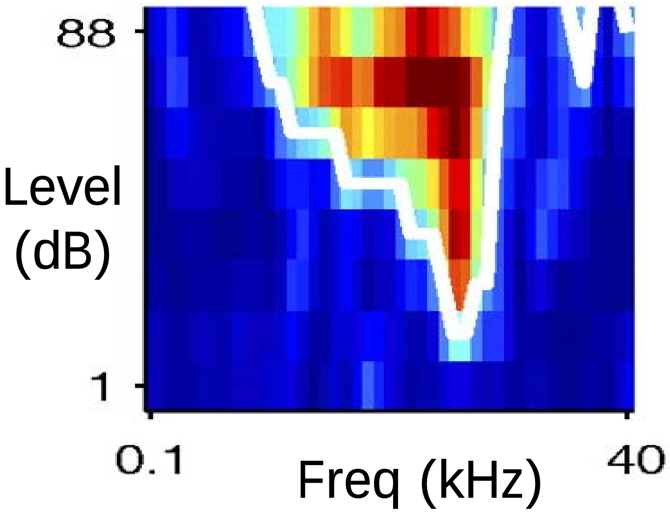


2. '<u>Auditory fovea</u>' (DSCF area) contains neurons with extremely narrow frequency tuning, centered around the dominant harmonic of the bat call (CF_2 , the 2nd harmonic). The narrowest frequency tuning in any animal's cortex.



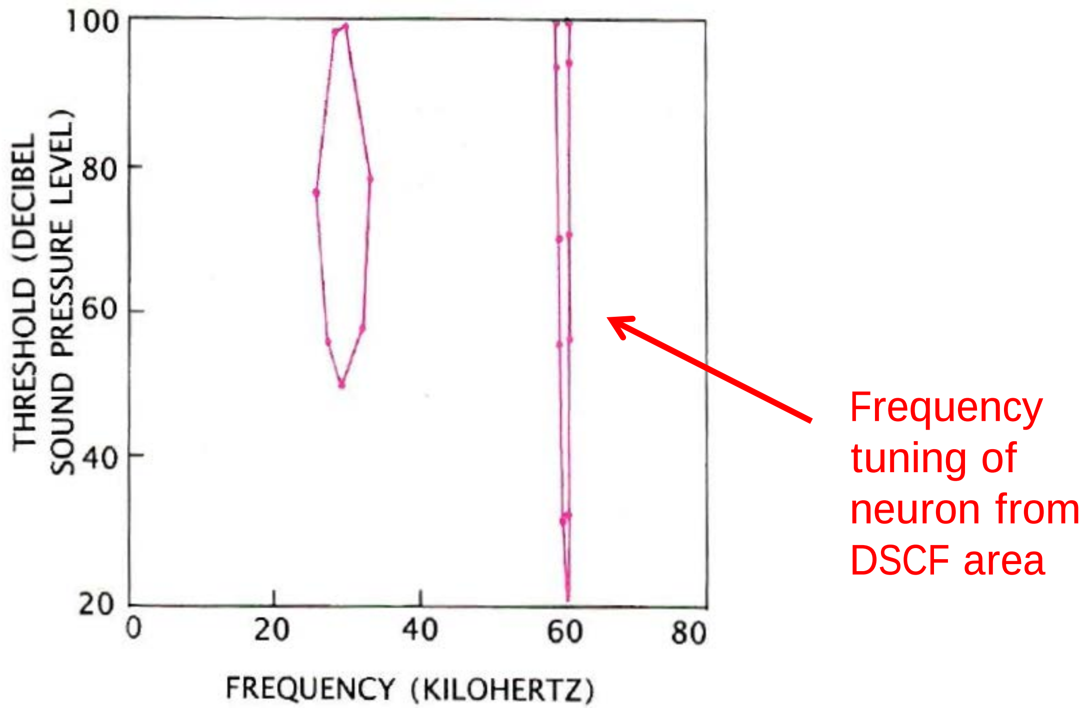
Frequency tuning of neuron from DSCF area

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

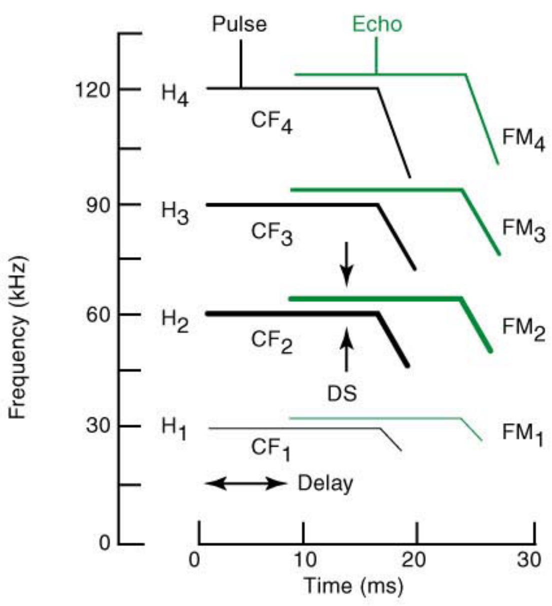


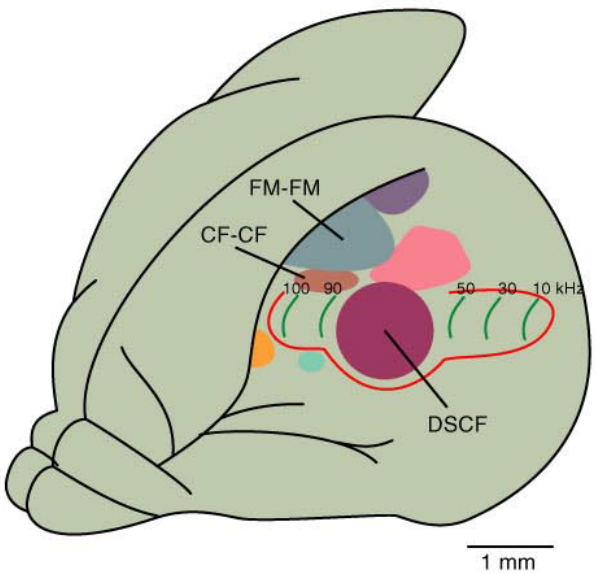
Neurons in the auditory cortex of all mammals (in this graph: the cat) serve as *filters*: They pass only signals within the frequency range of their "tuning curve" (white line).

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



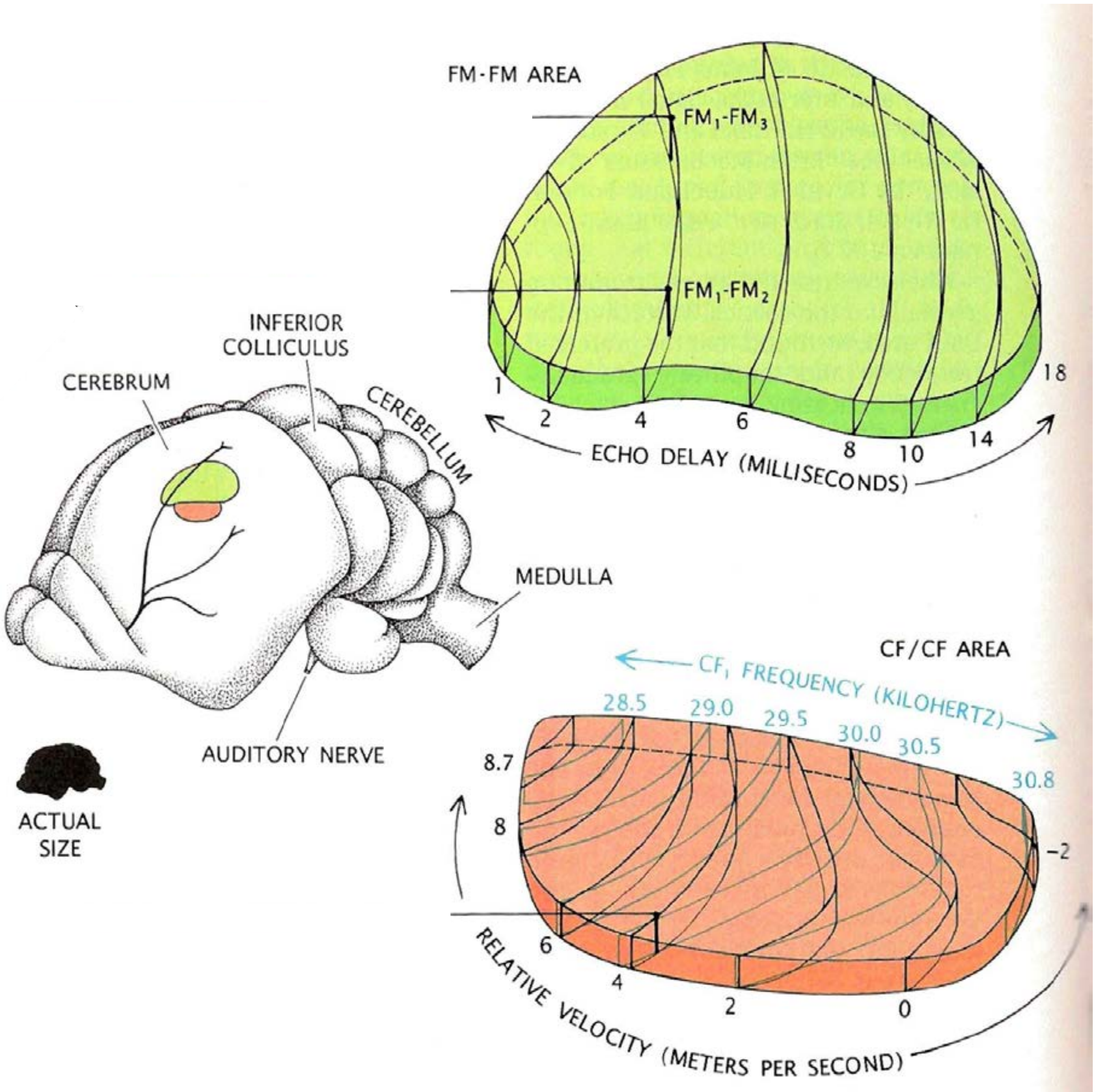
Neural processing of sonar signals in the mustached bat's brain





Neurons in the DSCF area specialize in detecting rapid Doppler modulations (*insect wing flutter*): Because of their exquisitely sharp frequency tuning, these neurons respond well even to the very small modulations in the CF frequency that are caused by the insect wing flutter (we will see examples below).

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



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

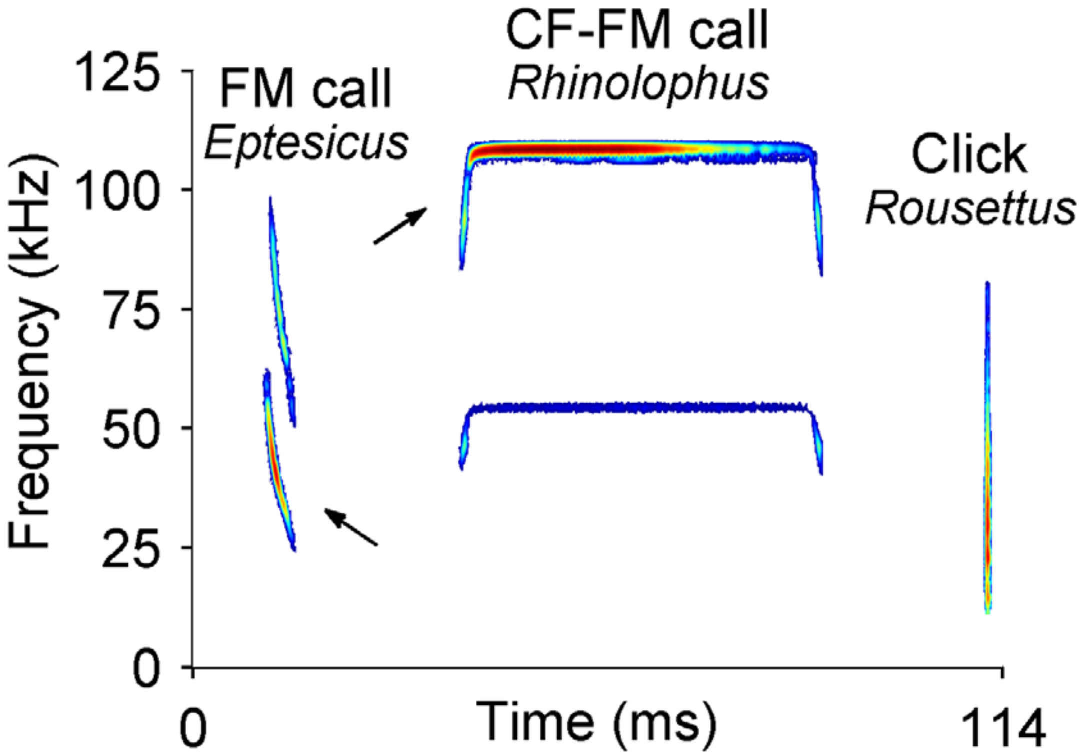
<u>FM–FM areas</u>: neurons specializing in computing pulse-echo delay (*target range*).

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

Doppler shift compensation: The only reasonably-studied example of neural control of a motor-sensory loop in bats

- An interesting and very reproducible motor-sensory behavior that occurs in CF–FM bats.
- In the remaining minutes I will focus on this behavior.
- What I will talk about
  - CF – FM bats: Behavior
  - CF – FM bats: More on the processing of sensory information in their auditory system
  - What is Doppler shift compensation?
  - A paper on the neural control of Doppler-shift compensation will be given for the exam.

Basic types of echolocation calls - REVISITED

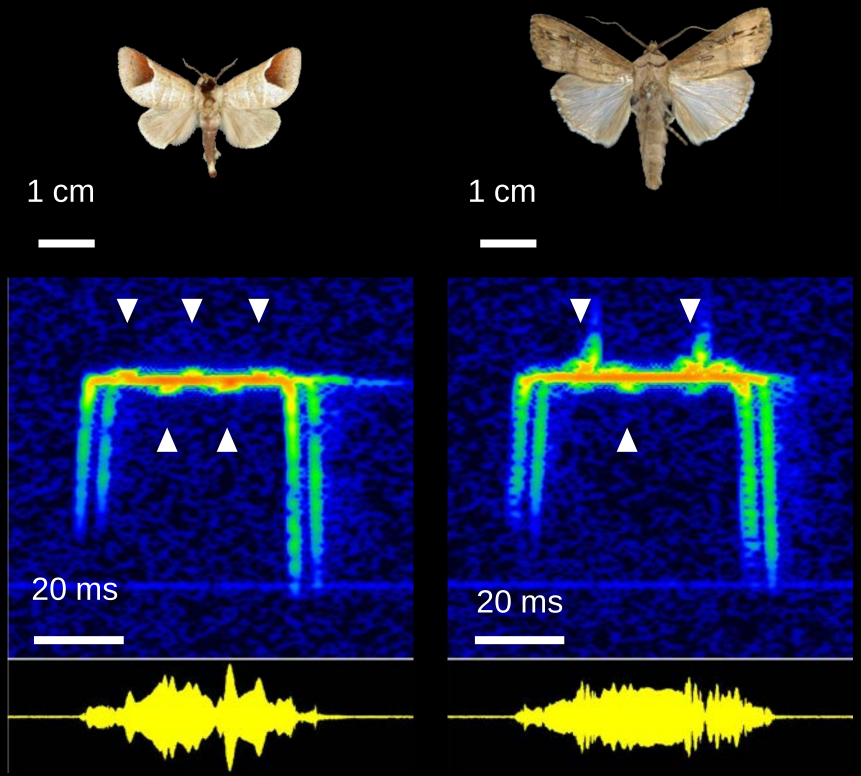


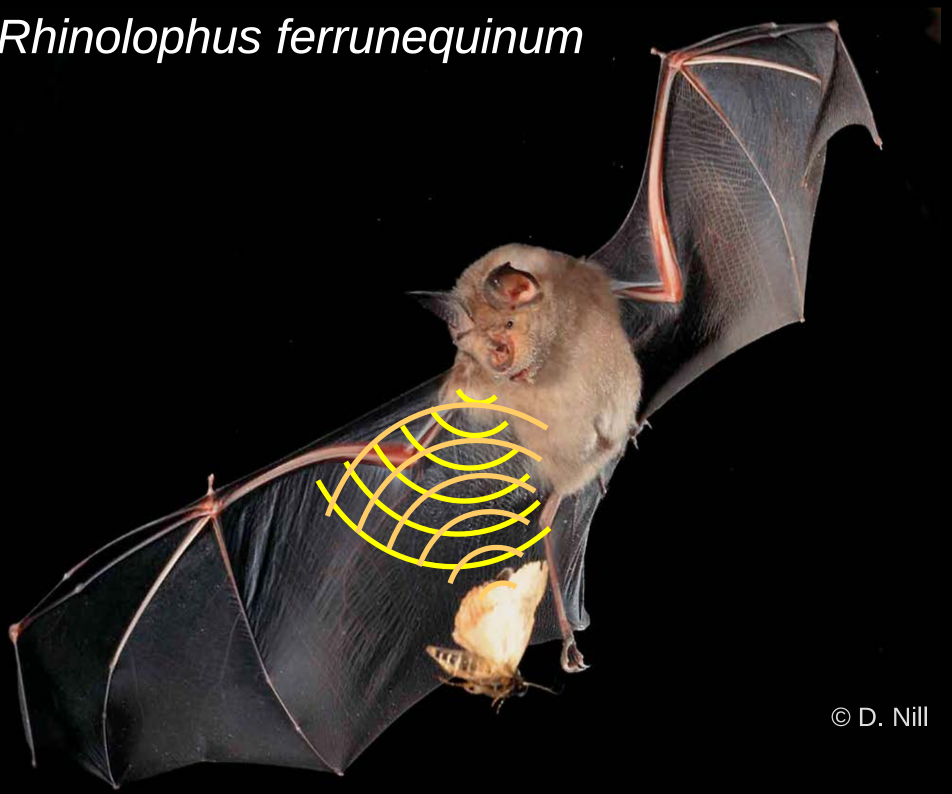
Ulanovsky & Moss,
PNAS 2008

CF–FM bats: Behavior - REVISITED

- CF-FM bats can compute the Doppler shift (target velocity).
- The CF-FM call is ideal for overcoming the clutter problems in highly cluttered environments, by doing Doppler processing. And indeed, CF-FM bats from the genus *Rhinolophus* (horseshoe bats), *Hipposideros*, and *Pteronotus parnellii* (mustached bat) can hunt insects inside dense vegetation / in cluttered areas.
- They can detect Doppler modulations caused by the insect's wing flutter.
- These bats can even tell apart different insect species based on their different flutter rate → can discriminate Δflutter-rates as small as ~ 5%.

CF–FM bats: Behavior

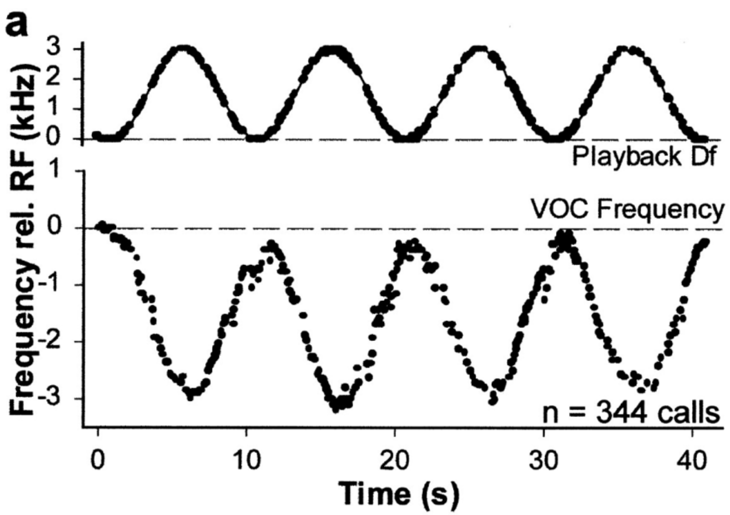




→ This is probably the reason why the CF-FM calls are so long = tens of ms (it's easier to identify the insect species if you have at least 2-3 insect-flutter cycles inside the call).

→ Moreover, CF-FM bats <u>increase</u> their pulse duration when exposed to fluttering targets.

Doppler Shift Compensation (DSC)



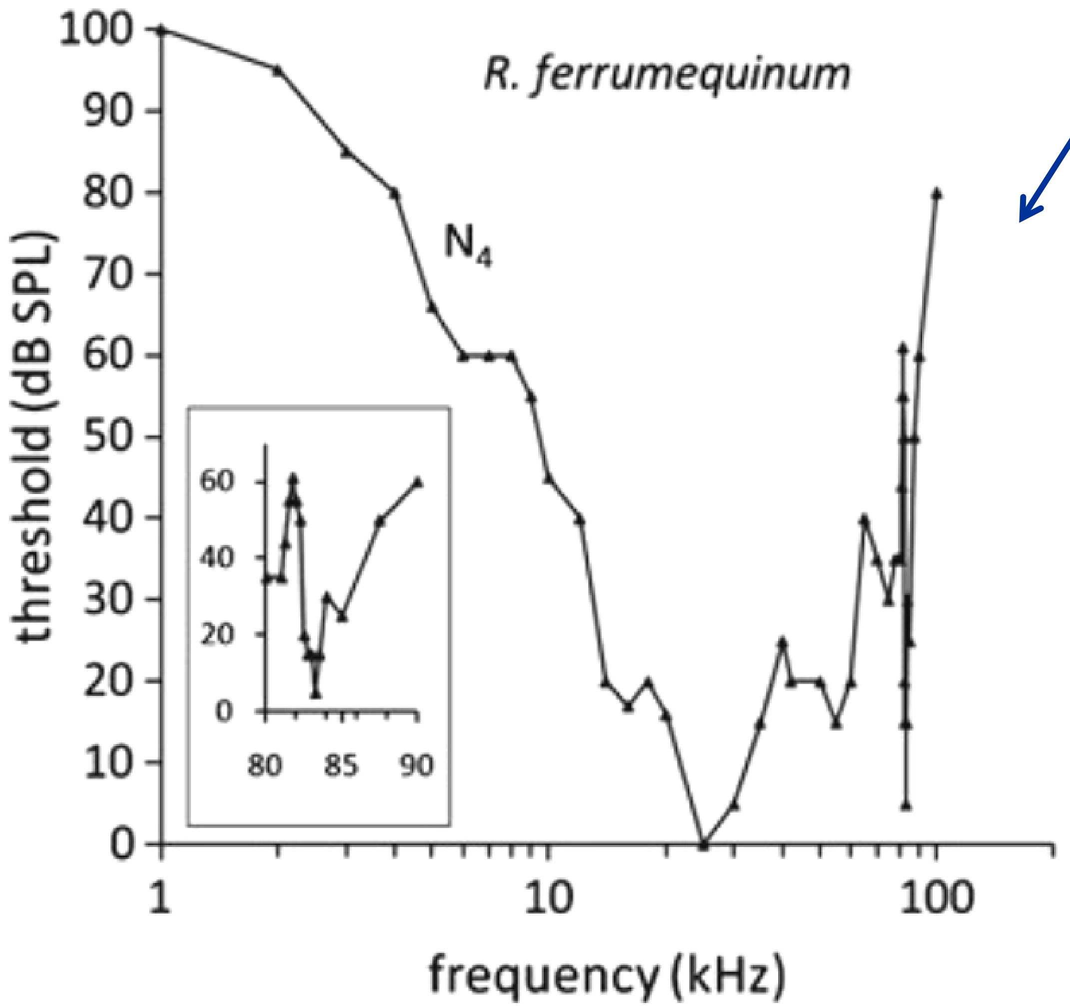
Doppler shift compensation in horseshoe bats on a platform – not flying (Smotherman et al. 2003)

Doppler shift compensation behavior: Mustached bat, as well as all other CF-FM bats (Horseshoe bats and Hipposiderid bats) shift their frequency so as to keep the frequency of the echo constant.

Why?

Because they have to keep the echo inside the narrow frequency tuning of their neurons – or else they will not be able to process the echo.

Doppler Shift Compensation (DSC) and auditory sensitivity

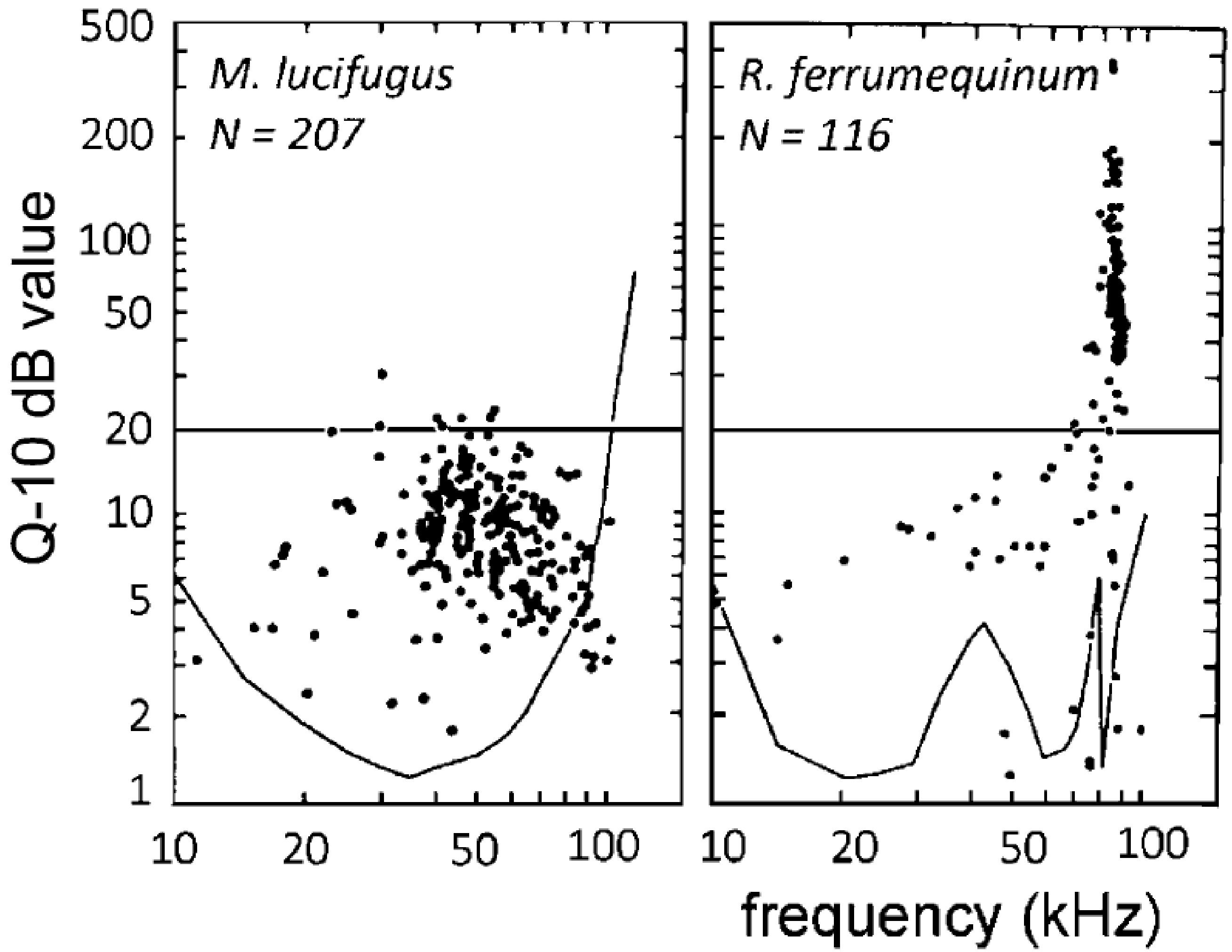


Sharp sensitivity peak in the audiograms of CF-FM bats around the resting frequency of the CF component (83 kHz).

In fact, it was shown that the frequency of this peak is tuned to the bat's own specific CF frequency – this is true both for the audiogram and for the frequencies of neuronal tuning curves in the auditory cortex ("The personalized auditory cortex of mustached bats").

This illustrates a general principle in bat echolocation, and in fact in many active-sensing systems: <u>Matching between the sensory side and the motor side</u>.

Doppler Shift Compensation (DSC) and auditory fovea

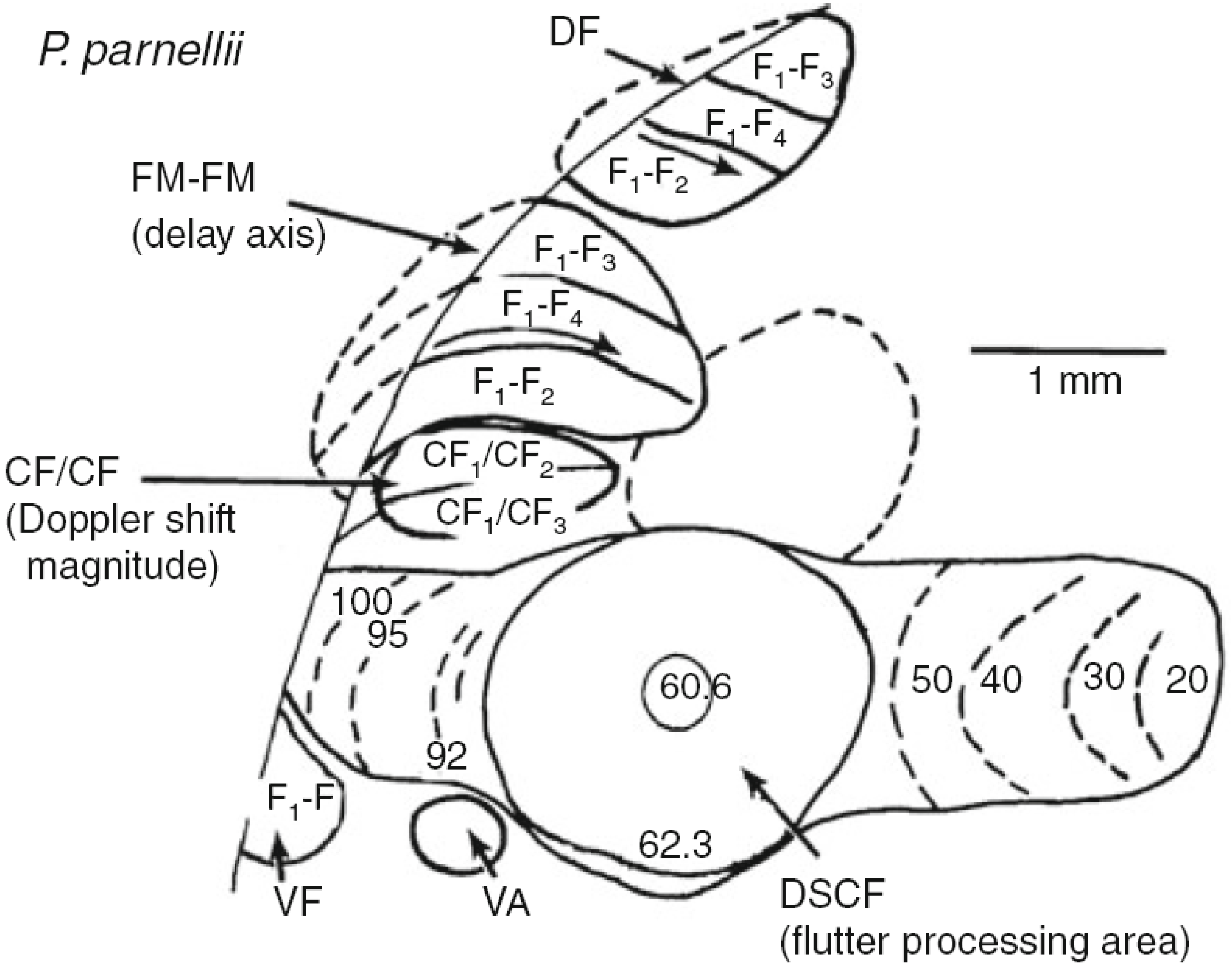


Over-representation and sharp tuning (high Q-value) of peripheral auditory neurons (in auditory nerve and cochlear nucleus): an <u>"auditory fovea"</u> in *Rhinolophus ferrumequinum.*

In contrast, an FM bat (*Myotis lucifugus*) foes *not* have such over-representation and such sharp neural tuning curves.

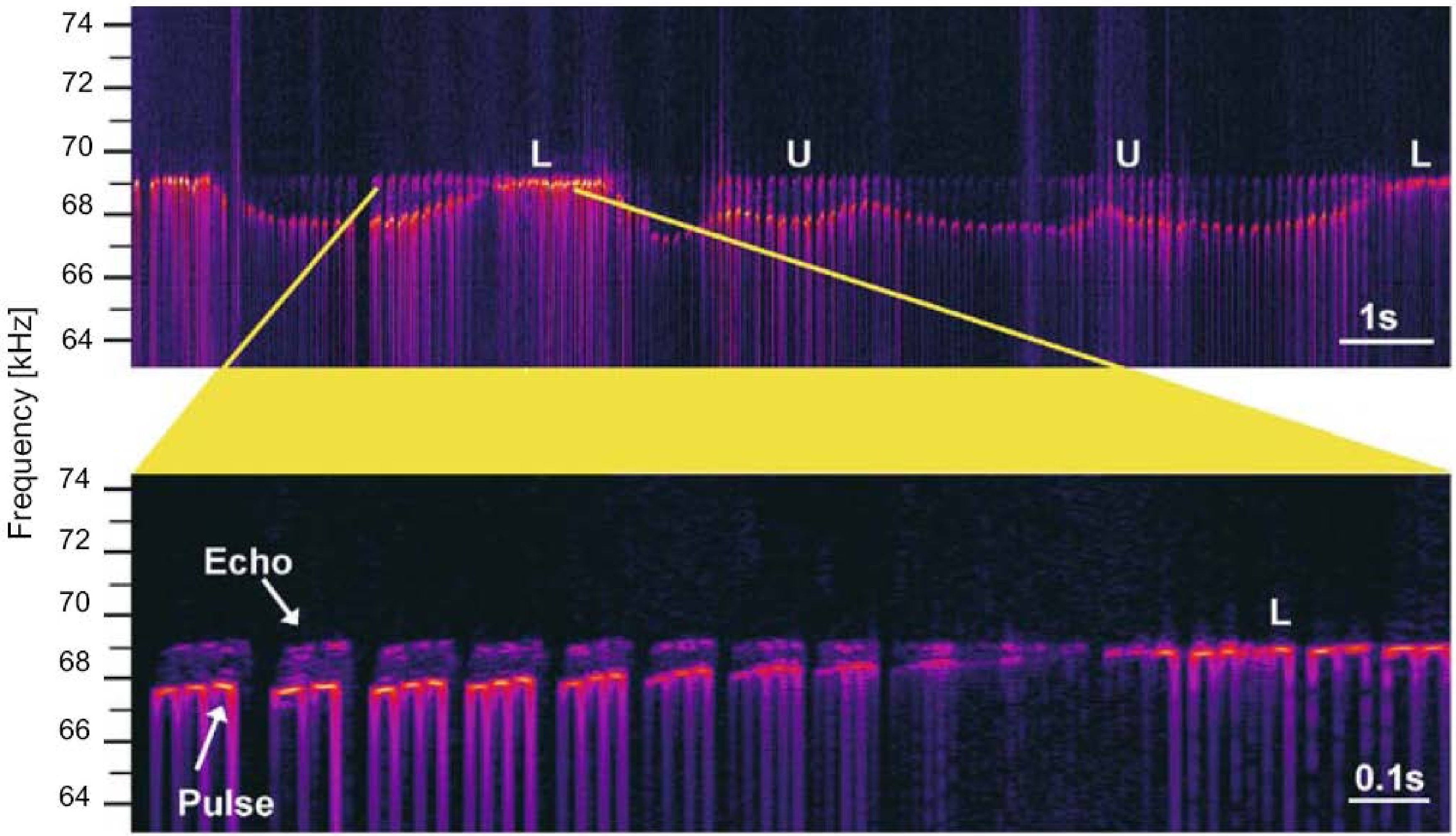
A large corpus of work studied the biomechanics, anatomy and physiology of how this auditory fovea is created already in the cochlea.

Doppler Shift Compensation (DSC) and auditory fovea



Primary auditory cortex (A1) of the mustached bat, *Pteronotus parnellii*, has an auditory fovea ("DSCF area") that over-represents the (personalized !) CF frequency emitted by each individual bat.

Stabilization of echo frequency by CF–FM bats in flight – measured by an on-animal telemetry microphone (Telemike)

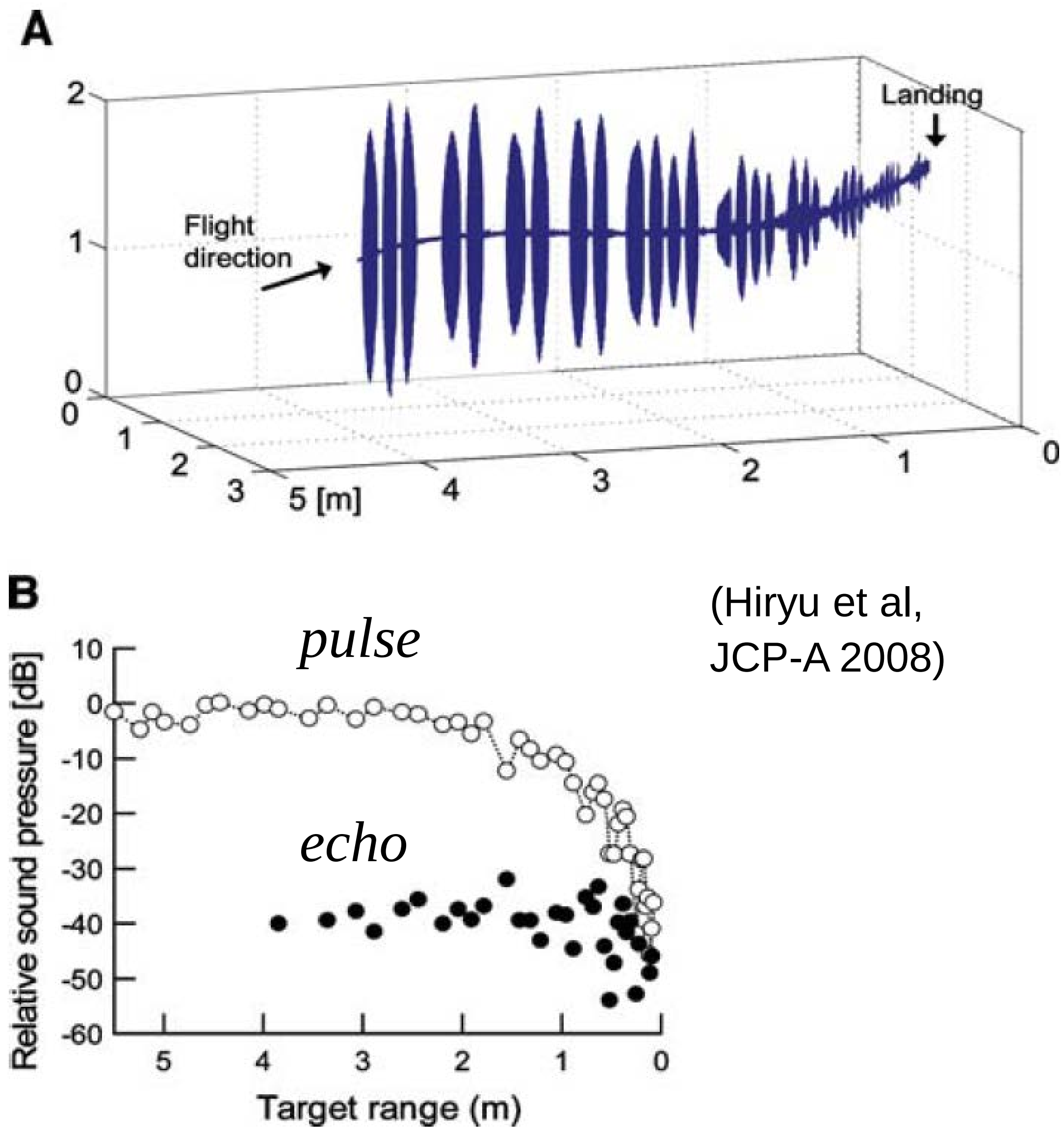


Echo freq stabilized to within 0.1%

(Hiryu et al, JCP-A 2008)

CF-FM bats exhibit Doppler Shift Compensation that stabilizes the echo frequency.
The echo frequency is controlled tightly (< 0.1%) and rapidly (< 100 ms) !

[Stabilization of echo amplitude by CF–FM bats – measured using an on-animal telemetry microphone (Telemike)]

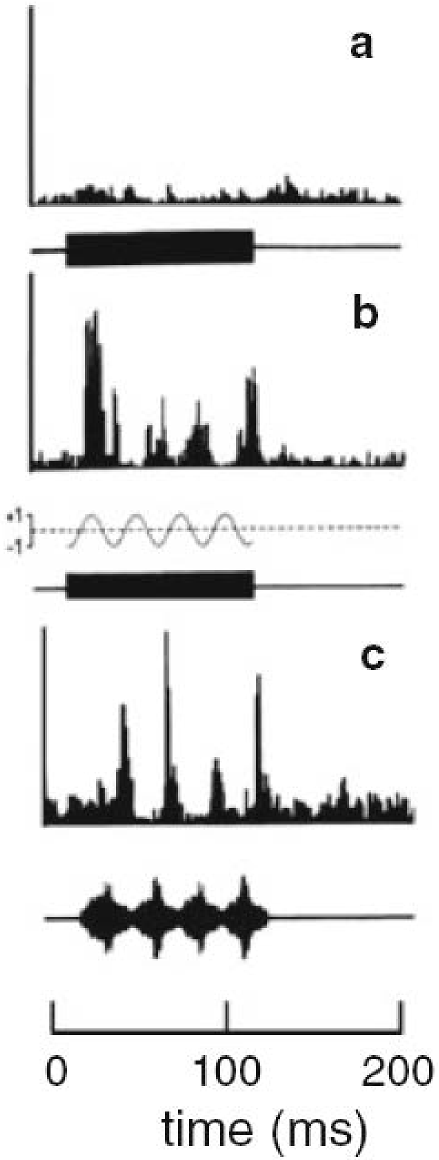


(Hiryu et al, JCP-A 2008)

CF-FM bats exhibit reduction in pulse amplitude as they approach a target or a landing wall – which <u>stabilizes the amplitude of the echo</u> (automatic gain control – AGC).

The echo amplitude seems to be tightly controlled in CF-FM bats – and in <u>many</u> other bats where it was tested, including some FM bats and clicking bats !

Doppler shift compensation allows the sharply-tuned auditory neurons of CF-FM bats to analyze the flutter information



No response to pure tone.

Strong response to frequency-modulated tone (modulation bandwidth ± 1 kHz).

Strong response to natural recorded flutter of an insect.

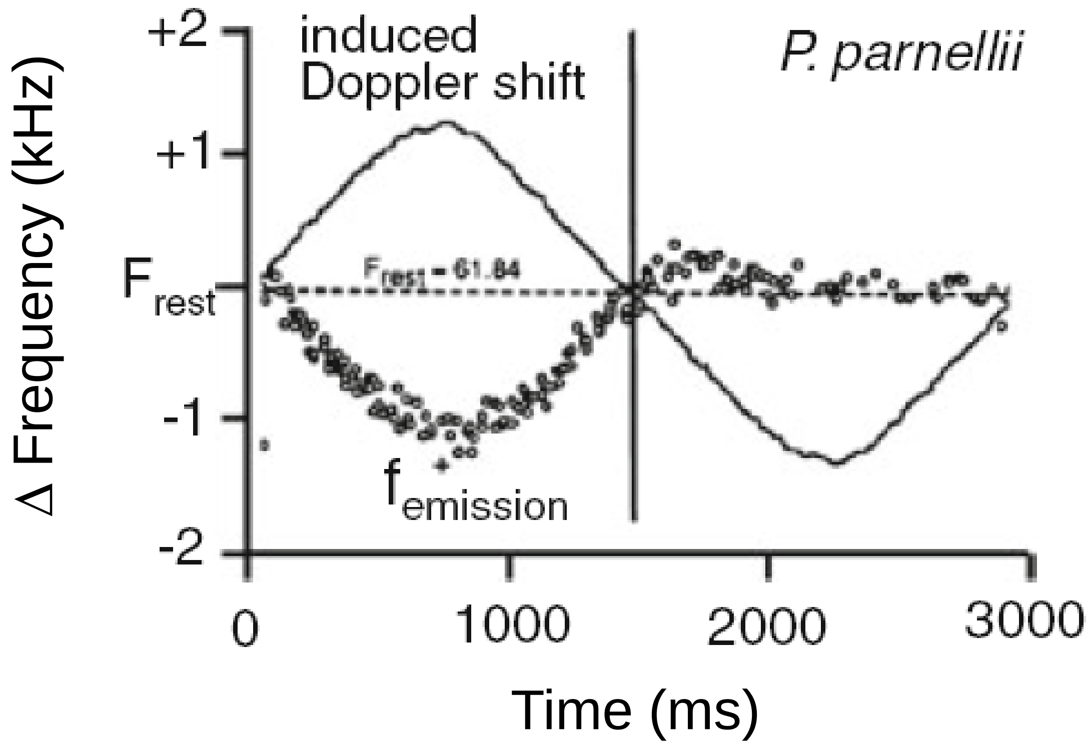
A neuron in the auditory cortex of *Rhinolophus ferrumequinum*.

Doppler shift compensation (DSC) must involve a negative sensory-motor feedback loop (rather than a forward model based on purely motor information = bat's flight speed)

- DSC is elicited correctly by target motion (pendulum) AND by bat's *passive* motion (bat placed on the same pendulum facing a stationary platform)
- DSC in bats flying in a flight tunnel is compensating for ground-speed, not air-speed (i.e., it must be based on sensory-motor information, not purely motor)
- DSC is elicited correctly in He-O_2 gas mixtures (when sound speed is increased)
- DSC is elicited correctly when bat is sitting on platform, in virtual-playback experiments (no real target at all)

Important property of the DSC feedback loop: Compensation is only for <u>positive</u> Doppler shifts (when approaching a target)

Bat sitting on pendulum swinging towards and then away from a stationary target:



A role for the midbrain tegmentum (paralemniscal zone) in the neural control of the DSC negative feedback loop

A possible neuronal basis for Doppler-shift compensation in echo-locating horseshoe bats

Walter Metzner*

NATURE · VOL 341 · 12 OCTOBER 1989

I will give this paper to read for the exam.

A much more detailed discussion of the neural basis of DSC is given in the course “Active Sensing”.

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 <u>simple</u> 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 want to achieve, 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, freely-moving animal, using microphone arrays (in many ways it is much more difficult to do this in other active-sensing systems, such as rat whisking 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: 140 dB : much 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