

Three-dimensional space representation by echolocation in bats

KITP Research Seminar
July, 2017

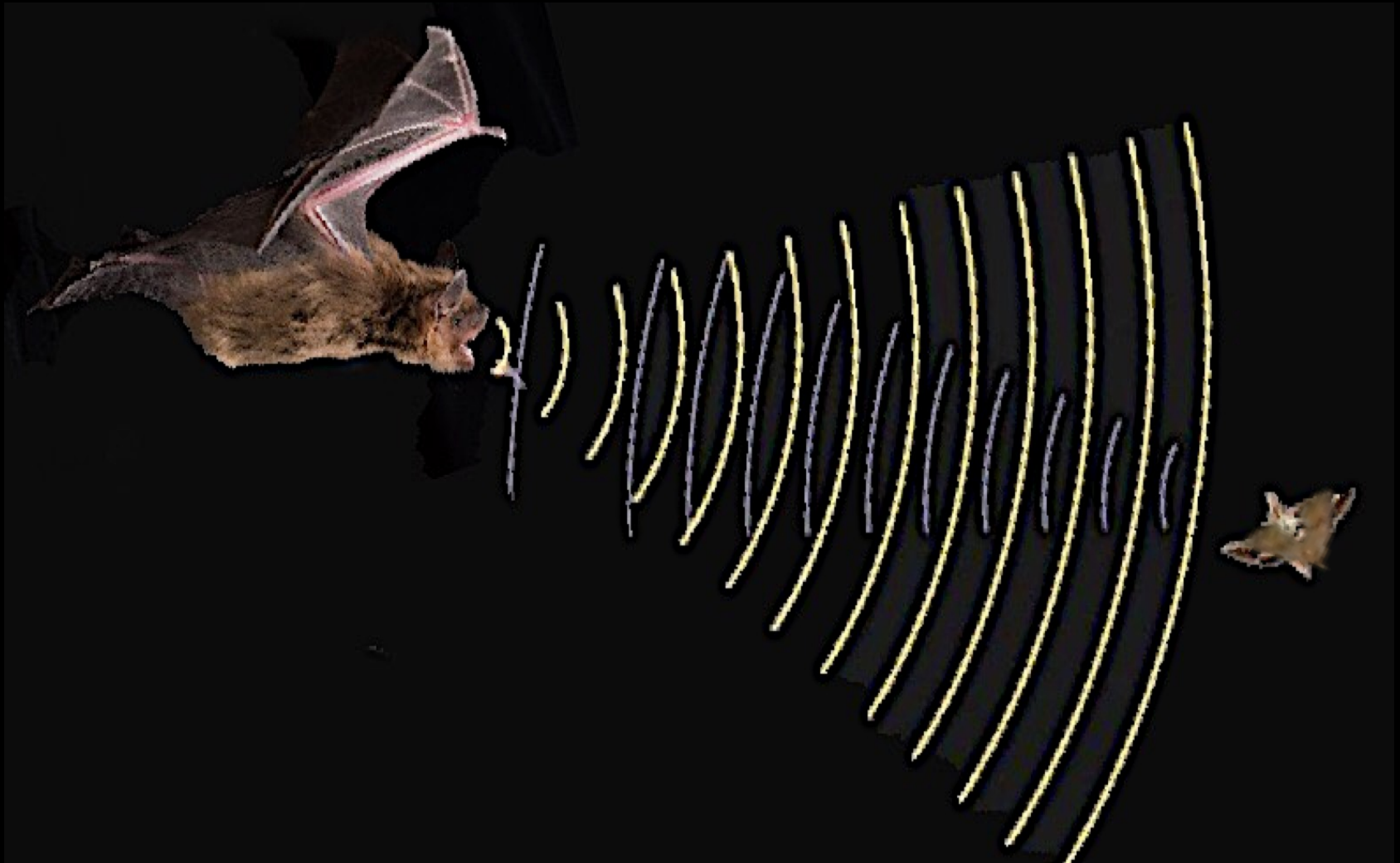


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Active Listening by Echolocation

Perceiving the location and features of objects in the world by producing sounds and listening to reflected echoes



Why bats? Echolocating bats are valuable models for studies of mammalian hearing

- Bat echolocation makes use of a standard mammalian auditory system.
- This active sensing system provides a direct window to the information bats use to guide behavior.
- Comparative studies can help to separate specializations from general principles.



Bat echolocation depends on systems that are common to a wide range of organisms

- Auditory localization
- Spatial perception and attention
- Adaptive behaviors



Talk Outline

Adaptive sonar behavior and spatial attention in bats

- Prey capture
- Obstacle avoidance
- Target discrimination

Neural mechanisms of echolocation

- Midbrain specializations
- Dynamic 3D representation





Big Brown Bat, *Eptesicus fuscus*

North American insectivore

Broadband sonar signal well suited for spatial localization

Horizontal Localization Accuracy

Comparing echoes at the two ears:

1 deg (Simmons et al., 1983)

Vertical Localization Accuracy

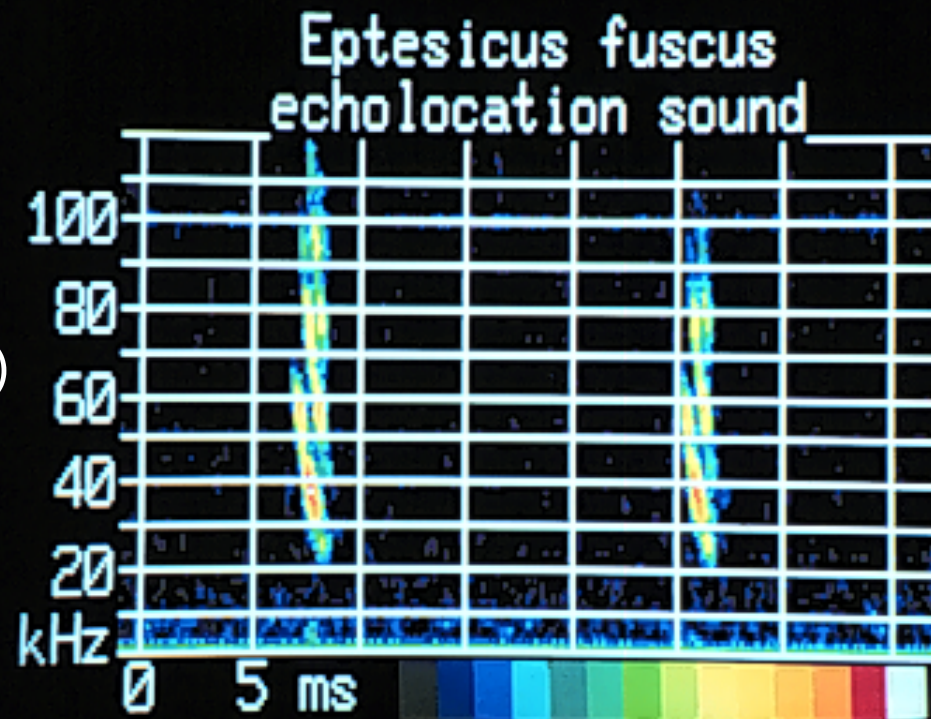
Analyzing echo spectrum:

3 deg (Lawrence and Simmons, 1982)

Distance Localization Accuracy

Measuring the time delay between echolocation sound and echo:

< 1 cm (60 μ sec) (Simmons, 1973)

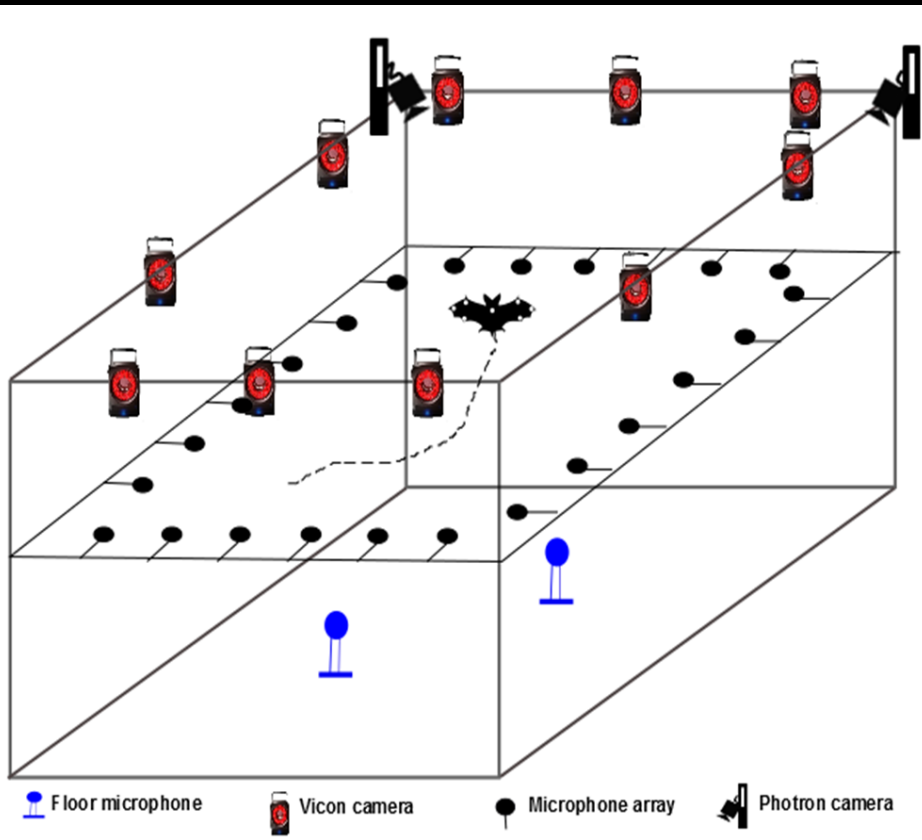


Echolocating bats dynamically modulate sonar signal design in response to 3D spatial information carried by sonar echoes



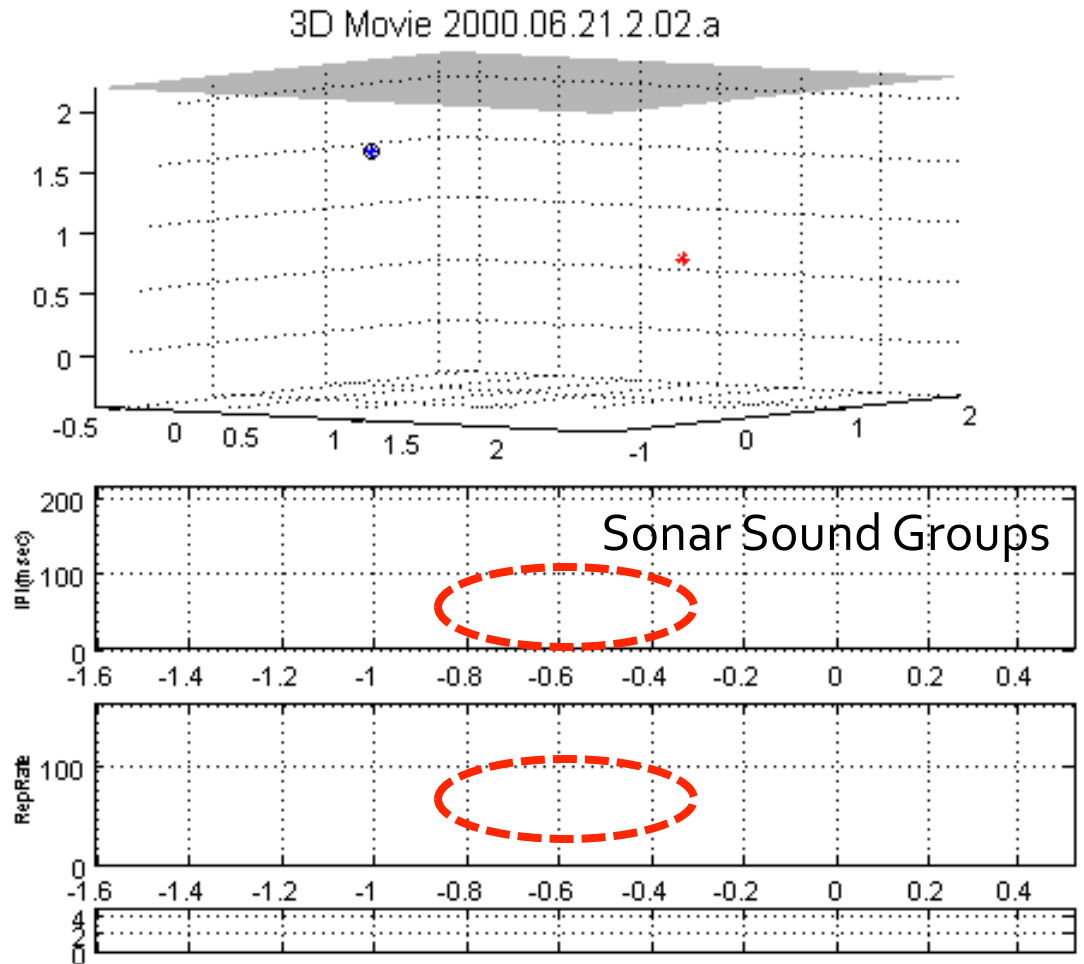
The linkage between action and perception is key to acoustic imaging by sonar.

Target tracking, discrimination and spatial navigation by echolocation in bats

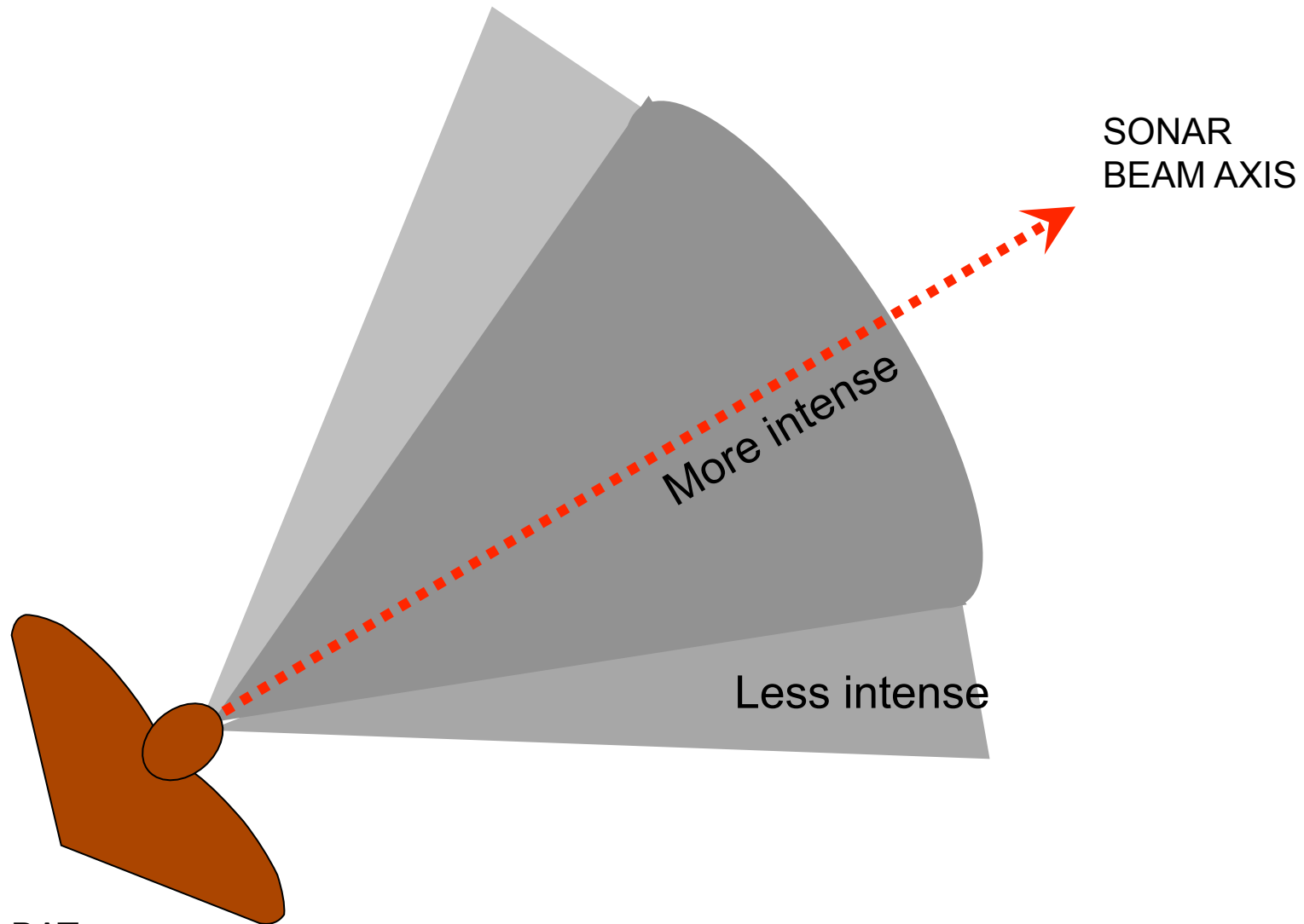


Multimedia Recordings:
Synchronized high-speed infrared cameras and ultrasonic microphones to measure and quantify the bat's echolocation patterns as it performs behavioral tasks.

Control of sonar call timing



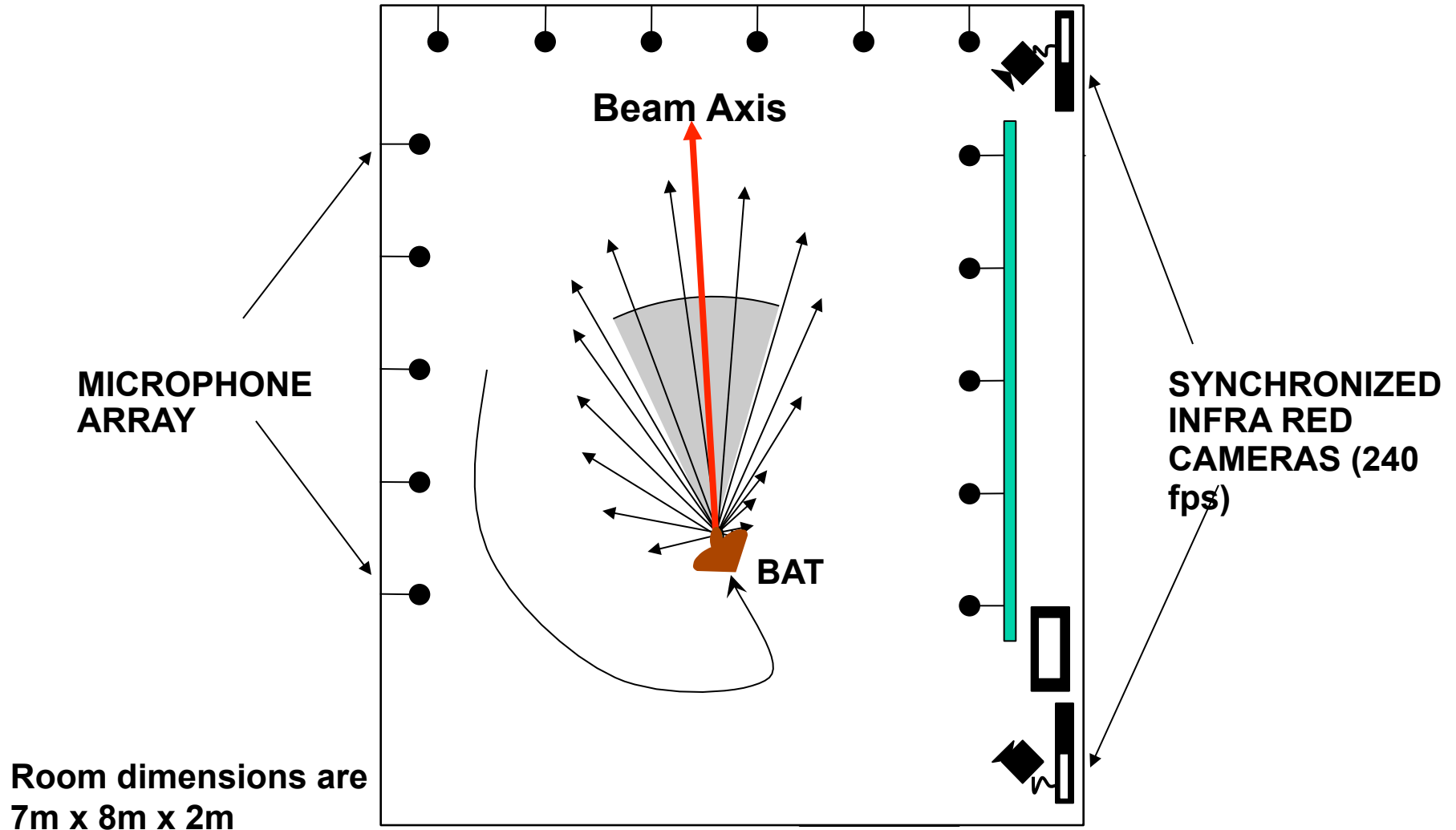
Sonar beam is a spatial filter



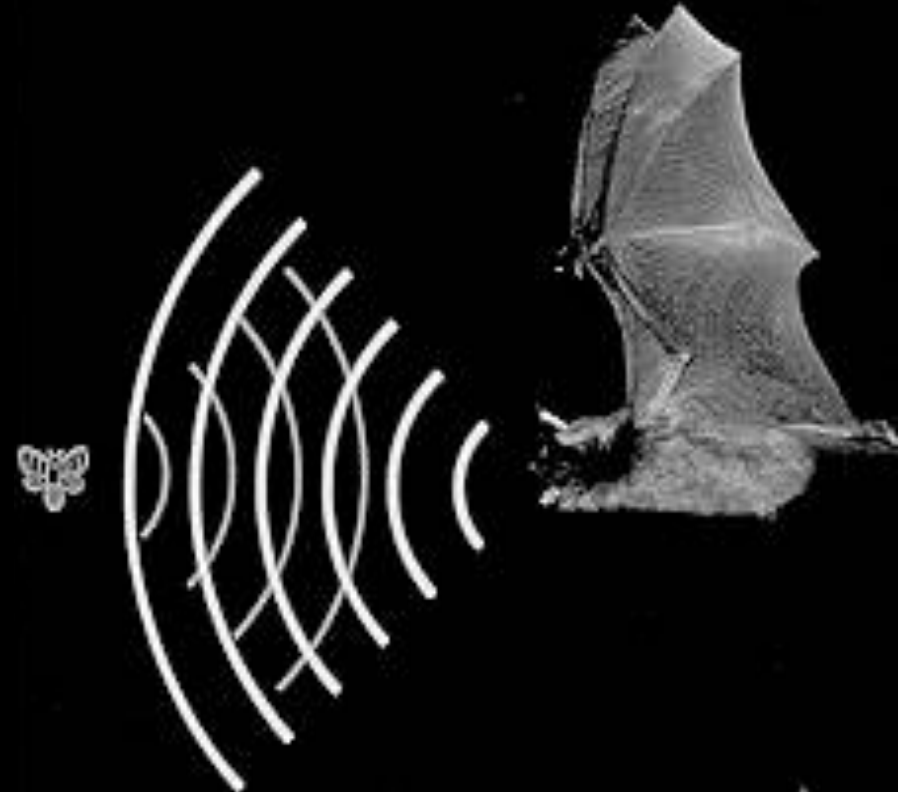
BAT

Griffin 1958, Hartley 1989

Measuring sonar beam direction



The bat's sonar beam aim reveals where it is attending in space



Adaptive Sonar Behavior

Call Adjustments in:

- Direction
- Duration
- Frequency
- Intensity
- Interval



Vocal adjustments directly influence echo returns used to determine the direction, distance and features of objects.

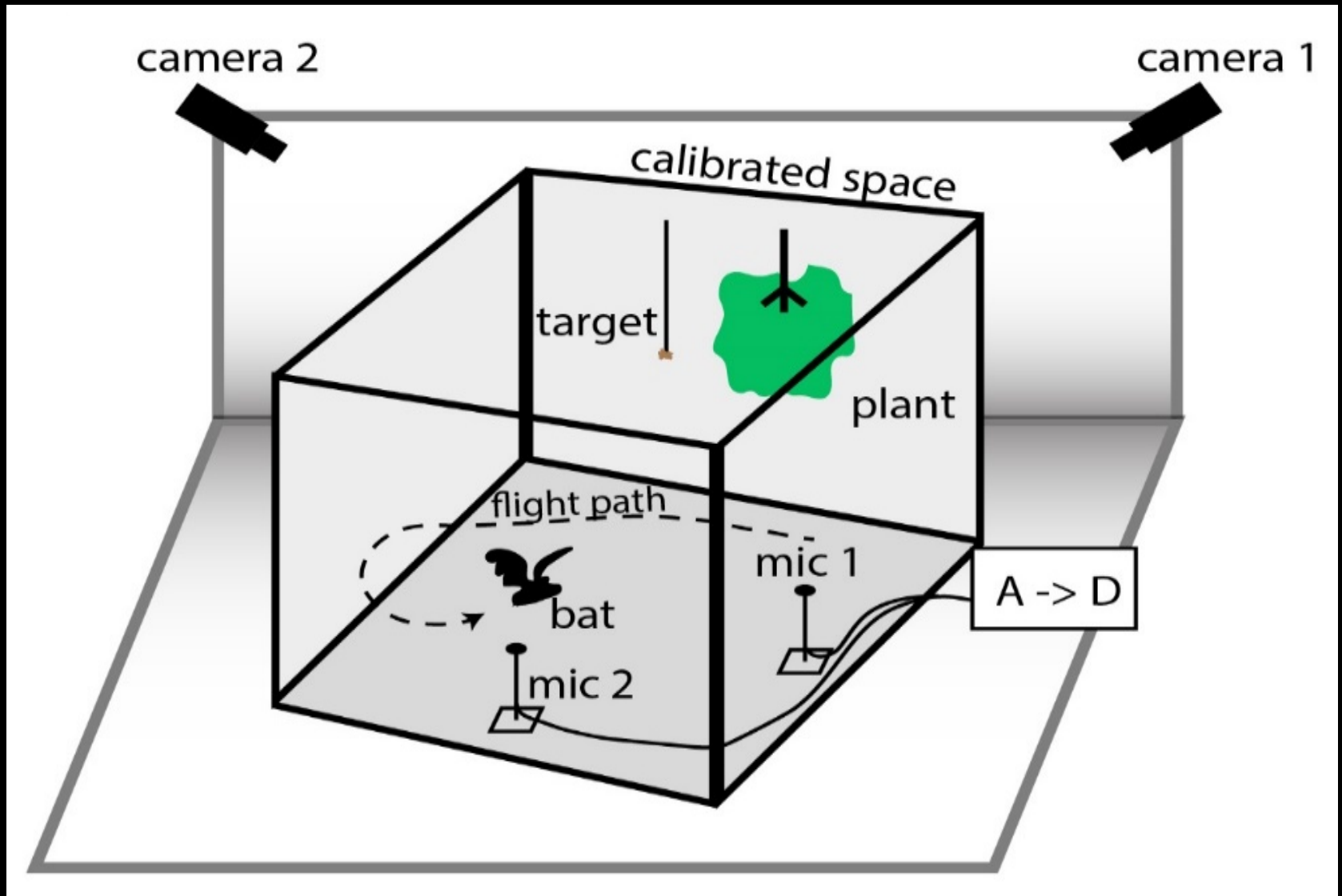
Adaptive vocal behavior:

- conveys acoustic information the bat is seeking
- provides an indicator of the bat's spatial attention to objects in its environment

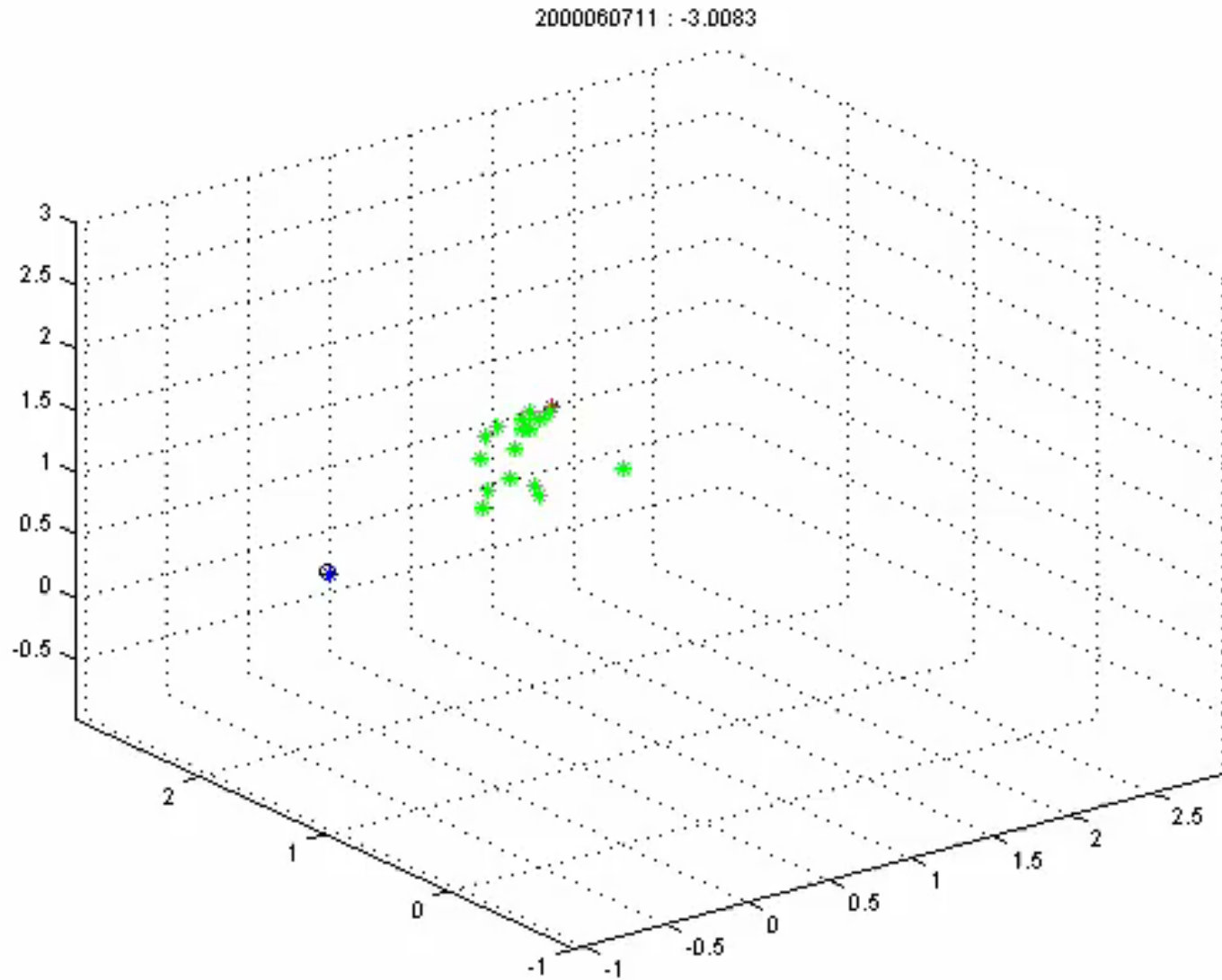


Hypothesis: Perception of the 3D echo scene
To forage in a cluttered environment, the bat
depends on active control of sonar signal
direction, duration, frequency and timing.
must sort echoes from different objects.

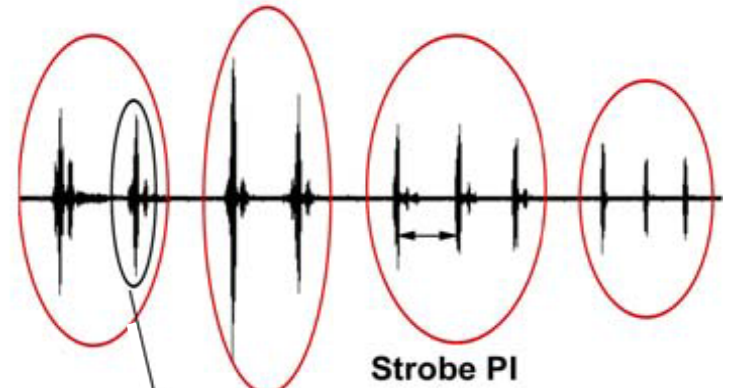
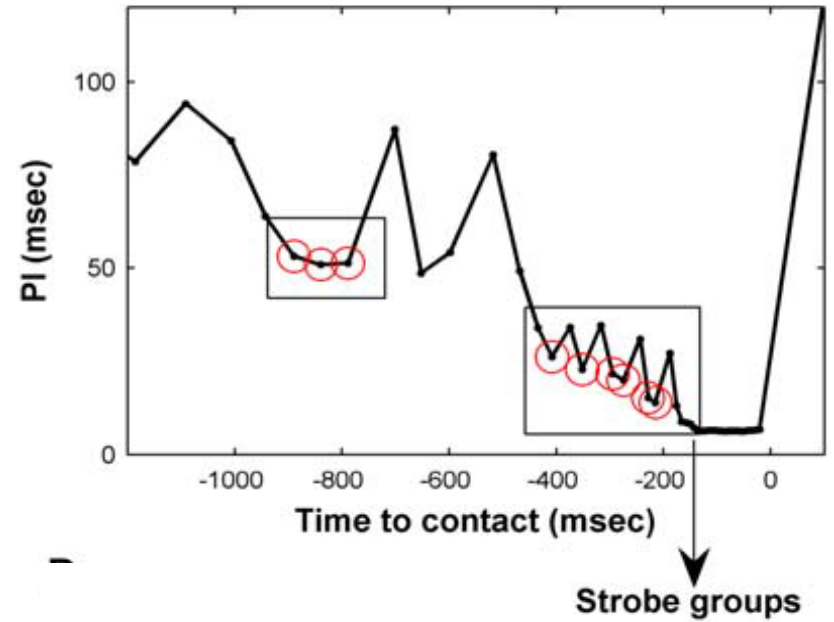
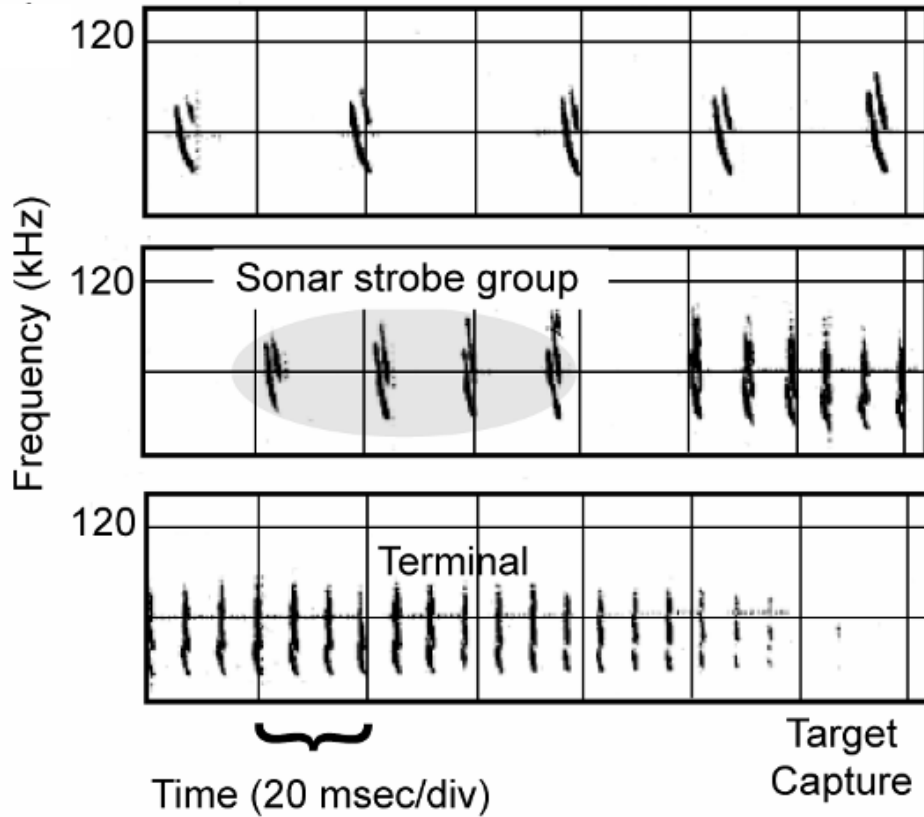
Target Capture in the Presence of Clutter



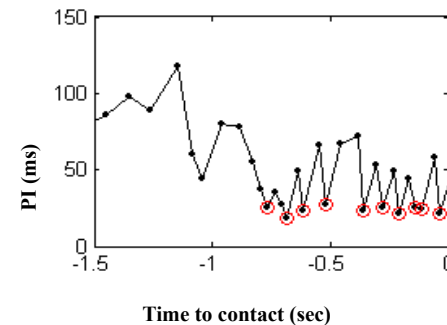
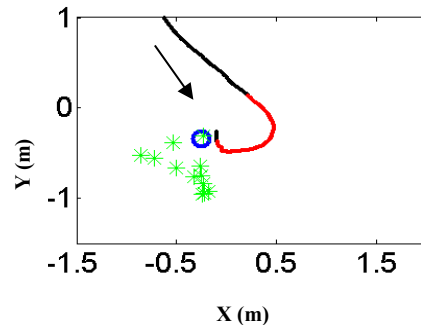
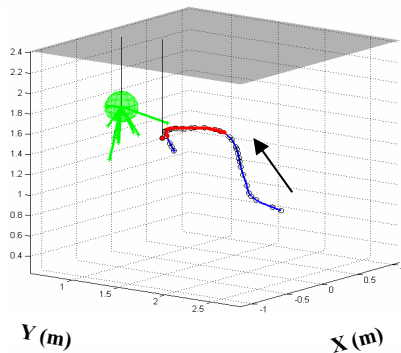
Sonar target tracking under clutter conditions



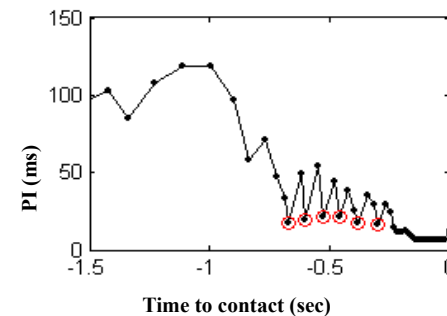
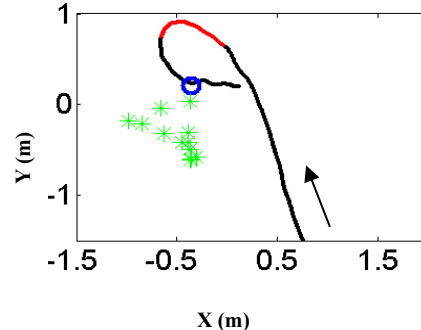
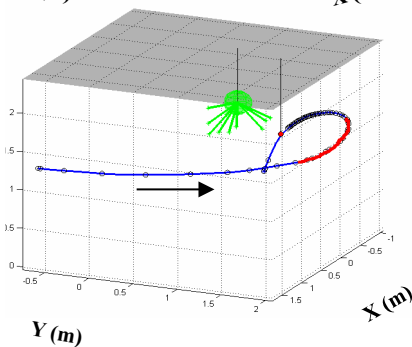
Sonar sound groups



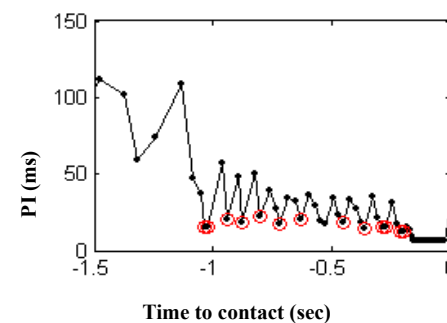
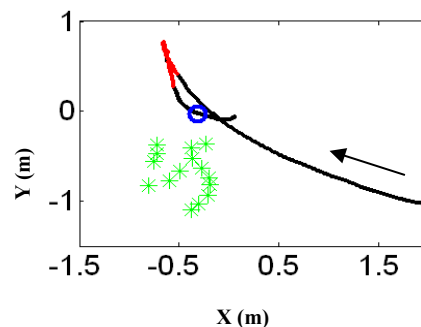
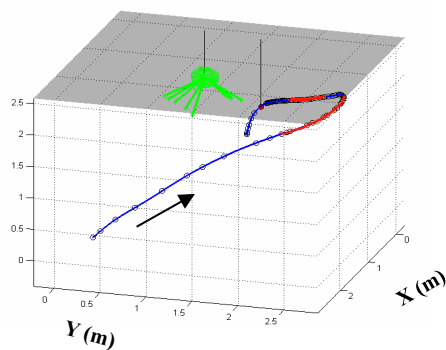
10 cm



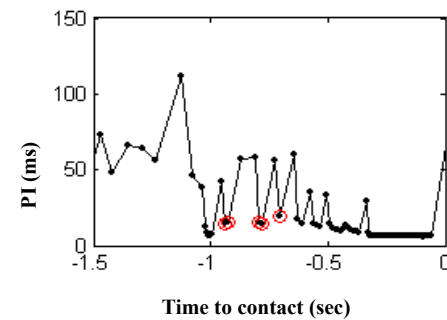
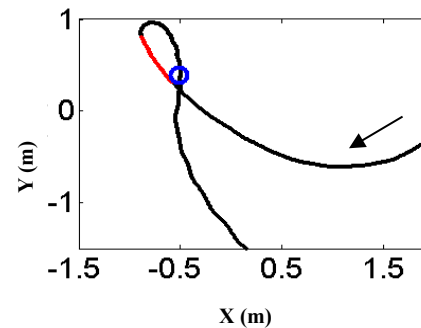
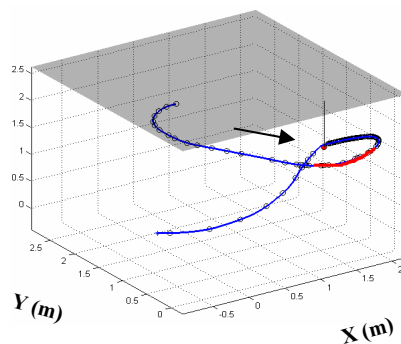
20 cm



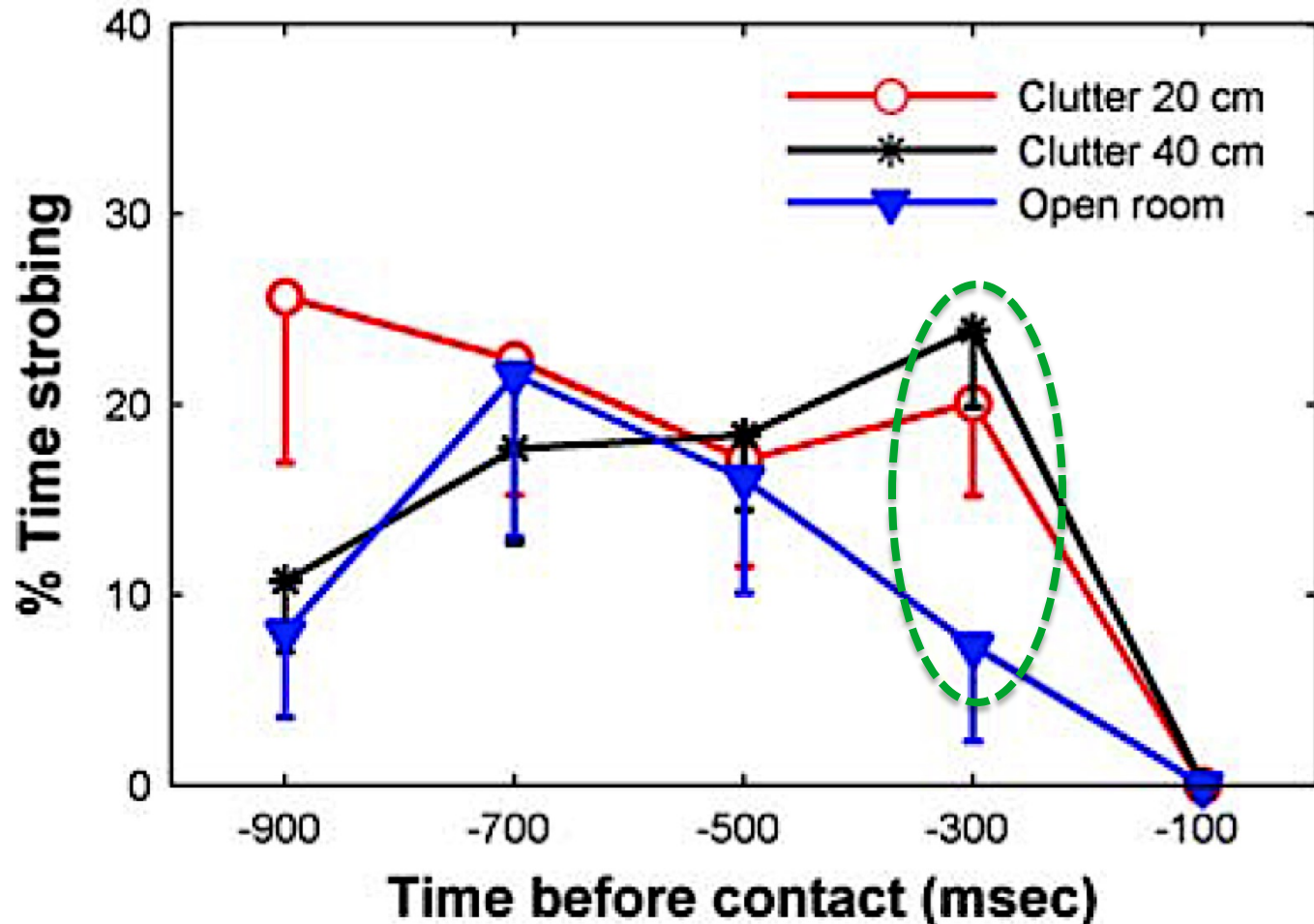
40 cm



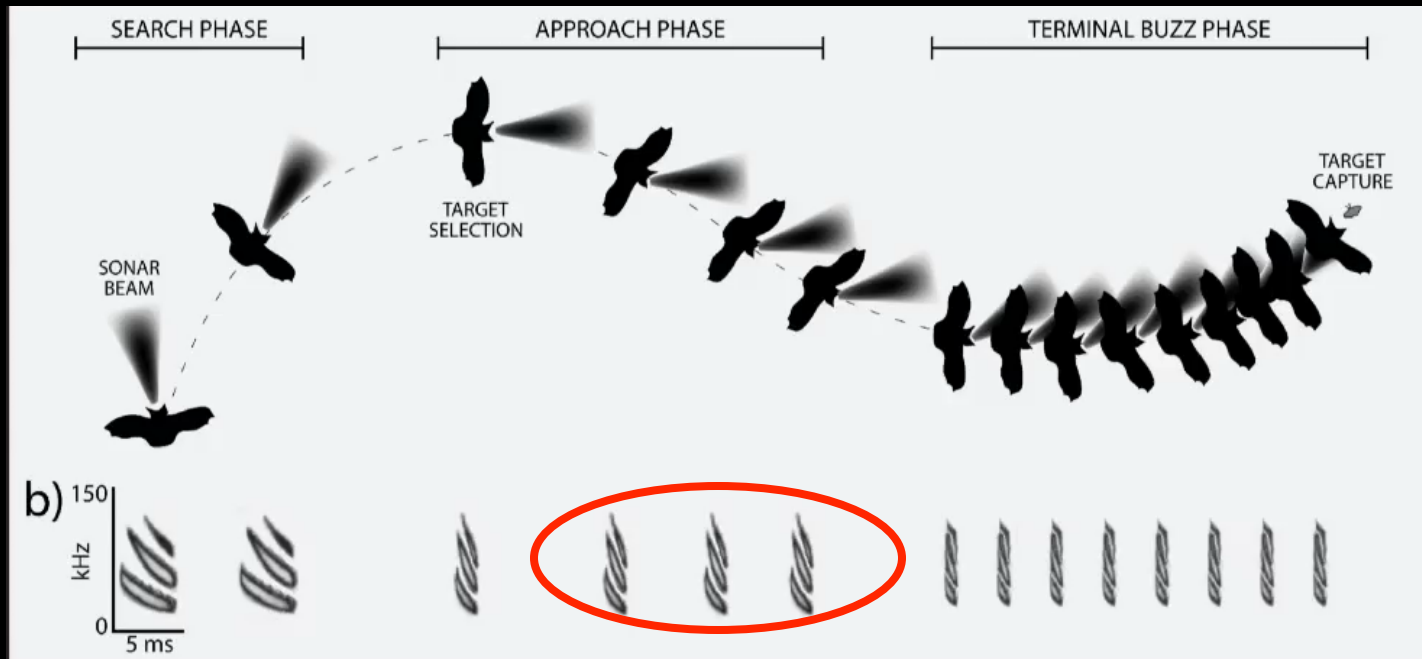
Open room



Sonar sound group production increases close to the time of insect capture when bats forage in the presence of clutter



Functional role of sonar sound groups?



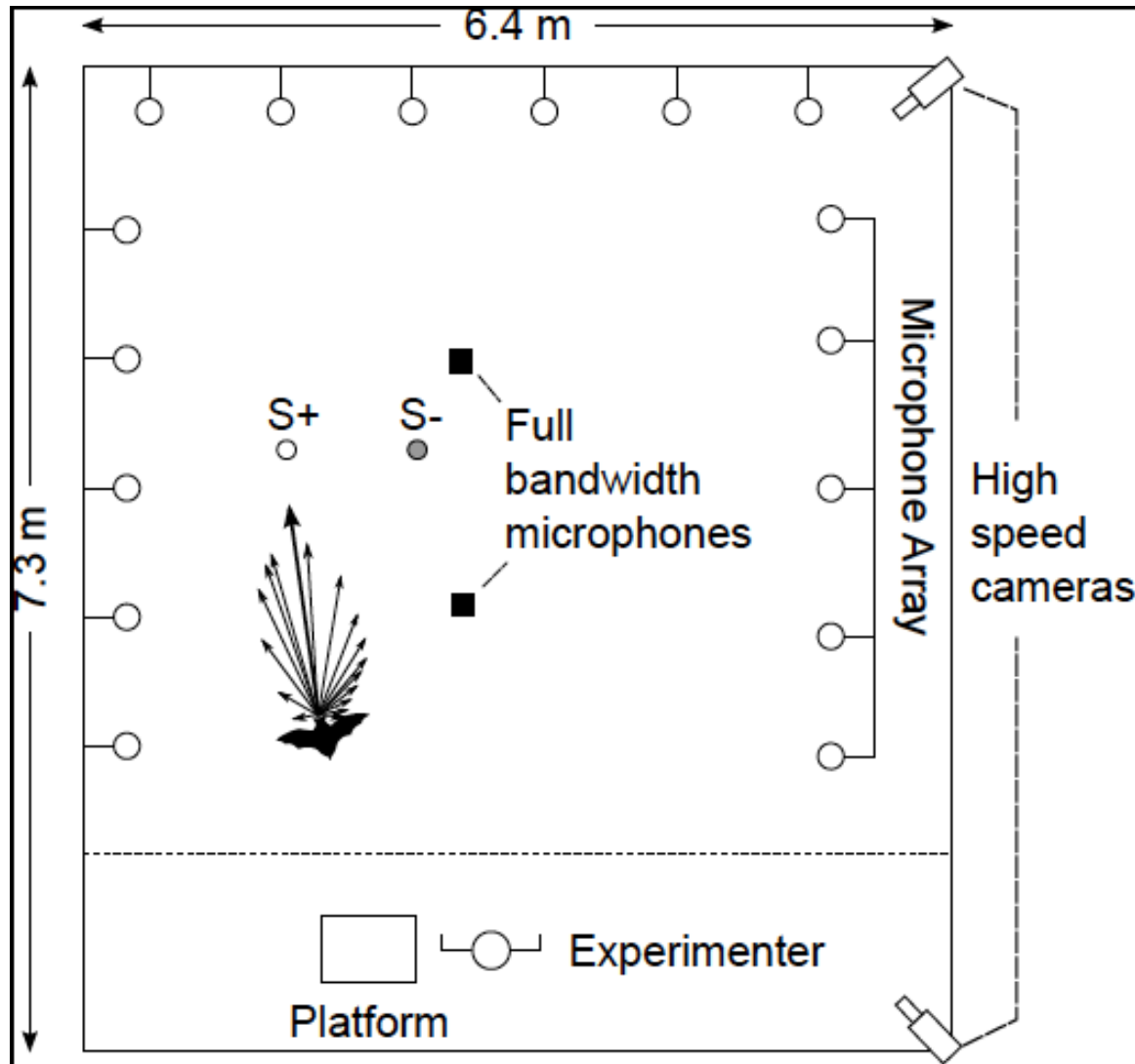
Hypotheses:

- Sonar sound group production is an indicator of spatial attention
- Sonar sound groups evoke a sharpened representation of sonar scene

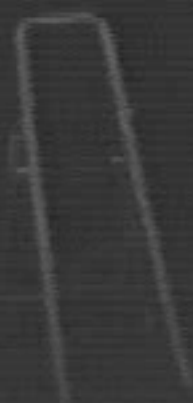
Adaptive Sonar Behavior Enables Sonar Target Discrimination



Target Discrimination by Echolocation

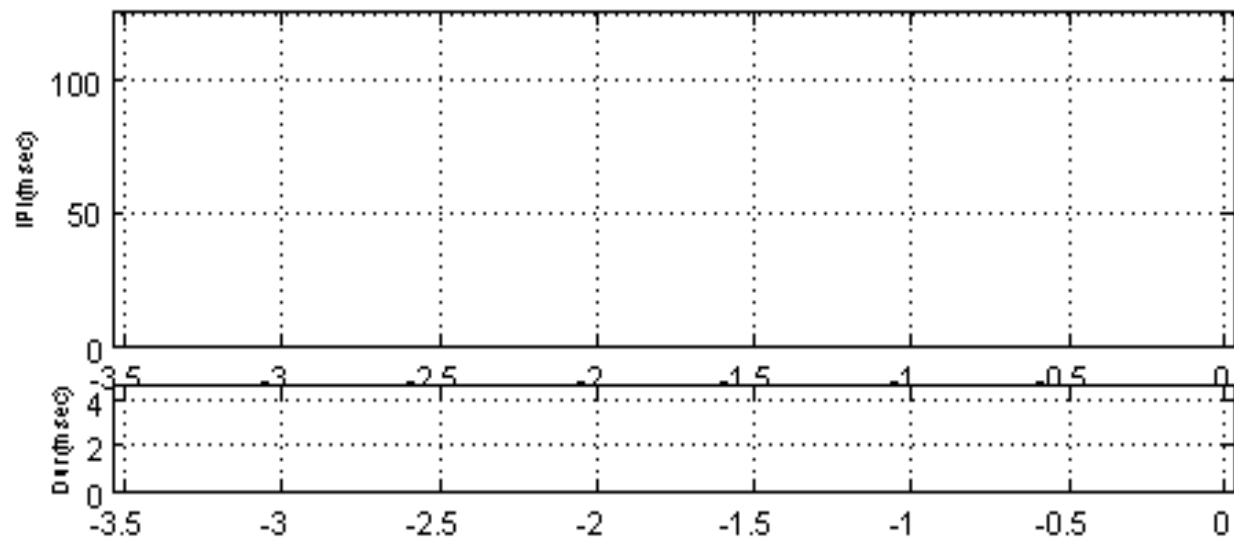
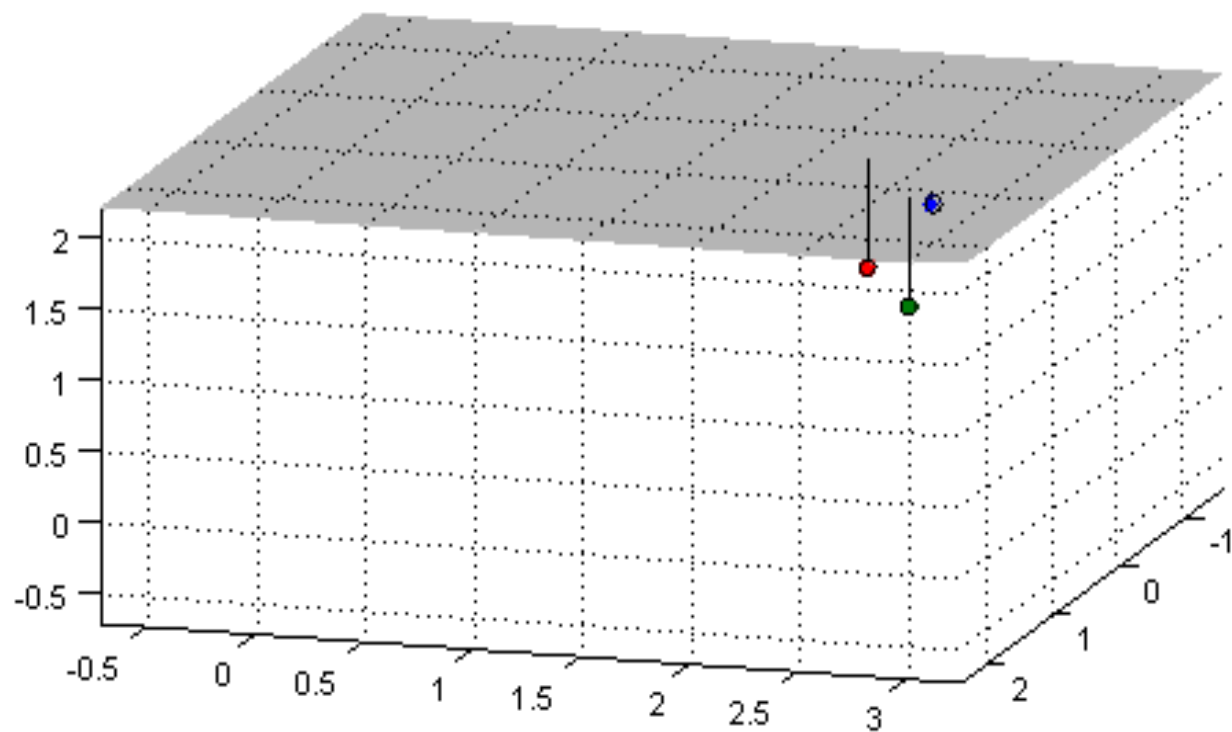


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-FWD30 -0007.7500sec

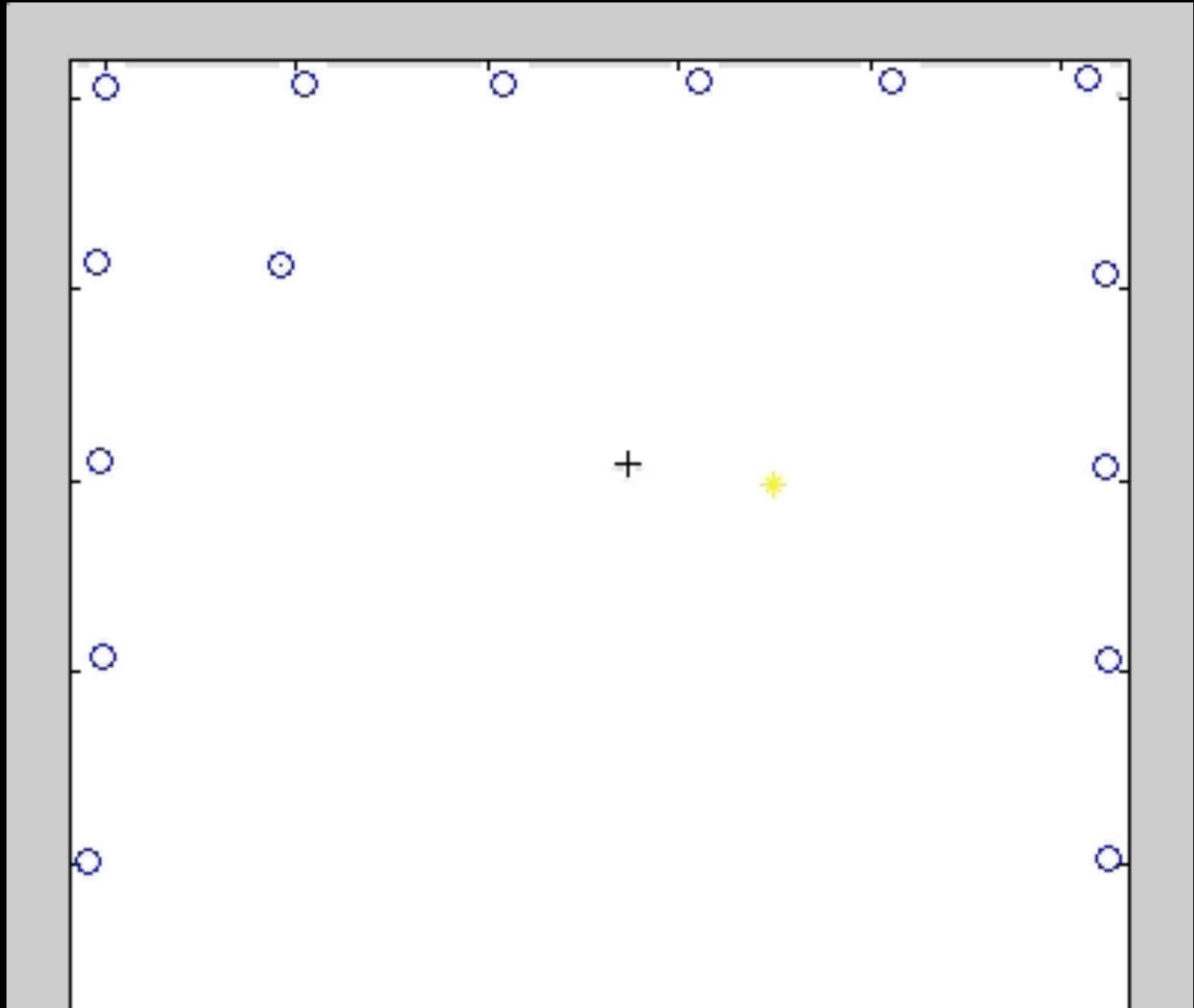




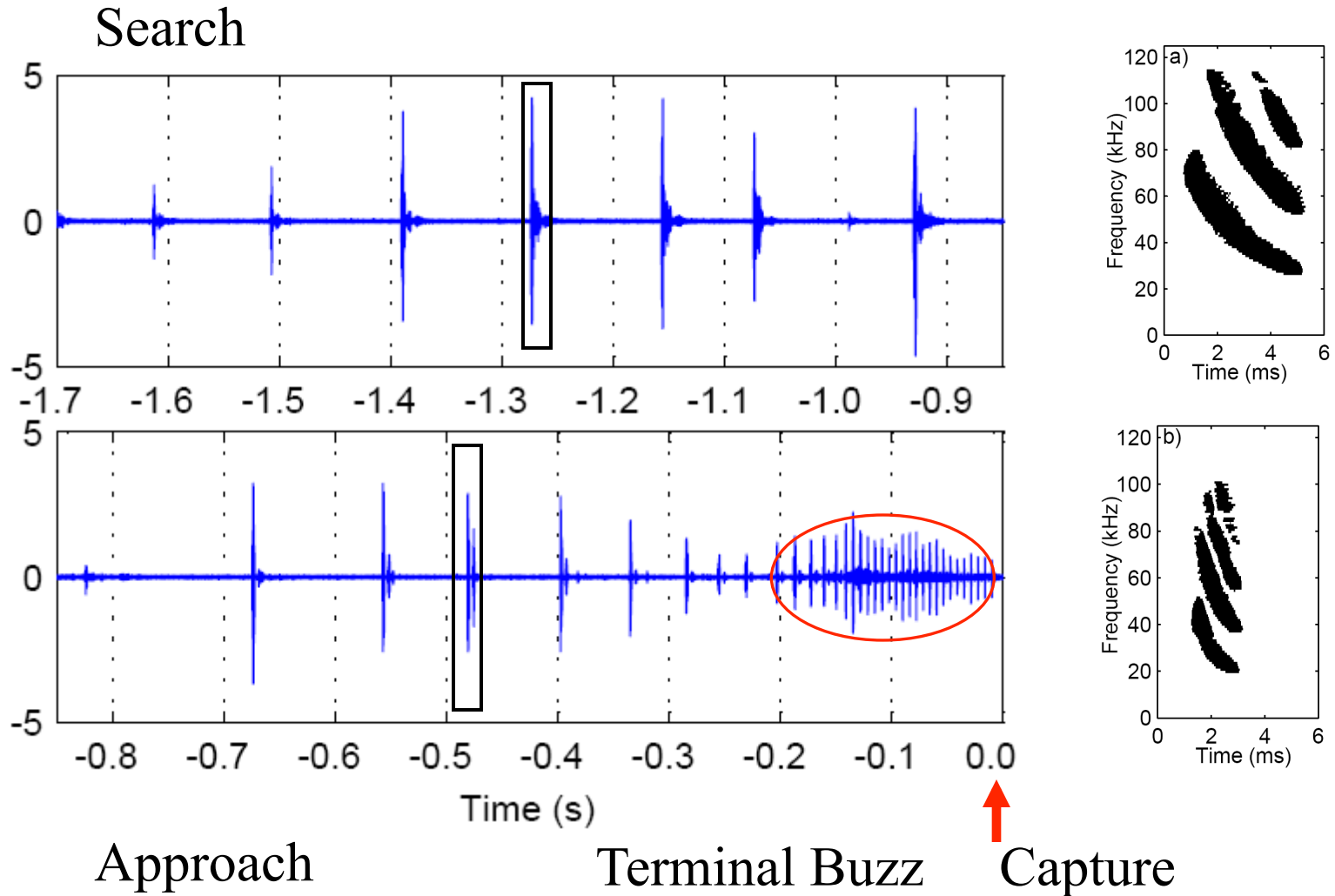
3D Movie 2004.09.06.1.01.a



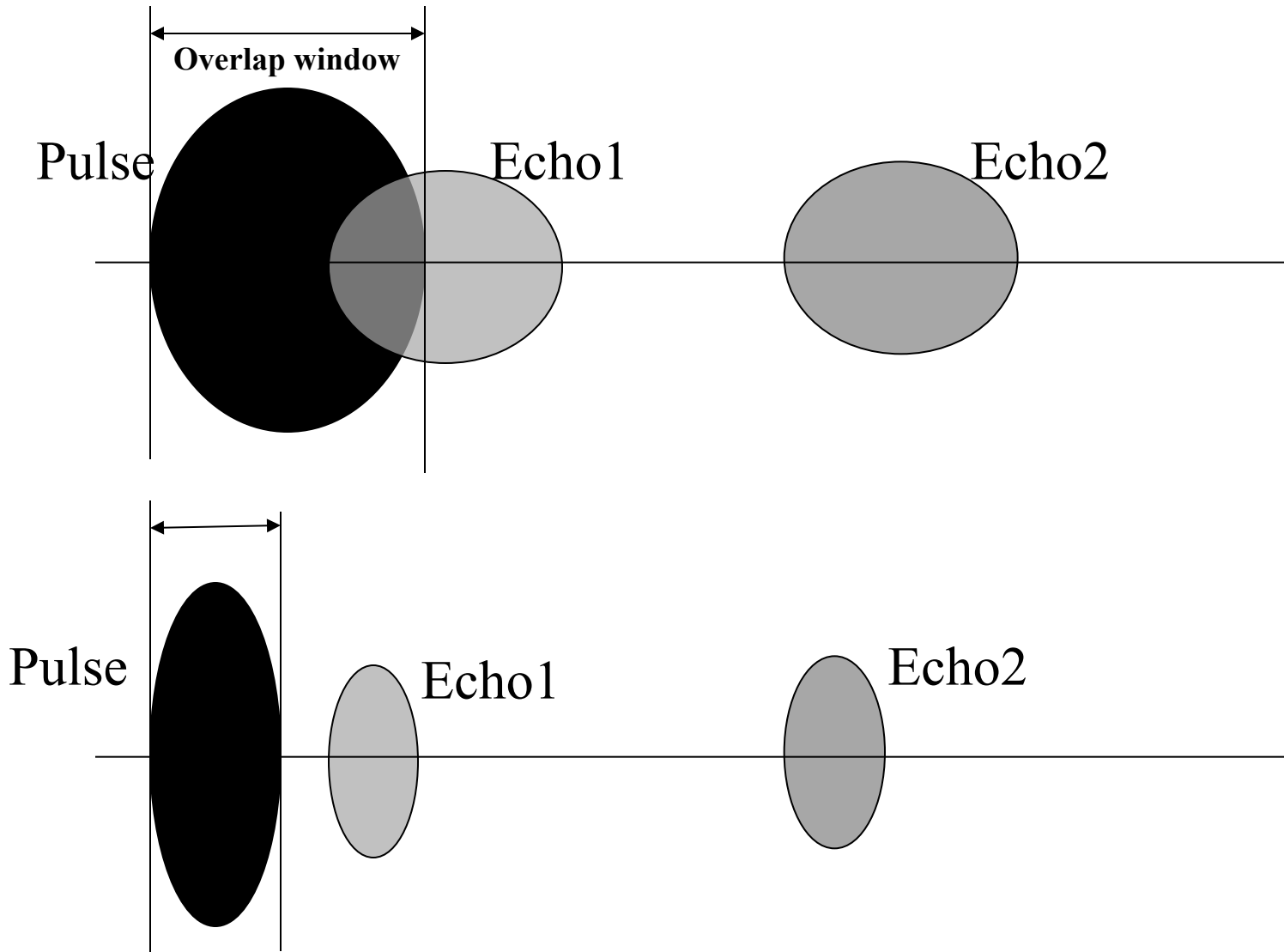
Control of sonar gaze in bead discrimination task



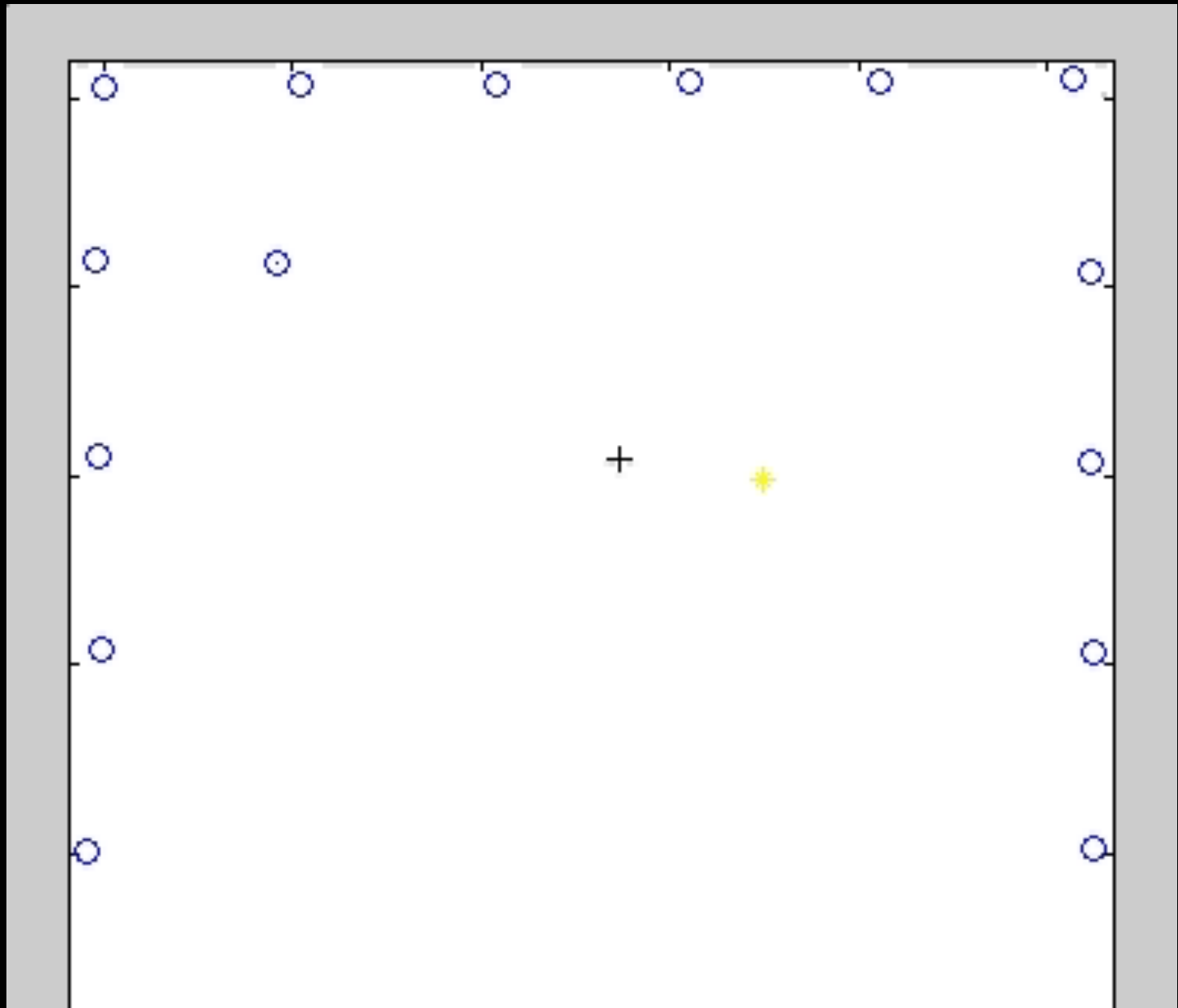
The foraging bat controls pulse timing



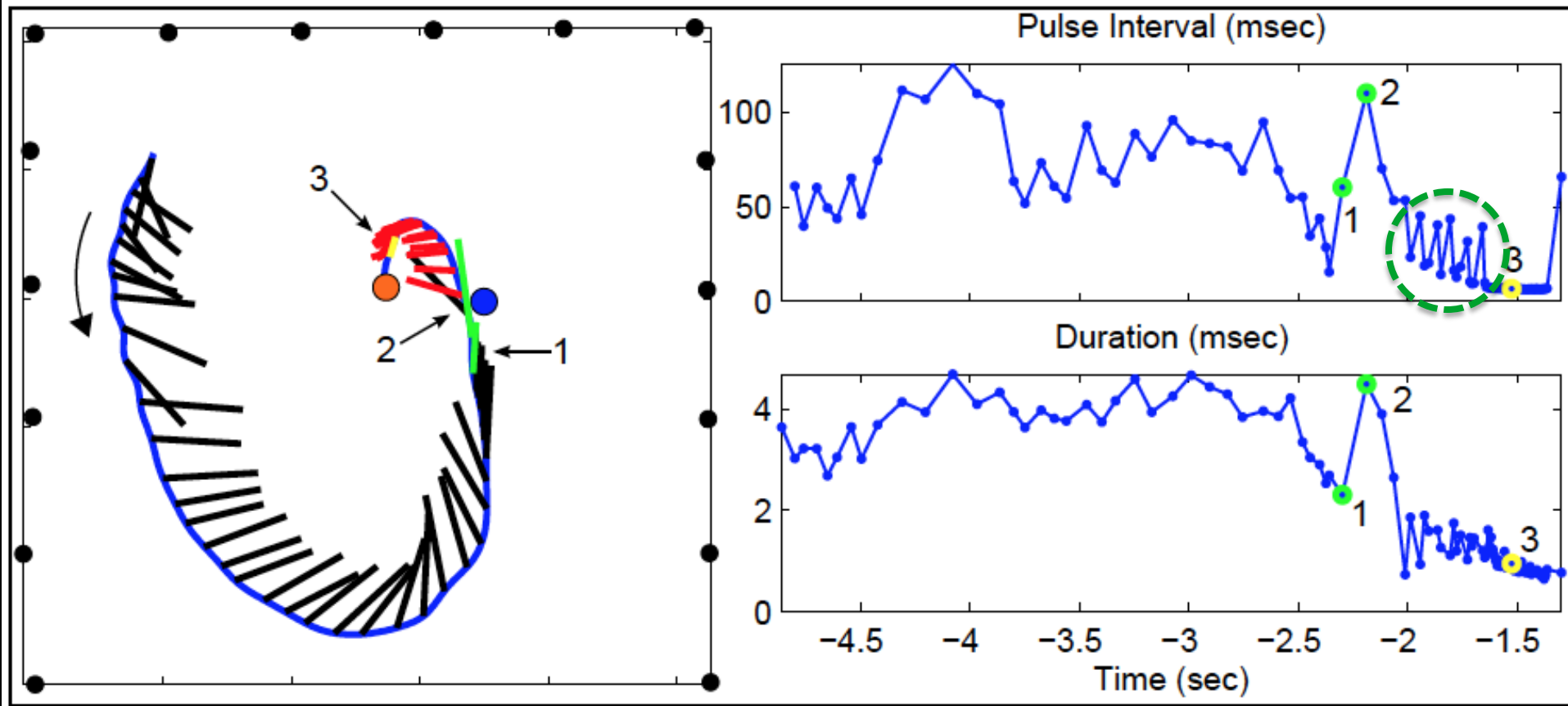
Pulse duration control with target distance



Control of direction and distance of sonar gaze in bead discrimination task



Bats point sonar beam to sequentially inspect targets

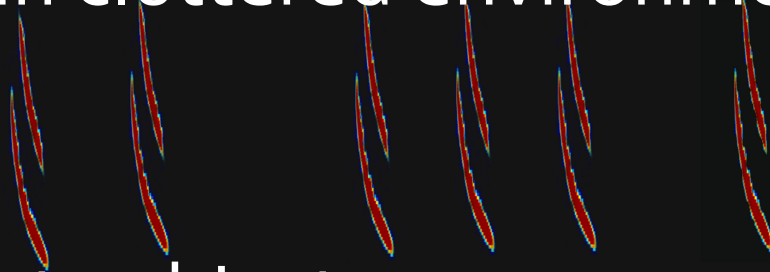


...while they also control call duration and produce sonar sound groups.

Sonar Sound Groups

Are prevalent when bat:

- Track moving, evasive prey
- Navigate in cluttered environments
- Discriminate objects



...tasks that require high spatial resolution
and figure-ground segregation

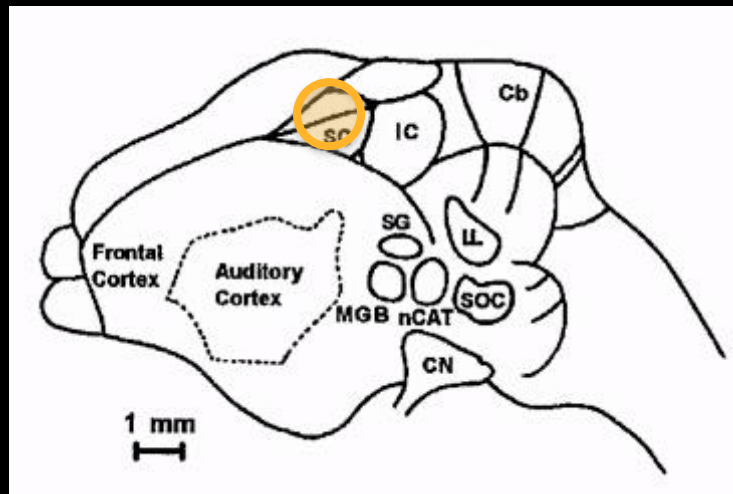
How does the bat's active control over call timing influence neural response profiles to echoes?



Hypothesis: Sonar sound groups evoke a sharpened representation of the sonar scene



Sensorimotor integration in bat echolocation: Specializations of the midbrain superior colliculus



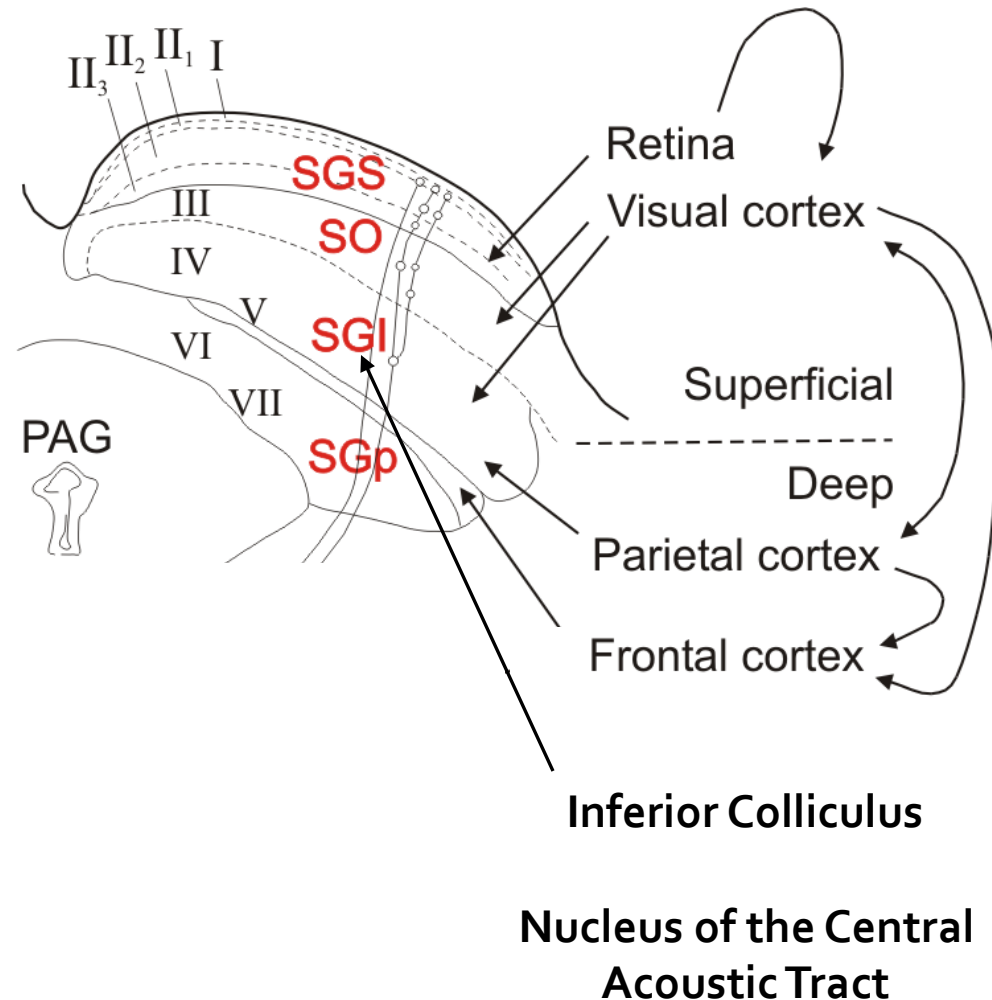
Superior Colliculus

Superficial layers of the superior colliculus

- neurons respond to visual stimulation (in most species)

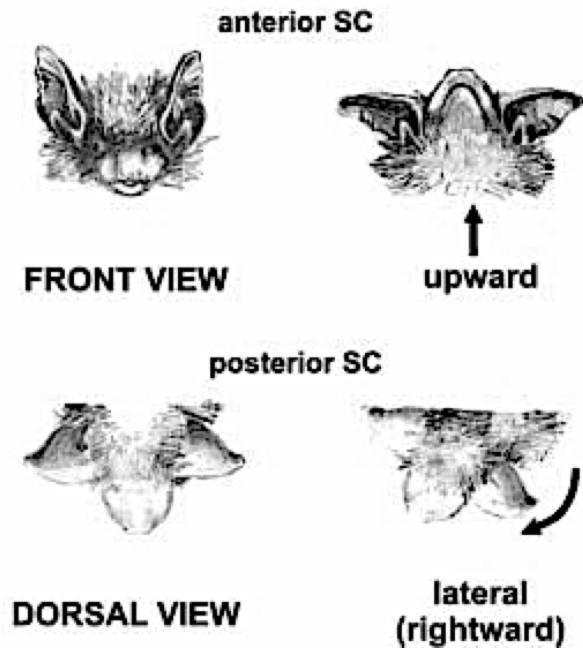
Intermediate and deep layers of the superior colliculus contain:

- neurons with multi-modal receptive field properties
- pre-motor neurons
- Sensory and motor maps in register

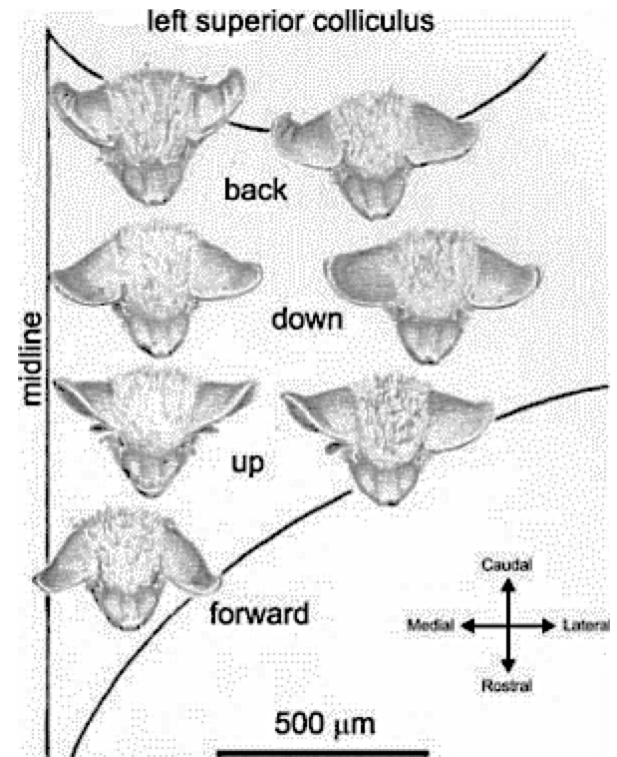


Microstimulation of the bat SC elicits orienting behaviors

Initial Position **Electrically-stimulated Head Movement**

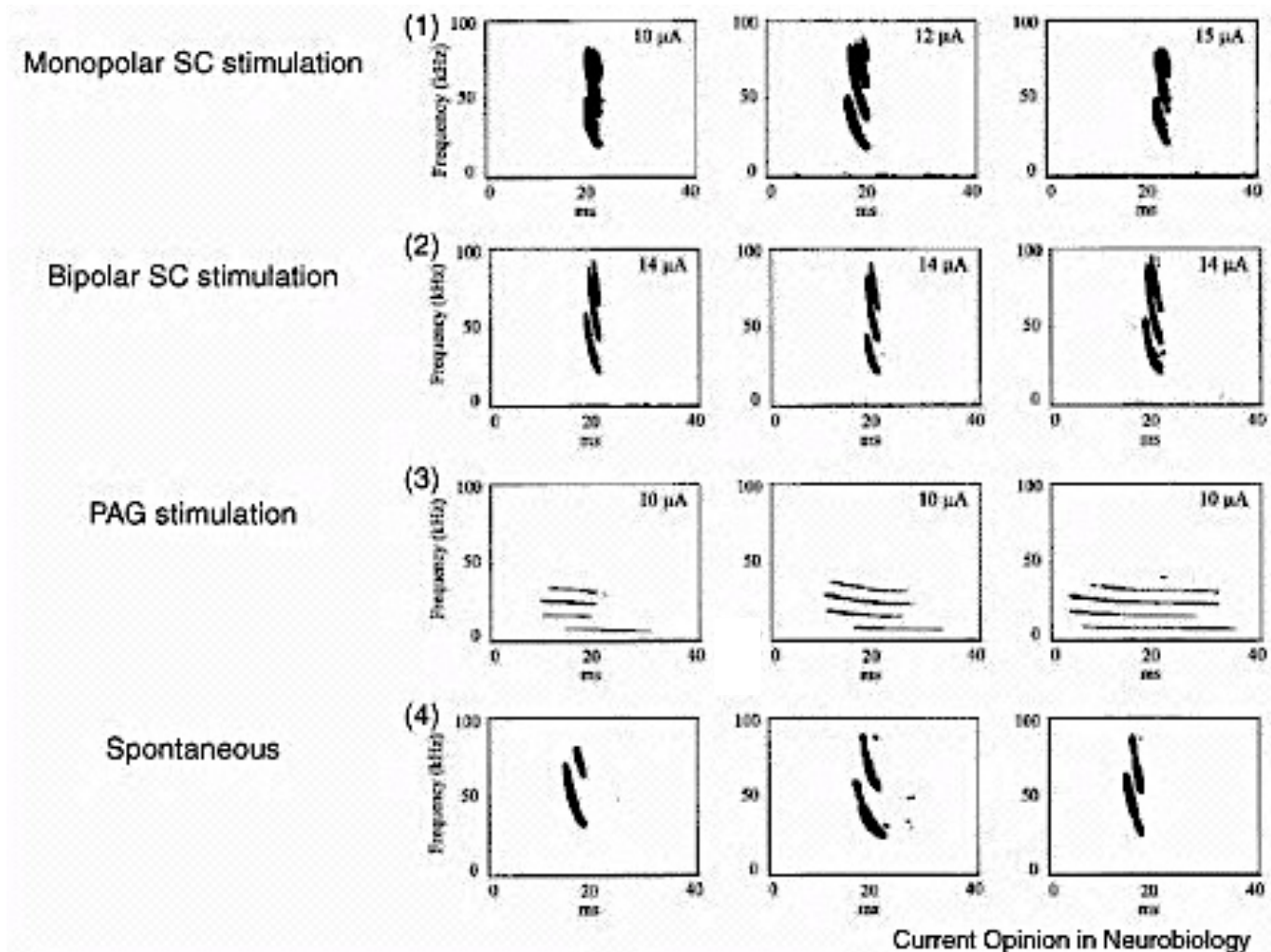


Head Movements



Pinna Movements

Microstimulation of the bat SC elicits species-specific orienting behaviors



Sonar Vocalizations

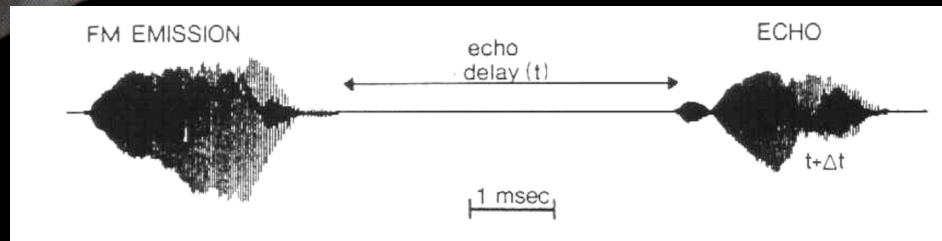
Recordings from the SC of the freely echolocating bat

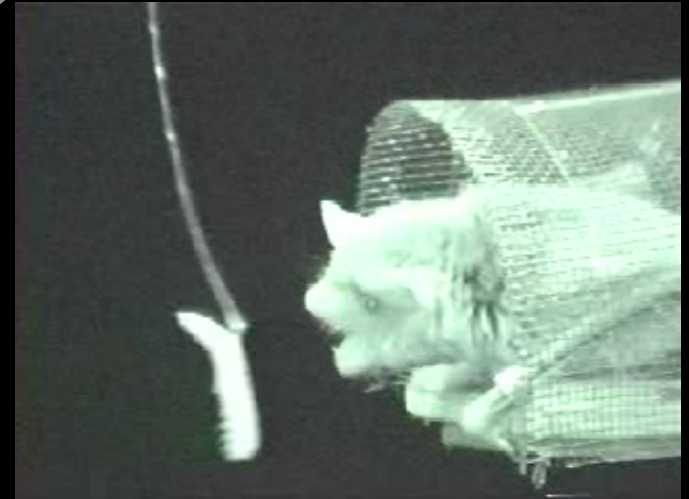
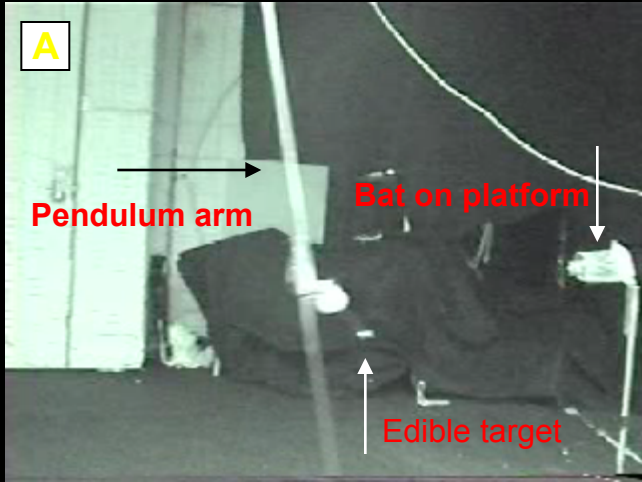
Accuracy of echo delay measurement ($\sim 60 \mu\text{sec}$) depends on a precise marker for vocal production time

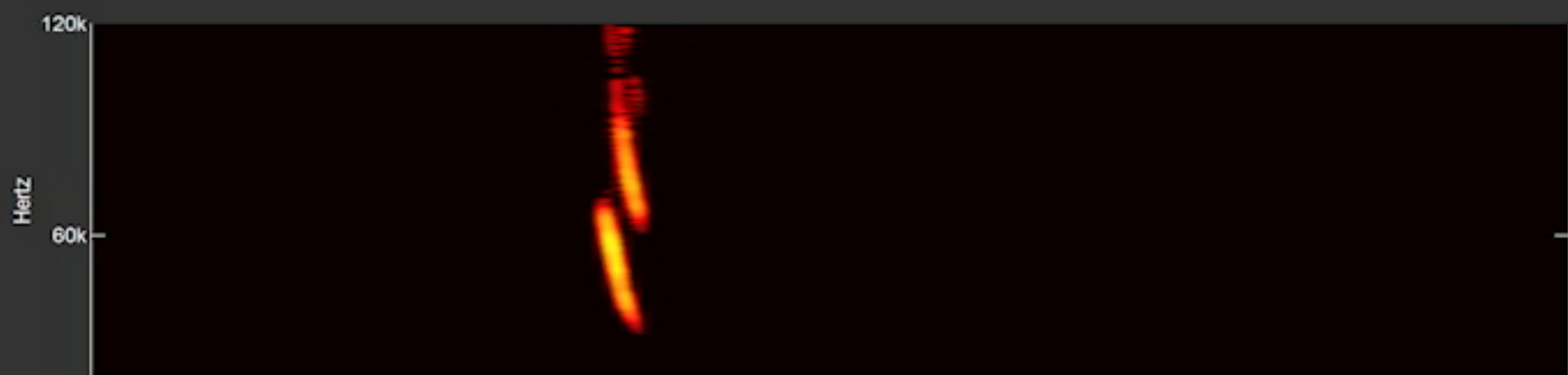
How is this accomplished?

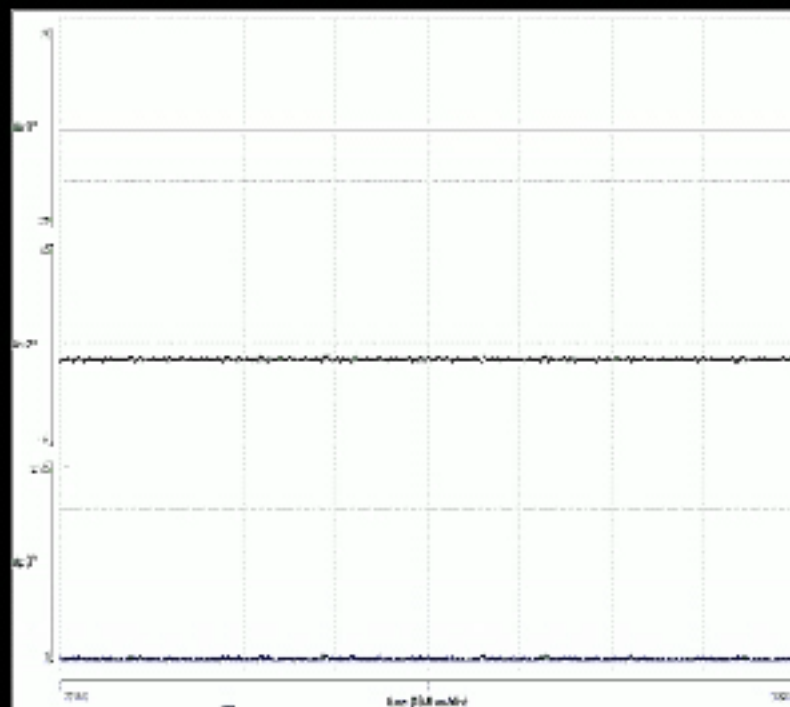
Direct reception of sonar call?

Reference copy?

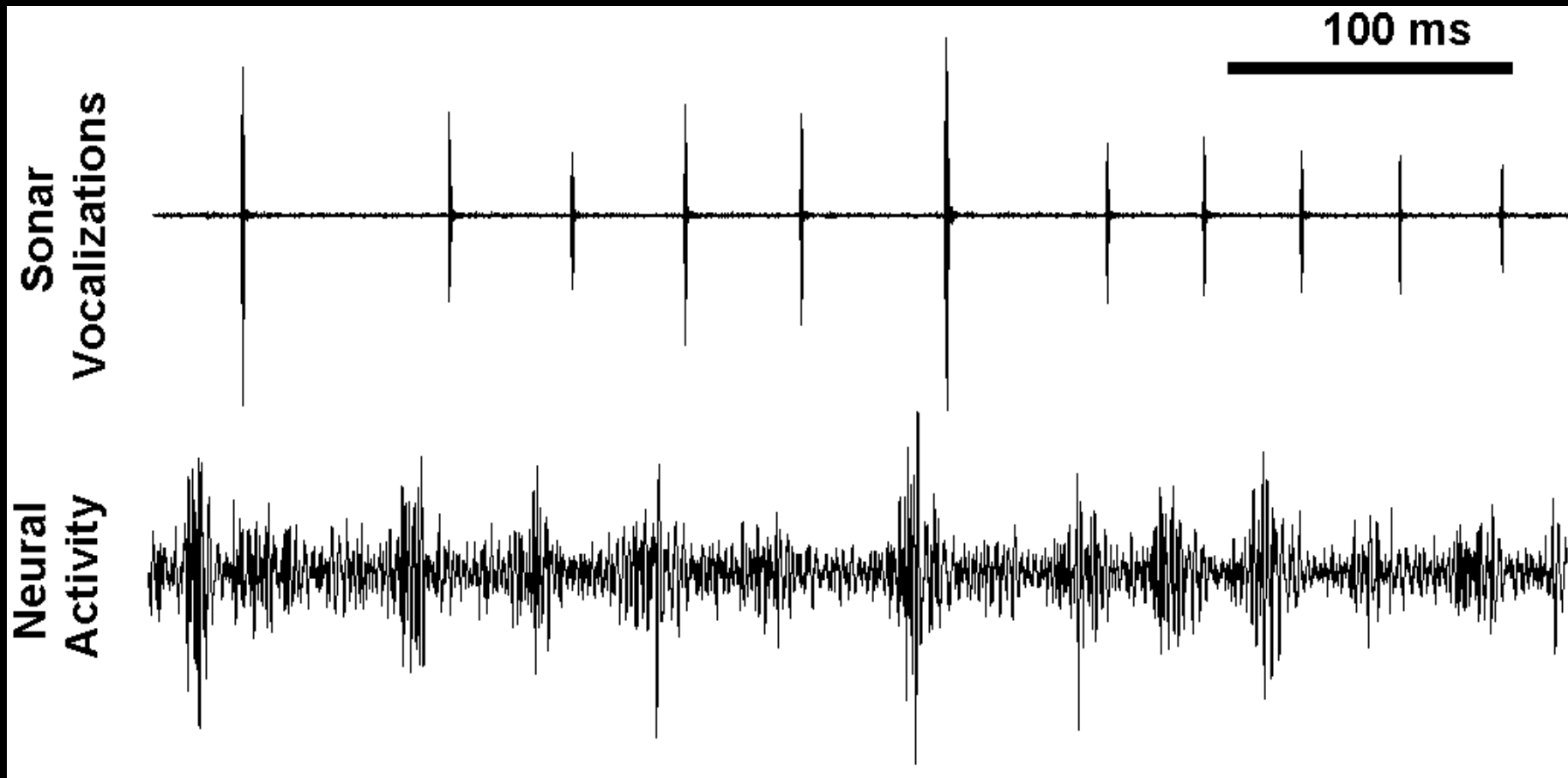




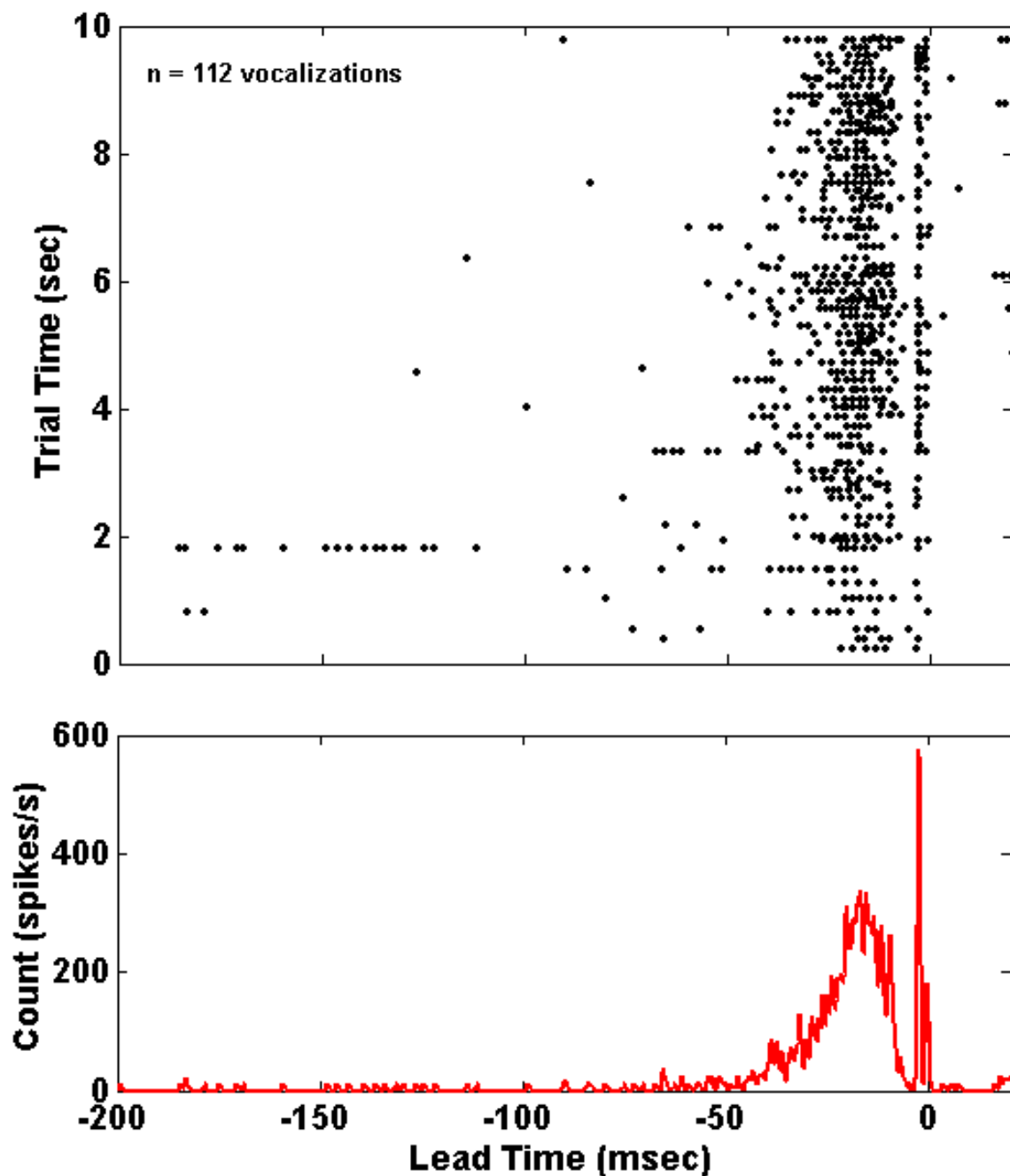




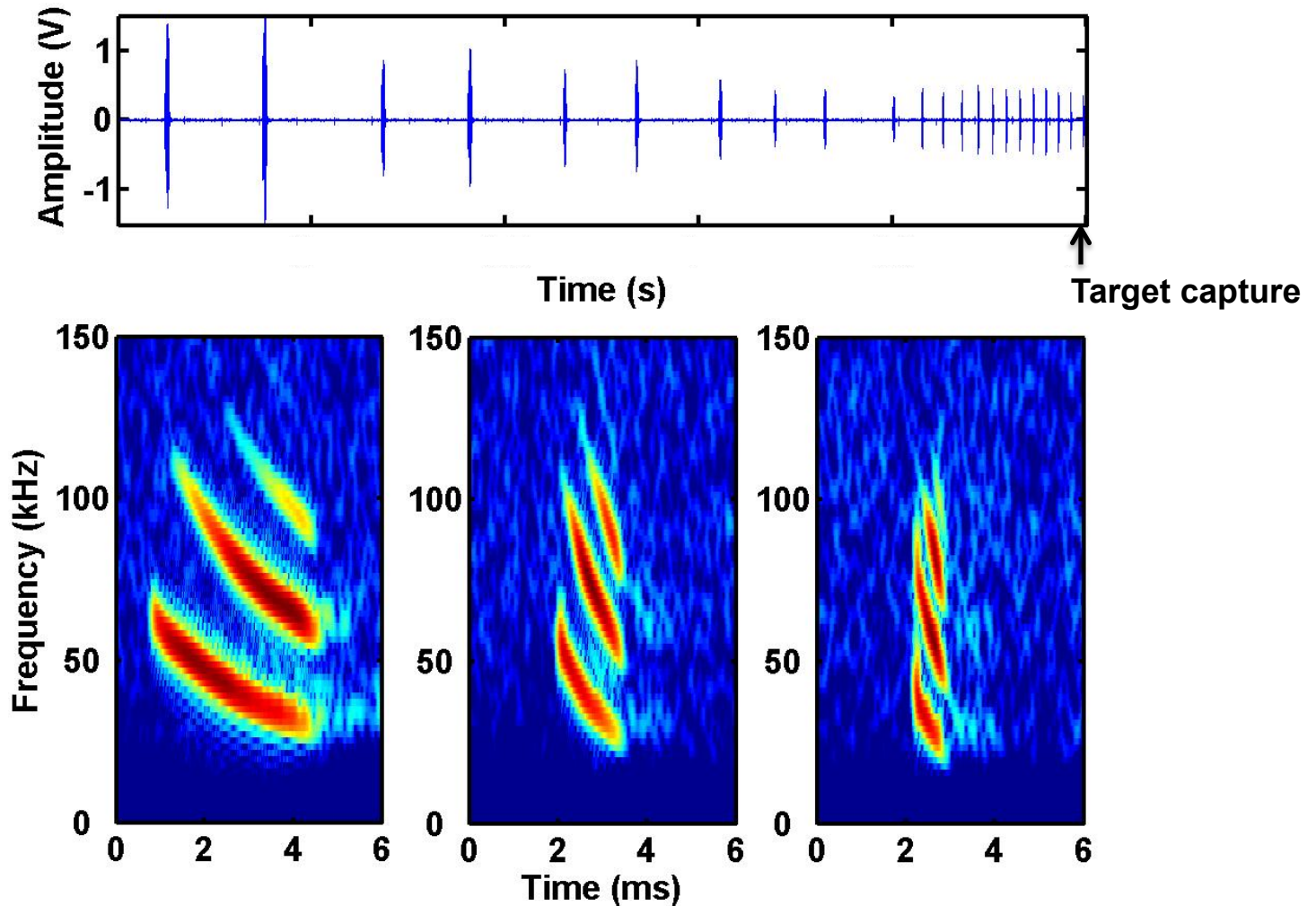
Neural activity in the SC is coupled to production of sonar vocalizations



Premotor Vocal-Motor Activity in the Bat SC

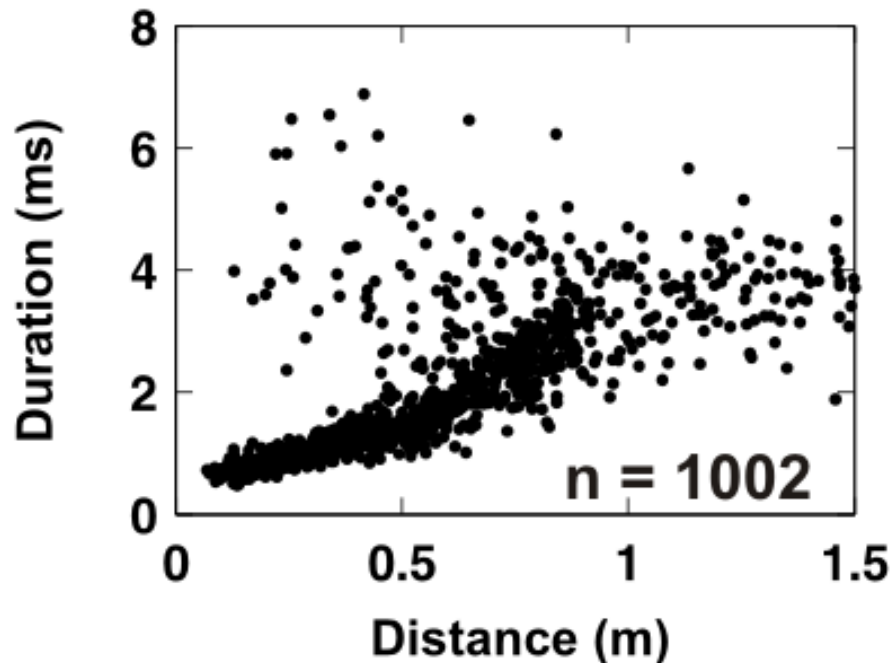


Bats adapt the duration of sonar calls in response to changes in target distance, computed from the time delay between sonar emission and echo.

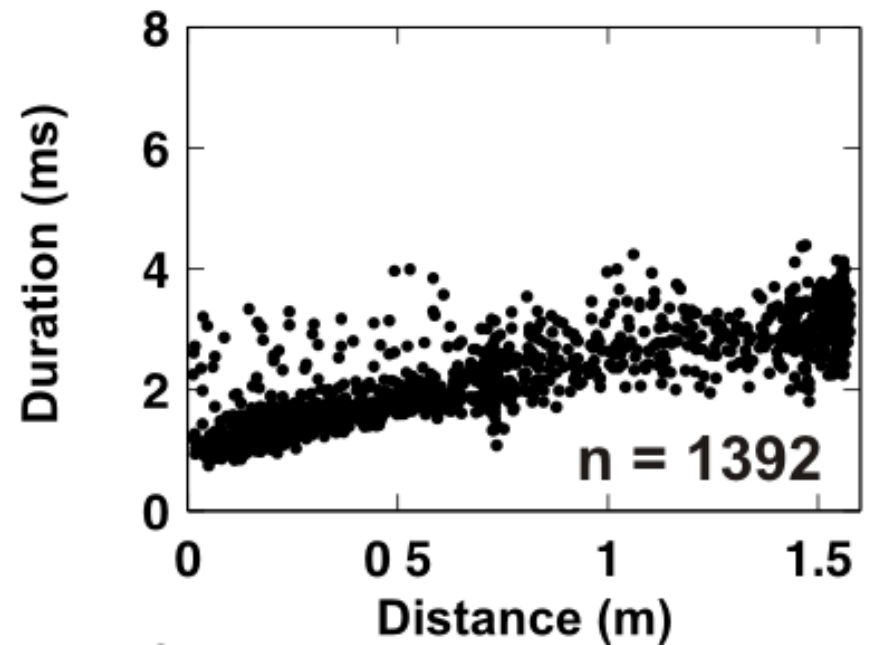


Bats adapt the duration of sonar calls in response to changes in target distance...in flight and on a platform

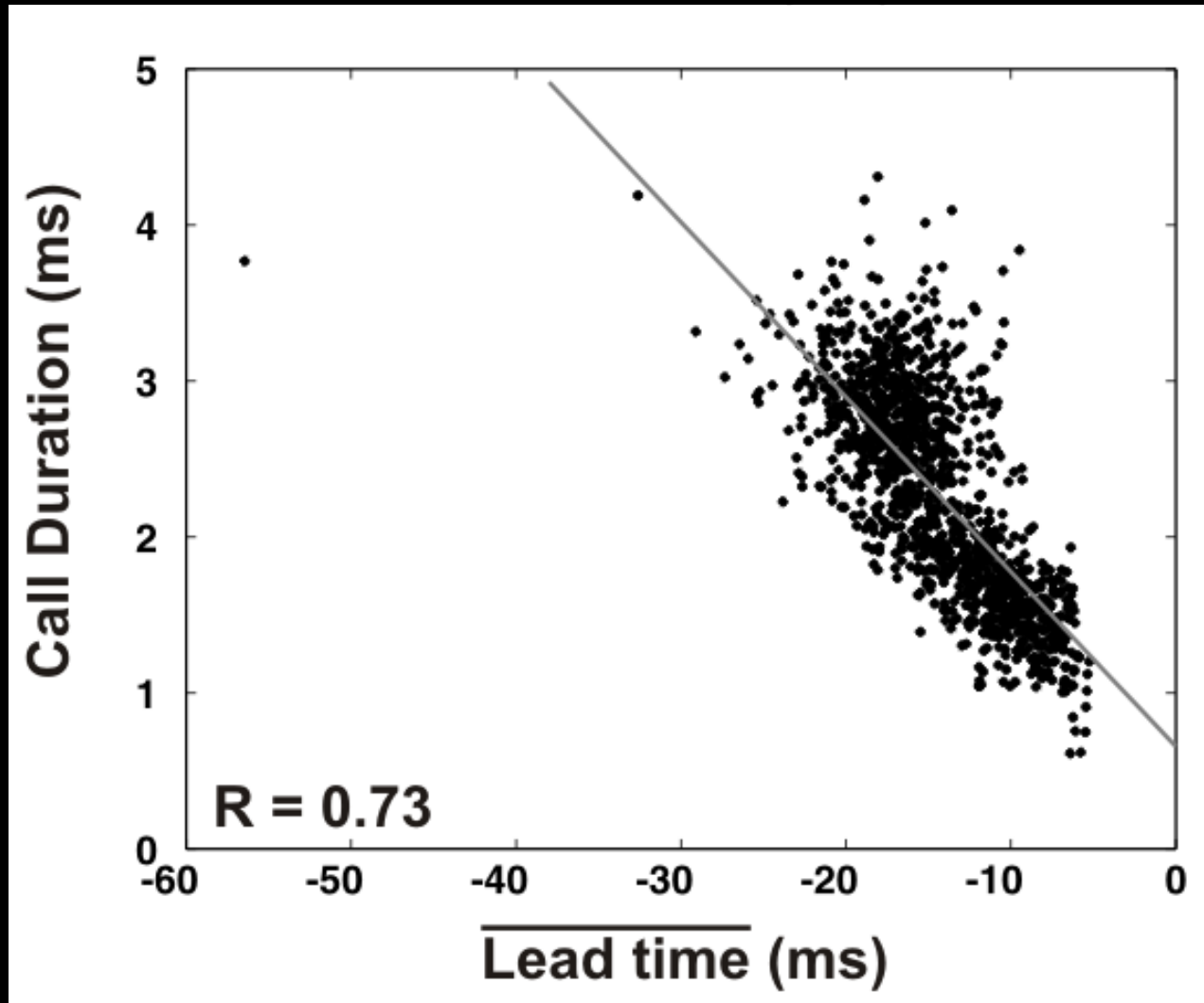
Free Flight



Oscillating Target

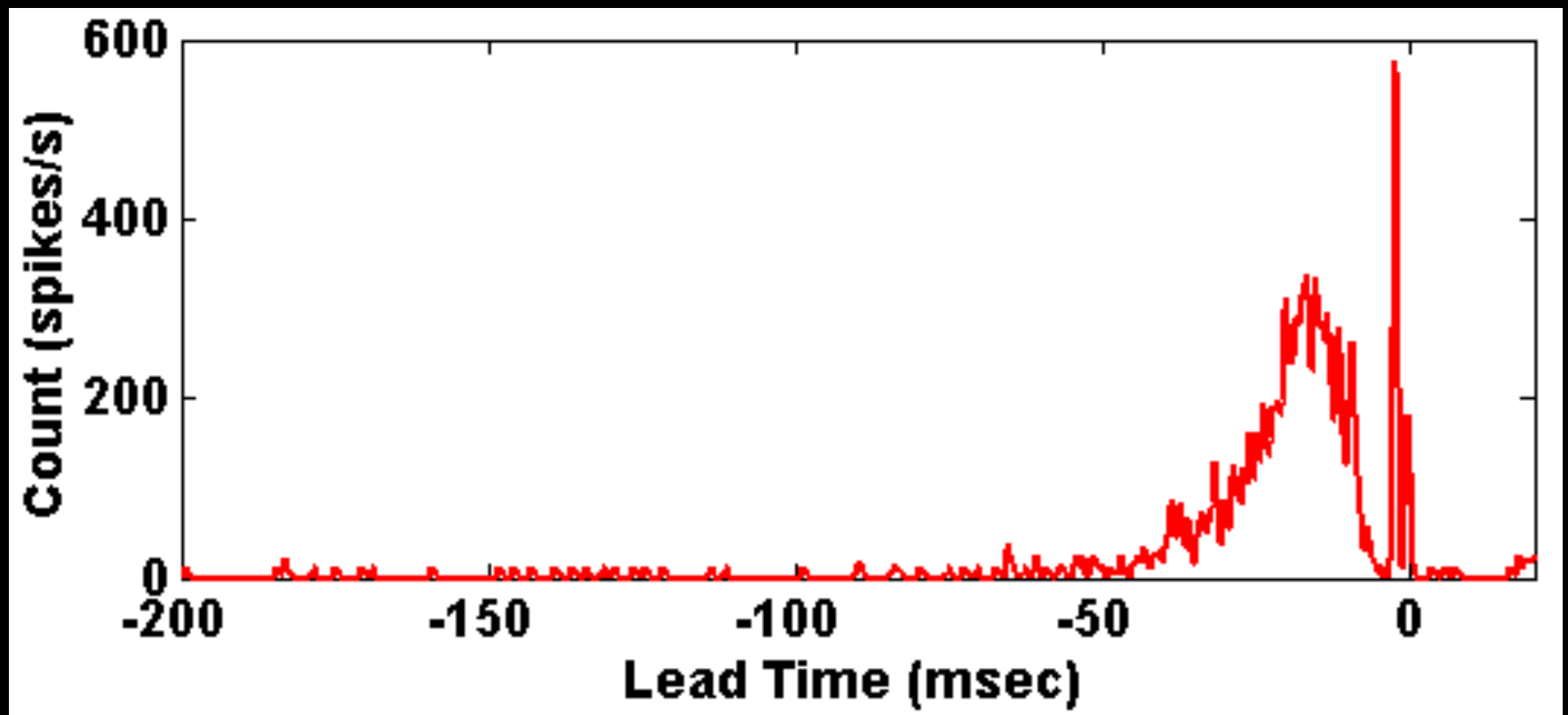


Timing of pre-motor long-lead activity changes with sonar call duration



Short lead activity can provide a marker for sonar emission time

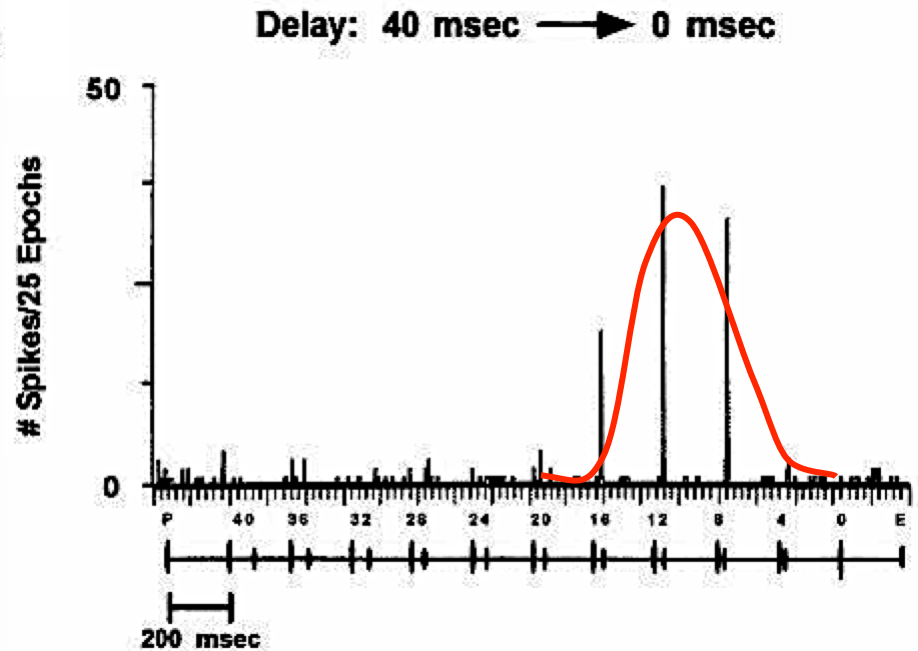
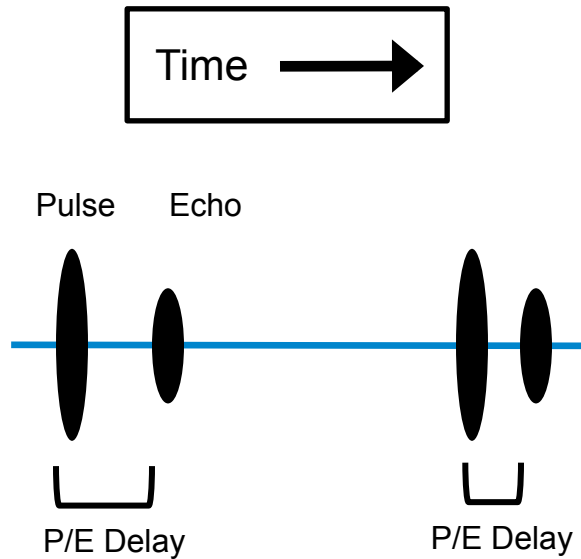
Used to measure echo delay/target distance?



Neural activity that precedes sonar call production may play a role in target tracking

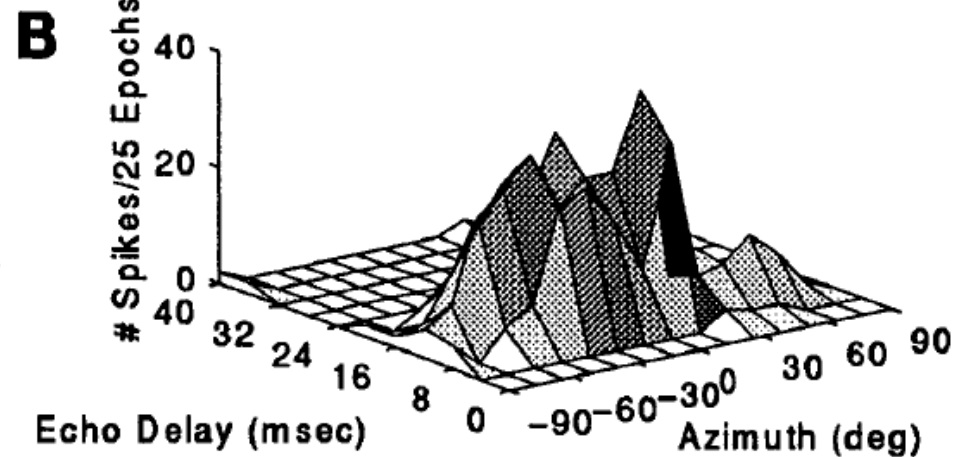
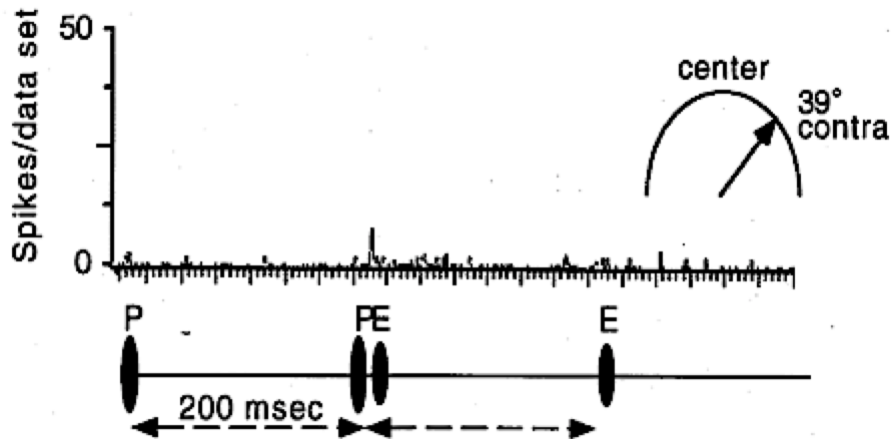
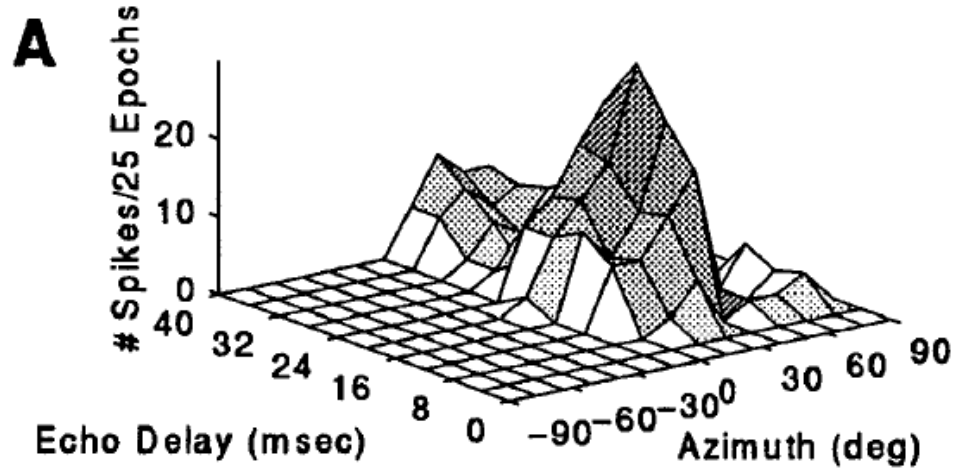
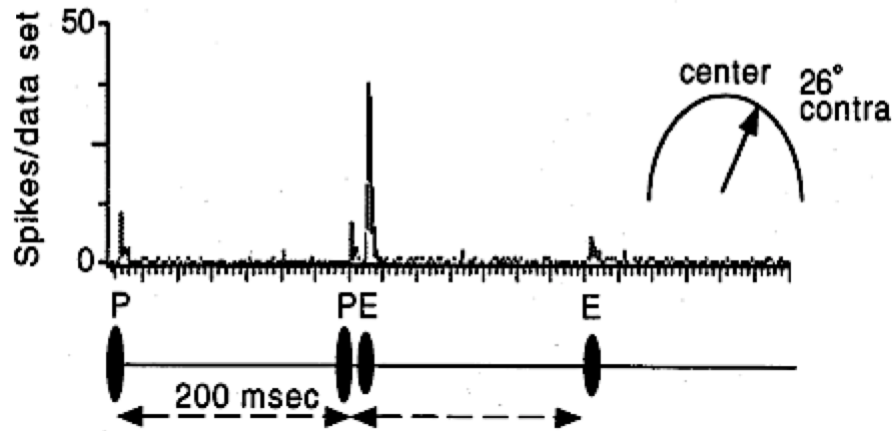
- **Long-lead activity** may be involved in the control of sonar cry duration, which changes with the bat's "acoustic gaze" along the range axis.
- **Short-lead activity** may play a role in marking the time of vocalization, important for accurate measurement of echo delay.

Range (echo delay) tuning of neurons in the bat SC



Echolocation call is often referred to as the pulse

A population of neurons in the bat SC show 3D auditory spatial tuning



How does the bat's active control over call timing influence neural response profiles to echoes?



Hypothesis: Sonar sound groups evoke a sharpened representation of the sonar scene

3D Auditory Response Profiles in the Free-flying Echolocating Bat

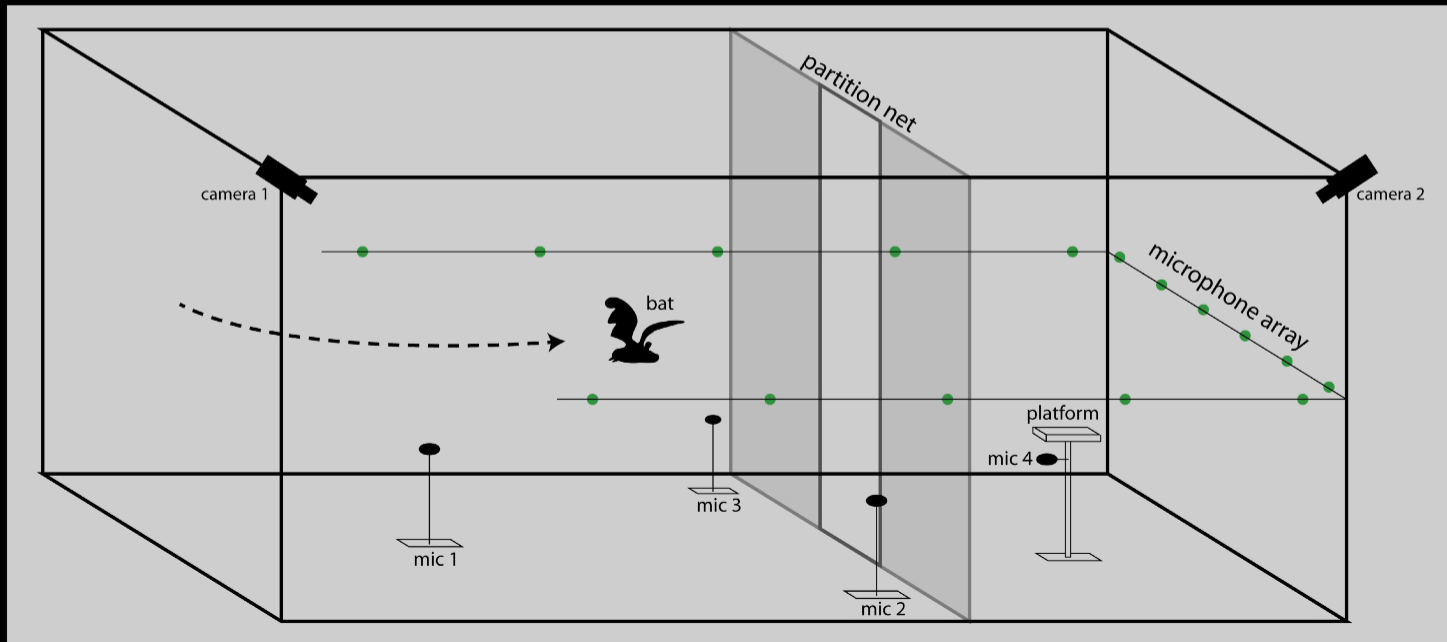


Ninad Kothari

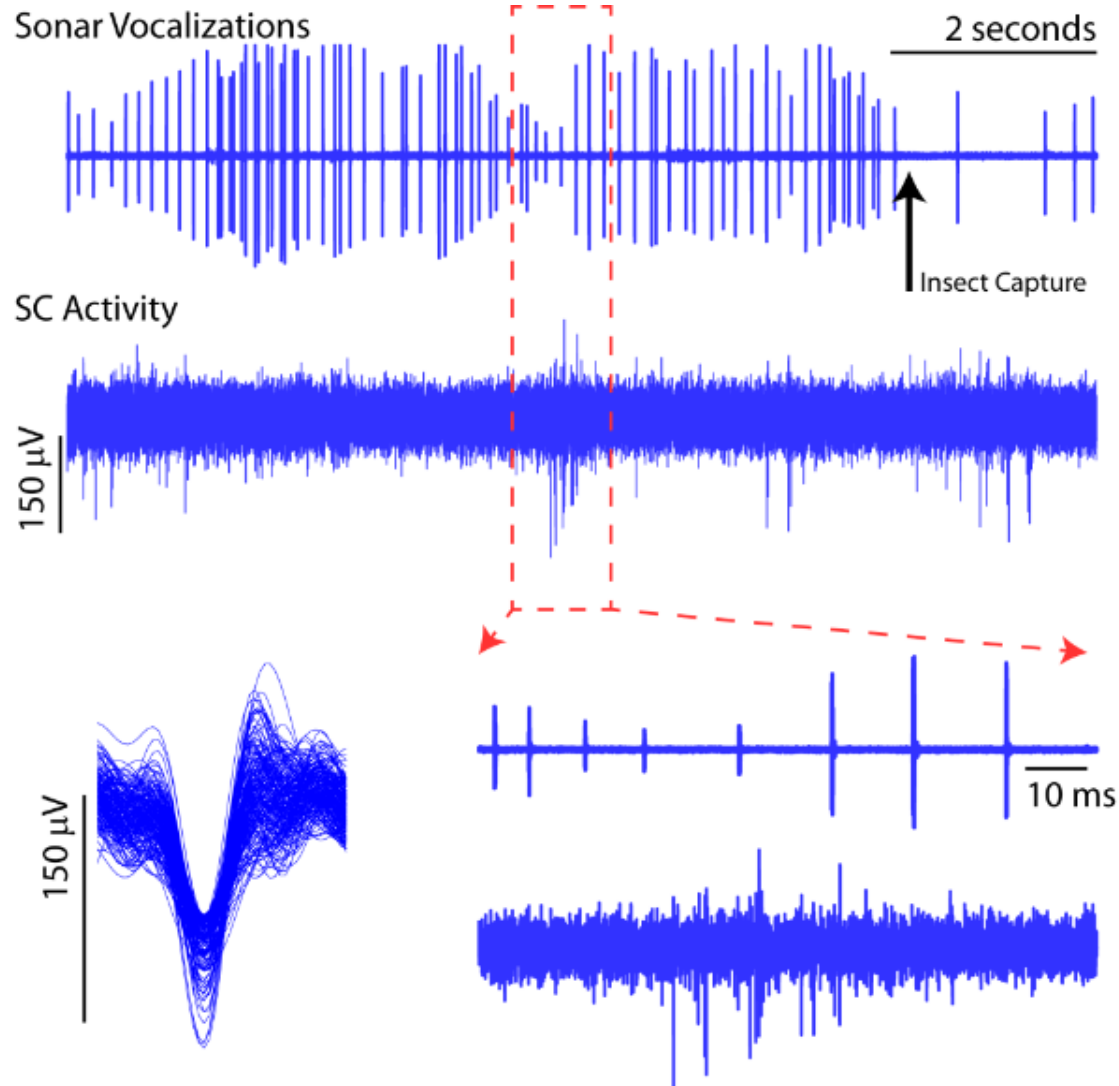


Mel Wohlgemuth

Recordings in the superior colliculus from the flying big brown bat, *Eptesicus fuscus*



SC recordings from a freely echolocating bat

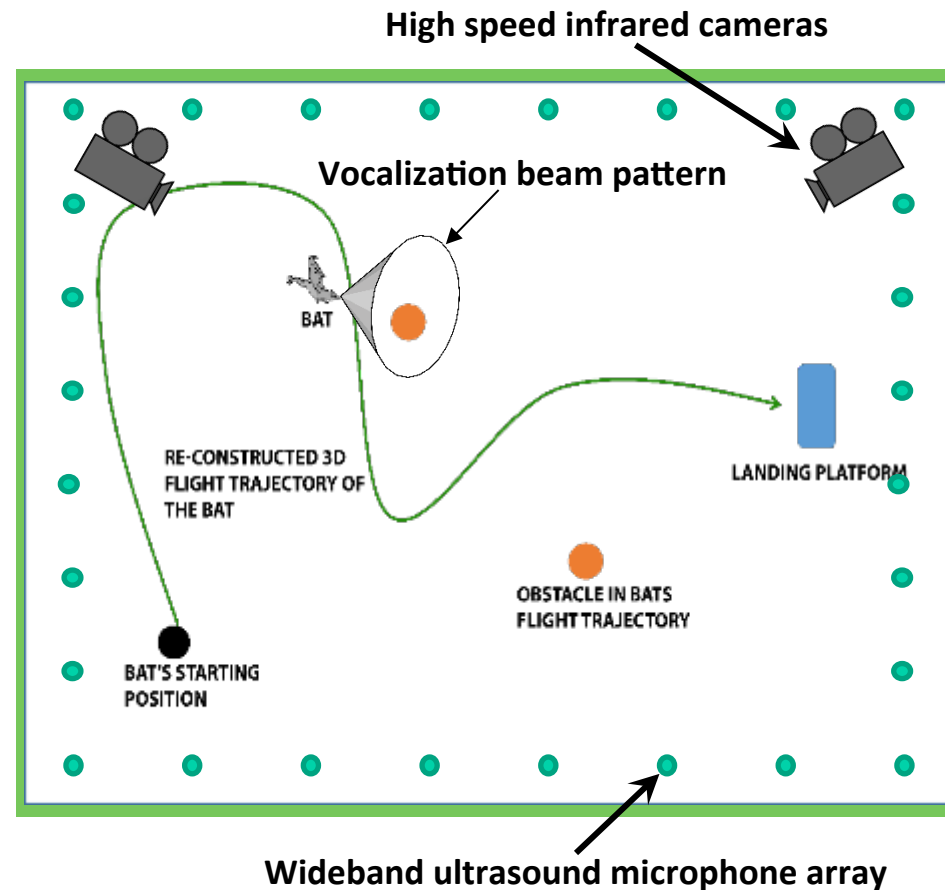


Computing the spatial characteristics of echoes arriving at the ears of a flying bat

Challenge: To determine the direction and arrival time of echoes at the ears of a free-flying bat.

Solution: **Echo Model**

- Using ultrasonic microphones, the bat's sonar vocalizations are recorded.
- And using high speed stereo video cameras, the bat's 3-D flight trajectory is reconstructed.
- Echo Model: Estimates the spatial location (direction and arrival time) of echoes at the bat's ears as it flies.

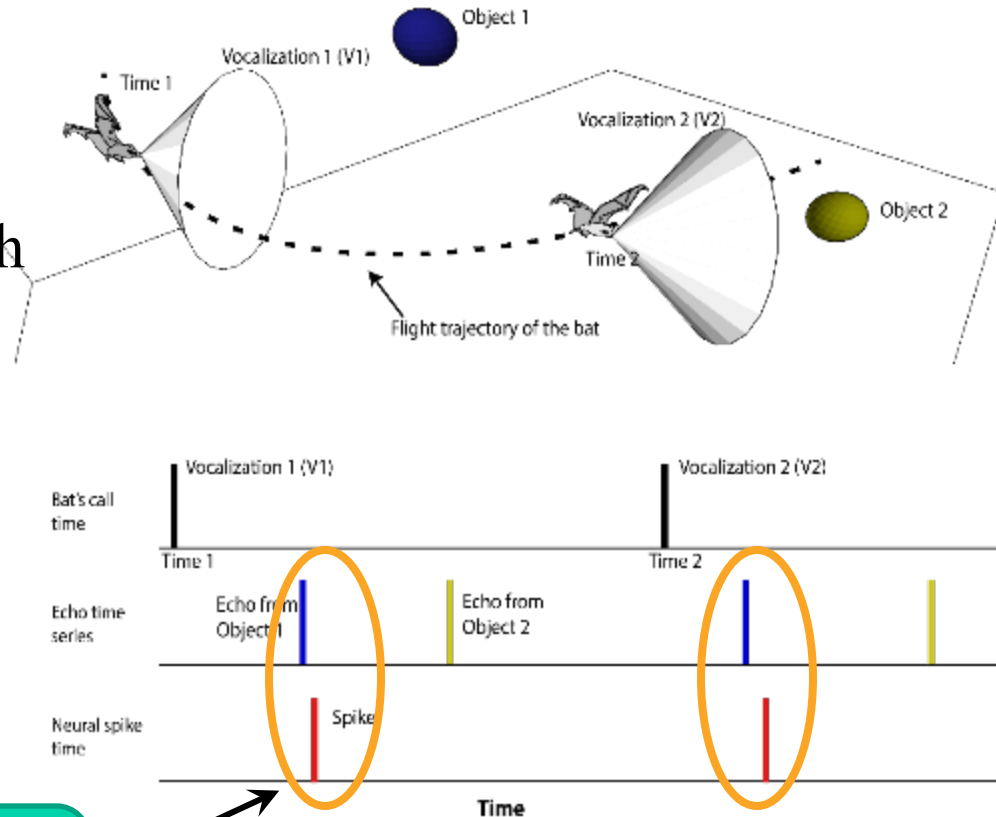


(See also Lee et al., JASA, 2014)

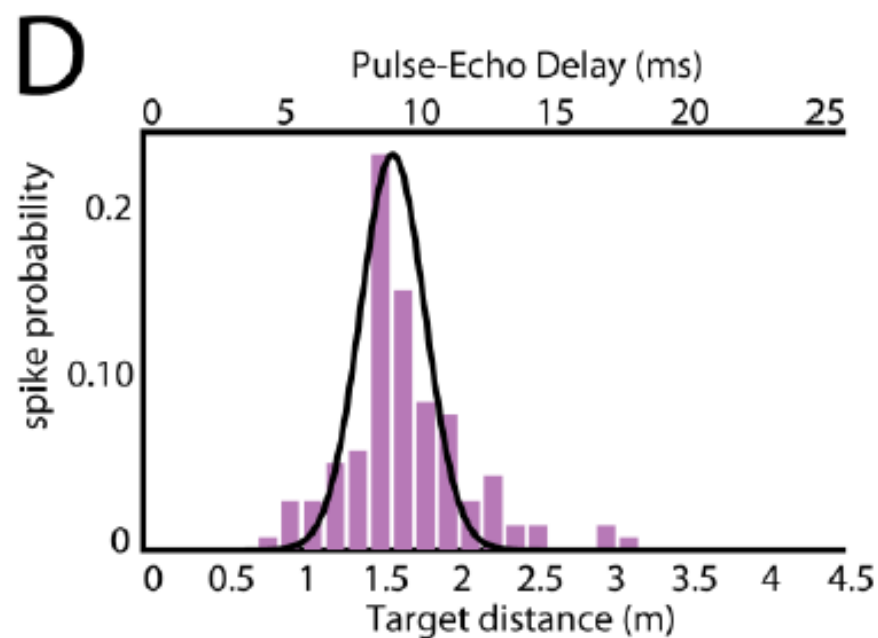
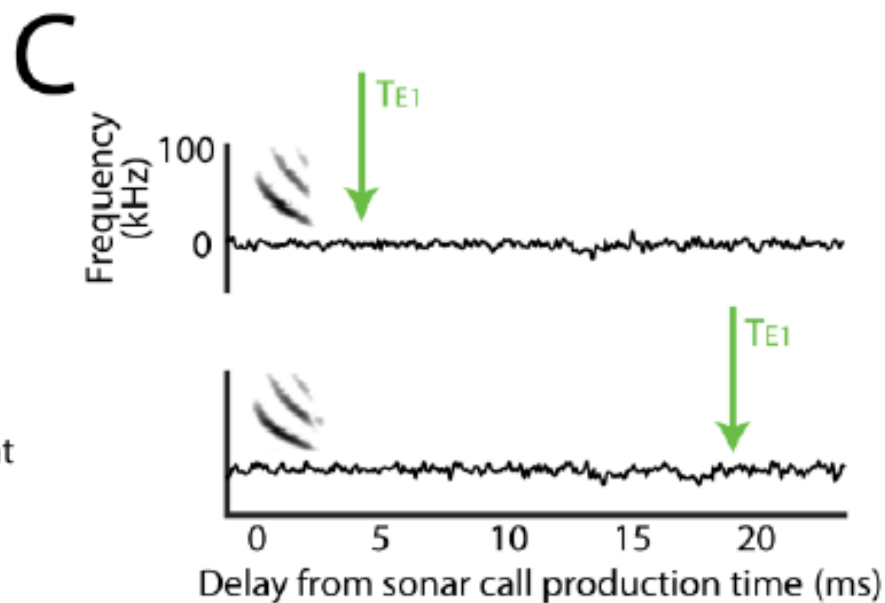
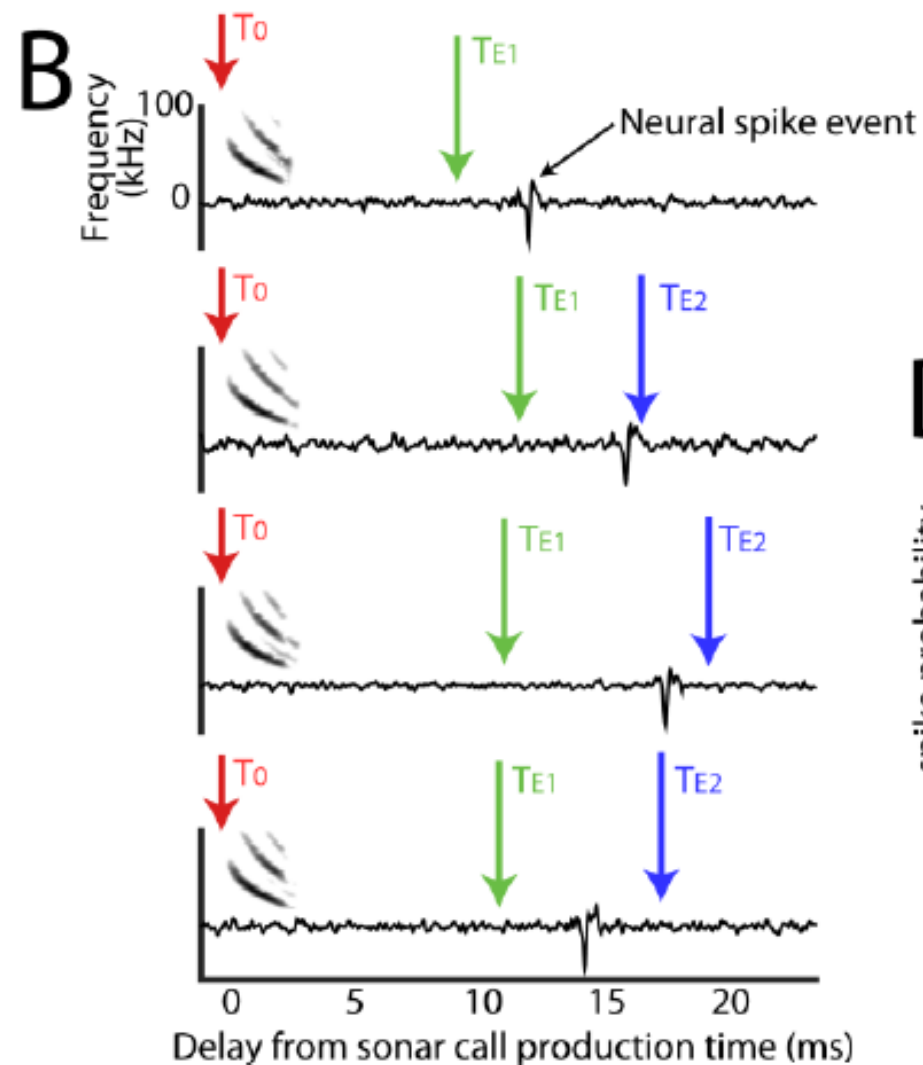
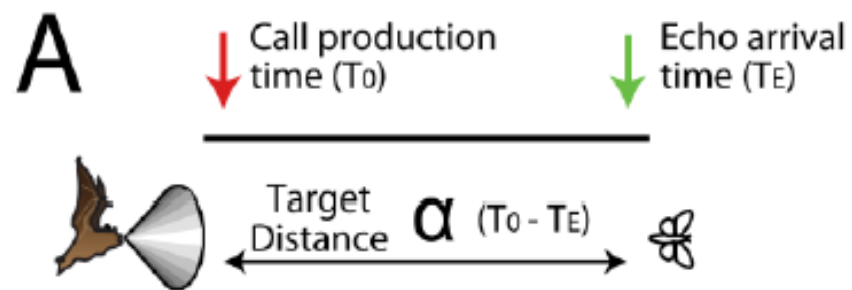
Reconstructing auditory spatial response profiles from recordings in a free-flying bat

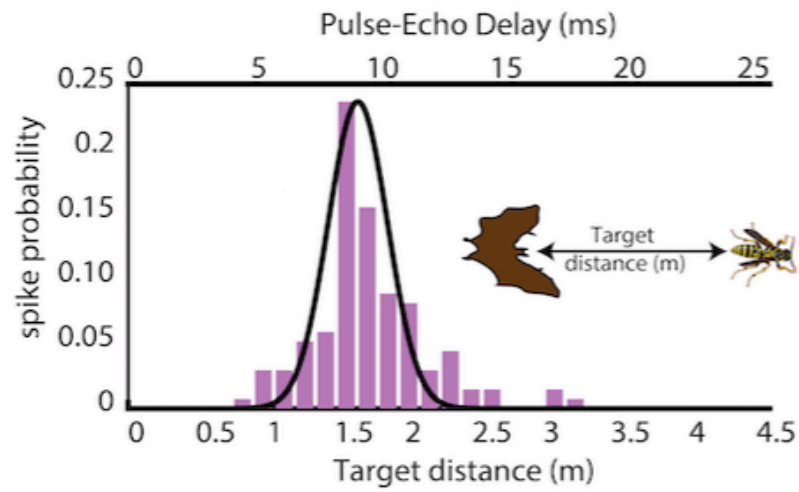
Representation of 3D space

Combining the echo model with neural recordings, we can construct response profiles of auditory neurons.

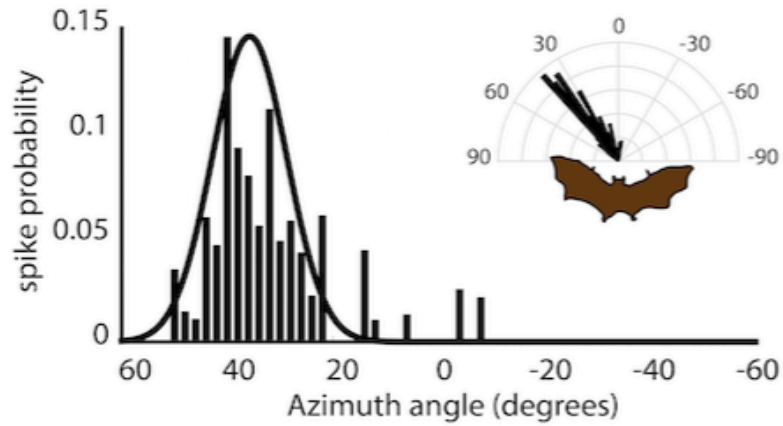


Combining echo times and echo directions with neural spike times

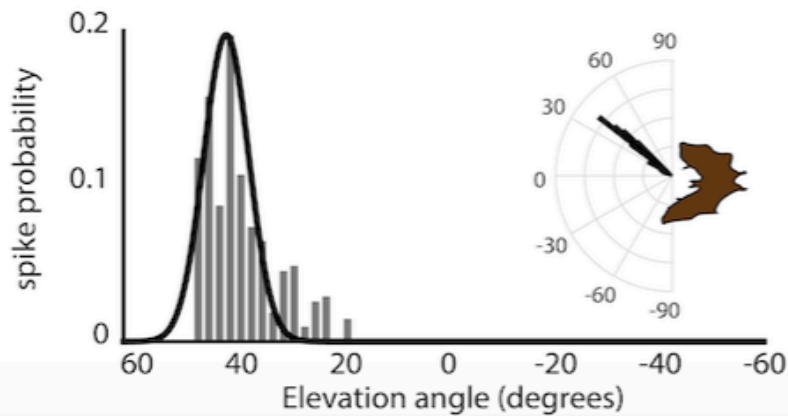




Delay/Range Tuning

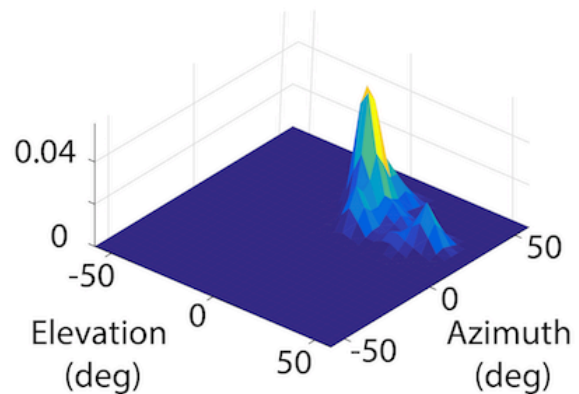
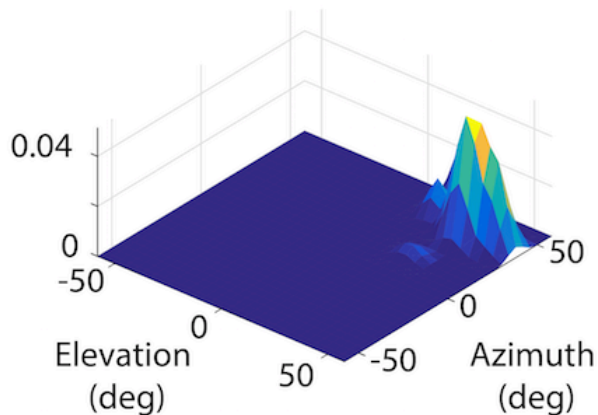
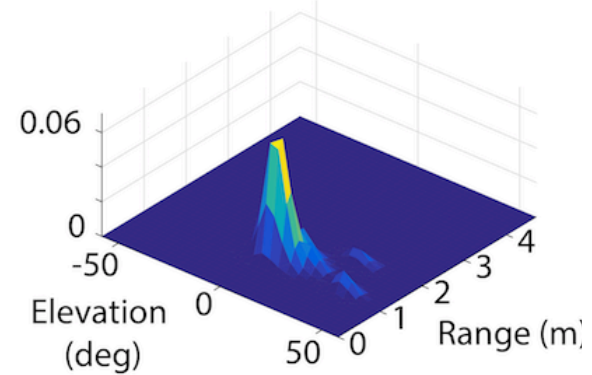
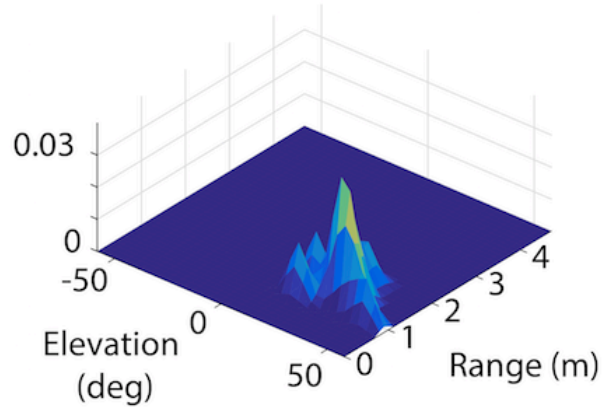
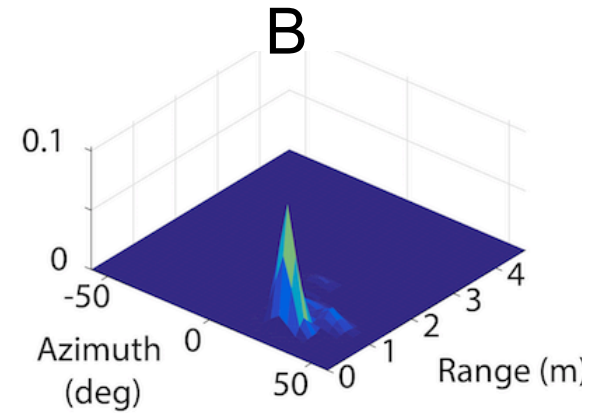
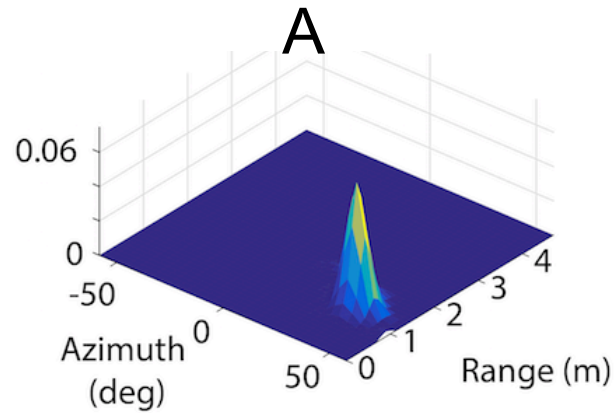


Azimuthal Tuning

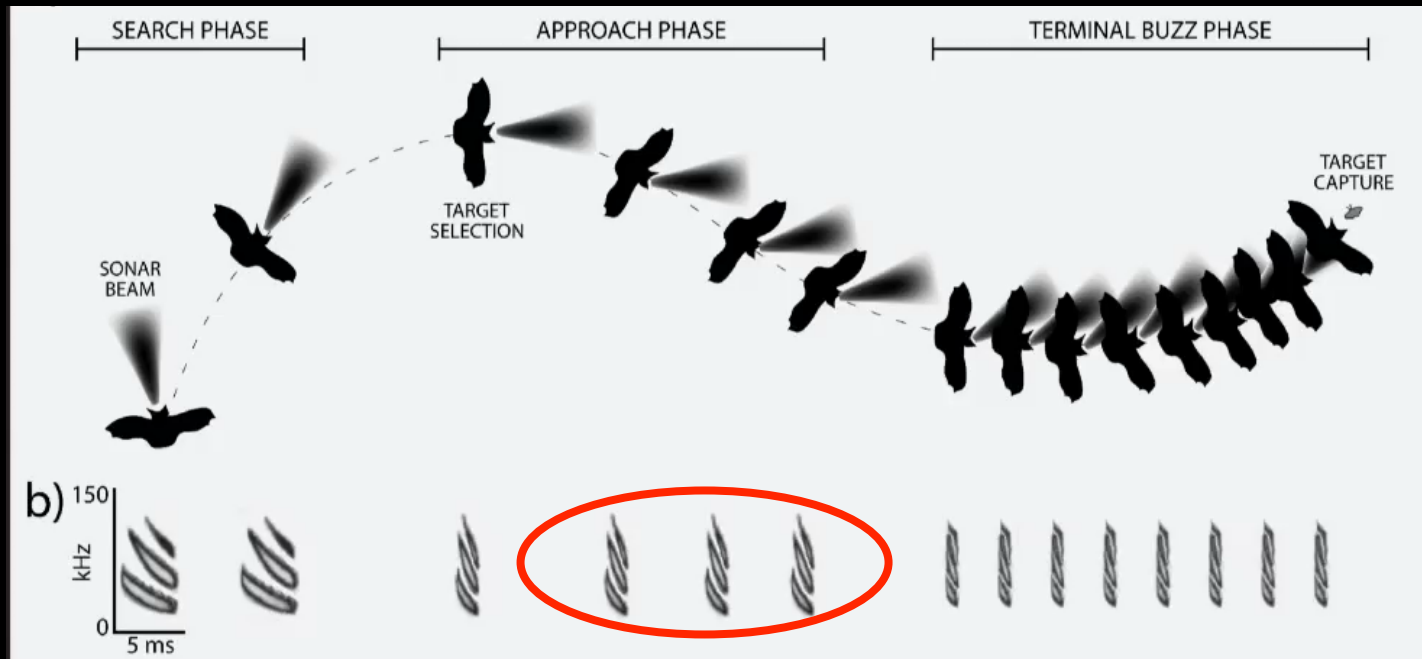


Elevation Tuning

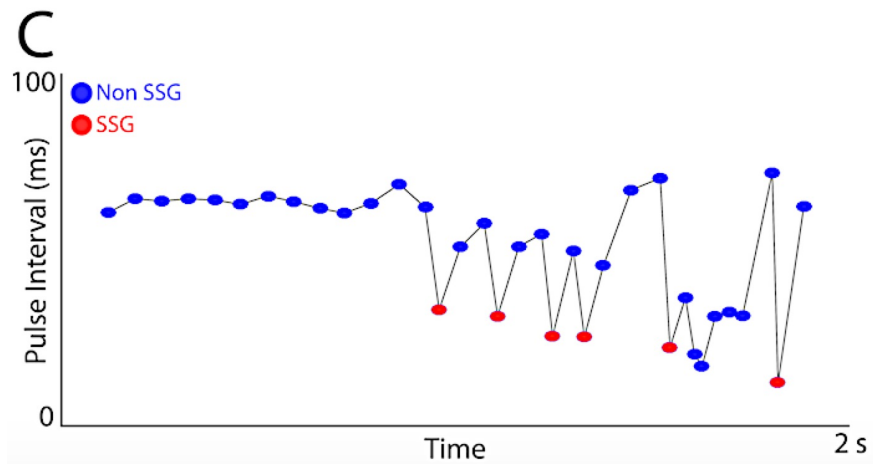
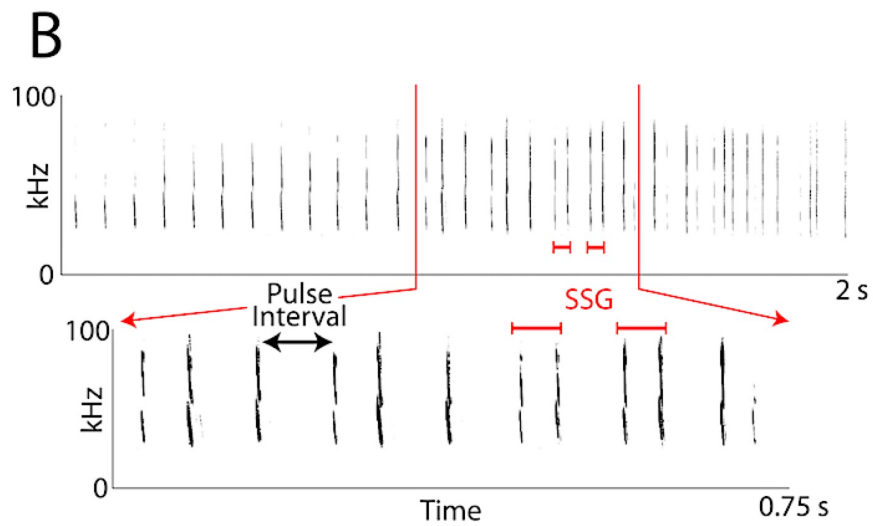
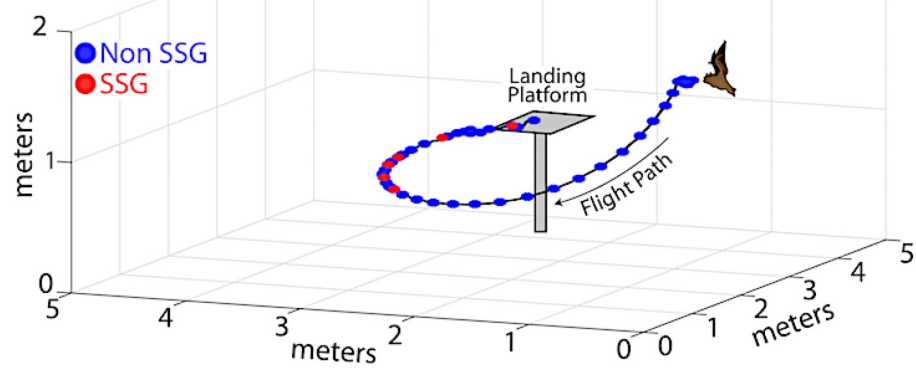
Spatially-tuned neurons in the SC of the free-flying bat



Functional role of sonar sound groups?

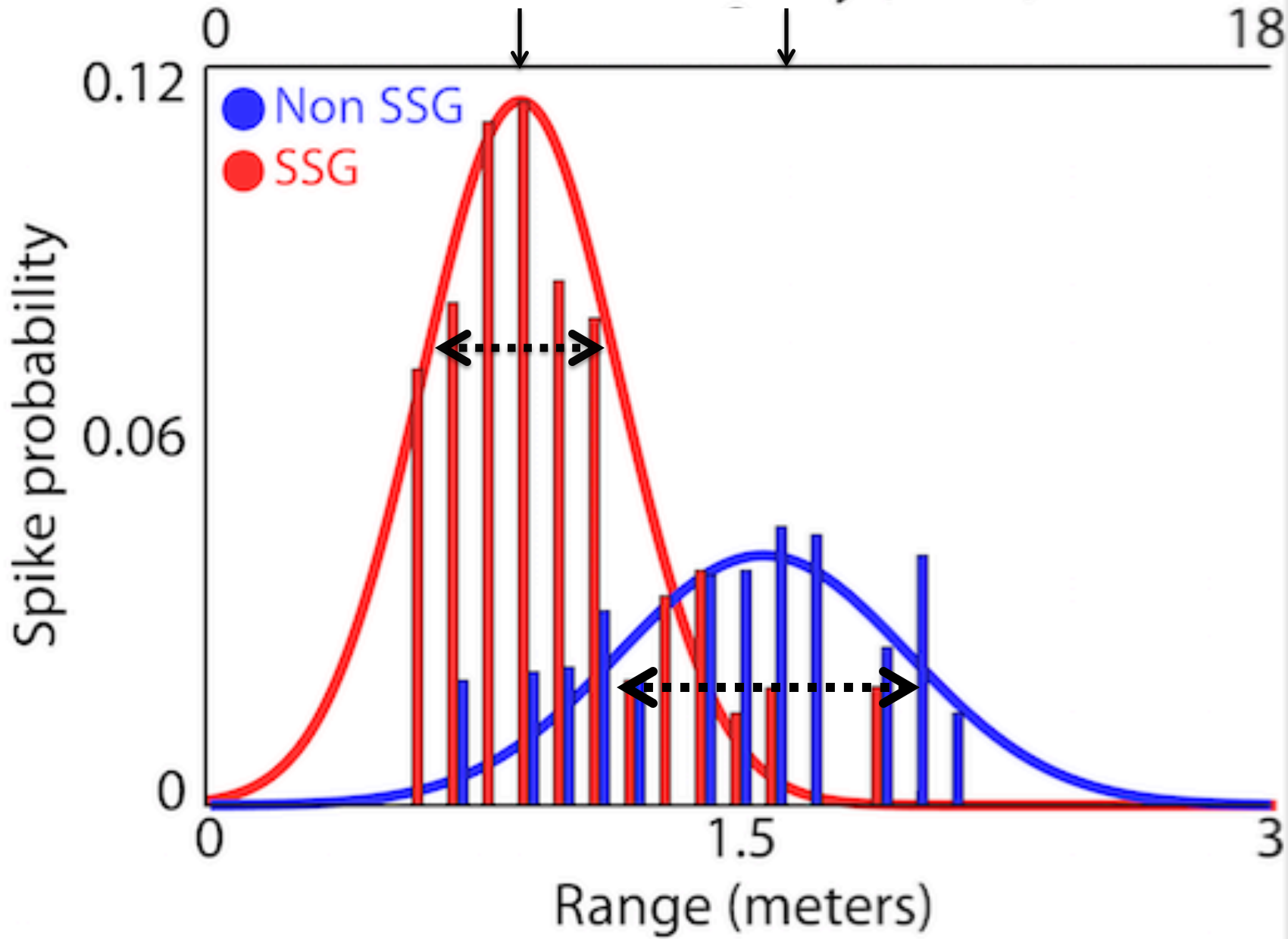


Hypothesis: Sonar sound groups evoke a sharpened representation of the sonar scene

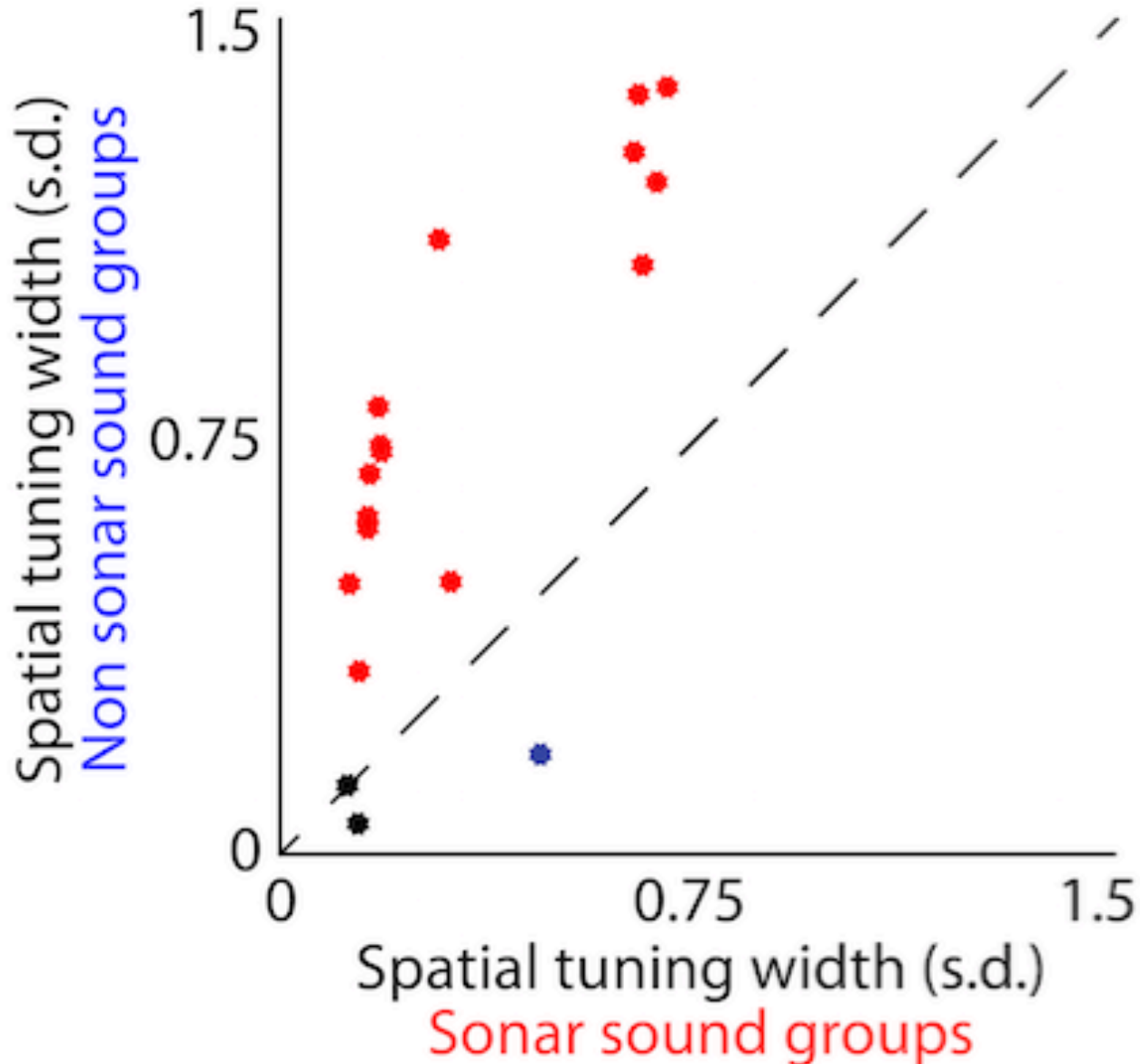


Pulse-echo delay (msec)

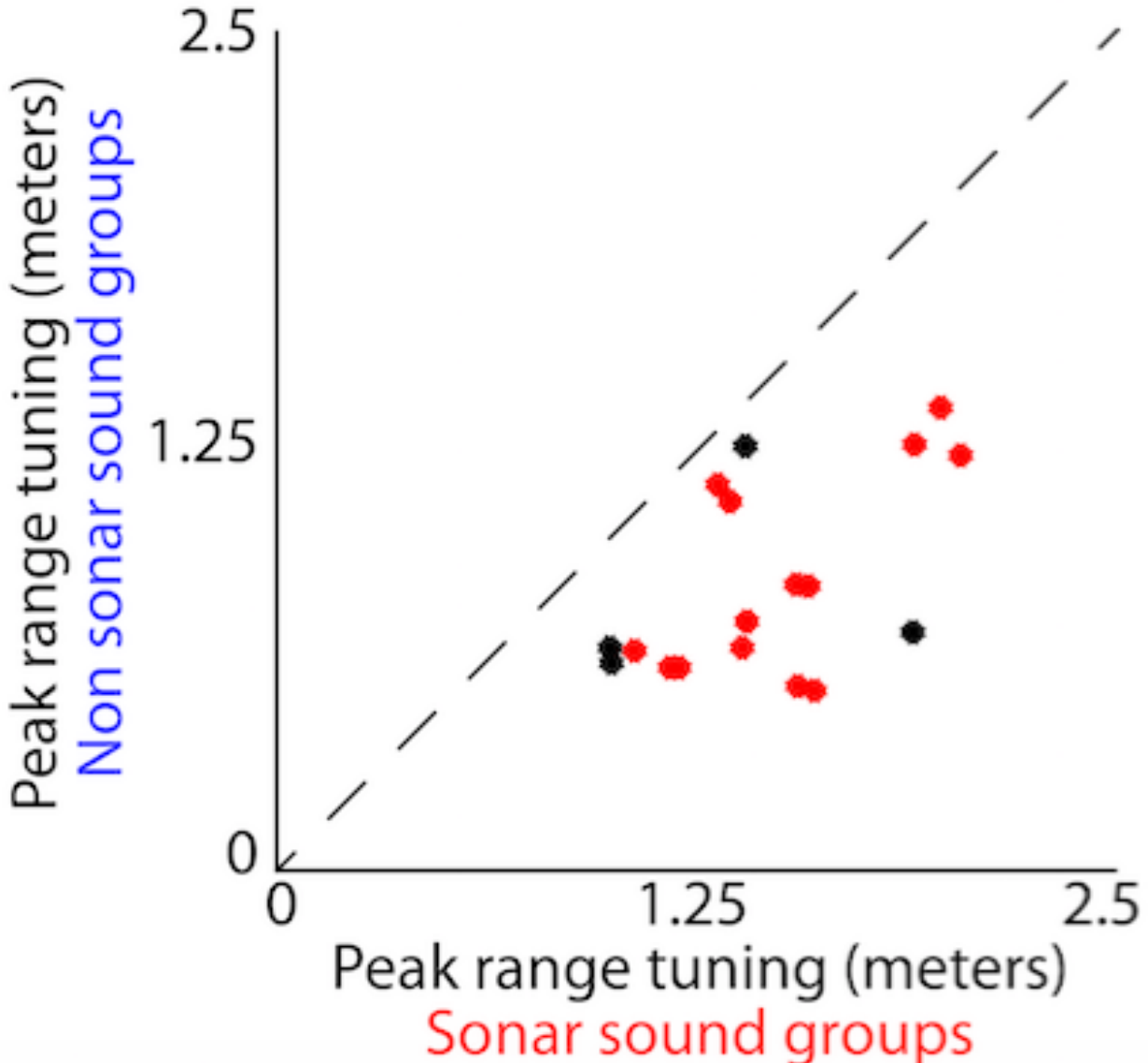
18



Sonar sound groups evoke responses in SC neurons with sharper spatial tuning



Sonar sound groups evoke responses in SC neurons at shorter target ranges (echo delays)



Summary



The echolocating bat's adjustments in sonar signal direction, duration and timing allow it to localize and track sonar targets in 3D.

Neurons in the bat midbrain SC show 3D selectivity to echo azimuth, elevation and delay (range).

3D neurons in the bat SC show sharper tuning and a shift in "best range/delay" to closer objects when bats inspect objects using sonar sound groups.

Acknowledgments



Ben Falk



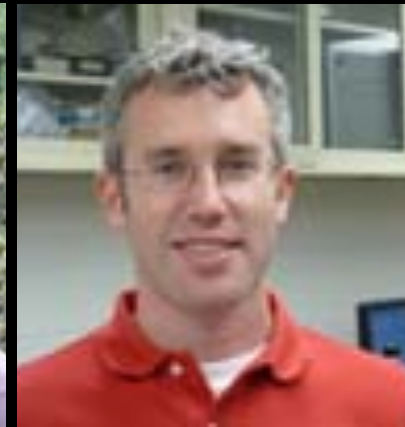
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