4_Bats

11 March 2025 16:49

Optimal Strategy for Stimulus Localization and Tracking

- **Challenging the Centering Strategy**
  - Traditional assumption: **Centering a stimulus in the field of view is optimal for localization and tracking**.
  - **Experimental and computational studies** using **echolocating Egyptian fruit bats** show that **this is not the case**.
- **Bat Sonar Targeting Strategy**
  - Bats trained to **localize a target in complete darkness**.
  - **Measured sonar click direction**:
    - **Bats do not center their sonar beam on the target**.
    - Instead, they **point the maximum slope ("edge") of the beam onto the target**.
- **Information-Theoretic Insights**
  - **Using the maximum slope** of the signal is **optimal for localization**.
  - **However, this comes at the cost of detection**, which is **optimized when centering on the stimulus peak**.
- **Proposed Tradeoff Between Detection and Localization**
  - **Detection is best when the stimulus is centered**.
  - **Localization is best when the maximum slope is used**.
  - This **tradeoff is likely a fundamental principle** in spatial localization across multiple sensory modalities:
    - **Hearing (echolocation in bats, auditory localization in humans and animals)**.
    - **Olfaction (odor gradient tracking in animals)**.
    - **Vision (edge-based object recognition and depth perception)**.

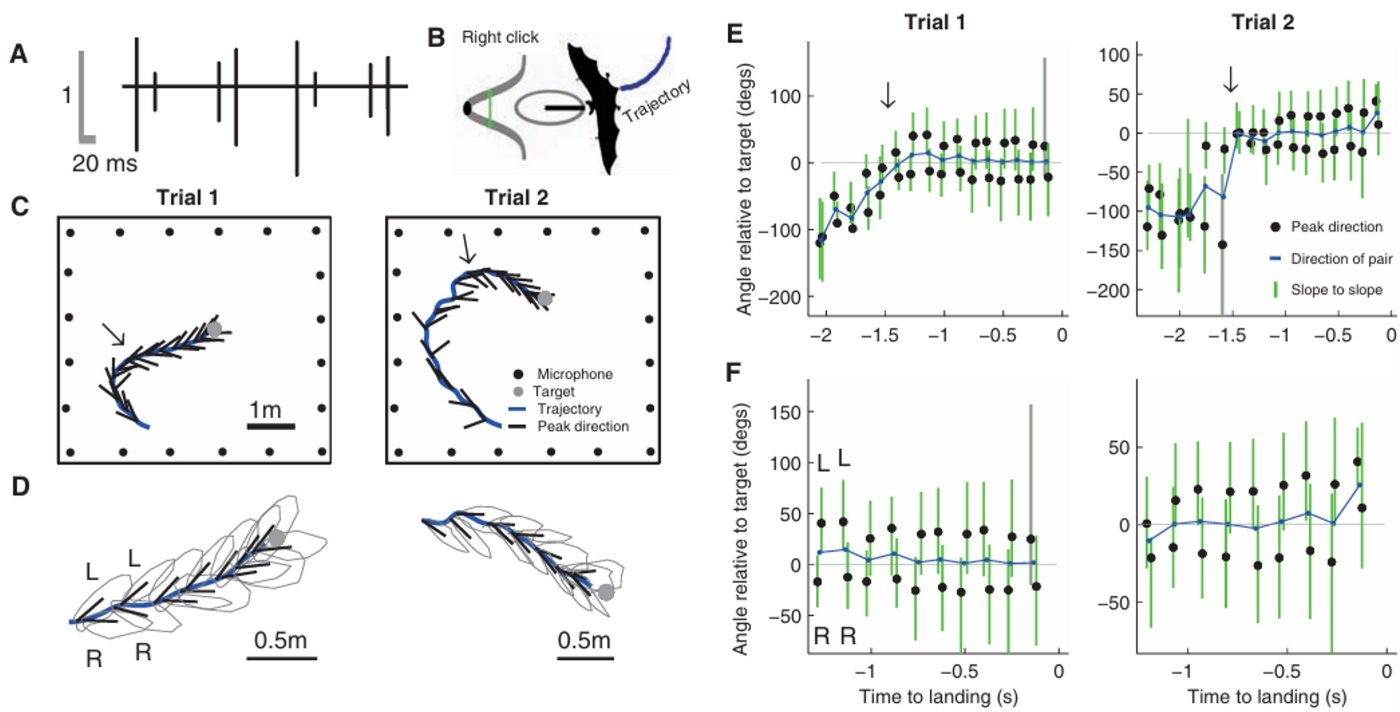
Active Control of Sonar in Egyptian Fruit Bats

Sensory Systems and Active Information Control

- Many **sensory systems** allow organisms to **actively control** how they acquire information (1–6).
- **Echolocating bats** are a prime example, as they:
  - **Modify their sonar signal design** (4, 7–16).
  - **Use returning echoes to navigate and forage in darkness** (4, 7–16).

Experimental Setup: Egyptian Fruit Bats and Sonar Tracking

- **Bats trained to fly and land on a spherical target**, relying only on sonar (17).
- **Measurement techniques**:
  - **3D tracking**: Two infrared cameras recorded **bat movement**.



  - **Sonar beam pattern tracking**: A **20-microphone array** measured the **shape and direction of sonar clicks** (17) (**Fig. 1, A–D**, and **movie S1**).
- **Flight behavior**:
  - Target position was **randomized at the start of each trial**.
  - Bats either approached the target in a **straight flight** or a **curved trajectory** (**Fig. 1C and fig. S1**).

Sonar Characteristics in Egyptian Fruit Bats

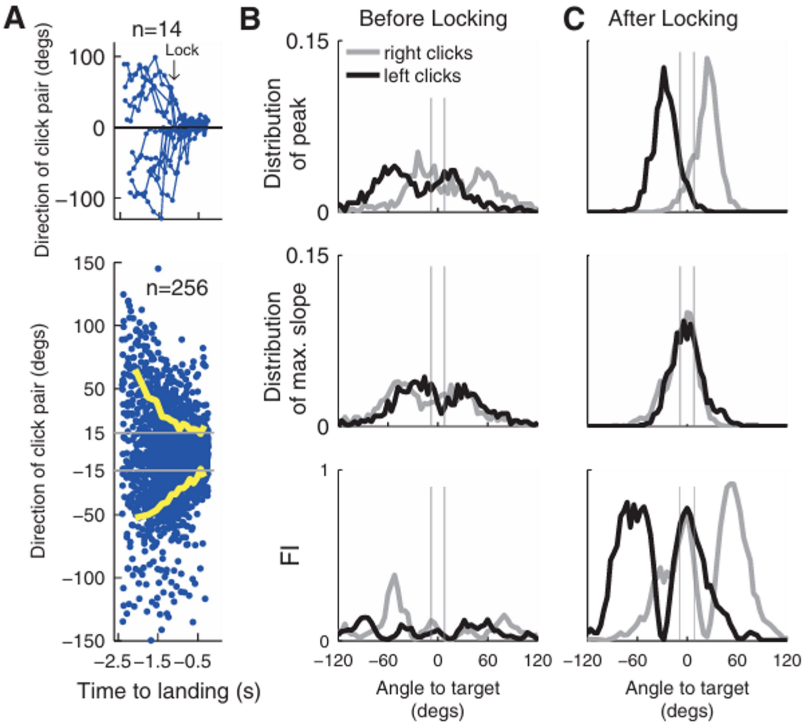
- **Different from microbats (microchiropterans)**:
  - Egyptian fruit bats **(megachiropterans)** do not emit laryngeal tonal calls.

    - Instead, they produce **very short impulse-like tongue clicks (50–100 µs)**.
    - Clicks are centered at **30–35 kHz (fig. S2)**.
- **Click Timing and Alternating Sonar Beam**:
    - Bats typically emitted **pairs of clicks** with:
        - **~20-ms interval within the click pair**.
        - **~100-ms interval between pairs (Fig. 1A and fig. S3)** (18, 19).
    - Sonar beam direction **alternated left-right** in a repeated pattern:
        - **Left → Right (100-ms gap) → Right → Left (Fig. 1D and movie S1)**.

Two Phases of Sonar Behavior: "Unlocked" vs. "Locked"

Unlocked Phase (Initial Search):
- **Bats did not consistently direct their clicks toward the target**.
- **Click directions were widely distributed**.

Locked Phase (Final Approach & Landing):



- **Bats directed click pairs so that their vector average pointed toward the target with high accuracy (~30° or better) (Fig. 1E, arrows; Fig. 2A, top; fig. S1C)**.
- **0.5 seconds before landing**:
    - **80% of click pairs were locked with accuracy better than 15° (Fig. 2A, bottom, gray lines)**.
    - **10% of trials achieved accuracy better than 5°**.
- **Left-right click alternation persisted**, implying that bats **did not maximize sonar intensity on the target**.

Key Finding: Bats Do Not Maximize Signal-to-Noise Ratio (SNR) for Echo Detection
- **Contradicts the traditional belief** that bats steer their sonar beam to **maximize the SNR of echoes** (13, 20).
- **Instead, they maintain an alternating left-right click pattern, even when locked onto the target**.
- Suggests an alternative **sonar localization strategy** that prioritizes **localization accuracy over echo intensity maximization**.

Bats Use Maximum Slope of Sonar Beam for Localization

Alternative Strategy: Directing the Maximum Slope Toward the Target
- Instead of centering the **maximum intensity** of their sonar beam on the target, bats may:
    - **Align the maximum slope of the beam's emission curve with the target**.
    - This strategy **maximizes changes in reflected echo energy** due to **relative motion** between the bat and the target.

Experimental Evidence
- **Directional span of sonar beams** (green lines in **Fig. 1E and F, fig. S1C and D**) shows:
    - **Bats consistently placed the maximum slope of their beams on the target (Fig. 1F and fig. S1D)**.
- **Population distribution of beam directions**:
    - **Before locking phase**:
        - Bats directed their sonar beams **over a wide angular range (>100° around the target) (Fig. 2B, top)**.
    - **After locking phase**:
        - **Maximum slope of the intensity curve**, not the peak intensity, was directed at the target (**Fig. 2C, middle row**).
        - **All six bats exhibited this behavior (fig. S4)**.

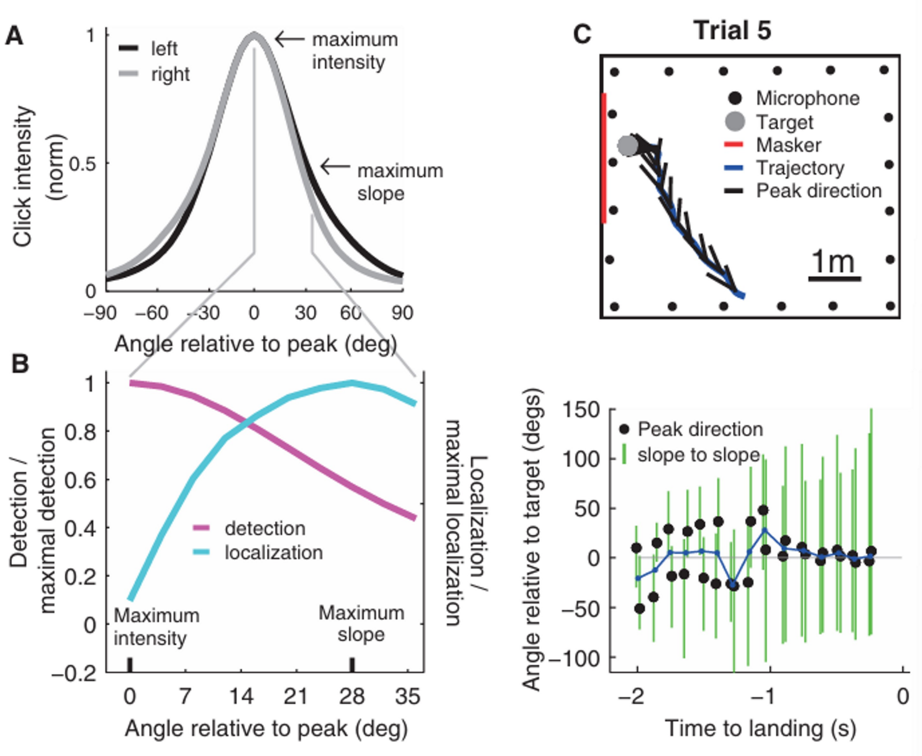
Why Use Maximum Slope Instead of Maximum Intensity?

- **Maximizing Sensitivity to Target Motion**:
  - If the **maximum slope of the beam is directed at an object**, then:
    - **Any motion of the object relative to the bat results in the largest possible change in echo intensity**.
    - The **sign of the intensity change (positive or negative) directly corresponds to the object's motion direction**.
- **Hypothesis**:
  - **Egyptian fruit bats use this strategy to enhance sensitivity to changes in target azimuth**, allowing for **better target localization**.

Testing the "Optimal-Localization" Hypothesis

Fisher Information (FI) as a Measure of Localization Sensitivity

- **FI is commonly used to assess sensitivity to small differences** (21).
- **Methodology**:
  - **Joint probability-density functions of intensities and angles** were computed for all sonar clicks (17).
  - After **locking onto the target**, the bats' **beam-steering strategy maximized FI in the target direction** (**Fig. 2C, bottom row**).



  - **Secondary FI peak** appeared due to the **two maximum slope points in the emission curve**.
    - The **secondary peak was higher** due to the **asymmetry of the sonar beam** (**Fig. 3A**).
- **Implication**:
  - Since **FI meets a theoretical optimality criterion (21)**, the bats' strategy is **optimal for localization based on reflected echo intensity**.

Ruling Out an Alternative Explanation: Edge Alignment Hypothesis

- **Alternative hypothesis**: Bats may have **aligned beam peaks to the edges of the target**.
  - **Prediction**: If this were true, the **angle between click pairs should increase as the bat gets closer** (because the target's angular size increases).
  - **Result**: No such increase was observed (**fig. S5**), ruling out this explanation.

Tradeoff Between Detection and Localization

Costs of Maximum Slope Strategy

- **Pointing the maximum slope at the target instead of the peak results in a 6 dB energy loss**.
  - **This reduces the amount of reflected energy, decreasing the detection range by ~16%** (17).
- **Hypothesis**:
  - **Bats use the area between the peak and the maximum slope to balance detection and localization**.
  - **Beam peak = optimal detection**, while **maximum slope = optimal localization**.
  - **Beam position can be adjusted based on task, target properties, and ambient noise**.

Adaptive Use of Beam Position

- **Experimental Context**:
  - In the experiment, **bats prioritized localization** to ensure **accurate landing on a salient object**.
- **Predicted Behavior in Other Contexts**:

    - If **detection is the primary challenge** (e.g., small targets, noisy environment, strong acoustic masking):
        - **Bats should center the beam peak on the target** for **maximum detectability** (22).
    - If **both detection and localization are required**:
        - **A compromise strategy is needed**, with the **beam directed between the peak and maximum slope** (**Fig. 3B**).

Evidence for Detection-Localization Tradeoff

- **Bats more frequently directed the area between the peak and the slope toward the target** than the area beyond the slope.
- **Statistical analysis**:
    - The **distribution of peak directions was significantly skewed toward the target (0° angle)**.
    - **T-test results**:
        - **Right side: gright=−0.42,P<0.001g_{\text{right}} = -0.42, P < 0.001**.
        - **Left side: gleft=0.26,P<0.001g_{\text{left}} = 0.26, P < 0.001**(17).
    - This **supports a detection-localization tradeoff strategy**.

Conclusion: Task-Dependent Sonar Beam Control

- **Bats actively control sonar beam positioning based on task demands**:
    - **Maximize localization (maximum slope on target) when precision is critical** (e.g., landing).
    - **Maximize detection (beam peak on target) when target is small, noisy, or masked**.
    - **Compromise strategy (beam between peak and slope) when both detection and localization are needed**.
- **This adaptive sonar strategy allows bats to optimize sensory processing in real time**, depending on environmental conditions.

Testing the Detection-Localization Tradeoff Hypothesis

Control Experiment with Acoustic Masking

- **A large reflecting board was placed 50–80 cm behind the target** to create a **strong echo masker**.
- This **secondary reflection interfered with target detection**, mimicking a **noisy acoustic environment**.
- **Observed change in bat sonar strategy**:
    - Initially, bats **maintained the alternating left-right sonar pattern**.
    - **~1 second before landing**, some bats **switched to a forward-directed beam**, aligning clicks **closer to the peak intensity of the beam** (**Fig. 3C, bottom, black dots; fig. S6**).
    - This **boosted echo energy and improved detection** by increasing the **signal-to-noise ratio (SNR)**.
- **Key finding**:
    - **Bats can flexibly adjust their beam-steering strategy** depending on environmental conditions.
    - This supports the idea that, in the main experiment (**Figs. 1 and 2**), the bats **actively chose to direct the maximum slope to the target** rather than being constrained by a fixed strategy.

Comparing Egyptian Fruit Bats to Other Echolocators

Do Other Echolocating Animals Use the Maximum-Slope Strategy?

- **Open question**:
    - **Microbats, dolphins, and swiftlets** have not yet been tested for this localization method.
- **Previous studies on microbat beam steering (13, 20, 23)**:
    - Focused on **small targets**, which **prioritize detection over localization**.
    - **Prediction**:
        - **When localization is the primary goal and detection is not a challenge, microbats might also use the maximum slope for localization**.

Differences Between Microbats and Egyptian Fruit Bats

- **Microbats use single sonar pulses**, while **Egyptian fruit bats use double-click sonar** (4, 7–10).
- **Microbat sonar strategy**:
    - **Each call would place one of the beam's slopes on the target**.
    - **Analysis of echo amplitude changes between successive calls** allows tracking of object movement.
    - Example: **Right → Right → Right → ...** instead of an alternating left-right pattern.
- **Egyptian fruit bats' left-right click alternation**:
    - Mechanism is **not fully understood (SOM text)**.
    - However, **comparing two different slopes doubles the intensity difference**, likely improving **localization accuracy**.

Neurophysiological Implications

Auditory Neurons and Echo Amplitude Processing

- **Previous studies in microbats** report **neurons tuned to echo amplitude changes** (24).
- **Hypothesis for megabats**:
    - **Megabat auditory neurons may be sensitive to the intensity difference between two successive echoes (20 ms apart)**.
    - This would allow them to **extract precise localization information** from their alternating click strategy.

Accuracy of Passive vs. Active Echolocation

- **Passive hearing localization accuracy**: **10°–15°** (25).

- **Active echolocation accuracy**:
  - **1.5°–5° during active beam control (12, 20)**.
  - This **suggests that active sonar beam steering significantly enhances spatial precision**.

Conclusion: Task-Dependent Adaptive Sonar Strategies

- **Egyptian fruit bats actively adapt their sonar beam positioning based on environmental demands**.
- **Localization vs. Detection Tradeoff**:
  - **Maximizing localization (maximum slope on target)** when precision is critical.
  - **Maximizing detection (beam peak on target)** when the target is small or the environment is noisy.
  - **Flexible switching between strategies when both are needed**.
- **Potential similarities with microbats**:
  - Microbats may use a **maximum slope strategy for localization**, but this remains to be tested.
- **Neural processing implications**:
  - **Megabats may have specialized neurons for comparing intensity differences between successive echoes**, enhancing **spatial accuracy** beyond passive hearing capabilities.

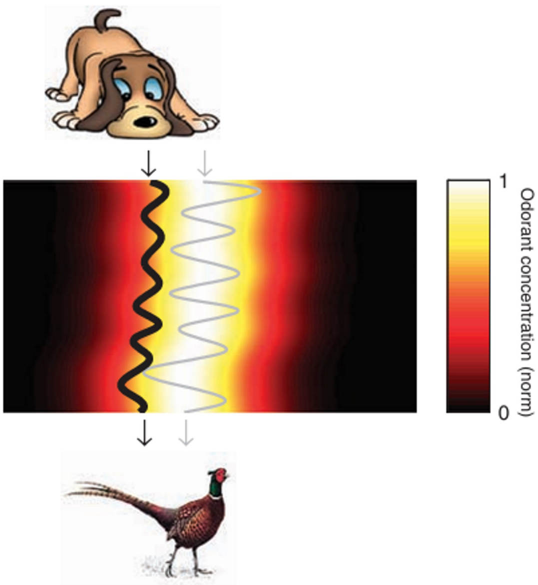
Generalizing the Detection-Localization Tradeoff Across Sensory Systems

A Fundamental Sensory Tradeoff

- The **tradeoff between detection (SNR) and localization** may be a **universal principle across sensory systems**.
- If **stimulus intensity is represented as a spatial contour**:
  - **Peak intensity is optimal for detection**.
  - **Maximum slope is optimal for spatial localization**.

Predictions for Other Sensory Modalities

Olfactory Tracking



- **Organisms following an odor trail should track the line of maximum concentration slope** for **better localization and minimal movement jitter (Fig. 4)**.
- **Experimental support**:
  - A study on **Drosophila larvae odor tracking** found that they follow a **trajectory between the odor peak and maximum slope** (26).

Visual Tracking

- **When tracking large moving objects, humans may align their fovea with the intensity slope** rather than the peak.
- This would allow for **smoother, more accurate tracking**.

Neural Basis for Maximum Slope Encoding

- Recent studies have identified **sensory neurons that encode stimulus location via the maximum slope of their tuning curve**, rather than the peak firing rate (**22, 27–29**).
- **Advantages of slope-based neural coding**:
  - **Maximizes discriminability** of stimuli near the slope.
  - **Parallels behavioral findings** where organisms prioritize maximum slope for localization.

Conclusion: A Universal Localization Strategy

- **The detection-localization tradeoff appears to be a fundamental principle across sensory modalities**.
- **Bats' sonar beam control mirrors strategies in olfaction, vision, and neural coding**.
- Future research should explore whether **other animals and sensory systems also optimize localization via maximum slope tracking**.