Effective biosonar echo-to-clutter rejection ratio in a complex dynamic scene

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Biosonar guidance in a rapidly changing complex scene was examined by flying big brown bats (*Eptesicus fuscus*) through a Y-shaped maze composed of rows of strongly reflective vertical plastic chains that presented the bat with left and right corridors for passage. Corridors were 80–100 cm wide and 2–4 m long. Using the two-choice Y-shaped paradigm to compensate for left–right bias and spatial memory, a moveable, weakly reflective thin-net barrier randomly blocked the left or right corridor, interspersed with no-barrier trials. Flight path and beam aim were tracked using an array of 24 microphones surrounding the flight room. Each bat flew on a path centered in the entry corridor (base of Y) and then turned into the left or right passage, to land on the far wall or to turn abruptly, reacting to avoid a collision. Broadcasts were broadly beamed in the direction of flight, smoothly leading into an upcoming turn. Duration of broadcasts decreased slowly from 3 to 2 ms during flights to track the chains' progressively closer ranges. Broadcast features and flight velocity changed abruptly about 1 m from the barrier, indicating that echoes from the net were perceived even though they were 18–35 dB weaker than overlapping echoes from surrounding chains.

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I. INTRODUCTION

Echolocating big brown bats, *Eptesicus fuscus* (Kurta and Baker, 1990) perceive the immediate three-dimensional environment using biological sonar (Griffin, 1958; Neuweiler, 2000). They emit trains of ultrasonic frequency-modulated (FM) chirps and analyze returning echoes to guide their flight, locate objects, and perceive the surrounding sonar “scene” (e.g., Moss *et al.*, 2006; Petrites *et al.*, 2009; Barchi *et al.*, 2013). The duration of broadcasts and the time interval between broadcasts, or its reciprocal—the repetition-rate (PRR), change as the bat adapts to features of the surrounding space—the distance to the nearest objects, the density of the objects distributed around the scene, and the depth of the scene (Griffin, 1958; Surlykke and Moss, 2000). The bat's broadcasts contain downward FM sweeps with a 1st harmonic (FM1) ranging from about 50–60 kHz down to 23 kHz, and a 2nd harmonic (FM2) from 100 to 45 kHz. Sometimes, there is a segment of the 3rd harmonic (FM3) around 80–100 kHz.

When a bat flies through a complex scene, each of its echolocation broadcasts is followed by a series of echoes at different delays (Moss and Surlykke, 2010; Simmons, 2014). In sonar or radar, this is the classic problem of *clutter interference*—locating a weakly reflective object in one direction when more strongly reflective objects surround it, to bury its

individual echoes in the series of echoes from the scene as a whole. Big brown bats often fly through vegetation while emitting trains of FM broadcasts, their flight path surrounded by numerous large reflecting surfaces such as branches and leaves. The extended series of echoes returning from the sides can mask the presence of echoes from an object located in the bat's upcoming path—a potential collision hazard.

A variety of obstacle-avoidance tests with flying bats have been carried out to assess the sensitivity of echolocation (e.g., Grinnell and Griffin, 1958; see review by Schnitzler and Henson, 1980; for *Eptesicus*, see Jen and Kamada, 1982; Sändig *et al.*, 2014). These experiments incorporate the dynamic conditions that surround flying bats, and their results vividly demonstrate the high maneuverability of bats flying around obstacles and the scope of their adaptive changes in broadcasts as they approach obstacles. However, these experiments typically use just one row of vertical wires as obstacles, which the bat approaches perpendicularly to pass through the gap between two adjacent wires. The scene therefore is shallow and does not extend in depth. For the new type of experiment described here (Petrites *et al.*, 2009), the configuration of cluttering objects consisted of multiple rows of obstacles that distributed their masking echoes to surround the bat on both sides (Fig. 1) so it could not turn its head to recover (i.e., unmask) echoes from the weakly reflective barrier in the presence of stronger echoes from the clutter.

In the relatively static conditions of two-choice psychophysical experiments, big brown bats can detect and locate a

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FIG. 1. Rationale for experiments. Bat is released into a darkened Y-shaped flight maze formed by rows of vertical plastic chains that strongly reflect the bat's incident sonar sounds (Barchi *et al.*, 2013). The center corridor diverges into two corridors, left and right, one of which is blocked on randomly selected trials by a thin net that reflects weaker echoes than the chains. The corridors are long enough that the net is not detected until the bat already has chosen the left or right passage, so that its reaction to the net (at **) depends on the strength of the net's echoes relative to the chains' echoes, not on knowing the net's position before entering the corridor.

test target in one direction from echoes that are equal in strength to clutter echoes arriving from 40° off to one side horizontally when the separation in distance is only about 1 cm, or $60\ \mu\text{s}$ in delay (Simmons, 1973; see Simmons and Grinnell, 1988). When the clutter echoes arrive from the same direction—no horizontal separation—and still have the same strength as test echoes, the threshold separation in distance of test and clutter echoes increases to about $300\ \mu\text{s}$, equivalent to about 5 cm of distance (Simmons *et al.*, 1989). In different experiments, when the clutter echoes are 22 dB stronger than test echoes and still from the same direction as test echoes, the threshold separation in distance increases to 11 cm, or almost $700\ \mu\text{s}$ in delay (Sümer *et al.*, 2009). Keeping the distance separation at 11 cm while moving the clutter off to the side, at a horizontal separation of 23° , the bat's sensitivity improved by 29 dB to reach approximately the sensitivity achieved in the absence of clutter. In a different study, electronically produced echoes arriving from an angle well above the bat and off to one side did not interfere with perception of test echoes arriving from in front of the bat (Warnecke *et al.*, 2014). Thus, differences in distance and direction both contribute to resisting the effects of clutter, and they reinforce each other to define a clutter-free zone around the target. Interference occurs when clutter encroaches within this zone, the size of which depends on the relative strength of the echoes.

Attempting to extrapolate measurement of the effects of clutter as measured in two-choice psychophysical experiments to the effects of clutter on bats in flying in complicated, cluttered surroundings requires separating the

potential advantages of the static conditions of psychophysics from the potential effects of the dynamic conditions of flight. The experiments reported here combine the two-choice procedure with flight tests in extended clutter to measure the strength of target echoes relative to clutter echoes at their just-detectable signal-to-clutter ratio for a collision-avoidance task in a complex scene (Fig. 1). Flying bats were presented with a weakly reflective obstacle (net barrier in Fig. 1) embedded in surrounding clutter (rows of vertically hanging plastic chains) so that turning the head would not isolate echoes reflected by the obstacle from echoes reflected by the clutter. The bat's reactions to encountering the obstacle were used to estimate the signal-to-clutter ratio adequate for detection, and to estimate the size of the space the bat considers necessary to maintain free of potential obstacles before it adapts to cope with the obstacle in cluttered surroundings. The experimental procedure that was built around this measurement problem was designed to isolate two additional confounding factors—the tendency of individual bats to favor a turn to the left or to the right (a version of “handedness”), and the bat's ability to remember the locations of objects through its familiarity with the scene.

II. MATERIALS AND METHODS

A. Animals

Subjects were three adult, wild-caught big brown bats, *Eptesicus fuscus*, collected at residential locations in Rhode Island under a state Scientific Collecting Permit. The bats (“Frosty,” “George,” and “Poe”; one female, two males) were housed in individual cages in a colony room controlled for temperature (22°C – 24°C) and relative humidity (40%–60%) and maintained on a 12 h light/12 h dark reversed light cycle. The bats were given vitamin-enriched water *ad libitum* and fed *Tenebrio molitor* (mealworm) larvae daily; food intake was adjusted to maintain animal body-mass between 16 and 18 g. All procedures were consistent with guidelines established by the National Institutes of Health and approved by the Brown University Institutional Animal Care and Use Committee (IACUC). These three individual bats were selected for their willingness to fly through the maze and land on the far wall.

B. Flight room

The experiments were conducted in a $8.5\text{ m} \times 3.4\text{ m} \times 2.4\text{ m}$ high flight chamber fitted with rows of black plastic chains hanging vertically, from floor to ceiling, to guide the bat's flight as described previously (Petrites *et al.*, 2009; Barchi *et al.*, 2013). The chains formed a symmetrical Y-shaped maze with two passageways for the bat to pass through to get to the other side of the room (Fig. 1). The bat's task was to negotiate the maze and arrive on the end wall of the room, where it was rewarded with food. On random trials, one or the other passageway was blocked by a movable net barrier, as depicted in Fig. 2. The Y-maze and surrounding active flight area were separated from a small release area at one end of the chamber by an entry net, which had an opening at the center through which the bat was

FIG. 2. Diagrams showing experimental procedure for flight tests and polar coordinates for plotting broadcast beam axis. (A) Plan view of flight chamber (black walls). Small black circles mark locations of vertical chains that form Y-shaped maze with corridors on left and right for the *narrow chain array* condition. Moveable net barrier (horizontal dashed line; randomly appearing at right, center, left positions on average every three trials or every 10 trials), 24-microphone array for acoustic tracking of the bat in flight (gray squares; four of the microphones are occluded by being at same position as other microphones on the plan), two infrared thermal-imaging video cameras for monitoring each flight, and a sample flight path tracked by the microphone array (curving line of gray dots). Black curving arrow shows segment where bat is engaged with left-right choice end flying in corridor. (B) Plan view for *wide chain array* showing individual chains that were removed from narrow array in A (open circles) to increase corridor width without sacrificing essential Y-shaped path for bat. (C) Plan view for *narrow chain array* showing individual chains added to wide array (gray circles; shown as open circles in B) to restrict corridor width and enclose Y-shaped paths. Note single row of chains at 6.2 m position on length axis with center gap for bat to fly into working area of the microphone array. Each sonar sound is localized acoustically to a particular position on the flight path, with a vector on polar-plot insert indicating the orientation of the acoustic axis of the broadcast beam relative to the instantaneous flight-path vector. Beam-axis vectors ultimately are plotted on a compound polar plot (in B, C) that combines left and right corridor flights to indicate beam direction to center of room or to outside, instead of just to the bat's left or right.

introduced into the maze. A single row of hanging chains, with its own opening in the center, paralleled the net and served as an entry point for flights [at length position 6.2 m in Fig. 2(A)]. The walls, ceiling and floor of the flight chamber were padded with sound absorbent foam to reduce reverberations (Sonex, Illbruck, IL), and the walls also supported an array of 24 ultrasonic microphones mounted at varying heights and surrounding the flight volume [Fig. 2(A), squares]. During the experiment the flight room was kept in complete darkness with the exception of dim red light emitting diode indicator lights on each microphone board.

The configuration of the chains was adjusted to expose the bats to two densities of clutter by varying the spacing between chains. The spacings were chosen to bracket the boundary, previously observed in the behavior of flying big brown bats between a low- or medium-density of clutter that the bats treated similarly to an open room and a high-density of clutter that caused the bat to use a characteristically different pattern of sonar sounds emission during flight (Petrites *et al.*, 2009). The chains were arranged to offer the flying bat a choice between two corridors once it entered the Y-shaped

maze, either of which could be blocked with a panel of mesh that was a weak acoustic reflector. On selected trials, the mesh net was randomly positioned as an obstacle in the path of the bat before it was released to fly along the left or the right corridor (Fig. 2). On other trials, the net was moved to the center of the configuration of chains, where it did not obstruct either corridor. The presence of the barrier would be expected to evoke obstacle-specific responses that might, however, be difficult to separate from the bat's ongoing responses to the corridor itself because the bat would be wholly occupied by navigating past the chains, which surrounded the bat in its approach to the location occupied by the obstacle itself. By exploiting the symmetric, effectively differential design of the Y-maze through combining results across bats for the left and right corridors, it should be possible to extract the effects of the barrier itself. The moveable net barrier was located about 2.5 m on the length dimension of the room [Fig. 2(A)]. It was constructed out of thin black plastic garden mesh (~2.5 cm squares), suspended from a horizontal rod, and weighted down at the bottom with a horizontal aluminum rod. The thin mesh of the net barrier was

chosen to minimize echoes reflected back to the bat, but the material was also light and yielding enough to cause the animal no injury should it crash into the barrier unexpectedly. The barrier and its supporting rods were suspended on a horizontal aluminum track at the ceiling and could be moved quickly by hand between flights to one the three positions—to block the left or right corridor of the Y-maze, or to be placed out of the bat's way, in the center of the cluster of chains separating the left and right corridors [Fig. 2(A)].

C. Experimental procedure

On any given testing day, each bat was flown in a series of repeated trials in one of three experimental conditions (see below). To start a trial, the bat was released by hand (alternating between the releaser's left and right hands) to fly from the release point at the opening of the net and row of chains that divided the room between the entry space [positions from 6 to 8 m room length in Fig. 2(A)] and the maze area itself [positions from 6 to 2 m length in Fig. 2(A)]. Upon release, the bat flew toward the maze and approached the area where it had to choose between the left and right paths through the maze. Although most flights ended with a landing on the far wall or the net barrier, the bat was allowed to fly until it landed. Sometimes the bat looped repeatedly through the maze, but only the initial track into the maze (until the bat landed or turned around) was considered in the analysis. Two persons (the experimenters) were present in the flight room and one person (the recorder) worked outside the flight room to operate the acoustic and video recording system (see below). At the conclusion of each flight, one experimenter collected the bat to begin the next flight while the other moved the net barrier to its assigned position (left, center, right) for the next trial [Fig. 2(A)]. Alternation of the net position was made, on average, every three trials or every 10 trials (on average, because a random sequence was used). In the case of no change on the upcoming trial, the net was still moved out of its current position and then moved back so that the bats could not learn to associate sound with a change in the net's position.

Three different sets of flight tests (Series 1, 2, and 3) were run with slightly different experimental parameters. In Series 1, bats were flown in the wide array of chains [Figs. 2(A) and 2(B)], while in Series 2 and Series 3 they were flown in the narrow array of chains [Figs. 2(A) and 2(C)]. The wide and narrow widths of the left and right corridors in the Y-shaped maze were determined from a previous finding that big brown bats shifted from a regime of pulse emission similar to that used in an unobstructed room when the chains making up a flight corridor in the array are moved closer to restrict the corridor to less than about 1 m (Petrices *et al.*, 2009). The spacing between the chains that formed the narrow corridors provided a width of about 0.8–1 m over a corridor length of about 2 m [Figs. 2(A)–2(C)]. The wide corridors had a width of 1.5–2.0 m, except at their most restricted point, where the width was the same 0.9 m as at the end of the narrow corridors. The wide and narrow conditions were coupled with different manipulations of the moveable net barrier [Fig. 2(A)]. In Series 1 (wide) and

Series 2 (narrow), the bats were flown for a block of 20 flights per day while the barrier position changed on an average of every three flights according to a pseudorandom schedule. In Series 3 (narrow), the bats were flown for a block of 25 flights per day while the net barrier changed on an average of every 10 flights, also in a pseudorandom schedule. In Series 1, “Control” flights with the net in the center of the room [Fig. 2(A)] were interspersed randomly among the other (i.e., left or right) trials. In both Series 2 and Series 3, a full set of control flights with the net in the center was run at the start of the series, and then the net was alternated pseudorandomly between left and right positions for the tests.

D. Data collection

1. Acoustic

The echolocation sounds emitted by the bat during flight were received with 24 ultrasonic microphones (MEMS, Knowles Type SMG-0291, Itasca, IL), mounted on custom-built preamplifier boards and distributed throughout the room [Fig. 2(A)]. Signals from the microphones were connected to analog bandpass filters with sensitivity from 10 to 100 kHz. Outputs of all 24 channels were digitized using a commercial audio processor (PCIe-424 with 2 × HD192, MOTU, Cambridge, MA) at a sampling rate of 192 kHz and stored to disk on a devoted computer (Mac Pro Early 2009/MacPro4.1, Apple, Cupertino, CA).

2. Video

The bats' flights were also recorded at 30 frames/s with two frame-synchronized thermal-infrared video cameras (FLIR, Merlin mid-IR, Billerica, MA) fixed in position to cover the flight space in stereo images [Fig. 2(A)]. Left and right video frames were combined using a Quad processor before being recorded (Supercircuits, Austin, TX). Videos were digitized along with the 24-channel acoustic data using a commercial multichannel audio-video system (V4HD, MOTU) and stored to disk on the host computer (Apple Mac). The real-time video images were used primarily to locate the place where the bat landed in the near-total darkness of the flight room after each flight so it could be recovered for the next flight. The video records also were used to determine whether they revealed any unusual maneuvering during passage through the maze because the sound tracking system only located the bat each time it emitted a sonar sound. Stereo video tracking of the flight path is less accurate than acoustic tracking, so the video was used just to validate the acoustic localization data.

3. Echo measurements

An artificial pulse-echo system was used to characterize the acoustic properties of the net barrier and the surrounding chains. This integrated system, constructed in-house, emitted a series of hyperbolic FM sweeps and recorded echoes from the targets *in situ* in the flight room. FM signals of 3 ms duration were synthesized in a Lenovo laptop computer with the 1st harmonic (FM1) sweeping from 50 to 25 kHz, the 2nd

harmonic (FM2) sweeping from 100 to 50 kHz, and a segment of the 3rd harmonic (FM3) sweeping from 100 to 75 kHz using MATLAB routines (Mathworks, Natick, MA). These signals were routed through a digital-to-analog converter (USB-1208HS-2A0, Measurement Computing, Norton, MA), amplified, and broadcast by an ultrasonic ribbon tweeter (LCY-K100; Madisound Speaker Components, Inc., Madison, WI), with a total effective bandwidth of 25–100 kHz, toward the net and the chains. Echoes reflected by the net barrier alone, by the nearby chains alone, and by the net barrier and chains together were picked up with an ultrasonic microphone (condenser microphone model 4135, windscreen removed; Brüel & Kjær, Nærum, Denmark), amplified, bandpass filtered to 20–100 kHz, and digitized by the same USB data acquisition unit before being stored in the laptop computer. Both the loudspeaker and the microphone were placed in the left chain alley, 1 m from the position of the net barrier, and aimed towards the center of the net, along the axis of the bat's flight. This distance was chosen after the analysis of results indicated that the approximate position of the bat during flight to the barrier when it first reacted unambiguously to the barrier's presence was 1 m. For each recording condition (net alone, chains alone, net and chains together), the echoes acquired from 50 signal presentations were averaged in the computer to reduce noise. To provide a standard for comparing echo strengths, echoes also were recorded (average of 50 trials) from a flat Plexiglas plane suspended at a distance of 1 m from the loudspeaker-microphone unit; echoes from the experimental conditions were compared to this reference acoustic "high reflector."

The big brown bat's broadcast beam is very wide (6-dB sound-pressure beam edges are $\pm 90^\circ$ at 25 kHz, $\pm 55^\circ$ at 40 kHz, $\pm 40^\circ$ at 60 kHz, $\pm 30^\circ$ at 80 kHz; Hartley and Suthers, 1989), so the bat ensonifies the chains off to the sides almost as strongly as the net barrier. The loudspeaker used for these echo measurement has a directional beam roughly half as wide as the bat (6-dB sound-pressure beam edges are $\pm 40^\circ$ at 25 kHz, $\pm 25^\circ$ at 40 kHz, $\pm 18^\circ$ at 60 kHz, $\pm 10^\circ$ at 80 kHz). Consequently, in these acoustic measurements, at an offside angle of 20° , which is a good approximation to the separation of the net and the chains from the bat's location, the strength of the clutter echoes relative to the net barrier's echoes is underestimated at different frequencies (by 2 dB at 25 kHz, 4 dB at 40 kHz, 10 dB at 60 kHz, 20 dB at 80 kHz). This limitation has to be kept in mind when interpreting the acoustic results.

E. Data analysis

1. Call detection and tracking

The bat's position during flight was reconstructed from the ultrasonic audio records off-line, using custom MATLAB software that implements a time-difference of arrival (TDOA) localization algorithm. Briefly, echolocation calls were detected on each channel using an energy detector that looked for threshold crossings of the audio waveform after low-pass filtering using a boxcar-averager with a 20 ms time constant. A window of time around each detector "hit" was

cut out of all audio channels and passed to the localizer, where the inter-channel arrival time differences were computed by crosscorrelation. These inter-channel arrival time differences were then used to compute a position estimate for the bat at the time it emitted that call (Barchi *et al.*, 2013; Gillette and Silverman, 2008; Wei and Ye, 2008). The TDOA position estimates were cross-checked using position data reconstructed from the stereoscopic video records via direct linear transform, but all further analysis was based on the localization data obtained from TDOA as they proved to be more reliable.

2. Broadcast beam measurements

The horizontal-plane emission direction of the sonar beam for each pulse was estimated from the relative amplitude of the signal at each microphone, corrected for spherical spreading (and atmospheric attenuation) based on the estimated position at which the call was emitted. The direction of the transmitted beam then was calculated as the resultant vector obtained by scaling each unit vector pointing from the bat to a microphone by the corresponding sound pressure at each microphone, and then summing over all such scaled vectors (Ghose and Moss, 2003).

3. Characterization of calling behavior

To best describe the acoustic parameters of each broadcast, an enhanced record of the bats' echolocation broadcast waveforms was created using an integrated delay-and-sum beamformer to follow the bat's track like a virtual telemike (Barchi *et al.*, 2013; Hiryu *et al.*, 2010). This enhanced call record used the entire microphone array, rather than a single microphone, to extract a clearer copy of each detected echolocation broadcast. Each extracted call was analyzed by a MATLAB analysis routine that estimated the 1st harmonic maximum frequency ($F_{\max}$), 1st harmonic minimum frequency ($F_{\min}$), and duration (Dur) using image analysis on the spectrogram of the call. Additionally, Inter-pulse intervals (IPIs) were measured as the interval between successive broadcasts, and the pulse repetition rate (PRR) was calculated from the IPIs with a 100-ms sliding time window. Finally, the occurrence of "strobe groups"—pairs of sounds emitted close together, interspersed with longer intervals (Petrites *et al.*, 2009; Surlykke and Moss, 2000; Moss and Surlykke 2010)—were identified from periodic fluctuations in the IPIs. To decide whether two sequential calls (k and $k+1$) constitute a strobe group, we used the following algorithm: Let $IPI(k)$ be the IPI preceding call k . Calls k and $k+1$ were identified as a strobe group if the "in-group" IPI [$IPI(k+1)$] was less than 45 ms, the preceding IPI was greater than 45 ms, and the "in-group" IPI was less than two-thirds of the preceding IPI. "Instantaneous" strobe group occurrence (% SG) was summarized as the percentage of calls within the interval 100 ms backward and forward in time that were assigned to strobe groups.

4. Definition of experimental events

On each flight, the bat entered the symmetrical chain maze and flew down either the right or the left path [Fig. 2(A)–2(C)]. This first passage through the maze constituted one “trial,” regardless of whether the bat circled back one or more times before landing. A flight was considered a successful trial if the bat flew from the hand, entered the maze, and flew within at least 2 m of the barrier’s length position in the room before landing or turning around. Two parameters were varied in three sets of experimental conditions. In Series 1 [Fig. 2(B)] the chain array was less dense, with a wider corridor (“wide”), and the net position was randomly altered every three trials (on average). In Series 2 [Fig. 2(C)] the chain array was more dense, with a narrower corridor (“narrow”), and the net position was altered every three trials (on average). In Series 3 [Fig. 2(C)] the chain array was more dense (“narrow”), and the net position was altered every 10 trials (on average). The reason for moving the net every three or 10 trials was to assess the potential effect of the bat’s memory for the space on its flight behavior (Barchi *et al.*, 2013).

The Y-shaped maze and overall symmetry of the room configuration allowed for several different schemes of separating the set of trials into meaningful classes. The first scheme is defined in terms of the path chosen by the bat—bat-left or bat-right, and the position of the barrier—barrier-left, barrier-right, or control (i.e., barrier-center). In order to specifically examine how the behavior of a bat changed when it encountered the barrier, the second scheme separated trials according to the bat’s path choice relative to the barrier—either “Same,” if the bat chose the blocked path, or “Opposite” or “Control” if the bat chose a path that was unobstructed (depending on whether the barrier was in either lane). Finally, to explore whether the bat’s memory of the previous trial influenced its behavior in the current trial, a third scheme divided the flights between those in which the position of the barrier was the same as the previous trial (Constant) and those in which the position of the barrier was different from the last trial (Move).

Although any one track is easily plotted, a simple overlay of all tracks for a given condition is not useful to characterize the data as a whole. There is variability in the tracks from bat to bat, and for each bat from trial to trial, in the exact path taken through the maze. Differences in flight speed would also confound a simple track-on-track overlay. Averaging the tracks is not useful, either, because so many of the times and locations involve zero values. To overcome this problem, the flight tracks were combined into visually intuitive two-dimensional “occupancy histograms” following a method developed previously to address this problem (Barchi *et al.*, 2013). These histograms illustrate the relative occupancy of sites on the horizontal plane of the flight chamber over all trials, thus providing a global picture of the bats’ flight behaviors. Occupancy histograms were computed by dividing the flight chamber into 2.5 cm square bins in the plan (width, length) dimension and then distributing all reconstructed bat positions for a given chain or barrier condition among these bins. The result is a two-dimensional map of the probability of bats occupying each bin in the room for

each condition. A similar approach was used to represent flight speed. In this case, the bat’s speed was calculated from sequential reconstructed positions along its flight path. The speeds were grouped into successive bins of 0.2 m in actual distance traveled along the flight path, and the mean flight speed in each bin was calculated for all flights in each experimental condition. The width of the distribution around the mean in each bin for each measured parameter of flight or acoustic parameter of broadcasts provided the information needed to carry out statistical tests, which were conducted chiefly to determine the location in front of the net barrier (“Same”) where the value of that parameter first diverged from the values on flights without the barrier (Opposite or Control). The tests were carried out as a running series of estimates along the track for the probability that the divergence of the parameter at each successive bin would have occurred by chance. The numerical value for the number of data-values in each bin, N , was the number of flights pooled across bats for each experimental condition (Series 1, 2, 3) and the category of flight (Same, Opposite, Control). Two methods were used—a rank sum test and a two-sample t -test, both implemented using the statistical toolbox in MATLAB.

III. RESULTS

A. Acoustic measurements of the auditory scene

The results of acoustic measurements of the echoes from the thin net barrier and the surrounding chains at a distance of 1 m from the net are presented in Fig. 3 (see below for why 1 m was used). From these measurements, the barrier net alone [Fig. 3(A)] produced a weak cluster of overlapping reflections (low amplitude XCR) with an uneven pattern of amplitudes across frequencies in the spectrogram, which is approximately 60 dB weaker compared to the flat-spectrum echo from a Plexiglas plane at the same distance (density shading of spectrogram). In contrast, by themselves, the immediately surrounding chains [Fig. 3(B)] produced multiple, comparatively strong echoes (higher XCR peaks), with only 35–45 dB attenuation compared to the Plexiglas plane. When the net barrier was placed in its blocking position among the surrounding array of chains [Fig. 3(C)], its reflections were 15–25 dB weaker than those of the chains. The net thus was significantly obscured by the much stronger echoes from the surrounding array of chains. This satisfied our intention that the net would likely be less detectable than the chains, and therefore difficult for the bat to detect until it had progressed well into the corridor that was being blocked. These measurements were made with a loudspeaker that had a narrower transmitting beamwidth compared to the bat (see Sec. IID3). Consequently, the bat’s beam ensonified the chains more than did the loudspeaker, which caused the estimate of 15–25 dB for the strength of the echoes from the chains relative to the net to be an underestimation by about 3 dB in FM1 and about 10 dB in FM2. Depending on frequency, then, the strength of echoes from the net actually experienced by the bats would have been about 18–35 dB weaker than echoes from the surrounding chains.

FIG. 3. Echoes from the net barrier and the chain maze at 1 m range. Pairs of panels show cross-correlation function (XCR) for broadcast and stream of echoes on top with spectrograms for (A) net barrier alone, (B) chains alone, and (C) net with chains on bottom. Broadcast is synthesized 3-harmonic FM sound; all waveforms averaged with 50 presentations to improve signal-to-noise ratio. The net returns multiple, relatively weak reflections; the chains return multiple, strong reflections. The XCR series is lower for the net than for the chain echoes at all delays. Spectrogram density scale at bottom displays decibels of attenuation compared to reference echo from a Plexiglas reflector at 1 meter from the emitter/microphone.

B. Flight behavior in the chains

The three bats completed a total of 922 trials (in 960 flights) in all three experimental series. In Series 1, a total of 216 trials were completed from 240 flights; in Series 2, 226 trials were completed from 240 flights, and in Series 3, 480 trials out of 525 were completed. These differences reflect the rejection of otherwise successful flights due to a momentary failure of the acoustic/video recording system while the bat was in flight. After entering the maze, each bat flew a consistent path until about 1 m before the position of the moveable net barrier, after which its behavior became conditional upon the state of the barrier. Figure 4 shows flight paths and broadcast-beam directions for three representative trials. The acoustic tracking system produced a smooth track for each trial, and the broadcast axis was well-defined for each sound on the track, except when the bat landed and its turning maneuver caused the beam to shift rapidly away from the direction of flight and possibly away from the microphone array. Each broadcast was emitted in the direction of flight, but pointed slightly in the direction of an upcoming turn, to lead into the turn.

Several different laboratory members served as the experimenter for releasing the bat at the start of each flight. While releasing the bat, that person alternated between using the left and the right hand, to avoid an externally imposed bias for the bat to fly to one side or the other. Nonetheless, all three bats developed a strong preference for either the left or the right corridor through the maze. Two of the bats (Frosty and George) preferred the right corridor, while one of the bats (Poe) preferred the left corridor (Fig. 5). These preferences were maintained throughout the course of the experiments, except for a single day in Series 2 during which George preferred the right rather than the left path. This is an interesting result, as handedness has been shown theoretically to improve homing in swimming and flying animals (Bandyopadhyay, 2013).

Aggregate flight paths and flight speed are illustrated in Fig. 6 for all three bats. Flight paths are shown as occupancy histograms in the top panels, grouped by experimental series and then by the state of the net—either blocking (same) or not blocking (opposite) the bat's chosen path. The lower three graphs in Fig. 6 plot average flight speed as a function of distance traveled, with this distance calculated relative to the barrier position (0 m). This allowed data from all flights to be combined and aligned to a common reference at $d=0=d_{\text{net}}$. Flights to the left or right side blocked by the net barrier all ended with landings on the net, while on flights to the non-blocked side the bat generally continued through the corridor and ended in the portion of the flight chamber beyond the chain array (length positions $<2\text{ m}$ in Fig. 2). In Series 1, with the wide chain array [Fig. 2(B)], the spread of the histogram about the flight path was greater than for Series 2 or Series 3, with the narrower chain array [Fig. 2(C)]. When the bats were in the wide corridor, the width of the occupancy histogram was roughly 20 cm, and when they were in the narrow corridor, the width was roughly 10 cm. The bats kept clear of the chains by flying approximately down the middle of the corridor, and responded to the narrowing of the passageway by tightening the spread of their flight paths (see Petrites *et al.*, 2009). The flight speed of the bats ranged from about 2 m/s to 4 m/s depending on conditions (Fig. 6). In Series 1 and Series 2, speed was lower (2–3 m/s) during the approach to the barrier than in Series 3 (3.5–4 m/s), where the bat had more experience with the placement of the barrier on one side or the other before it was changed. Flight speed in blocked flights fell to zero when the bat landed on the net, while in unblocked flights speed remained relatively stable as the bat simply continued flying along the unobstructed corridor. The point where the flight speeds began to diverge between blocked and unblocked conditions indicates the point at which the bat initiated locomotor action in response to the net. In these conditions, with numerous echoes from the highly reflective chains (Fig. 3), that is also likely to be the point where the bat detected the net. In Series 1 and 2, flight speed in the Same condition diverged from the Opposite and Control conditions at a point slightly less than 1.0 m before the position of the net; in Series 3, the speed divergence appeared earlier, suggesting earlier detection. (See statistical

FIG. 4. Tracks for three representative flights in narrow chain array showing broadcast beam axis relative to flight path. (Localized positions are circles, acoustic axes are arrows) (A) Moveable net barrier in center. (B) Net barrier on right. (C) Net barrier on left. During each flight, the bat moves smoothly along its course and aims its sound beam in the direction of flight, with a tendency to “lead” into the turn as it flies along the chosen corridor. Wide alternating scanning movements to the left and right do not occur. The gray shaded sector in C shows the approximate reaction zone where the presence of obstacles induces specific responses compared to the ongoing behavior associated just with the corridor.

FIG. 5. Left-right side preferences for each bat over all flights in Series 1, 2, and 3. Series 1 was conducted in the wide array between 2/8/2010 and 3/24/2010. Series 2 was conducted in the narrow array between 4/9/2010 and 6/10/2010. Series 3 was conducted in the narrow array between 9/2/2010 and 9/17/2010. Each of the three bats developed a strong preference for the corridor on one side or the other and generally maintained this preference throughout the course of the experiments.

tests in Fig. 8.) The distance for measuring the echoes from the net in the context of the scene thus was set at 1 m.

C. Acoustic behavior during flights

Analysis of the acoustic recordings yielded a multidimensional characterization of the bats' biosonar broadcasts during flights in the chain maze. The graphs in Fig. 7 show the mean PRR, highest frequency in 1st-harmonic sweep (Fmax), lowest frequency in 1st-harmonic sweep (Fmin), duration (Dur) and percent calls in strobe groups (% SG) (see Sec. II) for each 0.2 m distance bin relative to the net barrier's position along the length of the room. The standard error of the mean at each bin's data-point along each curve is sufficiently narrow that the place where the bats started to behave differently when the barrier was present (Same) versus when it was absent (Opposite, Control) is reasonably well-judged just by eye (Fig. 7). For all of the acoustic parameters plotted, in Series 1 (wide array) and Series 2 (narrow array), with random movement of the net barrier on average every three trials, values in the Same condition diverge from values in the Opposite and the Control conditions slightly less than 1 m before the bat reaches the net's position. In Series 3 (narrow array), with random movement of the net barrier on average only every 10 trials, these parameters diverge earlier in the flight, about 1.0–2.0 m before the net's position. The distribution of values in the occupancy histograms provides the information necessary to carry out statistical tests to locate the point of divergence more rigorously. Figure 8 shows the probability that the

FIG. 6. Two-dimensional occupancy histograms (plan view, top) for flight paths and mean flight-speed measurements (bottom) for all bats' flights through the chain maze in three experimental conditions. (A) All flights from Series 1 superimposed, with wide chain array [as in Fig. 1(B)] and random changes in net barrier [Fig. 1(A)] every 3 trials on average. (B) All flights from Series 2, with narrow chain array [as in Fig. 1(C)] and random changes in net barrier every 3 trials on average. (C) All flights from Series 3, with narrow chain array [as in Fig. 1(C)] and random changes in net barrier every 10 trials on average. To make occupancy histograms, 1 for each flight, the bat's X and Y positions [i.e., width vs length in Fig. 2(A)] were calculated at 20 ms intervals, and the resulting X-Y data were placed into 0.0025 m^2 position bins on the plan view of the flight chamber before combining across all flights and all bats. Occupancy histogram plots on left show flights with bat's choice of the left or right corridor the same as the position of the net barrier; plots on right show the bat's choice on opposite side. Note that flights on same side as net barrier end with landing on the barrier. The width of the occupancy histogram is wider in the wide chain array (Series 1, A) compared to the narrow chain array (Series 2, B and Series 3, C). Graphs at bottom show average flight speed versus distance to the barrier's location. On each flight, the bat's speed was determined for sequential positions in 0.2 m bins. The mean flight speed in each bin was then calculated for all flights in Control (C; barrier in center), Same (S; barrier on same side of bat's left-right choice), and Opposite (O; barrier on opposite side of bat's left-right choice). Error bars denote standard error around the mean flight speed.

FIG. 7. Acoustic behavior during flight to the net barrier. Graphs plot the mean pulse repetition rate (PRR), highest frequency in 1st-harmonic sweep (Fmax), lowest frequency in 1st-harmonic sweep (Fmin), duration (Dur) and percent calls in strobe groups (% SG) (see Sec. II) for each 0.2 m distance bin relative to the net. Individual curves show data from Control, Same, and Opposite flights in Series 1 (A), Series 2 (B), and Series 3 (C). Error bars denote standard error about the mean. In Series 1 (wide array) and Series 2 (narrow array), values in the Same condition diverge from values in the Opposite and the Control conditions slightly less than 1 m before the bat reaches the net's position. In Series 3 (narrow array), these parameters diverge earlier in the flight, about 1.0–2.0 m before the net's position. (See statistics in Fig. 8.)

FIG. 8. Statistical comparisons for behavior between flight conditions. Graphs show probability of difference between Same and Opposite conditions occurring by chance for flight velocity (black lines) and five acoustic parameters of broadcasts (in legend) at different distances from the net barrier. For each experimental condition (Series 1, 2, 3), the null hypothesis that the series of values at 0.2 m distance bins for each parameter of the Same flights was drawn from a population identical to that of the opposite flights. At each distance from the barrier (x axis), the α value for rejecting the null hypothesis is plotted on a log scale (y axis). Two statistical tests were performed—a rank sum test (plotted here) and a two-sample t -test (see Results), which produced nearly identical results. The horizontal dotted line denotes the threshold value for rejecting the null hypothesis after adjusting for the multiple comparisons for the data depicted in Figs. 6 and 7 (six measured parameters at 24 spatial distance bins = 144 paired comparisons). These tests confirm the view from Figs. 6 and 7 that the distance of reaction to the net is only slightly less than 1 m from the net for Series 1 and Series 2, but 1–2 m from the net for Series 3.

difference between the flights with the barrier present (Same) and the flights with the barrier absent (Opposite) occurred by chance (α values for rejection of null hypothesis) for each of the measured flight or acoustic parameters. (Plotted probability values, on a logarithmic scale, are from the rank sum test; values from the two-sample t -test were indistinguishable.) In Fig. 8, the range of distances where the probability values fall below $\alpha = 10^{-3}$ to 10^{-4} , which bracket the horizontal dashed line on the plots, agree well with the impression gained by eye from Fig. 7: In Series 1 and Series 2, the bats reacted to the barrier at a distance slightly less than 1 m in front of the barrier; in Series 3, they reacted between 1 and 2 m in front of the barrier.

In Fig. 9, the angle of echolocation emission is plotted relative to the bat's flight direction for the three experimental series and for four different segments of the maze. Series 1 is depicted in Fig. 9(A), series two in Fig. 9(B), and series three in Fig. 9(C). The angle of echolocation emission is plotted in polar coordinates, with 0° indicating emission directly along the flight path. Flights were combined in a side-agnostic manner; a positive angle indicates that the direction of call emission was biased toward the center-line of the room, and a negative angle indicates that call emission was biased away from the center-line of the room. The maze was divided into four segments, with the first two before the division point between the corridors (see Fig. 6) and the second two after the bat had chosen one of the side branches

[see Figs. 2(B) and 2(C) for an illustration of the chain mazes in relation to the polar plots]. For all three flight series, the axis of echolocation call emission aligned with the flight direction for the first two maze segments—while the bat was flying in the initial “stem” of the Y. Once the bat had chosen a side, in segments three and four, the axis of echolocation call emission deviated somewhat from the flight direction, but did so consistently. In all cases, once the bat had entered a side arm of the Y, it directed its echolocation calls away from the axis of flight toward the center of the maze—that is, in the direction of its turn. In effect, the bats consistently directed their echolocation calls into the turn, and toward the net barrier.

IV. DISCUSSION

In the experiments described here, big brown bats flew along the left or right corridor of a Y-shaped maze flanked by multiple, strong reflecting sources—the hanging chains [Fig. 3(B)]. In confirmation of previous observations for bats flying in clutter (Petrites *et al.*, 2009), their flight paths kept to the center of the corridor, thus approximately equalizing the flow of the surrounding objects moving past the bat on its left and right. Moreover, the orientation of the bat's broadcast sonar beam was aligned in the direction of flight, with additionally a tendency to anticipate an upcoming turn by leading in the direction of the turn (Fig. 9). Notably, the bats did not alternate their acoustic “gaze” (Ghose and Moss, 2003; Surlykke *et al.*, 2009) to the left and right to scan the scene as they passed the chains but instead maintained their gaze down the center of the approaching corridor. Several recent studies have examined big brown bats flying to capture suspended mealworms in a complex, but sparse scene relative to the dense, distributed clutter provided by multiple rows of chains used here (e.g., Falk *et al.*, 2014; Surlykke *et al.*, 2009). These sparse scenes can be characterized as consisting of a number of salient obstacles that impede the bat in its search and approach to the target. During flights to find and capture the mealworm, the bat aimed its sonar beam first at one obstacle and then at another as the obstacles were encountered. In contrast, in the experiments described here, during flights along the Y-maze of chains the bat kept its sound beam pointed in the direction of flight. It is likely that the greater uniformity of surroundings provided by the chain arrays, particularly the lack of a small number of highly salient objects comprising the scene, caused the bat to treat its surroundings not as a sequence of discrete obstacles but as a “clutter field.” The absence of side-to-side scanning may be related to the bat attempting to stabilize its view of the scene to equalize acoustic flow on the left and right sides. In addition, the density of the surrounding clutter and the proximity of the chains to the net barrier may make it difficult for the bat to separate the barrier from the chains simply by scanning in different directions. Its broadcast beam is too wide to achieve much segregation based solely on directionality. A further consideration is that, when the bat receives echoes from chains on its left, it also is receiving echoes from chains on its right at about the same moment. So, just when it is receiving echoes from the net that stimulate both

A wide chain alley (barrier alternates ~ every 2 trials)

B narrow chain alley (barrier alternates ~ every 2 trials)

C narrow chain alley (barrier alternates ~ every 10 trials)

FIG. 9. Mean direction of acoustic axis for broadcast beams of all bats at different locations in flight. (A) Flights in wide array with barrier moved approximately every three trials (Series 1). (B) Flights in narrow array with barrier moved approximately every three trials (Series 2). (C) Flights in narrow array with barrier moved approximately every 10 trials (Series 3). [See Figs. 2(B) and 2(C) for explanation of polar coordinates collapsed over left and right sides and four regions of the chain array; see Fig. 4 for example flights.] Vectors are combined for sounds emitted in each of the four regions of chain array. In all three experimental conditions, when entering the array (Region 1) and flying prior to the Y-shaped left-right separation (Region 2), the bats aim their sounds straight ahead relative to the flight direction. After entering the left or right corridor (Region 3), and passing through the most restricted space (Region 4), the bats aim their sounds toward the center of the room relative to the direction of flight, “leading” in the direction of the upcoming turn.

ears dichotically, it also is receiving echoes from multiple chains that overlap at both ears, to create a pattern of potentially dichotic stimulation that would be indistinguishable from echoes returned from “phantom” chains located in the flight path, when the actual chains are off to the left and right. This is the main reason why some powerful echo-rejecting mechanism not dependent on binaural differences must be present to suppress off-side clutter (Simmons, 2014).

In the presence of multiple, strong reflecting sources [the chains; Fig. 3(B)], big brown bats react abruptly to the

presence of a less reflective barrier [the net; Fig. 3(A)] only when they are about 1 m away (Figs. 7 and 8), at a point where their flight velocity is such that contact with the net barrier is likely to occur in only a few hundred milliseconds (Fig. 6). The two-choice (i.e., differential) design of the Y-maze allowed the bat’s relatively short-range reaction to emerge from the data in spite of strong side preferences in individual bats (red curves, Fig. 6). These principal findings are consistent with results from previous studies on obstacle avoidance (Grinnell and Griffin, 1958) and on flight in cluttered environments (Barchi, 2013; Petrites *et al.*, 2009;

Hiryu *et al.*, 2010). This leads to the most important result—that echoes from the net barrier were 18–35 dB weaker than echoes from the chains at the moment when the bat reacted by slowing down (Fig. 6) and changing its sound emission patterns (Figs. 7 and 8). The ability to detect the barrier at such a low signal-to-clutter ratio is a good index of the practical efficiency of biosonar in a complex scene.

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