Oscillating Ears Dynamically Transform Echoes in Constant-Frequency Bats

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Abstract. The oscillatory movements of the pinnae in constant-frequency (CF) bats have long been documented, yet their role in actively transforming echo signals has remained underexplored. Inspired by Perrine's foundational description of Doppler effects in oscillating receivers, I hypothesised that bat ear oscillations could serve as dynamic signal modulators, introducing time-varying Doppler shifts to received echoes. I tested this hypothesis using both computational simulations and controlled experiments. In the simulations, each ear was modelled as an angularly oscillating structure receiving echoes from a CF pulse, with motion parameters systematically varied across frequency (5–50 Hz) and excursion angle (15–45°). The received echoes were synthesised as composite signals comprising delayed, Doppler-shifted components based on instantaneous ear segment velocities. Results showed pronounced spectral broadening, instantaneous frequency fluctuations, and binaural disparities that scaled with tip velocity. These effects were then validated using a subwoofer-driven oscillating reflector that emulated the ear's motion while reflecting a stable 80 kHz tone. Recordings showed consistent bandwidth expansion to over 1.2 kHz at 30 Hz, with phase warping evident in the time-domain waveforms. These findings confirm that oscillatory motion alone, without source modulation or target motion, can dynamically restructure the spectral and temporal profile of echoes. I argue that in CF bats, such echo transformations represent an active encoding strategy, enabling spatial and temporal contrast enhancement within the auditory fovea. This reconceptualises ear motion not as passive filtering, but as a means of dynamically enriching incoming sensory information.

Keywords: Echolocation, Constant-Frequency Bats, Oscillating Ear Motion, Doppler Shift, Binaural Cues, Spectral Modulation, Receiver Dynamics, Bioacoustics, Sensorimotor Encoding, Computational Simulation

1 BACKGROUND

The Doppler Shift (DS) as a result of motion relative to sound is a perceptually and functionally significant sensory aspect for echolocating bats that rely on heavy-duty cycle constant frequency (CF) call types. Studies have shown how Rhinolophid and Hipposiderid bats compensate for DS by varying the calling frequency so that they receive frequency matches the auditory fovea [1]. Such a compensatory phenomenon is of further significance when the actively moving ears are taken into account. The experiments by Schneider and Möhres [2] provide direct behavioural proof for the relevance of oscillating ear movements. They observed that bats compensated for disabled ear muscles by vigorous head movements.

Experimental measurements of call to ear movement correlations by Pye and Roberts (1960) [3] and Griffin and Dunning (1962) [4] show that the alternating ear oscillation movements are not random but correlated to the timing of pulse emission, but not always one-to-one. Griffin and Dunning observed during their trials that when the target was nearer to the *Rhinolophus* bats,

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the calls were shorter and more frequent, which they attributed to the need for more accurate information.

SUMMARY. Echolocating bats belonging to families such as *Rhinolophidae* and *Hipposideridae* emit sonar calls characterised by long-duration constant-frequency (CF) components, often extending up to 100 ms. In contrast, families such as *Vespertilionidae* produce frequency-modulated (FM) calls that are typically shorter than 10 ms. A striking behavioural feature of CF-calling bats is their rapid oscillatory ear movements. Early experiments demonstrated that when the muscles controlling these ear motions were disabled, bats compensated by vigorously moving their heads, indicating a critical role for ear motion in successful echolocation. Pioneering studies by Donald Griffin and J.D. Pye in the 1960s quantitatively described these movements, reporting oscillation rates of 30–35 Hz or higher. While some theories have proposed that such ear motion enhances directional sensitivity, the precise acoustic consequences of these movements on the received echo have remained unexplored. Since relative motion between a source and receiver induces Doppler shifts, I hypothesised that these oscillatory ear movements modulate incoming echoes in a dynamic, frequency-rich manner—not merely as a static frequency shift, but as a continuous spectral transformation. Moreover, because the ears move in antiphase, this transformation should differ between the two ears, producing enhanced binaural cues through greater interaural frequency and amplitude disparities.

To test this hypothesis, I developed a computational model simulating echo reception by oscillating ears with defined velocity profiles. To experimentally validate the model, I devised a novel setup: I used a large subwoofer as a dynamic reflector, driving its membrane to oscillate up to 10 mm at low frequencies (5–50 Hz). A stable 80 kHz CF tone was played toward the moving reflector, and the returning echoes were recorded in the same plane. Spectral analyses of the recorded echoes revealed phase-locked frequency modulation patterns, consistent with Doppler-induced spreads. Crucially, the frequency spread observed within a −20 dB intensity band reliably fell within the 200–400 Hz range—the very band of maximal sensitivity (the "auditory fovea") in CF bats. This suggests that ear movements ensure that, regardless of the bat's relative motion to a target, some part of the echo remains within its sensitive hearing range. In effect, the bats achieve information stability through movement-induced modulation. These findings reconceptualise the role of ear movements in CF bats: not as passive directional filters, but as active modulators of acoustic input. The integrated simulations and novel experimental design presented here shed light on how CF bats dynamically reshape incoming signals, ensuring effective perception under varying acoustic and kinematic conditions.

The experiments by Pye and Roberts (1960) provide a rich source of measurements for the ear movements of six species of Rhinolophids and four Hipposiderids. They report ear oscillations of 30–35 cycles/s with a mean linear velocity of about 30 m/s, and an arc of 30°. The DS induced by movements at that velocity is immediately obvious—for 50 kHz and 100 kHz tones, this amounts to 4.3 kHz and 8.7 kHz (or 0.12 octaves), respectively.

The movement of the ear produces a velocity gradient along its length, with the ear tip showing the highest linear velocity. The studies by Yin and Müller (2019) [5] model this phenomenon and provide evidence to conclude that the bats could use the DS produced by rapid ear movements as a sensory encoding mechanism.

The call durations of CF bats are typically much longer than those of FM bats, reaching up to 50–100 ms in some species of *Rhinolophus*, and several tens of milliseconds in Hipposiderids. Even at a more conservative ear oscillation frequency of 10 Hz, and a short pause in between (as reported by Pye and Roberts), it is evident that the major part of ear movement occurs while the echo arrives. This raises a crucial question—what signal transformation does this bring about? With a velocity gradient on the moving ear, which generates a small difference in the DS as the echo continues in the auricular space, the close frequencies in a given interval would interact. This continuing transformation would therefore give rise to signal features that are defined by the acoustic phenomenon of interference, and effectively produce different transformations in each ear, since the ears move out of phase. Moreover, the bat itself is in flight with relative motion to the echo, which carries a baseline DS defined purely by the relative velocity.

The foundational principles of Doppler acoustics laid out by Perrine [6] describe how motion between a sound source and a receiver results in measurable shifts in frequency—a principle that has since underpinned numerous applications in sonar and radar. Crucially, Perrine noted that even oscillatory motion of the receiver can impose dynamic modulations on the returning sound, especially when the speed and direction of motion vary over time. Inspired by this insight, I hypothesised that the periodic ear oscillations observed in constant-frequency (CF) bats do not merely enhance directional gain but actively transform the structure of incoming echoes. Specifically, I proposed that these motions induce time-varying Doppler effects that manifest as spectral broadening and temporal phase warping. In this view, the ear serves not as a static filter but as a dynamic acoustic interface—one that modulates and encodes incoming echoes through continuous motion, much like the Doppler modulation systems described by Perrine. This conceptual framework guided both the simulation and experimental studies presented here, which test the hypothesis that oscillating receivers—like bat ears—act as biologically embedded signal transformers.

Therefore, I sought to understand the precise nature of the signal transformation in oscillating ears typical of CF bats. I hypothesised that: 1) the oscillatory movements generate a much richer set of binaural cues both in frequency and amplitude, and these transformations are not simply inverses of each other; and 2) the phase-accounted instantaneous frequency shifts must be greater than DS alone, thus producing greater binaural differences than expected from DS.

To test these hypotheses, I developed a computational framework simulating binaural echoes received by oscillating ears during the emission of a CF pulse. Each ear was modelled as a 2 cm long vertical lever, oscillating sinusoidally in antiphase around its base at angular frequencies ranging from 5 to 50 Hz, and reaching a maximum deflection of 45°. The echo signal was synthesised as a sum of Doppler-shifted tones arriving from different segments along the ear, each contributing a delayed sinusoidal component whose frequency reflected its instantaneous velocity relative to the sound source. This allowed me to reconstruct the frequency and amplitude profile of the binaural echo signals as they would be perceived by each ear during the call–echo period. I further accounted for the baseline Doppler shift induced by forward flight (e.g., 2 m/s) and used the Hilbert transform to estimate instantaneous frequency and envelope level in each channel.

The resulting simulations revealed that the dynamic modulation of echo structure due to ear motion introduces prominent time-varying features that are not predicted by classical Doppler theory alone. In particular, the instantaneous frequency, derived from the phase trajectory of the

analytic signal, showed strong fluctuations aligned with the sinusoidal tip velocity profile, confirming that the movement of the ear introduces significant frequency modulation beyond what is captured by average velocity-based Doppler shifts. These frequency shifts, often exceeding 0.5 -1 kHz across the ear cycle, interacted with the amplitude envelope to produce alternating dominance between left and right ears in both frequency and level domains. The resulting binaural differences (in both instantaneous frequency and level) scaled with oscillation frequency and were not simple mirror images across the ears. Taken together, the results support the hypothesis that antiphase ear oscillations in CF bats serve not only to modulate directional sensitivity but also actively transform echo structure in a way that could enrich spatial or temporal coding of targets.

To empirically investigate the effects of oscillatory motion on an incident constant-frequency tone, I developed a controlled laboratory setup in which a high-frequency tone (80 kHz) was reflected off a 20 cm subwoofer driven with sinusoidal signals at various frequencies (5–30 Hz). The oscillation waveforms were generated in MATLAB and played through a custom ESP32-based system equipped with an I^2S DAC and a Class D amplifier. The playback system delivered sinusoidal oscillations by reading pre-generated `.wav` files from a microSD card, and the tone reflections were recorded using a Sanken CO-100K microphone connected to an RME Babyface Pro interface at 192 kHz.

I analysed the recorded waveforms using short-time Fourier transform, quantifying frequency spread (Δf) as the bandwidth within 20 dB of the peak power in the 75–85 kHz range. As expected, the Control condition showed minimal frequency spread (mean $\Delta f = 234$ Hz), with clean and stable sinusoidal waveforms. As oscillation frequency increased, the reflected signals exhibited both temporal warping and significant spectral broadening, with mean Δf rising steadily (e.g., 445 Hz at 15 Hz and over 1240 Hz at 30 Hz). Manual fanning produced broadband and irregular spread (mean Δf 850 Hz), highlighting the influence of aperiodic motion.

Together, these results confirm that oscillatory reflector motion introduces complex, biologically relevant acoustic transformations beyond Doppler shifts expected from a constant and linear relative velocity difference, and may serve as a rich source of dynamic cues in CF bat echolocation.

2 METHODS

To investigate the echo-acoustic effects of dynamic ear motion in constant-frequency (CF) bats, I developed a simulation framework that models binaural echoes received by oscillating pinnae. The model computes time-varying echo waveforms, their frequency content, and binaural acoustic disparities as a function of ear motion, simulating conditions relevant to CF bats known to exhibit antiphase ear oscillations during echolocation.

2.1 Simulation Approach

2.1.1 CF Call and Simulation Parameters

A 100-ms constant-frequency call at 80 kHz was synthesised at a sampling rate of 192 kHz to approximate narrowband pulses typical of CF bats. The bat was modelled as flying forward at a constant velocity of 2 m/s in still air (speed of sound: 343 m/s). The simulated echo was

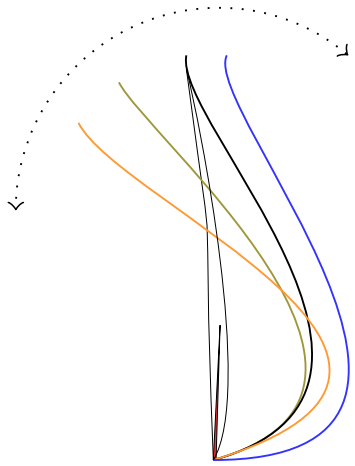

Figure 1: Mechanism of Doppler-induced signal transformation across an oscillating bat ear. As an echo impinges on the bat's ear, it reaches different regions of the ear surface with a slight delay due to the ear's spatial extent. Simultaneously, different points along the ear move at different velocities due to the ear's oscillatory motion. This combination of delayed arrival and spatially varying velocity results in a gradient of instantaneous Doppler shifts. Each point along the ear effectively receives a frequency-shifted version of the echo, with the tip of the ear contributing the largest shifts due to its highest velocity. This dynamic velocity profile imparts a time-varying phase transformation across the reflected wavefront, causing phase warping and the generation of interference patterns in the time domain. In the frequency domain, these effects appear as a spread of energy around the carrier frequency, resulting in a widened spectral band. This phenomenon is distinct from the classical Doppler shift induced by linear relative motion, which produces only a uniform frequency offset.

computed for binaural receivers (left and right ears), with time-varying motion profiles imposed on each ear in antiphase. (Figure 2 top panel)

2.1.2 Ear Kinematics and Doppler-Shifted Echo Modelling

Each ear was represented as a vertical structure of height 2 cm undergoing angular oscillation with maximum deflections of 15°, 30°, or 45°, and frequencies ranging from 5 to 50 Hz. The peak linear velocity at the ear tip was computed as:

$$v_{\text{tip}} = \theta_{\text{max}} \cdot \omega \cdot h, \tag{1}$$

where $\omega = 2\pi f_{\text{ear}}$ is the angular velocity, θ_{max} is the angular displacement (in radians), and h is the ear height.

The ear was discretised into 100 vertical segments from base to tip. For each segment, the instantaneous linear velocity followed a sinusoidal pattern scaled by height. The Doppler-shifted frequency at each time point was computed as:

$$f(t) = f_0 \left(1 + \frac{v(t)}{c}\right), \tag{2}$$

where f_0 is the CF frequency, $v(t)$ is the segment velocity, and c is the speed of sound. The echo was constructed by integrating the instantaneous phase at each time point:

$$\phi(t) = \int 2\pi f(t)\, dt, \tag{3}$$

Thus, modelling frequency shifts due to motion as continuous phase warping. Each segment's contribution was delayed based on its one-way travel time, and the total echo was synthesised

by summing across segments. A toggle allowed switching between summation and amplitude-averaging across segments (testing), but all presented results used summation. The methods of the simulation are depicted in Figure 2.

Instantaneous Frequency Estimation

The analytic signal of each echo was computed via the Hilbert transform. Instantaneous frequency was obtained from the temporal derivative of the unwrapped phase:

$$f(t) = \frac{1}{2\pi} \cdot \frac{d\phi(t)}{dt}, \tag{4}$$

where $\phi(t) = \arg[z(t)]$ and $z(t) = x(t) + j \cdot \hat{x}(t)$. Regions with envelope magnitudes below 1% of the maximum were excluded, and the frequency trace was smoothed using a 50-sample moving average. Only the central 60 ms of each trace (excluding the first and last 20 ms) was retained for analysis to avoid onset and offset artefacts (Figure 2 bottom panel).

2.1.3 Spectrogram and Visualization

Time–frequency representations were obtained via short-time Fourier transforms using a 2048-sample Hamming window and 95% overlap. Spectrogram overlays were constructed with grayscale encoding for the left ear and red channel encoding for the right ear. Other panels included waveforms, ear tip velocity profiles, and plots of $\Delta f(t)$ and BLD with dual y-axes and consistent colour themes. (Figure 4)

2.1.4 Parameter Sweep and Output Summary

Simulations were conducted for 18 combinations of angular frequency (5–50 Hz) and displacement (15–45°). For each run, the resulting echo metrics and figures were saved. The peak tip velocity, Δf bandwidth, standard deviation of Δf, and BLD were collected in a summary table. The full output was saved as CSV and MATLAB ‘.mat‘ files. (Figure 6)

Binaural Frequency and Level Differences

Binaural frequency disparity was computed as:

$$\Delta f(t) = f_{\text{right}}(t) - f_{\text{left}}(t), \tag{5}$$

and binaural level difference (BLD) as:

$$\text{BLD}(t) = 20 \log_{10} \left(\frac{A_{\text{right}}(t)}{A_{\text{left}}(t)} \right), \tag{6}$$

where $A(t)$ denotes the envelope of the analytic signal. The standard deviation of both Δf and BLD was computed from the valid region. The Δf bandwidth was defined as the maximum of $|\Delta f(t)|$ within the selected segment. (Figure 5)

2.1.5 Implementation

All simulations and post-processing were conducted using MATLAB R2023a. Custom scripts handled the synthesis of CF calls, Doppler and phase transformations, segment-wise integration,

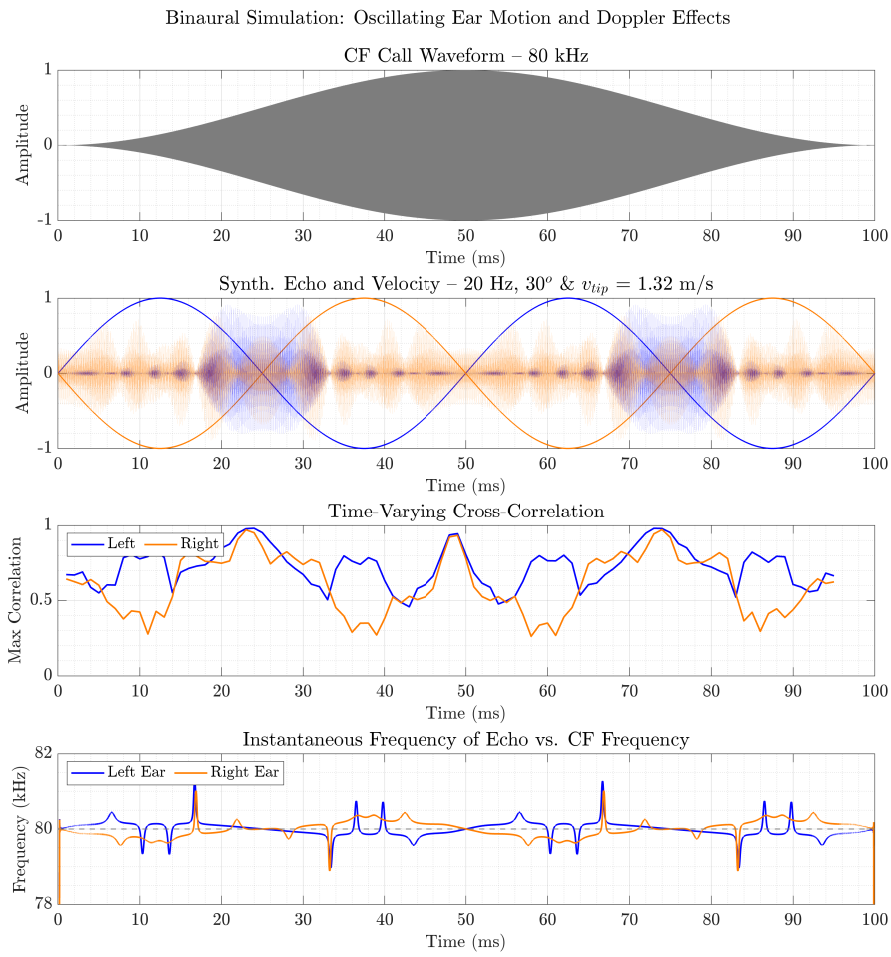

Figure 2: Binaural simulation of echo transformation by oscillating ear motion. This figure illustrates the simulated effect of ear oscillations on binaural echo reception for a constant-frequency (CF) call. The top panel shows the 80 kHz synthetic CF call waveform lasting 100 ms. The second panel displays the simulated echoes received at each ear as translucent coloured patches (left: blue, right: orange), overlaid with the corresponding normalised tip velocity profiles (solid lines). Due to opposing sinusoidal ear motions (20 Hz, $\pm 30^\circ$), the echoes are dynamically warped in both amplitude and phase. The third panel shows the time-varying cross-correlation between the left and right ear signals, revealing dynamic changes in binaural timing alignment induced by phase distortion and frequency shifts. The bottom panel plots the instantaneous frequency in each ear, demonstrating the divergent Doppler-induced modulation imposed by the oscillating ear motion. Together, these panels reveal how even a CF echo is transformed into a spectrotemporally rich, binaurally asymmetric signal through biologically plausible ear kinematics.

Figure 3: Experimental setup for measuring motion-induced Doppler effects. A custom-built ESP32-based playback system was used to generate oscillations in a 20 cm subwoofer via an I^2S DAC (PCM5102) and a 50 W Class D amplifier (ZK-TB21). Oscillatory waveforms at 5–30 Hz were created in MATLAB, saved as `.wav` files, and played back from a microSD card using custom firmware flashed via PlatformIO. An 80 kHz tone was generated and recorded using an RME Babyface Pro interface. A Sanken CO-100K microphone was aligned with the tone playing speaker, both directed at the centre of the subwoofer, positioned 20 cm away. Control trials were recorded with the subwoofer inactive.

and Hilbert-based feature extraction.

2.2 Experimental Approach

2.2.1 Oscillation Playback System

I developed a custom tone modulation system using an ESP32 microcontroller connected to a 20 cm subwoofer. The ESP32 was interfaced with a PCM5102 I^2S DAC for digital audio output, which was amplified via a 50 W Class D amplifier module (model ZK-TB21, China). The ESP32 firmware was developed and compiled using PlatformIO and flashed to the board over USB. This firmware was programmed to read and play back `.wav` files stored on a microSD card. Oscillation waveforms were generated in MATLAB as pure sine tones with frequencies ranging from 5 to 30 Hz, sampled at 44.1 kHz, and saved in 16-bit `.wav` format. These tones were looped in sequence by the ESP32, driving sinusoidal motion in the subwoofer cone (Figure 3).

2.2.2 Recording Configuration

Recordings were made using a Sanken CO-100K microphone aligned parallel to the ScanSpear tweeter at a distance of 20 cm, both aimed at the centre of the subwoofer membrane. The microphone signal was routed through an RME Babyface Pro (RME GmbH, Haimhausen, Germany) audio interface operating at 192 kHz. A MATLAB script was used to generate a series of 100 ms long 80 kHz tones with 1-second intervals. These tones were simultaneously played back and recorded in MATLAB using the RME interface. An internal trigger loopback signal was recorded on the second channel to assist signal segmentation.

To synchronise playback with the subwoofer oscillation, the MATLAB recording script was manually triggered immediately after ESP32 playback began. Each trial consisted of 10 repetitions of the tone, and the entire sequence was recorded for analysis. Control recordings were taken at the end of the session with the subwoofer powered off to assess baseline frequency spread without motion.

Trial	Ear Freq(Hz)	Ang.(°)	Tip v (m/s)	Excur.(mm)	Δf BW(Hz)	Δf σ(Hz)	BLD σ(dB)
2	5	15	0.08	5.2	23.1	8.8	3.6
3	5	30	0.16	10.5	67.9	30.9	5.4
4	5	45	0.25	15.7	113.0	43.6	6.2
5	10	15	0.16	5.2	107.4	65.4	3.6
6	10	30	0.33	10.5	201.8	95.1	5.5
7	10	45	0.49	15.7	213.2	109.9	6.2
8	15	15	0.25	5.2	160.8	83.2	3.6
9	15	30	0.49	10.5	318.8	129.8	5.4
10	15	45	0.74	15.7	420.7	187.6	6.2
11	20	15	0.33	5.2	214.1	107.8	3.6
12	20	30	0.66	10.5	423.7	179.2	5.5
13	20	45	0.99	15.7	558.8	236.7	6.2
14	25	15	0.41	5.2	267.4	139.0	3.6
15	25	30	0.82	10.5	528.4	232.7	5.4
16	25	45	1.23	15.7	695.9	309.4	6.2
17	30	15	0.49	5.2	320.3	182.0	3.6
18	30	30	0.99	10.5	631.7	301.9	5.5
19	30	45	1.48	15.7	831.2	400.8	6.2
20	35	15	0.58	5.2	373.1	206.6	3.6
21	35	30	1.15	10.5	734.5	340.2	5.4
22	35	45	1.73	15.7	965.8	446.8	6.2
23	40	15	0.66	5.2	425.6	224.1	3.6
24	40	30	1.32	10.5	836.6	381.4	5.5
25	40	45	1.97	15.7	1099.0	521.2	6.2
26	45	15	0.74	5.2	477.9	251.6	3.6
27	45	30	1.48	10.5	937.5	417.1	5.4
28	45	45	2.22	15.7	1231.7	547.8	6.2
29	50	15	0.82	5.2	530.1	290.8	3.6
30	50	30	1.64	10.5	1038.2	480.0	5.5
31	50	45	2.47	15.7	1364.2	629.4	6.2

Table 1: Summary of simulated binaural Doppler conditions across combinations of ear oscillation frequency and angular excursion. Each trial reports the resulting tip velocity and corresponding tip displacement (Excursion), along with the peak binaural frequency disparity (Δf bandwidth), its standard deviation, and the standard deviation of the binaural level difference (BLD). All simulations assume a constant forward flight velocity of 2 m/s and a 20 mm ear length.

2.2.3 Spectral Analysis

Recorded signals were segmented based on a synchronisation trigger embedded in the second channel. Each 100 ms segment was analysed using a short-time Fourier transform with a 2048-sample window, 1800-sample overlap, and a 4096-point FFT. The frequency spread (Δf) of each segment was defined as the bandwidth containing spectral energy within 20 dB of the peak, constrained to the range 75–85 kHz. The Doppler-induced broadening was quantified by comparing Δf across conditions (Figure 5).

RESULTS

To evaluate the effects of oscillating receiver motion on the acoustic structure of returning echoes, I conducted both numerical simulations and controlled acoustic experiments. The simulations modelled the reception of constant-frequency (CF) echoes by antiphase-oscillating ears over a range of kinematic conditions, systematically varying oscillation frequency and angular displacement. In parallel, I performed physical measurements using a stationary speaker and microphone with an oscillating reflector to emulate the relative motion of the bat's pinna. Together, these two approaches provide converging insights into how dynamic receiver motion transforms echo features, particularly in terms of frequency bandwidth, amplitude envelope, and binaural disparity. The following sections present the results of these simulations and experiments, illustrating their alignment and divergence across different conditions.

Origin and Characteristics of Spectral Spread

Unlike classical Doppler shifts resulting from linear flight, where a fixed relative velocity induces a single frequency offset, oscillatory motion introduces a dynamic velocity profile throughout each echo interval. Because CF bat calls can last 50–100 ms, and the echo arrives while the ear is in motion, the reflected signal experiences time-varying phase shifts. These result in not just a shift, but a spectral broadening—a band of frequencies reflecting the changing instantaneous velocity of the reflector.

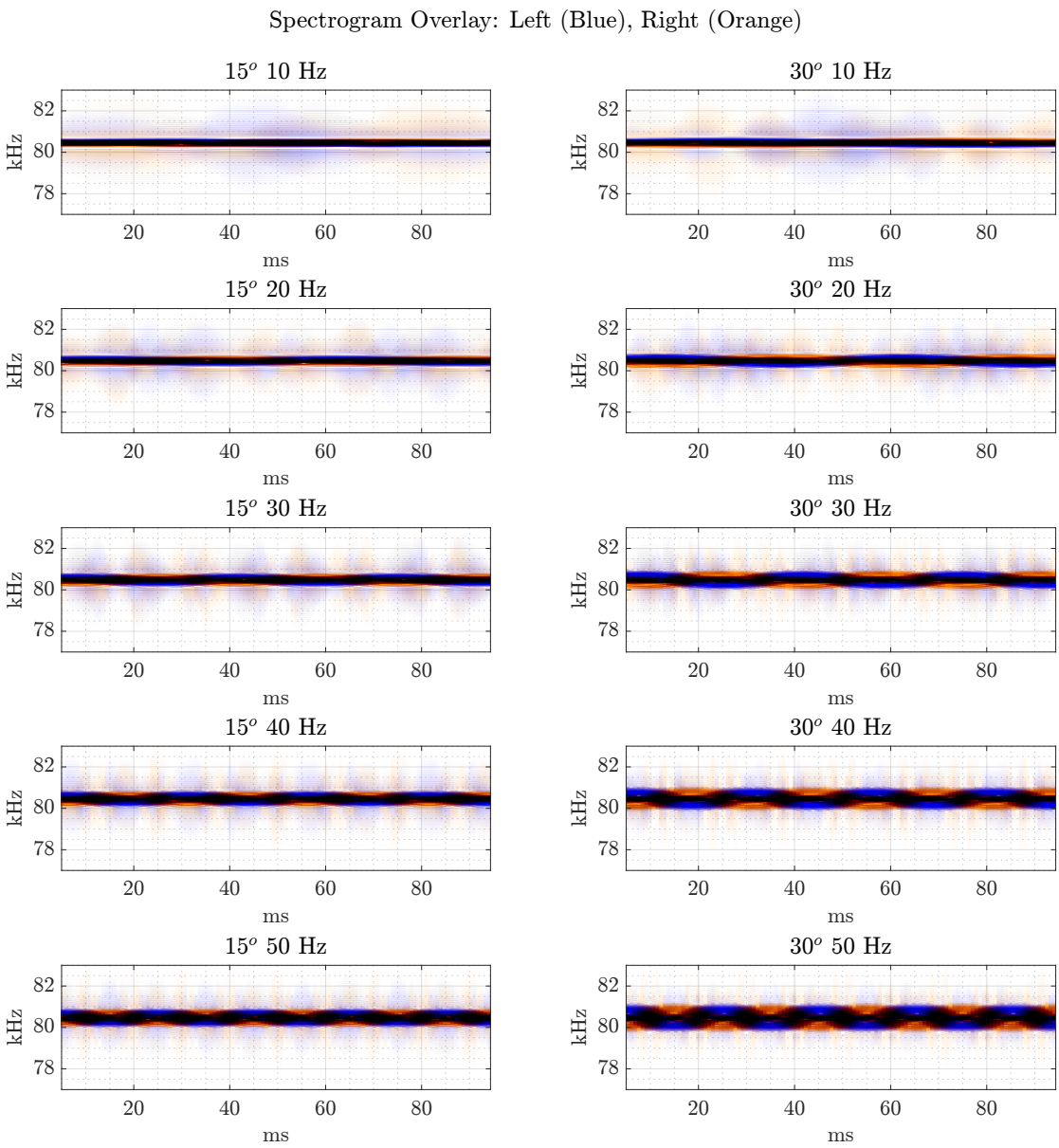

Figure 4: Spectrogram overlays of binaural echoes for varying ear oscillation conditions. Each subplot shows time–frequency representations of echoes received at the left (blue) and right (orange) ears under different angular displacements (15°, 30°) and ear oscillation frequencies (10–50 Hz). As oscillation frequency and angular displacement increase, spectral modulation deepens and broadens, producing pronounced dynamic variation around the 80 kHz CF tone.

This effect is fundamentally different from the classical Doppler shift caused by constant linear velocity. In the case of a bat flying steadily at 3 m/s, the relative velocity between source

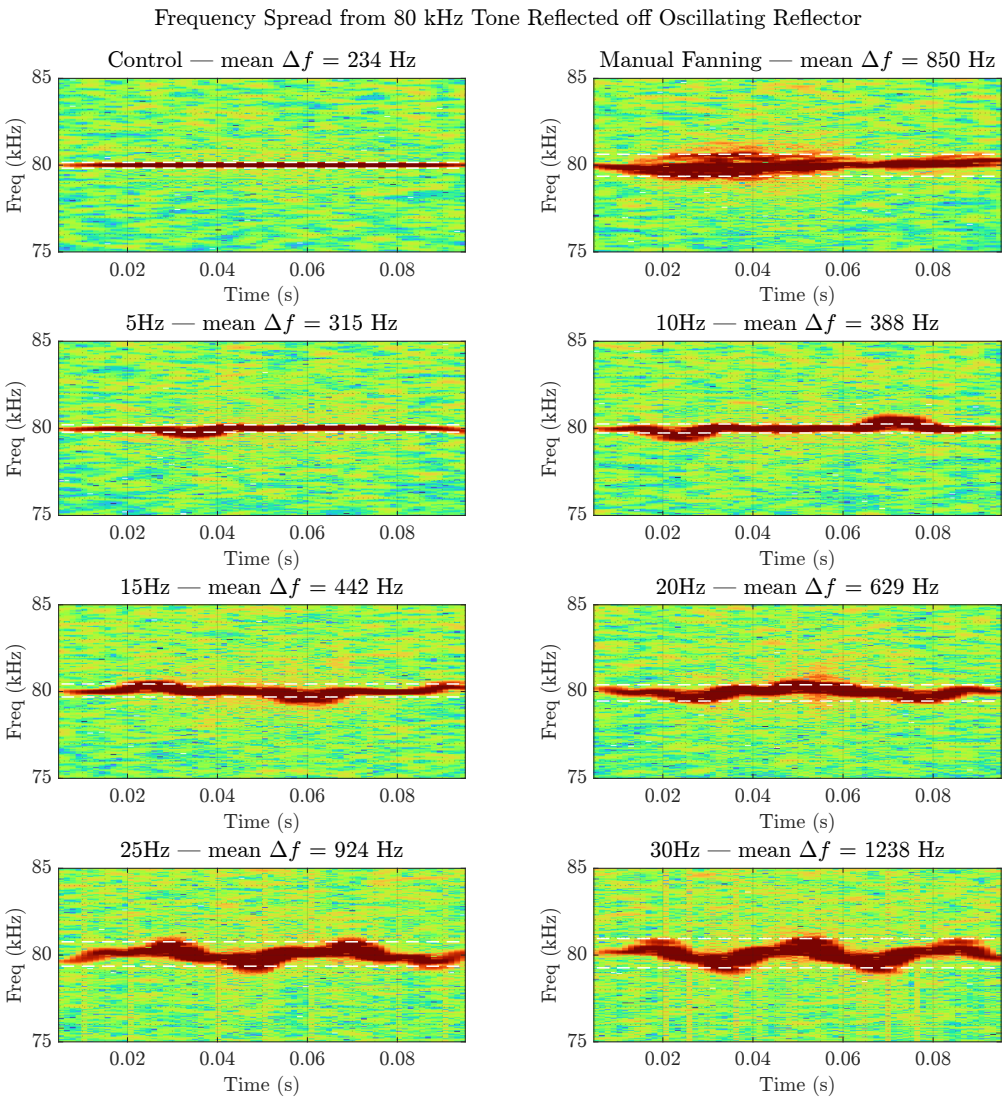

Figure 5: Spectrograms of reflected 80 kHz tone showing frequency spread across conditions. Each panel displays the time–frequency representation of a 100 ms segment extracted from the reflected signal for the corresponding trial condition. The analysis was performed using short-time Fourier transform with a window length of 2048 samples and a 90% overlap. Dashed white lines indicate the upper and lower frequency boundaries of the tone's spectral energy within the **-20 dB** band relative to its peak power. The numeric label in each title represents the mean Δf (frequency spread) across all segments in that condition. In the **Control** condition, the spectrogram shows a narrowband, nearly stationary tone centred at 80 kHz, with minimal frequency spread (mean Δf = 234 Hz). As reflector motion increases (from 5 Hz to 30 Hz), the signal exhibits progressively broader frequency modulation, with Δf increasing accordingly. This spread reflects the Doppler effect induced by oscillatory motion, which introduces instantaneous frequency shifts. At higher modulation frequencies (e.g., 25 Hz and 30 Hz), the bandwidth widens considerably, indicating more pronounced phase distortion of the reflected wave. The **Manual Fanning** condition also produces a large frequency spread, though with more irregular temporal structure, likely due to non-sinusoidal, variable-speed motion. These results indicate what may be expected from oscillating ears, with increasing oscillation frequency leading to greater spectral broadening of the reflected signal, consistent with motion-induced Doppler dynamics.

and receiver remains fixed. The Doppler effect in such a scenario causes a uniform frequency shift given by the well-known relation:

$$\Delta f = \frac{2v}{c} \cdot f_0 \tag{7}$$

For a tone of 80 kHz and $v = 3\,\mathrm{m/s}$, this yields a constant Doppler shift of approximately 1400 Hz. Importantly, **the entire frequency spectrum is translated**, and the output remains spectrally narrow–only offset in frequency. There is no spread, modulation, or temporal variation in spectral content.

By contrast, when a bat's ear oscillates sinusoidally, the velocity of the reflective surface (i.e., the ear) is continuously changing throughout the echo duration. The instantaneous velocity $v(t)$ varies as a sinusoidal function:

$$v(t) = r \cdot \theta \cdot 2\pi f \cdot \cos(2\pi f t) \tag{8}$$

where r is the length from the base to the ear tip, θ is the angular amplitude in radians, and f is the ear oscillation frequency. This variation in $v(t)$ results in a continuously changing instantaneous Doppler shift, rather than a constant one. The received echo is thus not simply shifted, but frequency modulated.

Mathematically, this is equivalent to applying a time-varying phase term to the reflected signal. The result is not a displaced tone, but a signal whose spectrum is spread across a range of frequencies. This manifests as spectral broadening (bandwidth spread), which depends on the velocity range of the ear tip during the echo interval.

Table 1 summarises the outcomes of 30 binaural Doppler simulations, systematically varying ear oscillation frequency and angular amplitude. The tip velocity, computed from ear kinematics, ranged from 0.08 to 2.47 m/s, corresponding to angular excursions of 15° to 45° and frequencies from 5 to 50 Hz. The resulting binaural frequency bandwidths (Δf) showed a strong positive trend with increasing tip velocity, rising from 107 Hz at 5 Hz, 15° to over 1360 Hz at 50 Hz, 45°. The standard deviation of Δf also scaled with velocity, indicating that higher oscillation amplitudes not only broadened the frequency spread but introduced greater temporal variability. Interestingly, across all conditions, the binaural level difference (BLD) standard deviation remained relatively stable, clustering around 6.2 dB at peak excursions. These results confirm that rapid angular ear motion introduces dynamic frequency shifts and binaural disparities of biologically significant magnitude, consistent with the hypotheses on their functional importance in echolocating CF bats.

In my experiments, reflector oscillation at 30 Hz with $r = 2\,\mathrm{cm}$ and $\theta = 45°$ produced instantaneous velocities up to 2.96 m/s (Calculated based on speaker parameters). This yielded a dynamic frequency excursion of approximately 1.2 kHz around the 80 kHz carrier (Figure 5). Unlike the constant offset from forward motion, this spread is transient, phase-locked to the modulator, and results in temporally rich echo transformations. This modulation is further reflected in the waveform domain as phase warping, causing irregular zero-crossings and beat-like structures–features entirely absent in linear Doppler conditions (Figure 7).

These findings demonstrate that ear oscillations act as a signal transformation mechanism, not just a positional adjustment. They dynamically encode time-varying velocity and phase, and cannot be simplified to a static DS model. Therefore, the acoustic consequence of oscillating

ears in CF bats must be interpreted as *Doppler-based modulation*, not just shift, and forms a biologically distinct strategy for echo encoding.

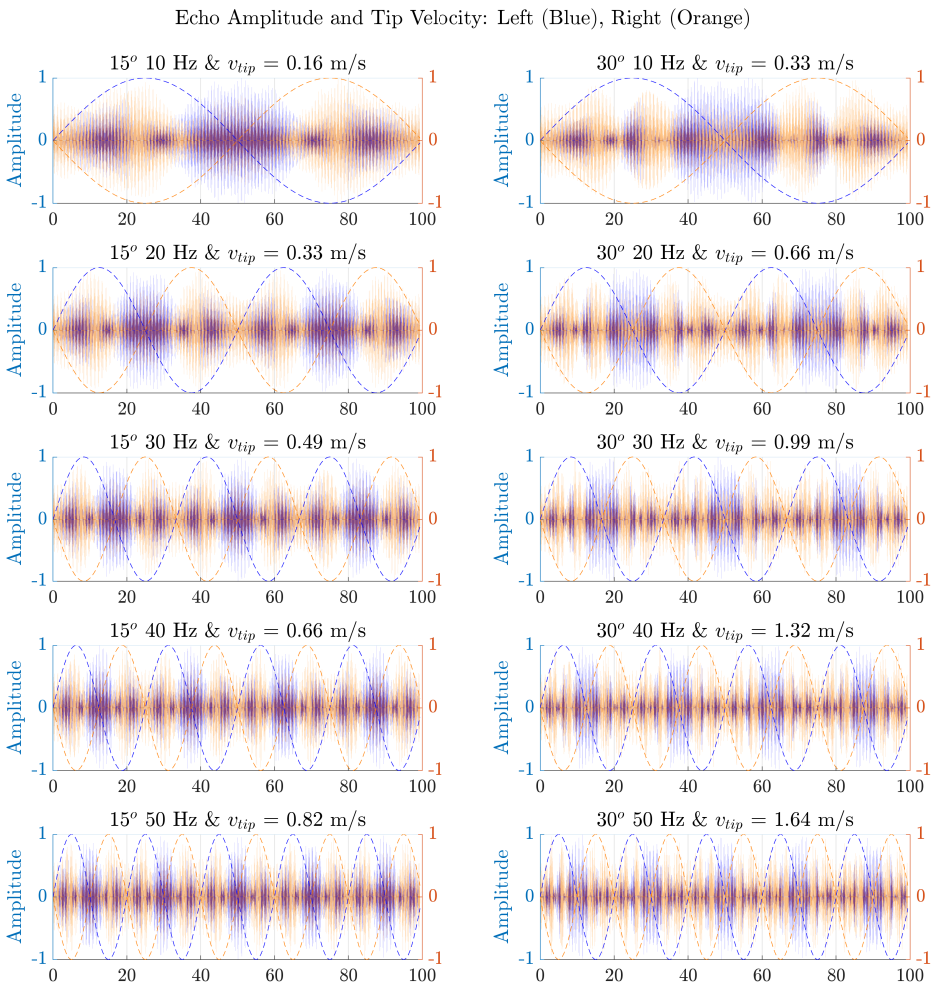

Figure 6: Simulated echo waveforms and corresponding ear tip velocity profiles. Left and right ear echoes are plotted alongside their respective velocity traces for multiple ear oscillation frequencies and angular displacements. Echo amplitudes and timing shift with velocity phase, illustrating dynamic modulation of the received signal imposed by oscillatory motion.

I systematically simulated the effects of oscillatory ear motion on echo reception across a range of ear oscillation frequencies (5–50 Hz) and angular displacements (15°, 30°, 45°). The simulations produced a set of echo waveforms for the left and right ears, which were analysed in terms of spectral characteristics (Figure 4), waveform and velocity dynamics (Figure 6), and binaural differences in frequency and amplitude (Figure 8).

2.3 Spectral Modulation by Ear Motion

Figure 4 shows the spectrograms of the left (blue) and right (orange) ear echoes across all simulated conditions. At low oscillation frequencies (e.g., 5–10 Hz) and small angular displacements,

the echo remained close to the transmitted constant-frequency (CF) tone at 80 kHz. However, with increasing ear frequency and angular range, I observed progressive spectral broadening and modulation. For instance, at 50 Hz and 45°, the spectral content extended over several hundred Hertz, indicating strong Doppler-induced shifts caused by rapid and large ear movements. Importantly, the left and right spectrograms diverged significantly due to their antiphase motion, with distinct spectral energy contours suggesting differential encoding of spatial information.

Similarly, the spectrograms from the recordings revealed that the frequency spread increased proportionally with oscillation frequency (Figure 5). Control trials showed narrowband reflections with Δf around 234 Hz. By contrast, 30 Hz oscillations produced spectral spreads approaching 1.3 kHz. These effects are temporally dynamic and phase-locked to the oscillator's motion. Waveforms also exhibited noticeable phase warping: zero-crossings became irregular, with beat-like modulations arising from interference patterns. Such distortions were absent in the Control and are not predicted by linear Doppler alone.

2.4 Temporal Alignment with Ear Velocity

The temporal structure of the echoes was also modulated by ear movement. As shown in Figure 6, the amplitude envelopes of the echoes vary in close synchrony with the sinusoidal velocity profiles of the ear tips. Echo peaks tended to align with peak velocities, while troughs coincided with direction reversals. This dynamic interaction between incoming echoes and moving receiver geometry led to periodic constructive and destructive interference in the waveform. The left and right ears displayed mirror-symmetric patterns, consistent with their opposite motion phases. These effects intensified with higher frequencies and greater angular sweeps. Figure 7 presents the waveforms of the recordings from the oscillating target. The expected phase warping and the resulting zero crossing distortion become increasingly evident with higher oscillation frequencies.

2.5 Binaural Differences in Frequency and Level

Figure 8 illustrates the instantaneous binaural frequency difference (Δf) and binaural level difference (BLD) as functions of time. At low oscillation frequencies, both Δf and BLD remained relatively stable and small in magnitude. As ear movement velocity increased, however, Δf fluctuated more rapidly and reached larger extrema. Similarly, BLD variation widened, reflecting the amplitude asymmetry introduced by differing Doppler and phase interactions at each ear. These features represent dynamic binaural cues potentially exploitable by the bat's auditory system for spatial localisation or motion tracking.

Overall, the results demonstrate that oscillatory pinna motion can impose rich, condition-dependent modulations on received echoes in both spectral and temporal domains. These transformations scale systematically with the biomechanical parameters of ear motion, offering a potential mechanism for sensory enhancement beyond directional gain.

These findings confirm that ear oscillations generate rich transformations to returning echoes–transformations that scale nonlinearly with velocity and encode motion phase. This suggests a role for ear dynamics in enriching spatial and temporal encoding in CF bat biosonar.

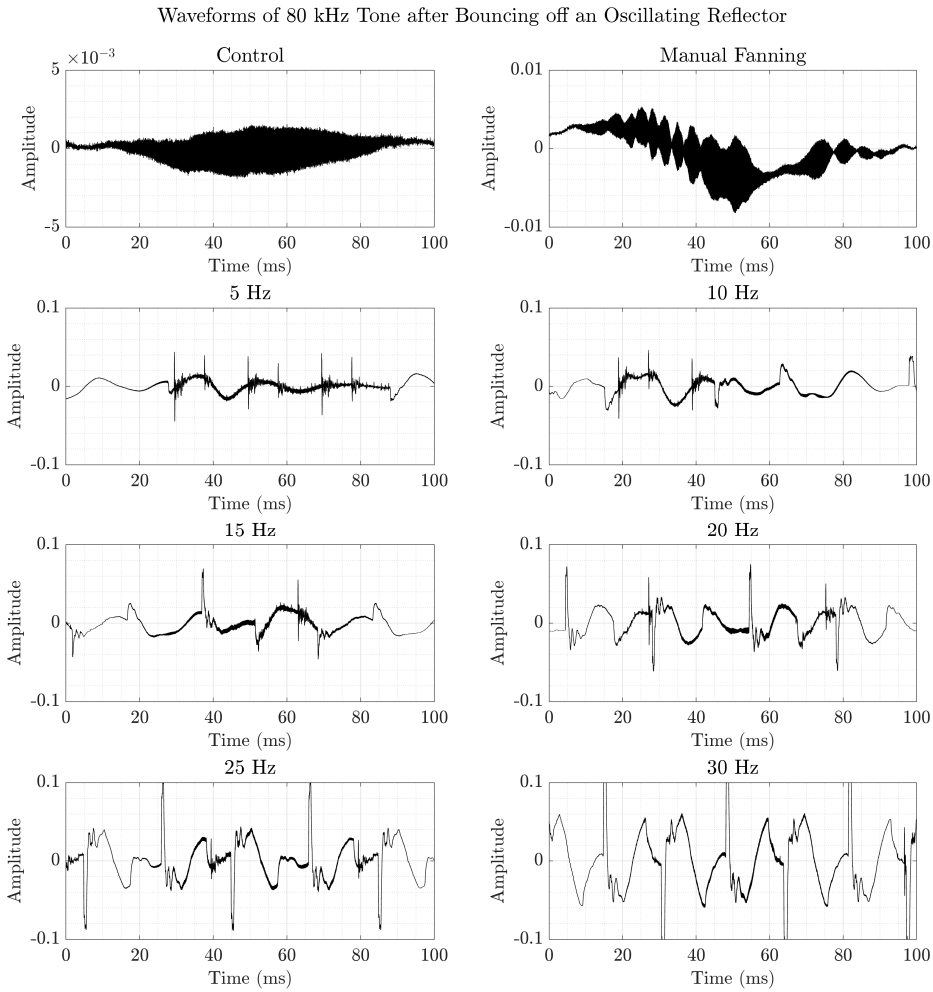

Figure 7: Time-domain waveforms of 80 kHz tone after reflection from an oscillating surface. Each panel shows a 100 ms segment extracted from the recorded signal for the corresponding condition. The **Control** condition (top left) reveals a clean and stable sinusoidal waveform, characteristic of a continuous tone with no motion-induced modulation. In contrast, all other conditions introduce varying degrees of non-stationarity due to surface movement. At low modulation rates (5–10 Hz), the reflected waveform exhibits periodic amplitude fluctuations and mild distortions. As the oscillation frequency increases (15–30 Hz), the waveform becomes increasingly distorted, with prominent changes in both amplitude and zero-crossing structure. This reflects **phase warping** caused by the Doppler shift imparted by the moving reflector. Notably, in the higher frequency conditions (especially 25 Hz and 30 Hz), the waveform appears stretched and compressed in a quasi-periodic manner, producing variable intervals between zero-crossings–unlike the uniform spacing seen in the Control. Manual fanning yields a complex, irregular pattern resembling fluctuating velocity components, which also alters zero-crossing symmetry. These features demonstrate how relative motion between emitter and reflector induces instantaneous frequency modulation and waveform distortion even in a nominally constant-frequency tone.

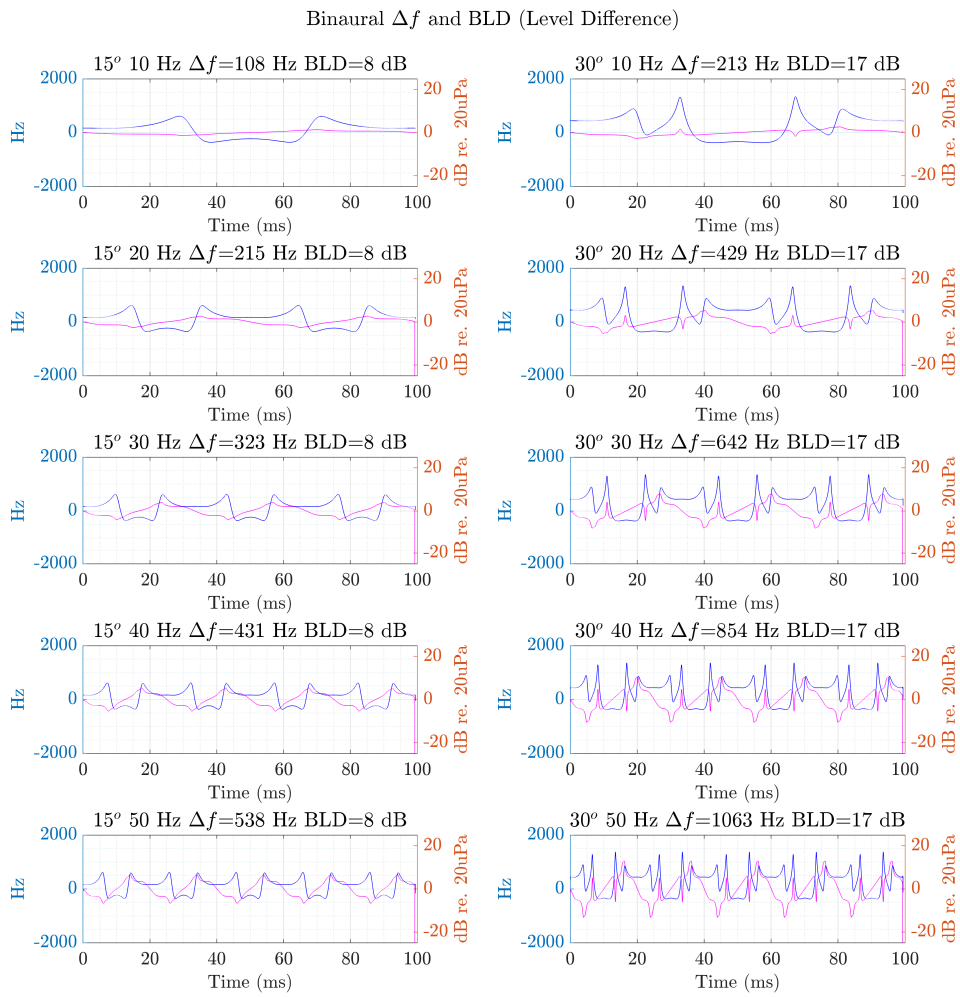

Figure 8: Instantaneous binaural frequency difference (Δf) (*magenta*) and binaural level difference (BLD) (*blue*) traces for each simulation condition. Plots show how dynamic ear motion produces non-linear binaural disparities. Higher oscillation frequencies and angular displacements lead to stronger modulations in both frequency and amplitude, highlighting the potential role of ear kinematics in encoding spatial acoustic cues.

DISCUSSION

The results presented here demonstrate that oscillatory motion of a reflective surface–analogous to the ear movements observed in CF bats–can impose substantial spectral and temporal modulations on returning echoes. These modulations go beyond a simple Doppler shift, producing dynamic frequency spreads and phase warping that vary continuously with the velocity profile of the motion. In contrast to traditional models where Doppler effects are treated as constant frequency offsets due to steady flight, the data here reveal that even periodic, localised motion can introduce rich and time-varying transformations to acoustic signals. The experimental evidence confirms that such motions generate spectral broadening proportional to the modulation frequency, with observed bandwidth spreads exceeding 1.2 kHz at 30 Hz ear-like oscillation. These findings suggest that ear movement in CF bats is not merely a morphological adaptation for directional gain, but potentially a source of biologically encoded signal dynamics that may be exploited for fine-scale echo discrimination.

The mechanism by which an oscillating ear transforms incoming echoes is rooted in the spatial and temporal structure of Doppler shifts across its surface. As an echo arrives, the first point of contact is typically the base of the ear, which–due to its anatomical anchoring–experiences minimal or no oscillatory motion. The frequency content of the signal at this point reflects only the baseline Doppler shift induced by the bat's translational flight velocity. However, as the sound wave continues to travel across the surface of the ear, it interacts with regions that are in motion due to ear oscillation. Because different parts of the ear move at different velocities and in different directions at any given moment, the echo is subjected to a cascade of instantaneous Doppler shifts that vary both spatially and temporally. This effectively applies a dynamic frequency modulation to the reflected signal, overlaid on top of the constant shift due to forward motion. The result is a composite transformation: the initial frequency offset from the bat's motion combined with a sweeping modulation induced by the oscillating ear tip, which can reach velocities comparable to or greater than flight-induced Doppler. This creates a distributed phase transformation across the ear, manifesting in both broadened spectral energy and characteristic waveform warping. Such a structure likely imposes a unique spectro-temporal signature onto each echo, which the bat's auditory system could exploit for extracting directional or textural information.

The simulation results presented in Table 1 and the experimental measurements shown in Figure 5 & 7 both demonstrate that oscillatory motion of a reflective surface introduces pronounced spectral modulation in echoes of constant-frequency (CF) signals. Notably, both simulation and experiment reveal a consistent increase in spectral bandwidth with increasing oscillation frequency and excursion amplitude—key parameters that govern the velocity of the reflecting surface. This supports the hypothesis that oscillating bat ears dynamically transform incoming echoes in a manner that could enhance the encoding of spatial or temporal cues.

In the simulations, I modelled the bat ear as a vertical structure segmented into 100 discrete positions from base to tip. Each segment contributes a Doppler-shifted and delayed component to the received signal. The cumulative echo is therefore a constructive and destructive interference of sinusoidal components with varying instantaneous frequencies and phases. This method captures not only the classical Doppler shift but also the additional phase warping introduced by distributed motion across the ear's surface. The result is a temporally fluctuating signal with

modulated envelope and instantaneous frequency, and rich binaural contrasts that grow with increasing tip velocity (Figure 4, 6 & 8).

The experimental data in Figure 5 & 7 corroborate these findings. When a pure tone was reflected off a flat surface oscillating at 5–30 Hz (using a subwoofer or a manually fanned cardboard), the spectrogram of the recorded signal revealed increasing frequency spread with increasing modulation frequency. At 30 Hz, the observed bandwidth reached over 1.3 kHz. This closely matches the simulations, where similar tip velocities (e.g., ∼1.0–1.5 m/s) resulted in comparable Δf bandwidths. While the reflector used in the experiments lacked the distributed velocity gradient of the simulated ear, the agreement in modulation depth across velocity ranges validates the acoustic relevance of the model.

The alignment between simulation and measurement underscores the robustness of the underlying mechanism: velocity-induced echo transformation is not merely a function of instantaneous speed, but a result of compound effects from distributed delays, phase accumulation, and amplitude variation across the receiving surface. These interactions generate spectral sidebands and temporal envelope modulation—features which may serve as internal sensory references in bats, enabling them to detect subtle target-induced amplitude modulations such as insect wingbeats.

From a functional standpoint, this suggests that the spectral broadening observed is not a liability, despite CF bats possessing highly tuned auditory foveae. Rather, dynamic ear movements may transiently enrich the signal within the foveal band through phase-driven amplitude and frequency modulations. These modulations, when detected binaurally and temporally resolved, may enhance the bat's ability to infer motion direction, flutter, or surface irregularity from echoes.

Taken together, these results highlight a novel acoustic function of bat ear motion: to actively modulate and probe the acoustic return, transforming an otherwise stationary narrowband echo into a dynamic and information-rich signal that enhances spatial and temporal resolution. The interplay between physical motion, phase dynamics, and biological filtering merits further neurophysiological and behavioural investigation.

Despite this induced spectral broadening, CF bats are known for their highly selective auditory processing. Many species possess an auditory fovea—a narrow frequency band with exceptionally high sensitivity and neural tuning precision [7, 8]. For example, *Rhinolophus ferrumequinum* maintains echo frequencies within a 200–400 Hz window around the foveal best frequency via Doppler shift compensation (DSC), adjusting call frequency in real-time to negate forward flight velocity [9, 10]. This raises an apparent contradiction: If CF bats are only sensitive to a narrow spectral window, what functional role might dynamically induced spectral broadening serve?

I propose that the role of broadband echo transformation by moving ears is not to expand spectral analysis per se, but rather to enhance the temporal and spatial contrast of echo features available to the bat's auditory system. The results presented here demonstrate that even modest ear motion introduces fine-scale amplitude and phase variations in the received echo. When the echo is constructed from a summation of delayed and Doppler-shifted contributions along the ear, these components interact via constructive and destructive interference, generating complex modulations and rapid transients in both amplitude and instantaneous frequency. Importantly, these interference patterns differ between the left and right ears, due to their antiphase motion, resulting in strong binaural contrasts.

Such contrasts could be functionally advantageous for encoding spatial cues or detecting movement-related modulations in targets (e.g., insect wingbeats). Although the cochlear filters are narrow, the auditory system may be exploiting the temporal envelope or phase transitions within the foveal band. Neural coding strategies in the midbrain or auditory cortex could detect these temporal modulations or relative phase cues, even if the frequency content remains tightly constrained [11]. This would allow CF bats to benefit from the echo structure shaped by ear motion without violating the constraints of their auditory fovea.

The dynamic ear motions observed in CF bats may also serve a compensatory function in maintaining perceptual access to relevant echo information under varying flight-induced Doppler conditions. During forward flight, especially at high velocities or while closing in on a target, the returning echo can be shifted by several kilohertz, often beyond the sharply tuned range of the bat's auditory fovea. Given that many CF bats possess extremely narrow frequency tuning, with foveal bandwidths often less than 1000 Hz, any substantial shift in the incoming signal could impair the bat's ability to extract echo features with high precision. By oscillating the ears, bats may induce a deliberate frequency modulation that effectively sweeps the incoming echo across a broader spectral range. This has two consequences: first, it increases the probability that some portion of the modulated echo passes through the foveal band, thereby ensuring perceptual accessibility even when the absolute arrival frequency is unpredictable; and second, it may convert frequency offsets into dynamic patterns–such as periodic sweeps or interference beats–that could be decoded temporally. In this way, ear motion acts not merely as a passive directional filter but as an active mechanism for spectral remapping, potentially ensuring robust echo encoding under diverse acoustic conditions.

A particularly intriguing implication of these results concerns the timing of ear oscillations relative to the emitted call. Behavioural studies of CF bats have shown that ear movements are not consistently locked to pulse emission [3, 4]. Rather than being tied to the timing of vocalisation, I suggest that ear movements may instead be phase-locked to the anticipated arrival of the echo from a selected target range. In my simulations, the richness of the spectral and temporal modulations — including peak instantaneous frequency shifts and binaural level differences — is strongly influenced by the velocity phase of the ear at the time of echo reception. When the echo arrives during the high-velocity phase of the ear swing, the induced Doppler shift is maximised and more structured modulation appears in both frequency and amplitude domains. This supports the idea that the functional timing of ear oscillation is designed to optimise echo transformation, not vocal production. Such a strategy would allow CF bats to tune their auditory biomechanics dynamically, aligning their sensory filters to extract maximum information from specific objects in space at the expected time of echo return.

These findings also prompt a re-evaluation of how CF bats process echo modulations arising from fluttering insect targets. Experiments show how the wing flutters are important cues for detecting prey for CF bats [12]. Traditionally, wingbeat-induced fluctuations have been interpreted as low-frequency amplitude modulations (AM) imposed on the returning echo. However, based on the experimental evidence presented here, it is more appropriate to describe wingbeats as oscillatory motions that actively transform the incoming signal–much like the bat's own ears do. Insect wings act as moving reflectors with periodic velocity profiles, and their motion imparts time-varying Doppler shifts on the reflected signal. As a result, the echo from a fluttering insect is not only amplitude modulated but also spectrally spread due to transient frequency

modulation (FM). This reframing aligns the physics of fluttering targets with that of oscillating receivers: both generate dynamic spectrotemporal transformations via distributed Doppler effects.

Importantly, this means that CF bats are navigating an echo scene where both the emitter–receiver system and the target are capable of inducing non-stationary modulations. The challenge, then, is not merely to detect low-frequency AM cues but to distinguish between self-induced and externally sourced spectral structures. In this context, ear oscillation may play a compensatory role–not by suppressing flutter-induced cues, but by remapping the incoming echo to ensure that flutter-induced spectral energy remains within the auditory fovea. The resulting echo signature–now a combination of FM and AM patterns–could enhance detectability through temporal contrast and binaural differentials. This interaction between two biologically oscillating surfaces–ears and wings–suggests a more dynamic acoustic ecology than previously appreciated, and invites future work exploring the co-evolution of signal structure and sensory adaptation in CF bat prey detection.

Taken together, these results support a reconceptualisation of CF bat ear motion as an active encoding process. The dynamic transformation of echo signals by oscillating pinnae introduces rich temporal structure into an otherwise spectrally narrow channel, which the bat may exploit for enhanced spatial resolution, motion detection, and scene analysis.

Future Experimental Testing of the Hypothesis

While the computational simulations and the experiments presented here demonstrate how oscillatory receiver motion transforms incoming echoes, it remains essential to evaluate whether CF bats exploit these transformations behaviourally. I propose a targeted psychophysical experiment using trained CF bats under controlled laboratory conditions. The experimental setup would involve an array of loudspeakers positioned at fixed spatial locations in front of the stationary bat, each capable of playing desired CF tones modulated with specific frequency offsets. High-precision laser vibrometry would be employed to monitor both the instantaneous ear kinematics and the phase relationship between the two ears during echolocation. Based on the real-time vibrometry data, the system would dynamically select which speaker outputs a tone falling within the bat's foveal sensitivity range, while the remaining speakers would produce tones outside the bat's auditory tuning window. The speaker selection would be randomized across trials and synchronized with the ear movement cycle. The bat's task would be to report the perceived audible speaker (e.g., by calling towards it a number of time in a given time widnow). This paradigm directly tests whether ear oscillations actively enable the animal to extract echo information that would otherwise fall outside its narrow foveal band. Crucially, if the hypothesis is correct, the bat's ability to detect the target should covary with whether the ear kinematics align to place the transformed echo within the auditory fovea. Such experiments would provide decisive behavioural validation of the proposed function of oscillating ear motion as an active encoding mechanism in CF biosonar.

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DATA AND CODE

The simulation code, experimental data, and analysis scripts will be made available upon publication. Requests for access to data and code during the review process may be directed to the author via email.

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