Spatial perception and adaptive sonar behavior

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Bat echolocation is a dynamic behavior that allows for real-time adaptations in the timing and spectro-temporal design of sonar signals in response to a particular task and environment. To enable detailed, quantitative analyses of adaptive sonar behavior, echolocation call design was investigated in big brown bats, trained to rest on a stationary platform and track a tethered mealworm that approached from a starting distance of about 170 cm in the presence of a stationary sonar distracter. The distracter was presented at different angular offsets and distances from the bat. The results of this study show that the distance and the angular offset of the distracter influence sonar vocalization parameters of the big brown bat, *Eptesicus fuscus*. Specifically, the bat adjusted its call duration to the closer of two objects, distracter or insect target, and the magnitude of the adjustment depended on the angular offset of the distracter. In contrast, the bat consistently adjusted its call rate to the distance of the insect, even when this target was positioned behind the distracter. The results hold implications for understanding spatial information processing and perception by echolocation.

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I. INTRODUCTION

Echolocating bats emit brief ultrasound pulses and listen to the echoes reflected back from objects in the path of the sound beam.¹ To negotiate a complex environment, an echolocating bat controls the timing, duration, and time-frequency structure of its sonar pulses in response to the echo information it receives.² This control is important to obtain the information sought in a dynamic and noisy environment, which may contain a mixture of target echoes and interfering echoes from obstacles, as well as calls produced by conspecifics.^{2–4} Hence, a bat's sonar signal production patterns can serve to indicate the information the bat has processed from echoes and new information it actively seeks from the environment.

Echolocation pulses vary within and across bat species, and bat sonar signals are adapted to the conditions of the environment in which they forage,² as well as the task at hand. For instance, by condensing the energy of sonar calls to a narrow bandwidth, a bat increases the distance over which returning echoes have sufficient acoustic energy to be detected, thus extending the operating range of its biosonar. Long constant frequency (CF) signal components are well-suited to carry echo information about flying insect prey through Doppler shifts introduced by fluttering wings.⁵ Frequency modulated

(FM) signals are well-suited to localize a target's position in space or to identify object features such as depth, structure, and texture.^{6,7}

Dynamic modulation of sonar pulses during target capture has been reported for many different bat species.^{1,8} As a bat approaches a target, its sonar pulse emissions become increasingly more frequent.^{9–12} The increase in vocalization rate suggests the bat's need to increase the rate of information flow as it approaches prey. In particular, during the terminal phase of target capture, *Eptesicus fuscus*'s vocalization rate is typically 150 pulses per second.¹³ Bats sometimes alter the distance-pulse rate pattern by using short bursts of pulses with regular intervals, also referred to as sonar strobe groups.⁴ Production of strobe groups is observed in field studies and laboratory experiments when bats must capture prey positioned close to vegetation,^{4,13} suggesting that bats operating in complex acoustic environments may use sonar strobe groups to obtain the information necessary to separate echoes from targets and obstacles.

Bats that use FM sweeps shorten their pulse duration while approaching a target and they appear to do so to avoid overlap between outgoing calls and returning echoes.^{10,11,14} Although long-duration pulses are well-suited to detect echoes from prey at large distances, long pulses result in echoes that overlap in time with outgoing vocalizations for objects at short distances. This overlap could compromise a bat's ability to detect the echoes through forward masking.^{2,7} Similarly, if a target is sufficiently close to clutter, echoes received from both sources may overlap and reduce a bat's ability to detect the target's echo through backward masking. By adjusting

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pulse duration to target and obstacle distances, bats minimize masking effects.^{10,11}

It is important to note, however, that the structure of FM pulses permits time-frequency separation of prey echoes that overlap with echoes from clutter. Echolocating bat species *Myotis nattereri*, and *Eptesicus nilssonii*, both of which use FM signals, can detect prey within the clutter-overlap zone.^{15,16} Simmons *et al.*¹⁷ has shown that *Eptesicus fuscus* can discriminate two echo sources with 2–5 ms duration sonar calls, that overlap up to 92%. Furthermore, Hartley¹⁸ reported that *Eptesicus fuscus* can identify which of two phantom target echoes is louder in the presence of extensive signal overlap.

The spatial relationship of the clutter and the target stimulus also plays a role in the amount of masking a bat experiences. Bats have been shown to prefer approach paths to targets that maintain clutter at an angular offset.⁴ In a recent study Sümer *et al.*¹⁹ showed that, for a stationary target and clutter, backward masking decreased not only with the temporal separation between target and clutter echoes but also with their angular separation. In the same study the authors also reported a decrease in pulse duration with a decrease in clutter-target angular separation.

The present study investigated sonar vocal control by an echolocating FM bat, *Eptesicus fuscus*, as it tracked a moving, tethered prey item from a stationary platform. Here we present a detailed analysis of the sonar vocalization behavior under controlled conditions to investigate how bats adapt their signal parameters in relation to a moving target and a stationary object. The distracter object was placed between the bat and the target at different ranges and angular offsets. This allowed us to observe the influence of the distracter and the target on the bat's sonar vocalization behavior.

We hypothesized that the bat's sonar call duration profile would depend on both the distracter and target distances. We also predicted that the influence of the distracter on sonar behavior would vary with its angular offset from the target motion path.

II. METHODS

A. Animal subjects

Four echolocating bats, *Eptesicus fuscus*, served as subjects: Two males (Bat 45 and Bat 49) and two females (Bat 24 and Bat 39). Bats were maintained at 80% of their *ad lib* weight and normally fed mealworms only during experiments. Animal care and experimental procedures were approved by the University of Maryland Institutional Animal Care and Use Committee.

Complete data sets were obtained from two animals, Bat 45 and Bat 49. Bat 24 and Bat 39 were not able to complete the experiments due to illnesses. Results presented in the study are from the two bats that performed in all conditions. The overall sonar behavior of bats 24 and 39 was similar to that of 45 and 49 for the conditions they performed.

B. Experimental setup

The experiment took place in an echo-attenuating room of dimensions 2.7 m wide, 2.7 m high, and 7.9 m long. The floor was carpeted, and the ceiling and walls were lined with

acoustic foam. To eliminate the bats' reliance on vision, while allowing sufficient visibility for the experimenters to operate, the room was dimly illuminated with long-wavelength lighting (>650 nm). A platform (9 cm by 7 cm) was positioned at equal distances from the side walls and 6.2 m from the most distant wall. The platform was maintained at a height of 1.5 m from the floor to minimize the echoes from the floor and ceiling. A linear motor (STPM-SL-05-80-R, Optimal Engineering Systems Inc.) moving on a 2 m long rail was used to control the distance of a tethered mealworm from the bat's listening position on the platform. The rail was positioned such that it extended along the length of the room at an equal distance from the side walls, directly in front of the platform [Figs. 1(a) and 1(b)]. The distance between the platform and the closest end of the rail was 4 m. The speed, acceleration, and direction of the forcer moving along the rail were controlled by a computer via a stepper motor control system (Allegra-1–10, Optimal Engineering Systems Inc.). The motion of the forcer was relayed to the target, tethered mealworms, via a pulley system [Fig. 1(a)]. The movement of the target was limited to the axis of the rail and within a range of 2 m from the platform. The cable that ran through the pulleys was about 1.8 m high, 30 cm above the platform. Strings were attached between the pulley cable and the tether to reduce swinging of the target caused by sudden changes in velocity during the initial acceleration at the start of each approach and the deceleration before the target's stop.

To minimize the noise generated by the movement of the forcer, the rail was encapsulated in a wooden box, that was padded with ultrasound absorbing foam (Sonex-1) on the internal walls [Fig. 1(a)].

A 1/2 in. thick and 2 m high metal rod was placed at different angular offsets (5° , 10° , 20° , 30° , and 40°) from the target motion axis on the left side of the platform. The influence of the distracter on the bat's sonar pulse parameters was tested at distracter distances of 45 and 70 cm from the platform [Fig. 1(a)].

Two microphones (Ultrasound Advice) were placed on each side of the target motion axis, 2.8 m from the bat. A third microphone (Ultrasound Advice) was placed under the platform and oriented toward the target to record acoustic signals from the bat's listening position. Microphone outputs were amplified (Ultrasound Advice, SM3) and bandpass filtered (Krone-Hite 3550) between 10 and 100 kHz and acquired via an analog-to-digital converted board (National Instruments, PCI-6071E). An infrared-sensitive camera (Sony Handycam) was used to monitor the bat's body orientation and movements on the platform.

The distance of the target from the platform was measured by an optic encoder (USDIGITAL, EM1-0-200) placed on the forcer. A linear transmissive strip (USDIGITAL, LIN-200-0.5-N), placed parallel to the rail, was optically read by the encoder as the forcer moved along the rail. A quadrature signal generated by the encoder was converted to an analog output (USDIGITAL, EDAC2), whose magnitude was linearly related to the position of the target, and acquired simultaneously with the microphone signals.

Computer control of the target movement and synchronized data acquisition was accomplished with custom software written in MATLAB-2007b.

FIG. 1. (a) The experimental setup included a pulley system that carried the target (mealworm), moved by a linear stepper motor housed in a sound-proof box. The distracter object was placed at a given distance from the platform at different angular offsets relative to the target motion axis. Sonar vocalizations were monitored by two microphones on each side of the platform over 2 m distance and by one placed under the platform, (b) Overhead view of the setup showing target motion axis and angular offsets (5° , 10° , 20° , 30° , and 40°) and distances (45 and 70 cm) of the distracter. (c), (d) Target position (c) and velocity (d) with reference to the platform during a standard (solid lines) and a low velocity trial (dashed lines): The desired target speeds were 0.77 and 1.27 m/s for low velocity and standard target approach trials, respectively.

C. Animal training and procedure

The bats were trained to rest on a platform and associate the presentation of a mealworm with a clicking stimulus generated via a pet-training device. The mealworm, tethered to a 30-cm-long fishing line, was attached to the pulley cable and positioned about 5 cm from the platform. Using the linear motor the mealworm was brought to the platform following a click. As the bat learned to attend to a tethered mealworm target, the distance of the target and its approach speed were gradually increased. The training continued until the bats consistently tracked the sonar target approaching from 170 cm at 1.27 m/s. The training period for each bat varied between 2 and 4 weeks.

D. Data collection

A trial started with a clicker stimulus, while the target was positioned 170 cm away from the platform. Using a pre-set

acceleration the target achieved a pre-set speed before coming to a complete stop at the platform. After waiting for 4 s, to allow the bat to grab the mealworm from the tether, the target was moved back to the initial position. Sonar vocal data acquisition started 0.5–1 s before the movement of the target and continued for another 2.5 s. Observational notes on the bat's behavior were entered on the computer following each trial. An infrared camera was also used to record the bat's head orientation in each trial for visual inspection after data collection.

E. Experimental conditions

The experiment included baseline and 10° distracter conditions. All subjects were initially tested in the baseline condition with no distracter at a speed of 1.27 m/s. The distracter conditions included two distracter distances (45 and 70 cm) and five angular offset conditions (5° , 10° , 20° , 30° , and 40°).

Data were collected from each bat for a minimum of 2 days per condition and about 20 trials per day.

Probe trials were randomly interspersed in daily sessions to monitor the bat's vocal behavior under altered or halted target approach. During the no-target and stationary target trials the linear motor moved as usual: The target was not attached to the pulley cable in the no-target trials and remained at its initial position during stationary target trials. Probe trials included the following: Low target velocity (0.77 m/s), target stopped at 25 cm from the platform, no-target, and stationary target. These trials helped maintain the motivation of the bats and also probed the consistency of the animal's tracking behavior.

F. Target motion

Figures 1(c) and 1(d) depict the position and velocity profiles of the target during a standard velocity (solid lines) and a slow velocity trial (dashed lines) with reference to the platform. The target started moving 0.5–1 s after data acquisition began. In a typical trial the velocity and the acceleration were set to 1.27 m/s and 0.5 m/s^2 , respectively. The constant velocity for a standard trial was achieved starting at a target distance of 83.4 cm [Fig. 1(d), solid line]. The target's speed before and after this point changed as linear function of time. The constant velocity range for a slower target motion (0.77 m/s with an acceleration of 0.5 m/s^2) was larger [Fig. 1(d), dashed line]. Constant target speed was achieved during lower target speed probe trials at target distances between 31 and 136 cm.

G. Data analysis

1. Computation of sonar pulse duration

Extraction and analysis of the echolocation pulses was done automatically using custom software written using MATLAB-2007b. Using a simple threshold technique on the signal energy, we identified the times within a given trial's record when sonar pulses were recorded. The pulse durations were then estimated as the time differences between the beginning and end times of the signal envelopes determined by using a second threshold. This threshold was selected as the level 97% below the peak value of the pulse envelope, to avoid inclusion of background noise in call duration measurements.

2. Pulse structure analysis

Harmonic components of the sonar pulse were identified based on a process that involved grouping peaks in the spectrogram image into clusters. A similar algorithm used to identify time-frequency structure of the echolocation pulses was previously reported.²⁰ The peaks that were below threshold were excluded from the analysis. The threshold was determined by the intensity level which corresponded to the 70th percentile of the intensity distribution of the spectrogram and was obtained within a window that started ~ 2 ms before and ended ~ 2 ms after the recorded pulse. Remaining peaks were linked, using heuristics consistent with bat sonar pulse spectrograms, to their local neighbors and labeled as a group. Groups that were harmonically

related and overlapped in time were classified as the fundamental and harmonics, based on their frequency relationship. The estimations of harmonic components were then used to extract fundamental and first harmonic components from the spectrogram of the signal. The extracted spectrogram pieces were later used to estimate the power spectra of harmonic components.

III. RESULTS

A. Sonar pulse duration and pulse interval control

Figures 2(a) and 2(b) plot the time interval between sonar pulses (pulse interval, PI), and the pulse duration, respectively, as a function of target distance in two example trials: One baseline (line with solid circles) and the other from a distracter condition (line with open circles) for Bat 49. The distracter was positioned at 70 cm with a 5° angular offset.

The PI decreased with the target distance in both trials from 75 ms (13 pulses/s) at the starting target distance of 170 cm down to 7 ms (143 pulses/s) at a target distance of 33 cm from the bat. At target distances below 33 cm, the bat's vocalization rate was constant at around 143 Hz. The bat's vocal production rate in this segment of the trial corresponds to that typically observed in the terminal buzz phase of prey capture in flight.^{12,13}

When the distracter was present, the PI pattern followed an overall similar pattern to that observed during the baseline trial. It is noteworthy, however, that the bats alternated between longer and shorter PIs around the average PI as the target moved closer to the bat. The shorter PI calls were clustered in groups of two, hereafter referred to as pulse pairs. The clustering of three or more calls with stable intervals within the approach sequence has been referred to as sonar "strobe groups."⁴ The alternating PI observed in the presence of the distracter is consistent with earlier findings that the presence of obstacles in the environment affects the temporal patterning of a bat's sonar vocalizations.^{4,13,21} We investigated the effect of the distracter on PI in relation to the distracter angle by fitting Markov chain models to the PI changes between subsequent vocalizations. The Markov models consisted of three states: Increase in PI, decrease in PI, and unchanged PI. A change in PI was categorized as an increase in PI if the PI change was larger than half a standard deviation above the average PI, as a function of target distance. Similarly, if PI decreased more than half of the standard deviation it was categorized as decreasing PI. Remaining PI changes were categorized as unchanged.

Table I lists a subset of the state transition probabilities for baseline and (30° , 70 cm) and (10° , 70 cm) distracter conditions. We found that the likelihood of a long PI following a short PI, and vice versa, increased with decreasing distracter angle, whereas long to longer and short to shorter PI changes were less likely. Similarly, the estimated likelihood of PIs remaining unchanged following a long PI were 0.321 (baseline), 0.224 (distracter at 30°), and 0.212 (distracter at 10°) and the likelihood that short PIs to stay short were 0.284 (baseline), 0.167 (distracter at 30°), and 0.087 (distracter at 10°). These results reflect the increased production of sonar pulse pairs with increasing distracter interference. Similar observations on pulse interval patterns were reported

FIG. 2. Sonar pulse intervals (a), (c) and durations (b), (d) from two example trials (a), (b) and from 16 and 12 other trials (c), (d) for baseline and distracter conditions, respectively. The distracter was positioned at 70 cm with 10° offset from the target motion axis. The lines with solid and open circles represent baseline and distracter conditions, respectively. The distracter distance is indicated by a vertical line at 70 cm.

earlier by Petrites *et al.*²¹ in relation to the bat's navigation through dense clutter.

The bat's adaptive changes in sonar pulse duration with target distance were distinctly different between the baseline and the distracter trials [see Fig. 2(b)]. Under baseline conditions, the pulse duration decreased steadily from 3 ms at the

TABLE I. Likelihoods of PI changes for baseline and (30° , 70 cm) and (10° , 70 cm) distracter conditions for Bat 49 for target distances between 70 and 150 cm. The likelihood of long to short and short to long PIs increased with the presence of the distracter and decrease of its angular offset.

	Long to longer	Long to short	Short to long	Short to shorter
Baseline	0.083	0.595	0.537	0.179
Distracter at 30°	0.075	0.702	0.758	0.076
Distracter at 10°	0.035	0.752	0.861	0.052

target's initial position to 0.5 ms at target distances shorter than 33 cm. When the distracter was placed 70 cm from the platform at a 10° offset from the target motion axis, the pulse duration was consistently lower than the baseline trial by 0.5 ms, between target distances of 170 and 57 cm. At shorter target distances, the call duration in the distracter trial was reduced systematically to 0.5 ms, showing a similar pattern to baseline data as the target neared the bat.

The PI and duration data are summarized across 16 and 12 trials for the baseline and distracter conditions, respectively, in Figs. 2(c) and 2(d). Trials for each condition were obtained in a single experimental session. The PI values for both conditions were very similar.

The duration profiles for the baseline and distracter conditions were similar for target distances below 40 cm [Fig. 2(d)]. Beyond this distance, the pulse duration in the baseline condition continued to increase with target distance, whereas

FIG. 3. Sonar pulse duration versus pulse interval for baseline (a) and a distracter condition (b). The solid and open circles represent average pulse interval and pulse duration for baseline and the (10°, 70 cm) distracter condition, shown in (a) and (b), respectively. The lines are the four-degree polynomial fits to the average values. The dots are the data points obtained from all trials of a single session. The average trend for the baseline condition is re-plotted in (b) for comparison, and shows that the relationship between the two parameters was altered when the distracter was present.

pulse duration in the distracter condition remained below the baseline values (about 0.5 ms lower) at target distances between 40 cm and 170 cm, i.e., behind the position of the distracter.

The conditions created by our experimental paradigm allowed us to examine the relation between PI and pulse duration. In Fig. 3 pulse duration values, obtained from the same set of trials presented in Figs. 2(c) and 2(d), are plotted against the PI values for both the baseline and the distracter conditions. Sonar pulses recorded under each condition are represented by gray dots. The average Pi-duration relation is depicted by connected black dots and triangles for the baseline [Fig. 3(a)] and distracter conditions [Fig. 3(b)], respectively. In Fig. 3(b), the average baseline trend is redrawn to highlight the differences between the two conditions. Compared to baseline, the PI in the distracter condition (10°, 70 cm) increased faster with pulse duration for durations above 1.5 ms.

In Figs. 4(a)–4(d) we show the average trend of the PI for all the distracter offset conditions for 45 cm (top row) and 70 cm (bottom row) distracter distances for Bat 45 (left column) and Bat 49 (right column). In the 10° distracter condition Bat 45's PIs were distinctly smaller in half of the trials than the average PI trend observed under most distracter conditions, causing a different average trend from the remaining data [Fig. 4(a)]. Otherwise, the average PI produced by both bats was qualitatively similar in baseline and distracter conditions, showing a decrease with a reduction in target distance. The bats' consistent dynamic adjustments in PI with target distance suggest that the animals were tracking the target when it was behind, as well as in front, of the distracter.

It is noteworthy that the angular position of the distracter had a direct influence on sonar call duration when the tethered insect was positioned beyond the distracter. The magnitude of the effect of the distracter on pulse duration was larger at smaller angular offsets (Fig. 5). Figure 5 shows that both bats decreased their pulse duration with target distance. The absolute range of pulse durations exhibited by

Bat 45 was larger, (1–4.7 ms), than that of Bat 49 (0.7–3.2 ms). The average pulse durations were systematically lower with decreasing distracter angle for all target distances beyond the distracter. When the target moved in front of the distracter the average pulse duration pattern followed a trend very similar to the baseline. At the closer distracter distance of 45 cm, the call duration profile, for both bats, broke away from the baseline pattern at a target distance of about 40 cm; this separation occurred at a target distance of about 55 cm when the distracter was at 70 cm. Consequently, the call duration values for target distances between 40 and 80 cm were lower for the distracter position of 45 cm, compared to the distracter distance of 70 cm, for a matching angular offset. Above 80 cm, the changes in call duration with target distance were similar for both distracter ranges for identical angular offsets.

B. Signal overlap zones

1. Pulse-echo overlap

It has been proposed that bats shorten sonar pulse duration with decreasing target distance to avoid overlap between pulse and echo.^{10,11,14} In Figs. 5(a)–5(d), Bat 45's and Bat 49's call duration profiles are plotted with changing target distance under different distracter angles and distances. The distracters were placed at 45 cm [Figs. 5(a) and 5(b)] and 70 cm [Figs. 5(c) and 5(d)] from the platform. The target distances for a given pulse duration where a pulse-echo overlap would have been experienced is shaded in light gray. Except for target distances below 15 cm, pulses produced by the bat were short enough to prevent pulse-echo overlap. At target distances smaller than 80 cm, the duration of the sonar pulses produced by Bat 45 was consistently 0.65 ms shorter than the maximum pulse duration which would still avoid an overlap [dark shaded area in Figs. 5(a) and 5(c)]. This nearly constant temporal gap may serve as a buffer zone assuring minimum interference between the outgoing sonar pulse and the distracter echo.

FIG. 4. Influence of the distracter's angular position and distance on pulse interval for Bat 45 (a), (c) and Bat 45 (b), (d) at 45 cm (a), (b) and 70 cm (c), (d) distracter distances.

FIG. 5. Influence of the distracter's angular position and distance on sonar pulse durations for Bat 45 (a), (c) and Bat 49 (b), (d) at 45 cm (a), (b) and 70 cm (c), (d) distracter distances. Pulse durations were kept well below the pulse-echo overlap zone (light shaded area). The dark shaded area represents the buffer zone. The dashed lines around the distracter distances represent the borders of the echo-echo overlap region. Pulse duration values represent averages within 5 cm intervals along the range axis. Baseline pulse durations are given for comparison with average pulse duration-target distance relation when the distracter was introduced.

The width of the buffer zone was around 1.2 ms for Bat 49, whose vocalizations were generally shorter in duration compared to Bat 45 [see Figs. 5(a) and 5(c)].

For a distracter at 70 cm, the pulse durations in almost all distracter offset conditions between the pulse and the distracter echo were well separated in time beyond the buffer zone (the dark shaded area). For the 40° angular offset condition, Bat 45's maximum average pulse duration was around 4.18 ms, causing a marginal temporal overlap between the outgoing pulse and the distracter echo. However, when the distracter was at 45 cm distance [Fig. 5(a)], both bats experienced overlap at target distances beyond the distracter. The modulation of the pulse duration in relation to distracter angle kept the pulse-echo overlap, experienced by Bat 45, below 20%–30% between 100 and 65 cm. No overlap between the pulse and the distracter echoes occurred at target distances closer than 80 and 65 cm for 20° and 40° distracter offsets, respectively [Fig. 5(c)]. Bat 49, on the other hand, experienced, at maximum, 25% overlap around 160 cm for 40° distracter position which diminished below 150 cm target distance.

2. Echo-echo overlap

A temporal overlap would also be expected between the target and the distracter echoes at short separations between these objects. In Fig. 5 the dashed lines around the distracter distances represent the borders of the region within which the echoes from the target and the distracter overlap. As the target approached the distracter the amount of temporal overlap between the two echo signals increased, reaching 100% when the target was at the distracter distance. Target echoes first overlapped with the distracter echoes at shorter distances behind the distracter as the angular offset was lowered. These distances correspond to the points where the distance-duration profiles intersect the dashed lines in Figs. 5(a)–5(d).

The influence of the angular position of the distracter on pulse duration and, consequently, the echo-echo overlap zone can be seen more clearly in Fig. 6. This figure depicts the effect of the distracter angle on the pulse duration at a target distance 15 cm behind the distracter (target distance 60 cm; distracter distance 45 cm). Points on the polar plot represent a decrease in pulse duration from baseline at a given distracter angle; the pulse duration decreased up to 1.2 ms at 10° and 0.73 ms at 5° for bats 45 and 49, respectively. A frontal view of the pulse duration decrease was obtained by mirroring the pulse duration decrease values, obtained for the angular offsets on the left hand side of the bat, to the right, using the target motion axis as the symmetry axis. At small angular separations between the target and the distracter both bats produced shorter pulse durations than under the baseline condition.

C. The influence of the distracter on sonar pulse structure

We predicted that spatial interference from the distracter would drive the bat to adapt its vocalizations to improve target position estimation accuracy. To achieve separation of closely spaced objects, echolocating bats can alter the time-frequency structure of their sonar pulses. We carried out signal analyses to capture the fine structure of the FM sweeps to

FIG. 6. Decrease in average sonar pulse duration from baseline as a function of distracter angle at a target distance of 60 cm (solid circles Bat 45, open circles Bat 49). The distracter is at 45 cm distance.

determine if there were changes related to the position of the distracter. We extracted time-frequency profiles of the fundamental and the first harmonic components of the sonar pulses, as well as their time waveforms. We limited this analysis to target distance ranges between 30 and 160 cm. The fundamental profile for pulses generated when target distances were below 30 cm could not be obtained reliably with the method we used, due to low resolution spectrogram representation of sonar calls with durations under 1 ms. The results shown in Fig. 7 were obtained for the baseline and two distracter conditions, 5° (45 cm) and 30° (45 cm), for Bat 49.

In Fig. 7(a) we show the start and end frequencies of the fundamental component in relation to target distance. In all three conditions the start frequency of the FM sweep decreased steadily with a reduction in target distance—from approximately 67 to 47 kHz between 160 and 45 cm. The rate of decrease in the FM start frequency became larger with decreasing distracter angular offset. In other words, the distracter at small angular offsets resulted in the reduction of fundamental start frequencies, for a given target distance behind the distracter.

The end frequencies of the FM sweeps produced across different conditions were less variable. The end frequency of the FM sweep also decreased with target distance from approximately 32–23 kHz. Start and end frequencies changed by an equal amount on a logarithmic scale, about 0.5 octave, between target distances of 160 and 30 cm.

Figure 7(b) depicts the average sweep rate of the fundamental with respect to target distance. Sweep rate of a pulse was calculated as the ratio of the bandwidth of the fundamental to the pulse duration.

The sweep rate increased for all conditions with decreasing target distance; from approximately 13–23 kHz/ms. This increase was smaller for distances above 100 cm and became larger below this distance in baseline conditions. Decreasing the distracter angle caused an increase of the sonar pulse sweep rate for target distances beyond the distracter. These results show that sweep rate increased with decreasing target distance and the rate of increase was highest for smaller distracter offset angles.

FIG. 7. (a) Average start and end frequencies of the fundamental component of the FM sonar pulses. Solid and open markers represent beginning and end frequencies, respectively, (b) the sweep rate of the sonar pulse fundamental increased with decreasing target distance, (c) peak frequencies of fundamental and first harmonic components, and (d) ratios of peak levels of the fundamental and first harmonic components of the sonar vocalizations. The measurements were obtained from the baseline (circles) and (5° , 45 cm; squares) and (30° , 45 cm; triangles) distracter conditions for Bat 49. Error bars represent standard deviations. The vertical line at 45 cm marks the distracter distance.

We investigated the coupling between pulse duration and sweep rate between the baseline and two distracter conditions. An analysis of covariance test with an independent linear model revealed that the regression lines representing the duration-sweep rate relation were significantly different across the three conditions (interaction $F(2,1511) = 75.42$, $p < 0.05$). The mean and confidence intervals for the slopes of duration-sweep rate relation under baseline and distracter conditions (5° and 30° at 45 cm) were -5.47 kHz/ms^2 (± 0.07), -5.98 kHz/ms^2 (± 0.07), and -6.66 kHz/ms^2 (± 0.07), respectively. These results reveal that for a given duration the time-frequency structures of sonar pulses under different distracter conditions were different.

In addition to the time-frequency profile of the bat's echolocation calls, the distribution of acoustic energy within the sonar pulse can be of consequence for the echo information received. For instance, by altering the peak spectral energy a bat could control the spatial coverage of its sonar beam. To quantify whether the bat altered the acoustic energy distribution within the fundamental and first harmonic sonar signal components, we computed the frequencies at which the acoustic energy was maximum [Fig. 7(c)] as well as the ratio of the magnitude of these peaks [Fig. 7(d), see methods]. In almost all the sonar pulses emitted, the power spectrum of the fundamental and the first harmonic had a single peak. The peak frequency for the fundamental remained constant at around 45 kHz. Below 50 cm target distance, the peak frequency of the fundamental dropped. This drop occurred more rapidly with decreasing target distance under the distracter conditions. The peak frequency for the

first harmonic, on the other hand, showed a decrease with target distance and distracter angle. It was lowest for the distracter at a 5° angular offset.

The intensity ratio of the fundamental and first harmonics at the peak frequency decreased with target distance and more so for the distracter at 5° angular offset than for distracters at larger angular offsets [Fig. 7(c)]. When the distracter was positioned near the target motion axis, the bat increased the first harmonic peak intensity relative to the peak intensity of the fundamental: For target distances above 60 cm, the peak intensity level for the fundamental was larger (maximum value around 5.2 dB). The relation between peak intensity ratio and target distance was very similar for the baseline and 30° distracter offset conditions. In comparison, for the 5° distracter offset the peak intensity ratio was smaller (maximum value around 2.5 dB). When the angular offset was 5° , the intensity of the first harmonic peak increased compared to that of fundamental at a greater target range, about 100 cm, compared to baseline and 30° distracter conditions.

IV. DISCUSSION

In this study, we found that the big brown bat, *Eptesicus fuscus*, echolocating from a platform, adjusted the duration and timing of its calls as it tracked an approaching tethered mealworm. The bat's sonar call structure in this target tracking task was influenced by the distance and angular offset of a stationary distracter, and we discuss below the implications of the bat's adaptive vocal behavior to spatial perception by sonar.

A. Adaptation of sonar pulses implies strategies for segregation of spatial information from multiple objects

Increasing vocalization rate, shortening sonar pulse duration, and controlling the time-frequency structure of sonar pulses can help a bat maintain an accurate representation of its immediate environment. Adjustment of these call parameters is discussed below.

1. Effect of distracter on pulse interval

Consistent with previous reports,¹⁸ the big brown bat decreased the time interval between sonar vocalizations with decreasing target distance. The tracking of the target at distances near the distracter could pose a challenge to the bat, due to interference between echoes from the target and distracter. One possible strategy for the bat to cope with such interference would be to decrease the pulse interval and thereby increase information flow to localize the target.²² Such sonar behavior has been observed in free-flying bats: Echolocating big brown bats produce groups of sonar pulses with regular intervals (strobe groups) while approaching a target close to clutter.⁴ For all the distracter conditions tested in this experiment the average PI pattern was very similar to that observed in the baseline condition; however, the bat produced more sound pairs separated by longer time intervals when the distracter was present. In other words, the mean PI was not influenced by the distracter, but the bat adjusted the temporal patterning of PI within the approach sequence to produce pairs of signals. We propose that the production of sonar call pairs aided the bat in separating echoes from the target and distracter.

In a recent study, Petrites *et al.*²¹ suggested that dynamic modulations of PI could help disambiguate potential pulse-echo registration problems. The pulse-echo registration problem refers to the ambiguity that a bat might experience in pairing echoes with their associated pulses when it receives a cascade of echoes that return from different sonar calls. In our experiment, we determined that the bat's PIs were sufficiently long to avoid pulse-echo ambiguity, thus eliminating it as a potential explanation. Consequently, we speculate that the bat's increased production of sonar pulse pairs with decreasing distracter angle might help enhance spatial resolution to maintain an accurate representation of the target and its movement.

2. Effect of distracter on pulse duration

The bat's sonar pulse duration was influenced by the angular offset and the distance of the distracter, however, as noted above, the PI was not. This finding suggests that the bat's dynamic changes in PI and duration can be decoupled during target approach in the presence of an obstacle (see Fig. 3).

The pulse duration-target distance relation was highly repeatable for a given condition for each bat. For each bat, pulse duration appears to be determined by the closer echo source: When the target was behind the distracter, the sonar pulse duration was influenced directly by the distracter distance and its angular offset (Fig. 7). The pulse duration was

affected by the distracter for a short time after the target moved in front of the distracter. The size of this zone was smaller at the shorter distracter distance of 45 cm than the longer distracter distance of 70 cm. This observation might be related to the increase in the clutter interference zone with longer object distances (see Simmons *et al.*).²³

Based on data reported by Sumer *et al.*¹⁹ it is expected that interference would decrease as the distracter's angular offset from the insect increases. Indeed, we found that the bat's distance-dependent adjustments in pulse duration were smaller at larger distracter angular offsets (Fig. 6). Thus, it is reasonable to conclude that the decrease in pulse duration is a behavioral strategy to minimize clutter interference. Note that in the Sumer *et al.* study the clutter object was in front of the target to be detected, and both objects were stationary. In our experiment, on the other hand, the bats tracked a moving target in the presence of a stationary distracter, which was sometimes in front of and sometimes behind the target. The animals dynamically adapted pulse duration when the target was in front of the distracter (see Fig. 7). Tracking a moving object in space requires continuous monitoring of its position. The reduction of pulse duration would aid segregation of the echoes in time and space, allowing perception of multiple objects. Temporal segregation is particularly important for objects that have small angular separation between them. Echoes from multiple objects in the scene are less likely to interfere with each other if they are short in duration, as their arrival times can be treated as discrete events, which may effectively increase the spatial resolution of the bat sonar receiver.

3. Effect of distracter on pulse design

Our investigation of the time-frequency structure of the sonar pulses emitted during target tracking revealed that the bats not only altered their pulse duration but also other measures of pulse design, potentially to enhance position information about the target. The increased signal sweep rate in the presence of the distracter may have served to improve the accuracy of the bat's range estimation.⁶

Another potential strategy the bat might employ to maintain accurate spatial information about the target is revealed by the relative energy in the fundamental and first harmonic components of the sonar pulses. The sonar signal's peak intensity of the first harmonic relative to the fundamental was the largest for the 5° distracter angle condition. Similar findings were also reported in a recent study by Siimer *et al.*¹⁹ Sonar beam width narrows with increasing call frequency²⁴ and consequently, the shifting of acoustic energy to higher frequencies results in strengthening of the target echo return relative to the echo from the distracter at an angular offset. The bat's adjustments in call frequency may therefore help the bat minimize the interference caused by the distracter.

The bat maintained the peak spectral energy of the fundamental and first harmonics of sonar pulses at 44 and 58 kHz, respectively, during the target's approach. By monitoring the relative changes in echo intensities from both objects at these frequencies, the bat could gain additional cues about the approaching target's distance under the predictable conditions in our experiment. Unlike the echo intensity of the stationary

distracter the target echo would not only change with the emission intensity but also with its changing distance. Note that given this proposed strategy, the echoes from the distracter would act as a reference against which the bat could compare the echoes from the target.

4. Signal overlap avoidance and control of pulse duration

Bats avoid temporal signal overlap by shortening pulse duration, presumably to prevent interference between the outgoing pulse and returning echo, or between two echoes from closely spaced objects.²

We predicted that bats would have adjusted call duration to minimize overlap between echoes from the target and distracter echoes (edge of the overlap zone, highlighted by the dashed lines around the distracter position in Fig. 7). Surprisingly, however, the bat tolerated overlap between the distracter and target echoes for a large range of target positions.

The bat also did not avoid pulse-distracter echo overlap completely when the distracter was at 45 cm distance. For target distances beyond 70 cm, overlap between the emitted pulse and distracter echo was up to 30% of the pulse duration. The bat, however, did maintain the target echo at a constant separation from the pulse-echo overlap zone when the target was in front of the distracter; 11 cm for Bat 45 and 20 cm for Bat 49 (Fig. 7).

Our results suggest that the bat was compensating for the interference caused by the presence of the distracter by altering the time-frequency structure of its sonar vocalizations under conditions when echo-echo overlap occurred. It is noteworthy that these signals can still be separated in the spectrogram domain;^{17,20} that is, echo frequency components of the sweep returning from closely spaced objects did not overlap. Simmons *et al.*¹⁷ proposes that two echo returns are perceptually separable to *Eptesicus fuscus* if the echoes are at least 300 μ s apart. This suggests that the spectrogram representation of target and distracter echoes may have merged only briefly when the echoes were separated by less than 300 μ s.

In the natural environment, echoes from foliage, for instance, would result in broadband echoes with complex time-frequency structure, creating a situation that would challenge the bat's sonar system to resolve insect echoes from background clutter. The free-flying bat can, however, control the direction of echo returns by adjusting its flight-path and head aim with respect to targets and clutter. This strategy would introduce additional cues for tracking insects close to vegetation, as observed in laboratory studies.⁴ The bat's vocal adjustments reported here suggest that rapid frequency modulation, combined with sonar beam directional control, can facilitate the perceptual separation of multiple closely spaced sonar objects.

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