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Vol. 157 • No. 3 • 03.2025



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AVAILABLE ONLINE: pubs.aip.org/asa/jasa

Published by the Acoustical Society of America through AIP Publishing LLC





Echolocating bats adjust sonar call features and head/ear position as they track moving targets in the presence of clutter

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ABSTRACT:

Echolocating bats often encounter clutter as they pursue insect prey. To probe the adaptive behaviors bats employ to mitigate the effects of clutter, this study quantified echolocation call features and head movements of big brown bats (Eptesicus fuscus) as they tracked a moving prey target in the dark. Bats were trained to rest on a perch and track an approaching target for a food reward. Clutter was positioned at different distances and angular offsets from the bat and the path of a moving target. This study hypothesized that bats dynamically adjust call features and head direction to facilitate target localization in the presence of clutter. The results show that bats shortened call duration and interval and increased head movements when the target was close to clutter. The study also revealed that bats increase the production of sonar strobe groups in cluttered environments, which may sharpen sonar spatial resolution. Spectral analysis showed that maximum call power shifted to lower frequencies when clutter was close to the target. These data demonstrate the big brown bat's range of adaptive behaviors that support target tracking in cluttered environments. © 2025 Acoustical Society of America. https://doi.org/10.1121/10.0036252

(Received 17 December 2024; revised 3 March 2025; accepted 6 March 2025; published online 27 March 2025) [Editor: JoAnn McGee]

Pages: 2236-2247

I. INTRODUCTION

Many bat and marine mammal species have evolved echolocation to navigate, forage, and avoid obstacles under low-light conditions.¹⁻⁴ Echolocating animals emit ultrasonic signals and analyze returning echoes to construct a representation of their environment.⁵ Species employ diverse sonar signal designs that are suited to the habitat, diet, and foraging behaviors of echolocating animals.^{1,6} The adaptability of echolocation is exemplified in the big brown bat, Eptesicus fuscus, a bat species that uses frequency modulated (FM) echolocation calls to expertly navigate and hunt insects in both open and cluttered environments.⁵

Big brown bats flexibly tune their echolocation call features in response to environmental stimuli.7 Specifically, they exhibit rapid adaptations in the duration, interval, and temporal patterning of echolocation calls with changing distance to a target.^{8,9} For example, the big brown bat decreases call duration and interval as it approaches prey, culminating in a "feeding buzz" just before interception.¹⁰ Shortening call duration and interval yields sharper information about target location, while avoiding overlap between sonar vocalizations and returning echoes.¹¹⁻¹⁴ Bats also adjust sonar signal design to the proximity of echoes from nearby vegetation or clutter. In cluttered environments, long

duration calls can produce call-echo overlap, and short call intervals could create ambiguity in call-echo assignment.^{14,15} In open environments, where bats may be searching for sparsely distributed prey, longer duration calls yield greater echo energy for target detection.¹⁶ The big brown bat skillfully manages the trade-off between call duration and interval to control the flow of echo information in different environments and tasks.¹⁷

In addition to modulating the temporal properties of echolocation calls, bats also modulate spectral properties to facilitate foraging in different environments. For example, as bats prepare to capture prey, they lower the frequencies contained in FM sweeps, producing wider beam patterns to monitor echoes from the surroundings, such as background vegetation.¹⁸⁻²⁰ Bats also modify the spectral content of their calls in areas occupied by large numbers of bats, potentially to avoid interference from calls of nearby conspecifics.²¹⁻²⁴ Bats also make adjustments to sound frequency in cluttered environments.^{14,25-27} These adjustments may aid in the discrimination between targets and background.

In addition to sonar call adjustments, head and pinna movements contribute cues that aid echo information processing. Big brown bats adjust their head orientation to direct their sonar beam at objects, enhancing localization of targets and obstacles.^{9,17,28} Head and ear movements are guided by echo feedback from the environment, allowing for environmental assessment, akin to visual scanning in other species.^{17,28,29} Likewise, movements such as head turning influence the directional aim of their echolocation calls, which, in turn, impacts target detection and localization.³⁰

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The present study dives deeper into the analysis of adaptive behaviors employed by bats to separate targets and clutter. Specifically, we quantify both adaptive echolocation behavior and head/ear movements in big brown bats tracking approaching targets in the presence of environmental clutter. We recorded synchronized audio and threedimensional infrared (3D IR) video to capture the dynamic echolocation calls and head movements of bats trained to track a moving target from a perched position in the dark. We hypothesized that bats would coordinate adjustments in sonar call features and head movements to separate echoes from targets and clutter. We therefore predicted that bats would shorten echolocation call duration, interval, and spectral content, while increasing head movements when targets are in close proximity to clutter.

II. METHODS

A. Study subjects

Six wild-caught, adult big brown bats (*Eptesicus fuscus*) served as subjects in the study. Five females (15BA, 68A7, 63E4, 11B5, and 6C1A) and one male (FD8F) were collected in the state of Maryland under a permit issued by the Department of Natural Resources (Permit No. 55440). Bats were housed together in three sets of cages in a colony room with controlled temperature (21°C–26°C) and humidity (30%–70%). Animal care and experimental procedures were approved by the Johns Hopkins Animal Use and Care Committee (Protocol No. BA23A45). Bats had unlimited access to water, but food was limited to the rewards offered during the experiment to reinforce target tracking from the perch. Bats were fed using live mealworms fortified with vitamins. The body weight of bats was closely monitored in accordance with established guidelines.

B. Training and environment

Experiments were conducted in a 5.25 m \times 2.9 m carpeted room; the walls and ceiling were lined with acoustic foam (Sonex1; Pinta Acoustic, Minneapolis, MN). The bats were trained to perch on a platform and track an approaching tethered target under red light (>650 nm) illumination to limit the availability of visual cues.³¹ Target motion was controlled by a pulley system driven by an BMS60 servo motor and Ensemble ML motor controller (Aerotech, Inc., Pittsburgh, PA) and custom code in MATLAB (Mathworks, Inc., Natick, MA).The motor was placed outside the anechoic room to reduce motor noise in the room (Fig. 1).

The training began with a tethered mealworm (target) approaching the bat via the pulley system at a close distance. The experimenter listened to the bat's sonar calls through a bat detector, Pettersson D10 (Pettersson Elektronik AB, Uppsala, Sweden), and rewarded the bat for increasing call rate with decreasing target distance. The experimenter used click training to reinforce the bat's successful sonar tracking, marked by high call rates at short target distances. As the bats learned to track the target, the distance between the bat and the target and the velocity of the target gradually



FIG. 1. Experimental apparatus. The bat was placed on a platform and tracks a tethered target controlled via a servo motor outside of an anechoic room. Vocalizations were recorded with a microphone mounted on the far wall (sonar call microphone), and the return echoes were recorded via a microphone mounted under the platform (echo microphone). Both microphones sampled at 250 kHz. Simultaneously, we recorded the bat's head movements and target location via four infrared (IR) cameras. The audio and video systems were synchronized using an external, manual trigger.

increased. The training concluded when the bat consistently tracked the target from a 3.0 m distance from the platform at a speed of 0.75 ms^{-1} . Each bat required 4–5 weeks of training.

C. Experimental design

Our study comprised five experimental conditions: four distinct combinations of clutter distance and angular offsets (labeled as clutter condictions C1, C2, C3, and C4) and a baseline condition with no clutter. The four clutter conditions were created by placing a pair of steel poles, referred to as distractors, at two different distances and symmetric angular offsets (C1, 45 cm away at $\pm 10^{\circ}$ angular offsets; C2, 45 cm away at $\pm 20^{\circ}$ angular offset; C3, 70 cm away at $\pm 10^{\circ}$ angular offsets; C4, 70 cm away at $\pm 20^{\circ}$ angular offset), as shown in Fig. 2(A). These conditions were selected to allow comparisons with prior studies of target tracking by big brown bats.^{14,25} The distractor poles were 2.5 cm in diameter, extended approximately 15 cm above the mealworm trajectory path, and were covered in black felt cloth on the top 30 cm to reduce interference with the IR video camera recordings. Source strength profiles of the poles and target can be seen in Figs. S1 and S2 in the supplementary material. Under all conditions, the bat tracked a tethered target that approached at a constant velocity of $0.75 \,\mathrm{ms}^{-1}$ [Fig. 2(B)].

Each experimental session comprised one of the four clutter condition and baseline (no clutter) trials. We adopted an "ABBA" design, where "A" and "B," respectively, represent the clutter and baseline conditions [Fig. 2(C)]; this design controlled for possible changes in the bat's performance over each session. Each session consisted of 25–35 trials. Catch trials were introduced every four to seven trials, in which the motor was operated but the tether did not carry a tethered mealworm. Catch trials controlled for the effects of motor noise and ensured the bat was actively tracking the target. The baseline trials on each session monitored session-to-session variations in the bat's behavior and established reference points for clutter condition comparisons.





D. Recording apparatus

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1. Video recording

We recorded bat head movements, target motion trajectory, and clutter pole locations using an arrangement of four Vicon Vantage V5 cameras (Vicon Motion Systems, Ltd., Oxford, UK), sampling at 100 frames per second (FPS), which tracked IR reflective markers on the clutter poles, the tethered target, and the bat's head, as shown in Fig. 3(A). The markers were used to reconstruct the target motion, the target distance from the clutter, and the bat head motion over time. Marker data recorded by the cameras were reconstructed as 3D trajectories using the Vicon NEXUS v2.1 software. The 3D reconstructions from the Vicon NEXUS software (Vicon Motion Systems, Ltd., Oxford, UK) were then converted to data structures in MATLAB with custom code.

2. Video processing

Using custom code, we calculated the target motion with respect to the bat and the bat's yaw head angle (α_{yaw}) in each trial from the marker data structures. Code is provided for calculating the absolute head angles, but our focus was on relative changes in head angle over a trial instead of

FIG. 2. Experimental design. (A) Overhead schematic of distractor placement. Two metal poles were placed at different distances and angular offsets from the bat perch. Only one clutter condition (two metal poles) was used per experimental day. (B) The tethered mealworm traveled directly towards the platform while the bat was tracking. The motion profile of the tether has the tether move 3 m with a velocity of 0.75 ms⁻¹ and an acceleration of 1.6 ms⁻². (C) Experimental schedule for two consecutive experimental days. On the first day, the experiment started with the baseline block (no distractors present). Each block consisted of five to eight regular trials plus one to two catch trials. On the second day, the experiment started with a clutter block (with distractors). C# refers to the clutter condition (i.e., C1, C2, C3, or C4) used for that experiment day.

absolute angle. For each trial, the change in yaw angle over time was calculated. The instantaneous angular velocity at each time point was calculated using finite differencing. For individual bats, the yaw rotational motions in each trial were aggregated by trial type. We also combined all individual bat data for trial type comparison across all bats. We analyzed differences in yaw angular velocities of each trial condition by comparing the root-mean-square (rms) motion across trial type.

3. Audio recording

Echolocation calls were captured using two custom ultrasound microphones, NEUmics (Ultra Sound Advice, London, UK), with 100% gain at 50 kHz. The NEUmic microphones have a flat frequency response in the spectral -4dB-4dB of 20 kHz-100 kHz, which is well suited to record big brown bat echolocation calls.⁵ The audio data were acquired at a 250 kHz sampling rate (PCIe-6353 board; National Instruments, Inc., Austin, TX). The first microphone's data were filtered with a Kemo VBF44 filter (Kemo, Ltd., Thetford, UK) that implemented a bandpass filter between 10 kHz and 125 kHz with 0 dB input-output gain. The second microphone's data were filtered with a Stanford Research Systems SR650 filter (Stanford Research



The 4-point, lightweight (<0.2 g) marker structure was glued onto the bat's head with water-soluble glue. (B) Using the marker structure, we calculated real time yaw of bat head movement. Yaw is the rotation about the bats coronal plane (*z* axis). In past publications yaw rotations were referred to as head turns (Ref. 25).

FIG. 3. Bat head movement angle. (A)

https://doi.org/10.1121/10.0036252

Systems, Inc, Sunnyvale, CA) that implemented bandpass filter between 10 kHz and 100 kHz with 0 dB input-output gain. Custom MATLAB code was used to extract the temporal and spectral features of echolocation calls recorded in each given trial.

4. Audio processing

We first identified the start and end of each echolocation call using the custom MATLAB script. This script creates envelopes around sonar signals and loops through each detected enveloped call in a given trial to obtain the start and stop times. Once we determined the start and stop times of each call, the durations and intervals were calculated as follows. For a given sonar call, *N*, we define

Call duration: $CD_N = end_N - start_N$,

Call interval: $CI_N = start_{N+1} - start_N$,

where start_N and end_N refer to the start and end times, respectively, of the *N*th call. Call start and end times were determined by finding the first time point where the call envelope magnitude crossed 3% of the envelope amplitude on the rising (start) and falling (end) edges, respectively. For each bat, sonar call durations and intervals of individual trials were aggregated by trial type. We subsequently combined all individual bat data for trial type comparison across all bats.

Sonar call intervals were also used to calculate sonar strobe groups (SSGs), which are often produced by bats operating in clutter.³² SSGs are groupings of echolocation calls with stable call intervals, surrounded by calls produced at longer intervals, defined as 1.2 times the call interval within the SSG. SSGs can occur in doublets, triplets, or groupings of higher numbers, although doublets and triplets are the most common. A set of echolocation calls was classified as an SSG if it met the following set of criteria (Fig. 4):

Island criterion:

Doublet: $CI_{N-1} \ge 1.2CI_N$ and $1.2CI_N \le C_{N+1}$.

Triplet and above: $CI_{N-1} \ge 1.2\mu$ and $1.2\mu \le CI_{N+k}$;

$$\mu = \frac{\operatorname{CI}_N + \dots + \operatorname{CI}_{N+(k-1)}}{k}.$$

Stability criterion:

Triplet and above: $\left|\frac{\mu - \operatorname{CI}_N}{\mu}\right|, \left|\frac{\mu - \operatorname{CI}_{N+1}}{\mu}\right|, ..., \left|\frac{\mu - \operatorname{CI}_{N+(k-1)}}{\mu}\right| \le T,$ T = 0.05 (tolerance).

SSG occurrences were aggregated by trial. We subsequently combined all individual bat data for trial type comparison across all bats. Since the occurrences of SSGs within a given trial were an order of magnitude less than the total



FIG. 4. Illustration of sonar strobe group (SSG) categorization. The island criterion, which determined if a set of calls have smaller internal call intervals than the calls directly before and after the set, was used for determining doublets and SSGs of higher order. The stability criterion, which determines if the internal call intervals of the set are of similar length, was used for determining triplets and SSGs of higher order.

occurrences of calls, we increased our time bins to be 350 ms or 26 cm in width for these analyses.

In addition to the temporal properties of the calls, we analyzed the spectral properties of the bat sonar calls. We used custom MATLAB code to calculate the power spectral density (PSD) of each call within each trial and collated the call PSDs by trial type. PSDs were calculated using the "pspectrum" function in MATLAB, with a frequency resolution of 3 kHz, a leakage of 0.85, and frequency limits of 0 kHz-120 kHz. We also used custom code to analyze the spectral properties of the call fundamental, including start and end frequencies and bandwidth of the FM sweep. This code generates sharpened spectrograms using timefrequency reassignment to identify the three spectral ridges (the fundamental, first harmonic, and second harmonic) in a given FM call and extracts the frequency content of each ridge. Ridges are generated using "pspectrum" in MATLAB with a frequency resolution of 3 kHz, leakage of 0.85, window overlap of 99%, frequency limits of 0kHz-120kHz, and the "Reassign" flag set to "true." For each bat, the spectral properties of the fundamental of each call across individual trials were aggregated by trial type. We subsequently combined all individual bat data for trial type comparison across all bats.

E. Testing room ensonification

To measure the reflective strength of our mealworm target and our clutter poles, we generated frequency sweep pulses (10 kHz–120 kHz in 2 ms) using a function generator (model DS345; Stanford Research Systems, Inc., Sunnyvale, CA) that was connected to an ultrasound amplifier (model S55; Ultra Sound Advice, London, UK). The amplified FM sweeps were broadcast from a custom-built ultrasonic speaker mounted in the same location of the bat



on the platform and echoes were recorded from the microphone mounted under the platform [see Fig. S1(A) in the supplementary material]. Sound power was chosen to have similar amplitude to average bat echolocation call.

We measured the reflective strength of objects during tracking by generating pulses when just the target was present [Fig. S1(B)], just the clutter poles were present [Fig. S1(C)], and when the target was 10 cm behind the clutter poles [Fig. S1(D)]. As can be seen in Fig. S1, the reflective strength of the poles was >12 dB stronger than the mealworm target. There was a weak, delayed echo, which was likely sound reflecting from the back wall of the room. We measured the strength of the clutter pole echoes and target at all clutter locations (Fig. S2) which verified the clutter reflective strength was 20 dB–24 dB stronger than the target reflective strength at all pole locations.

F. Statistical analysis

All the statistical analysis was performed using custom codes written in MATLAB R2024a (MathWorks, Natick, MA). Two types of statistical tests were performed in this study. We performed two-way analyses of variance (ANOVAs) with task type and subject as the two factors (MATLAB "anova" function) for call parameter comparisons between baseline and all other conditions. We also performed post hoc multiple pairwise comparisons of group means using Dunnett's test for call parameter comparisons between individual task types via MATLAB's "multcompare" function. Cohen's d effect size values are reported for each statistical comparison. The significance level was set to 0.05 for all statistical tests. The experimental data are provided as mean \pm the standard error of the mean $(\mu \pm \text{s.e.m.})$. The statistical tests used for each analysis are noted when the relevant statistic is provided. F and p values are reported for ANOVAs, and p values are reported for Dunnett's tests.

III. RESULTS

A. Bats produce shorter calls at a higher rate in cluttered environments

The modulation of call duration and call rate/interval is important for bats to obtain precise information about target location, by avoiding overlap between sonar calls and echoes and ensuring accurate call-echo assignment. Bats decreased call duration and call interval as the target approached under all conditions (Fig. 5), as expected from Refs. 14 and 25. Under cluttered conditions, bats decreased call duration by as much as $\approx 25\%$ compared to the baseline condition when the target was greater than 70 cm away $[F(4, 30021) = 1590.1, p < 1 \times 10^{-5}, d = 0.76;$ Fig. 5(A)]. Bats produced calls with shorter duration when the clutter was at 45 cm compared with 70 cm away (up to $\approx 10\%$ difference, $p < 1 \times 10^{-5}$, d = 0.21).). There was no statistical difference in call duration between the C1 and C2 conditions where poles were 45 cm away and 10° and 20° radially offset, respectively (p = 0.145, d = 0.046). There was a small but statistically significant difference in call duration between the C3 and C4 conditions, where poles were 70 cm away and 10° and 20° radially offset, respectively (p = 0.008, d = 0.08). These data indicate that the clutter pole distance had a larger effect on call duration than the angular offset, but that both distance and angle affected sonar call design. Bats initiated a high call rate sonar buzz when the target was less than 50 cm away under all conditions. At this target distance, call duration under clutter conditions was slightly greater than under the baseline condition, but with large individual variability.

Call interval, like call duration, decreased in the presence of clutter [Fig. 5(B)]. When the target was greater than 1 m away from the bat, call intervals under all clutter conditions were shorter by as much as \approx 50% compared with baseline [F(4, 29 342) = 93.8, $p < 1 \times 10^{-5}$, d = 0.21], but when the target was further than 1 m from the bat, call intervals under the clutter conditions were similar to those



FIG. 5. Sonar call duration and call interval. (A) Call durations for all bats across trial types. All clutter conditions had significantly different call durations than baseline. C1 and C2 had call durations that were less than those of C3 and C4 until the tether reached 45 cm from the bat (blue dashed line), after which call durations of C3 and C4 were less than those of C1 and C2. (B) Call intervals for all bats across trial type. For all clutter conditions, there was a significant difference in the call interval when compared to baseline. There was a very small but statistically significant call interval difference between the four clutter conditions.

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FIG. 6. Sonar strobe groups (SSGs) for all bats across all trial types. The production of SSGs under the baseline condition was lower than under all four clutter conditions until the target was less than 77 cm from the bat.

under the baseline condition. Unlike the substantial changes in call duration across conditions, there was a negligible, but statistically significant, difference in call interval between all clutter conditions ($p < 1 \times 10^{-5}$, d = 0.03 - 0.08). This means there was little effect of clutter distance or radial offset on call interval, which is instead globally impacted by the presence of clutter. The reduction in call duration and call interval in the presence of clutter serves to minimize call-echo overlap.

B. Bats increase SSG production in cluttered environments

The temporal clustering of sonar calls (SSGs) by freeflying bats has been shown to be particularly pronounced in clutter.³² Here, in perched bats, we found that the number of SSGs produced by a bat tracking a target increased in the presence of clutter and increased in baseline trials as the target approached the bat (Fig. 6). SSG production was less frequent in the baseline condition than all clutter conditions when the target was greater than ≈ 1 m from the bat $[F(4, 11717) = 113.06, p < 1 \times 10^{-5}, d = 0.38],$ for all bats except 11B5 and 68A7 (see Fig. S3 in the supplementary material). When the target was less than 1 m from the bat, there was a dramatic increase in SSG production under the baseline condition. Interestingly, for all bats except FD8F and 6A87 (Fig. S3) the production of SSGs under the baseline condition decreased when the target was within 25 cm of the bat. Notably, the overall increase in SSG production under the cluttered conditions compared to baseline is consistent with findings from previous work showing that free-flying big brown bats increase SSG production when tracking prey in the presence of clutter.^{8,25}

C. Bats decrease call power and lower FM sweep frequency in clutter

As bats tracked the moving prey item, their FM sonar calls typically spanned 20 kHz–120 kHz, with the call fundamental ranging from 20 kHz to 60 kHz. Figure 7(A) shows example spectrograms of calls produced by a bat tracking the moving target, with an enlargement on one call (red dashed box). We found that bats changed the spectral features of their calls when tracking in clutter and as the target distance decreased (Figs. 7 and 8). For all but two bats, 63E4 and 6A87 (see Fig. S4 in the supplementary material), there was more power in the first harmonic of the sonar call than in the fundamental.

Bats lowered overall call power (up to ≈ 10 dB) when tracking under the cluttered conditions throughout the target



FIG. 7. Call power spectral densities (PSDs). (A) Example echolocation calls produced by a bat tracking a target. The popout shows an enlarged version of the call boxed in the red dashed line. (B)–(E) The average PSD, with standard error of mean, of the echolocation calls within a certain time bin is shown for each trial condition. (B) Average PSDs of calls when target was between 1 m and 3 m away from the bat (which was before any clutter pole location). (C) Average PSDs of calls when the target was within 10 cm of the location of the C1/C2 distractor poles (45 cm). (D) Average PSDs of calls when the target was within 10 cm of the location of the C3/C4 distractor poles (70 cm). (E) Average PSDs of calls when the target was within 25 cm of the bat's location (which was after any clutter pole location).





FIG. 8. Sonar call fundamental frequencies. (A) Sonar call start frequencies for all bats across all trial types. All clutter conditions had significantly different start frequencies than baseline. C1 and C2 had start frequencies that are less than those of C3 and C4 when the target was greater than 45 cm away from the bat. (B) Call end frequencies compared across clutter conditions. End frequencies of cluttered conditions were less than those of baseline when the target was greater than 60 cm from the bat. (C) Frequency bandwidth of calls compared across clutter conditions. The call bandwidth under the cluttered conditions was lower than the bandwidth under the baseline condition when the target was greater than 45 cm away from the bat.

trajectory [Figs. 7(B)–7(E)]. We also found that the change in call power was dependent upon clutter distance and radial offset. Call power was lower when the clutter poles were closer to the bat (C1 and C2 poles at 45 cm) than when the poles were further away (C3 and C4 poles at 70 cm). For the conditions where the poles were 45 cm away, call power was lower when the poles were at a smaller radial offset (C1, 10°) than a larger radial offset (C2, 20°). Radial offset did not seem to have an impact on call power when the poles were at 70 cm away.

To further investigate sonar call power changes across target distance, the PSD of the echolocation calls was analyzed over four different time bins: when the target was 1 m-3 maway from the bat (far removed from clutter) [Fig. 7(B)], when the target was 10 cm within of the C1/C2 pole location (45 cm from bat) [Fig. 7(C)], when the target was 10 cm within of the C3/C4 pole location (70 cm from bat) [Fig. 7(D)], and when the target was within 25 cm from the bat [Fig. 7(E)].

The greatest difference in call power between baseline and the clutter conditions, ≈ 5 dB appeared in the early stages of tracking [Fig. 7(A)]. The smallest difference, ≈ 1.5 dB difference between call power under baseline and clutter conditions, appeared when the target was close to the bat, when the clutter poles were behind the target [Fig. 7(D)]. Overall, call power under the baseline condition tended to decrease throughout the target trajectory compared with cluttered conditions. It is noteworthy that call power was greatest during tracking under the clutter conditions when the target was within 10 cm of the clutter [Figs. 7(C) and 7(D)]. This indicates the bats increased call power when there was typically echo-echo overlap between the distractor poles and the target.

We also found that bats modulated sonar FM sweep start frequency, end frequency, and bandwidth in the presence of clutter (Fig. 8). Before the target was within \approx 70 cm of the bat, the start and end frequencies of calls in cluttered conditions were lower ([$F(4, 30021) = 1031.3, p < 1 \times 10^{-5}$, d = 0.53 and F(4, 30021) = 608.2, $p < 1 \times 10^{-5}$, d = 0.57, respectively) than those under the baseline condition [Figs. 8(A) and 8(B)]. The fundamental start frequency was slightly lower when the clutter was closer to the bat at 45 cm, under C1 and C2 conditions, compared with 70 cm, under C3 and C4 conditions $(p < 1 \times 10^{-5}, d = 0.23)$. However, there was only modest but statistically significant difference in start sweep frequency when the clutter was at the two different radial offsets at the two clutter distances $\times 10^{-5}, d = 0.12)$ 45 cm (p < 1)and 70cm $(p < 1 \times 10^{-5}, d = 0.10)$. Clutter distance showed a small but statistically significant effect on sonar call end frequency $(p < 1 \times 10^{-5}, d = 0.13)$ and an even smaller effect of radial offsets on end frequency ($p < 1 \times 10^{-5}, d = 0.02$ for C1 vs C2 and $p < 1 \times 10^{-5}$, d = 0.12 for C3 vs C4). These data indicate that the clutter pole distance had a larger effect on sonar call start and end frequencies than the angular offset.

Call start frequency remained relatively stable as the target approached the bat, until the target was less than ≈ 60 cm from the bat, but call end frequency decreased as the target approached the bat, consistent with previous findings.¹⁴ The difference in modulation between start and end frequencies over the course of tracking led to call bandwidth increases as the target approached the bat [Fig. 8(C)]. Surprisingly, call bandwidth was lower in clutter trials than in baseline, which mirrors findings of previous work,²⁵ but is counter to other research reports.²⁷ Notably, call bandwidth was lower when the clutter poles were closer to the bat. The impact of pole angular offset on sonar call bandwidth was highly variable across individual bats.

D. Bats increase overall head movements when tracking targets near clutter

It has been shown that bats turn their heads and shift the position of their ears as they echolocate.¹⁷ To understand



the impact of clutter on head/ear movement during prey tracking, we compared head velocity measurements of animals tracking targets under clutter and baseline conditions. To specifically explore the impact of clutter on head/ear movement, we focused on the portion of tracking when the target was within 10 cm of the clutter pole locations (60 cm–80 cm from the bat for C3/C4 and 35 cm–55 cm from the bat for C1/C2). Head movements under clutter conditions were directly compared to those in baseline conditions over comparable target distance bins (Fig. 9).

We hypothesized that bats would show an increase in head movements when the target was close to clutter. We found that, in general, the presence of clutter produced an increase in average yaw velocity. More specifically, the aggregated bat data showed an increase in head movement for all clutter conditions [Fig. 9(A)] in most individuals; a larger sample of animals may be needed to definitively conclude that head movements increase during target tracking in clutter. Bat 68A7 was one individual that did not increase head movement under any condition [Fig. 9(C)]. Individual bats also showed variability in head movements when the target was far removed from clutter (3 m-1 m and from the bat) (see Fig. S6 in the supplementary material). Each bat showed distinct patterns of head movement when the target was far from the clutter, revealing individual strategies for target tracking.

IV. DISCUSSION

Past research has quantified adaptive changes in sonar call design^{27,32} and flight patterns³³ of echolocating bats operating in clutter. While these studies offer key data on adaptive echolocation behavior and flight path selection in natural contexts, they do not capture the full suite of actions bats employ to successfully track prey, namely the

movement of head and ears. This study leveraged a behavioral paradigm that permitted detailed quantitative analyses of sonar call and head/pinna movements of big brown bats (*Eptesicus fuscus*) tracking a moving target in the presence of clutter. Our analysis of the spectral and temporal modulations of calls and head/ear movements reveals strategies bats employ to mitigate interference from clutter echoes.

A. Effect of clutter on call interval and duration

Our study yielded quantitative data on echolocation call dynamics in response to environmental clutter, addressing open questions raised by prior research.^{14,25} We show that bats consistently reduced both call duration and interval as targets traveled past stationary clutter objects. Previous studies demonstrate that a reduction in call duration may enhance target localization accuracy and minimize interference from clutter echoes.^{14,19}

Bats consistently decreased call interval under the cluttered conditions compared to baseline. Researchers have posited that a decrease in sonar call interval aids target tracking in clutter, by yielding more echoes per unit of time to localize sonar objects.^{25,34} We did not observe an effect of clutter angular offset or distance on call interval, as reported in previous studies that tested only two individual bats.^{14,25} Among the six individuals we tested, there was substantial variability in call interval and duration across the two clutter distances and radial offsets tested. The present experiments tested a more limited range of radial offsets than the Mao and Aytekin studies,^{14,25} and therefore, it is possible that larger radial offsets would haves revealed changes in call interval.

Sonar call duration was shorter in the presence of clutter and exhibited a less rapid decrease with target approach under cluttered conditions compared to baseline. Notably,



FIG. 9. Head angle velocity near clutter. (A) The rms yaw angle velocities across clutter conditions for all bats aggregated together. Yaw angular velocity was greater on average when tracking the target near the clutter pole locations when clutter was present (conditions C1–C4) than when there was no clutter present for the aggregated bat data. (B) rms yaw angle velocities for an example individual. All individuals except bat 68A7 followed the same trend as the aggregate, with clutter having an impact on head movement and head movement increasing generally when clutter is present. (C) The rms yaw angle velocities for bat 68A7, which did not follow the aggregate trend. Bat 68A7 seems to decrease yaw velocity under one clutter condition (C3), and other clutter conditions have nonsignificant impact on head movement.

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call duration was consistently affected by the distance of the distractor poles, a finding consistent with a previous report.²⁵ Shorter call duration improves sonar separation of the pole and target echoes by the big brown bat; however, the bats likely experience a merging of echoes from the two objects when they are a few centimeters apart. For single target echoes, big brown bats can discriminate differences in distance on the order of 1 cm or 50 μ s-60 μ s echo delay.³⁵ When big brown bats encounter echoes from closely spaced objects that return overlapping echoes, they exhibit an integration time of 200 μ s-400 μ s.³⁶ Echoes from two surfaces of a range-extended object, offset by 100 μ s, are represented as separate components of a single target. Psychophysical experiments show that the big brown bat converts the spectral interference pattern created by echoes offset by 100 μ s into a spatiotemporal display of the close and far edges of an object.³⁷

B. Effect of clutter on call temporal patterning

The present study demonstrates that big brown bats modulate SSG production during target tracking in cluttered environments. As the target approached, the bat increased production of SSGs across all conditions, likely to enhance spatial resolution.^{32,38,39} The bat's increase in SSG production when tracking a target under cluttered conditions aligns with prior findings.^{8,9,25} Increasing SSG production under cluttered conditions has been posited to enhance target localization in noisy and cluttered environments.

There was no significant effect of angular offset or distance on SSG production overall. Some bats produced fewer SSGs when the clutter poles were closer, while others produced fewer SSGs when clutter poles were further away (see Fig. S3 in the supplementary material). This variability underscores individual differences in echolocation strategies to mitigate clutter interference. In addition to individual variation, there is also cross-species variation in response to clutter. For example, the greater mouse-eared bat accomplishes clutter rejection without changing call source level, interval, or duration when operating close to background.⁴⁰

C. Effect of clutter on sonar call power and frequency

Our data show that bats reduced echolocation call amplitude by up to 10 dB in the presence of clutter. Previous studies in other insectivorous bat species have shown that lowering call power and shifting more power to higher frequencies may facilitate prey localization in background noise.⁴¹ Bats likely substantially lowered call power when the poles were closer as echoes from the closer poles would be stronger than those from the farther poles due to spreading loss. This may also explain why a lower angular offset did not impact the bat's modulation of call strength at far distance but did cause the bat to lower the call strength at close distance. When clutter is closer to the bats, they may need to further reduce the call volume for target discrimination. Additionally, all but two of the bats (see Fig. S4 in the supplementary material) shifted more power to the first harmonic of their calls than the fundamental, thereby creating more powerful high-frequency calls. Since higher-frequency emissions have weaker side lobes than those of lower-frequency emissions, the bats may put more power into the higher frequencies to blur echoes from the off-axis clutter.⁴² Higher-frequency emissions have weaker side lobes than those of lower-frequency emissions, so directing more power into the higher frequencies may enable the bat to blur echoes from off-axis clutter.⁴² In our study, however, the power difference between the fundamental and harmonic frequencies may not have been substantial enough to create a strong echo-blurring effect.

Echolocation call spectral adjustments also affect the directionality and strength of echo returns.^{20,42,43} In the present study, bats adjusted the FM sweep spectrum with respect to target distance and clutter. Across all conditions, the start frequency of the call fundamental remained relatively stable until the buzz phase of tracking, when it rapidly decreased. This allowed the bat to maintain high directionality of sonar tracking. The end frequency of the bat sonar calls, however, decreased as the target approached the bat. This mirrors previous reports of bats tracking in clutter.^{14,32} The decrease in sonar call end frequency likely allows bats to keep the target within the bat's "field of view" throughout its trajectory. These substantial decreases in frequency across the FM sweep when the target approaches the bat may partly result from biomechanical constraints, which prevent the bat from producing higher-frequency sounds when making more rapid calls during the terminal buzz phase.

When bats fly in dense clutter, each call returns a cascade of echoes, and the echoes from successive calls can be intermingled, creating ambiguity in call-echo assignment. Previous work has reported that bats overcome call-echo assignment ambiguity by alternating the spectral profile between successive sonar calls as they navigate in clutter.⁴⁴ This study showed that big brown bats can use even small frequency shifts (3 kHz-6 kHz) to distinguish echoes from successive calls. In the present study, clutter was limited to single distractor poles, which evoked shifts in the start and end frequencies of the bat's echolocation calls. The FM sweep frequencies were lower in the presence of clutter compared with baseline conditions. Bats further lowered sweep frequencies when the poles were closer to the bat than when the poles were a greater distance. Comparable to the report by Hiryu et al.,⁴⁴ shifts in sonar call frequency from baseline to cluttered conditions were only ≈ 2 kHz-6kHz. This suggests that FM bats can make use of small shifts in sonar call frequency to obtain a rich representation of the environment. Our findings that bats reduced sonar call frequency under cluttered conditions suggest that they make use of the wider sonar beam of lower sound frequencies to keep track of the clutter with respect to the target. Individual subject variation in call frequency adjustments under clutter conditions suggest differences in clutter tracking strategies among bats (see Fig. S5 in the supplementary material).



Sonar call bandwidth also decreased with clutter, which mirrors findings of previous work.^{25,40} The drop in bandwidth arises from unequal reductions in call start and end frequencies in the presence of the clutter poles. This counters an earlier report that higher sonar call bandwidth enhances target clutter discrimination.²⁷ That report comes from a cross-species comparison of static prey capture against a cluttered background, whereas the present study analyzed dynamic adjustments in sonar calls produced by bats tracking a moving target that traveled past clutter. The bat's adjustments to echolocation call bandwidth in the present study underscores its ability to dynamically modulate echo streams to navigate and forage efficiently under varying environmental challenges.

D. Effect of clutter on head movement

Head movements allow the bat to scan the environment and sample echoes from the clutter and target from different directions. It is worth emphasizing that head movements affect both the sonar beam direction with respect to the target and distractors and the acoustic information arriving at the bat's two ears, which process echo features to localize sonar objects in distance and direction.^{9,10,30,45} Since the ears are anchored to the bat's head, head rotational movements give rise to interaural difference cues.^{17,29,46,47}

Taking advantage of the perched bat engaged in target tracking allowed us to carefully measure head movements when the target was close to clutter. Specifically, we measured yaw head movements (i.e., head turns) in relation to cluttered environments and discovered that bats mitigate clutter interference.

We hypothesized that bats coordinate adjustments in sonar call features and head movements. However, the data showed no significant synchronization between head movements and call production.

Mao *et al.*²⁵ measured head movements indirectly by analyzing the relative amplitude of echolocation signals picked up by microphones positioned to the left and right of the bat. In contrast, the present study used high-speed video recordings to precisely track head/ear movements as the bat tracked the target under cluttered and uncluttered conditions. The video recording system permitted close analysis of head/ear movement at different stages of tracking, such as when the target was near clutter poles or when the target was far away from clutter poles.

Consistent with Mao *et al.*,²⁵ data from the present study show that bats increased head movements in the presence of distractors. Further, bats increase head velocity when tracking a target near clutter poles in comparison to tracking at the same target distance in baseline conditions with no clutter (Fig. 9). There was no significant effect of clutter distance or angular offset on head movement. Individual bats showed some variability in head movement patterns across conditions when tracking a target far away from clutter poles (see Fig. S6 in the supplementary material). Psychophysical experiments have demonstrated that the harmonic structure of big brown bat FM calls facilitates localization of on-axis target echoes and blurs off-axis clutter echoes.⁴² When the target is near clutter, bats may move their heads to find the head direction that maximizes target localization while minimizing interference of the pole echoes on target localization. It may be that bats move their head more when the target is close to clutter due to increased uncertainty caused by clutter interference, as has been reported in other species.⁴⁸ While we did not causally test if the bat's head motions are an adaptation to maximize localization, we observed that the movements are a consistent response to clutter interference.

E. Adjustments in clutter are part of closed-loop active sensing

Echolocation is a form of active sensing used by many species of bats to collect discrete acoustic snapshots of the environment,⁴⁹ in contrast to the continuous stimulus sampling available through vision. Like many biological systems, echolocation signal design is tied to the task at hand, which in this study was to track and intercept the tethered insect^{3,50–54} Echolocation operates in a closed-loop manner: Sonar calls return echoes, which give the bat sensory information about the environment, which in turn guides vocalmotor adjustments, and the loop continues until they capture their prey. For example, we see that as the target approaches the bat at each new "sample," the bats lowered the call duration, interval, and FM sweep frequencies to gain new pieces of information about the target and environment.

Along with rapid adjustments to call design with respect to the location of a selected object, bats can also make global adjustments to call parameters that facilitate sonar representation in a given environment. For example, the presence of clutter poles in the present study elicited global sonar call adjustments to duration, interval, and spectral profile of FM sweeps. These findings offer insight into a taskoriented active sensing mechanism by showcasing bats' use of momentary and general echolocation adjustments for prey capture in cluttered environments.

V. CONCLUSIONS

Echolocation employs a sensorimotor feedback system that depends on the coordination of movement and echo processing. Adjustments in the bat's vocal-motor control of sonar calls directly affect the features of echo returns, and head/ear movements shape the cues the bat uses to represent objects in the environment.

This study reports on the dynamic adjustments of head movements and sonar call parameters produced by bats tracking targets in clutter. Notably, video-based kinematic analyses revealed that bats increase their head movements when tracking targets near clutter.

The array of adjustments to echolocation behavior in this study underline the sophistication of this as goal-based active sensing mechanism. Future studies could explore the



neural mechanisms underlying these adaptive behaviors. This work provides new insights into the importance of both head/ear movements and sonar call modifications as interference mitigation strategies during predation in cluttered environments.

SUPPLEMENTARY MATERIAL

See the supplementary material for further information on target and clutter source strength profiles, dynamics of outlier individuals and inter-individual variability for a subset of sonar call properties, and examples of head movement in pre-clutter tracking.

ACKNOWLEDGMENTS

We gratefully acknowledge fellowship support from the Johns Hopkins Kavli Neuroscience Discovery Institute to M.G.T.W. This research was supported by the following research grants: National Institutes of Health (NIH) Grant No. R01 NS121413, Human Frontiers Science Program Research Grant No. RGP0045/2022, National Science Foundation (NSF) Brain Initiative Grant No. NCS-FO 1734744, NSF CRCNS Grant No. 2011619, and Office of Naval Research Grant Nos. N00014-23-1-2086 and N00014-17-1-2736 to C.F.M.

AUTHOR DECLARATIONS Conflict of Interest

The authors have no conflicts to disclose.

DATA AVAILABILITY

The data that support the findings of this study are openly available in the Johns Hopkins Research Data Repository at https://doi.org/10.7281/T1WF3NZ7. Preprocessed data used to perform the analyses and generate the figures in this manuscript are available in the Johns Hopkins Research Data Repository at https://doi.org/10.7281/T1WF3NZ7. Custom code was written to collect and analyze the datasets used in this study and to generate figures for this manuscript. This codebase is versioned. The codes used to perform the analyses and generate the figures in this manuscript are available in the Johns Hopkins Research Data Repository, at https://doi.org/10.7281/T1WF3NZ7.

Software dependencies:

- Audio Processing: MATLAB 2024a v9.13.
 - Packages: Signal Processing Toolbox v9.1, Curve Fitting Toolbox v3.8.
- Video Processing: MATLAB 2024a v9.13.
 - Packages: Signal Processing Toolbox v9.1, Statistics and Machine Learning Toolbox v12.4, Curve Fitting Toolbox v3.8, Simulink v10.6, Simulink 3D Animation v9.5.

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