

Analysing Biosonar Responsivity

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1 BIOSONAR RESPONSIVITY FRAMEWORK

1.1 Responsivity Parameters

Echolocating bats dynamically adapt their sonar output to effectively track and intercept moving targets. To quantitatively characterise this temporal adaptation, I introduced the *responsivity* metric \mathcal{R} , which captures the bat's moment-to-moment precision in adjusting interpulse intervals (IPIs) [1, 2].

The interpulse interval at call index n is defined as:

$$\Delta t_n = t_{n+1} - t_n \quad (1)$$

where t_n is the timestamp of the n th call.

Responsivity at index n is defined as the inverse magnitude of the change in IPI between successive calls:

$$\mathcal{R}_n = \left| \frac{1}{\Delta t_{n+1} - \Delta t_n} \right| \quad (2)$$

High values of \mathcal{R}_n indicate the system is making increasingly fine temporal adjustments, reflecting maximal sensory-motor engagement prior to the terminal buzz phase.

The echo delay, T_a , representing the two-way travel time for sound between bat and target, is given by:

$$T_a = \frac{2d(t) - \Delta s}{c} \quad (3)$$

where $d(t)$ is the instantaneous target distance, c is the speed of sound, and Δs is the distance covered during call emission, which may be ignored for calculation for short call durations and velocities.

The bat's biological reaction time window, T_b , is modelled as a proportion of the echo delay:

$$T_b = k_r \cdot T_a \quad (4)$$

where k_r is the dimensionless reaction constant encapsulating the total sensory-motor processing latency. k_r may be determined by empirical knowledge of known maximum call rate (see Figure 1 in Umadi & Firzlaff, (2025) [1]).

The interpulse interval is thus composed of echo delay and reaction time:

$$\Delta t = T_a + T_b = T_a(1 + k_r) \quad (5)$$

The call rate C_r is the inverse of interpulse interval:

$$C_r = \frac{1}{\Delta t} = \frac{1}{T_a(1 + k_r)} \quad (6)$$

The *buzz readiness* point, denoted n^* , corresponds to the call index at which responsivity approaches the physiological maximum call rate $C_{r,\max}$:

$$n^\downarrow = \arg \min_n |\mathcal{R}_n - C_{r,\max}| \quad (7)$$

At this point, the bat engages its finest temporal control, preparing to enter the terminal buzz phase characterized by maximal call rate.

Additionally, the fastest reaction time T_{b^*} at buzz readiness can be computed as:

$$T_{b^*} = |\Delta t_{n^*+1} - \Delta t_{n^*}| \quad (8)$$

reflecting the minimal IPI change and thus the temporal precision limit of the biosonar system.

To avoid call-echo overlap during approach, the emitted call duration t_{call} must satisfy:

$$t_{\text{call}} < T_a + T_{b^*} \quad (9)$$

The critical distance d_c at which call duration contraction must begin is given by:

$$d_c = \frac{t_{\text{call}} \cdot c}{2} + T_{b^*} \cdot v \quad (10)$$

where v is the bat's relative velocity to the target.

1.2 Calculating Echo Delay T_a from Interpulse Intervals

In biosonar studies, the echo delay T_a represents the two-way travel time of the sonar pulse between the bat and its target. While direct measurement of T_a requires precise knowledge of the target distance, it can be estimated from the observed interpulse intervals (IPIs) assuming a known responsivity scaling factor k_r .

Given the measured IPI at call index n :

$$\Delta t_n = T_{a,n} + T_{b,n} = T_{a,n}(1 + k_r), \quad (11)$$

where $T_{b,n} = k_r T_{a,n}$ is the bat's biological reaction time proportional to the echo delay.

Rearranging, the echo delay is derived as:

$$T_{a,n} = \frac{\Delta t_n}{1 + k_r}. \quad (12)$$

This relation assumes a constant responsivity factor k_r across calls, reflecting stable sensory-motor processing latency relative to target range.

By calculating T_a for each interpulse interval, one obtains an estimate of the echo delays that can be tracked over time without direct distance measurement. This approach enables inference of target approach dynamics and behavioral states (e.g., buzz readiness) solely from call timing data.

Importantly, this method allows biosonar responsivity analyses to be applied when 3D positional data are unavailable, broadening the applicability of the responsivity framework to field recordings where only call timestamps are accessible.

This framework thus links sensory-motor reaction constraints to observed temporal call adaptations, providing predictive power to detect behavioural transitions such as buzz readiness from call timing data alone. It captures the tradeoff between sensory update demands and physical kinematics that shape the dynamic sonar strategies of echolocating bats.

2 BIOSONAR RESPONSIVITY TOOLKIT: USER GUIDE AND METHODS

This section describes the `BiosonarResponsivity` MATLAB toolkit developed to analyse biosonar call timing and responsivity in echolocating animals. The toolkit combines interactive waveform-based call selection, temporal analysis, and visualization to facilitate biosonar behaviour studies.

3 OVERVIEW

The toolkit aims to:

- Allow manual annotation of echolocation calls via an interactive graphical interface.
- Quantify temporal call patterns using the *responsivity* framework, capturing interpulse intervals, echo delays, reaction times, and dynamic call rate changes.
- Provide clear visual summaries including call rates, buzz readiness points, and call timing distributions.

- Organize all data, analysis results, and plots within an object-oriented class interface for streamlined workflows.

4 CORE COMPONENTS

4.1 The `BiosonarResponsivity` Class

This class serves as the central hub for loading audio data, selecting calls, analyzing responsivity, and producing visualizations.

Properties

filename Path to the audio file (`.wav`).

waveform Loaded audio waveform data.

fs Sampling frequency (Hz).

callData Struct array with interactive call markers.

callTimes Vector of call emission timestamps (seconds).

t_call Vector of call durations (seconds).

results Struct containing responsivity analysis outputs.

kr Responsivity scaling factor relating biological reaction time to echo delay.

RcMax Maximum physiological call rate (Hz).

c Speed of sound (m/s), default 343.

Methods

BiosonarResponsivity(filename, kr, RcMax, varargin) Constructor that loads audio and sets parameters.

getCallTimestampsInteractive() Opens a GUI for manual selection and adjustment of call times and durations.

analyseResponsivity() Runs the responsivity analysis on the selected calls, computing IPIs, echo delays T_a , reaction times T_b , and responsivity \mathcal{R} .

summary() Prints an analysis summary including buzz readiness timing and reaction windows.

plotResponsivityCurve() Plots the responsivity curve highlighting buzz readiness points.

plotDetailedResults() Shows call rates over time with call timing and duration annotations.

exportResults(destFolder) Saves plots and analysis results into a subfolder named after the audio file for organized archiving.

4.2 Interactive Call Selection

The interactive call picker allows users to:

- Click to select call centers on waveform plots.
- Adjust vertical boundaries and widths of call regions with arrow keys.
- Detect local amplitude peaks automatically.
- Undo/redo markings and pause/resume input.

The output is a struct array with call start/end times, peak time/amplitude, and durations.

4.3 Responsivity Analysis

Using the selected call timestamps and durations, responsivity analysis computes:

- Inter-phonation intervals (IPIs) Δt_n .
- Echo delay T_a estimated as $\Delta t_n / (1 + k_r)$.
- Biological reaction time $T_b = k_r \cdot T_a$.
- Responsivity $\mathcal{R}_n = \left| \frac{1}{\Delta t_{n+1} - \Delta t_n} \right|$.
- Buzz readiness call index n^* , where \mathcal{R}_n approaches the maximum physiological call rate $C_{r,\max}$.

4.4 Visualization Tools

Two main plotting functions display:

- Call rate over time with buzz readiness markers.
- Call timings with vertical lines and call duration labels.
- Responsivity curves highlighting key temporal inflection points.

All plots are formatted for LaTeX compatibility.

5 TYPICAL USAGE WORKFLOW

```
% Create analysis object with audio file and parameters
bsr = BiosonarResponsivity('my_bat_call.wav', 5, 180);
```

```
% Select calls interactively
bsr.getCallTimestampsInteractive();
```

```
% Run responsivity analysis
bsr.analyseResponsivity();
```

```
% Print summary
```

```
bsr.summary();

% Plot responsivity curve and detailed results
bsr.plotResponsivityCurve();
bsr.plotDetailedResults();

% Plot temporal precision curves
bsr.plotIPI();

% Export all results and plots
bsr.exportResults('results/my_bat_call_analysis');
```

6 NOTES

- Responsivity coefficient k_r should be selected based on physiological or experimental calibration.
- Analyses are valid even when positional data are not available.
- The interactive GUI is optimized for ease of use but benefits from user familiarity with the control keys.
- An underlying requirement for the most reliable analysis is a complete call sequence collected in a direct pursuit setting. The field data provided is highly variable, and the regions of buzz readiness do not correspond to direct target pursuit; hence, interpreting the T_b^* must be approached with caution.

With great speed comes greater responsivity

REFERENCES

1. Umadi, R. & Firzlaff, U. *Biosonar Responsivity Sets the Stage for the Terminal Buzz* <https://www.biorxiv.org/content/10.1101/2025.06.16.659925v1>. Pre-published.
2. Umadi, R. *Temporal Precision Necessitates Wingbeat-Call Asynchrony in Actively Echolocating Bats* <https://www.biorxiv.org/content/10.1101/2025.06.18.660328v1>. Pre-published.