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ORIGINAL PAPER

Interpulse interval modulation by echolocating big brown bats (*Eptesicus fuscus*) in different densities of obstacle clutter

Anthony E. Petrites · Oliver S. Eng · Donald S. Mowlds · James A. Simmons · Caroline M. DeLong

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Abstract Big brown bats (*Eptesicus fuscus*) use biosonar to find insect prey in open areas, but they also find prey near vegetation and even fly through vegetation when in transit from roosts to feeding sites. To evaluate their reactions to dense, distributed clutter, bats were tested in an obstacle array consisting of rows of vertically hanging chains. Chains were removed from the array to create a curved corridor of three clutter densities (high, medium, low). Bats flew along this path to receive a food reward after landing on the far wall. Interpulse intervals (IPIs) varied across clutter densities to reflect different compromises between using short IPIs for gathering echoes rapidly enough to maneuver past the nearest chains and using longer IPIs so that all echoes from one sound can be received before the next sound is emitted. In high-clutter density, IPIs were uniformly shorter (20–65 ms) than in medium and low densities (40–100 ms) and arranged in "strobe groups," with some overlap of echo streams from different broadcasts, causing pulse-echo ambiguity. As previously proposed, alternating short and long IPIs in strobe groups may allow bats to focus on large-scale pathfinding tasks as well as close-in obstacle avoidance.

Keywords Bioacoustics · Echolocation · Interpulse interval · Clutter · *Eptesicus fuscus*

A. E. Petrites (✉)
Department of Ecology and Evolutionary Biology,
Brown University, Providence, RI, USA
e-mail: Tony.Petrites@gmail.com

O. S. Eng · D. S. Mowlds · J. A. Simmons · C. M. DeLong
Department of Neuroscience, Brown University,
Providence, RI, USA

Introduction

Eptesicus fuscus (Palisot de Beauvois 1796), the big brown bat (see description by Kurta and Baker 1990), is an insectivorous echolocating bat that emits frequency-modulated (FM) sonar sounds in the 20–110 kHz band. *E. fuscus* echolocation pulses consist of several harmonic frequency sweeps, with the first harmonic sweeping from about 50 to 22 kHz (Simmons et al. 1979; Hartley 1992; Surlykke and Moss 2000; Saillant et al. 2007). Overall signal bandwidth extends through the second and third harmonics up to about 105–110 kHz. Adaptive changes in broadcasts and head-aim tracking occur when *E. fuscus* is flying past obstacles or capturing a target in the vicinity of other objects (Jen and McCarty 1978; Moss et al. 2006).

In radar and sonar, *clutter* is the generic term for objects in the background or off to the side of the target of interest that return additional echoes which can interfere with processing of echoes from the target itself (Denny 2007). Clutter thus implies masking by echoes from extraneous objects, and, as such, is a perceptual phenomenon that is demonstrated for *E. fuscus* (Simmons et al. 1979). Objects comprising clutter usually are both obstacles to flight posing collision risks, and sources of interfering echoes. Infrared video observations confirm that *E. fuscus* operates successfully both in open areas and in edge spaces with background clutter (Simmons et al. 2001; Simmons 2005).

The periods of time between onsets of successive pulse emissions (interpulse intervals, or IPIs) become shorter as bats approach prey or obstacles, but they do not decrease monotonically as does pulse duration. In the original quantitative obstacle-avoidance experiments (Grinnell and Griffin 1958), *Myotis lucifugus* bats were induced to fly through a row of thin, vertical wires spaced 30 cm apart. The bats increased the repetition-rate of their sonar sounds as they approached and flew between adjacent wires in the row, then decreased the rate after passing through. IPI values changed more or less continuously from 150 to 170 ms as bats approached the wires down to as short as 10 ms while the bats flew between them. Subsequent experiments with a variety of different bat species confirmed this finding (reviewed in Schnitzler and Henson 1980), and it was observed in *E. fuscus* using both stationary and moving objects (Jen and Kamada 1982).

While approaching a target, a bat must reconcile two competing requirements: to emit sounds rapidly enough that it can maneuver with respect to the flying insect or any obstacles in the short range, while also monitoring the locations of objects in the background, and at longer ranges, for planning its future flight path in the scene as a whole (Moss and Surlykke 2001). To accommodate these requirements, echolocating bats frequently emit sounds that alternate between long and short IPIs—in effect broadcasting closely spaced pairs of sounds to perceive rapid changes in the scene followed by longer intervals between pairs to probe farther into the scene. These pairs, or occasionally triplets, of sounds are called "strobe groups" (Moss and Surlykke 2001). Strobe groups are commonly used by *E. fuscus* when echolocating for insects near obstacle clutter (Moss et al. 2006). It has been hypothesized that the short, fixed IPIs between pulses within strobe groups make the perceptual problem of organizing returning echoes from multiple features on multiple targets easier for the signal processing system of the bat. Stable IPIs seem to provide the most effective stimulation to delay-tuned neurons in the bat's auditory system, which may facilitate neural representation of the distance to particular targets (Moss and Surlykke 2001). IPIs are related to other sound features even in horseshoe bats (*Hipposideros terasensis*) that emit constant-frequency sounds to sense Doppler shifts in echoes (Hiryu et al. 2005).

We tested the hypothesis that a species of bat known to operate in different amounts of clutter will adapt the pattern of emission of its sonar broadcasts to suit these conditions (see Obrist 1995). The experiments presented here employed an artificial three-dimensional clutter environment using a matrix of vertical obstacles—plastic chains suspended from the ceiling of a flight room and arrayed in multiple columns and rows, analogous to branches and leaves of vegetation. The chain matrix presents bats with a long sequence of echoes stretching away in time following each broadcast, rather than the narrow cluster of echoes returned by a single row of wires in a typical obstacle-avoidance test. The effective density of the obstacle array was manipulated by clearing corridors of different widths through the matrix of chains (corridors with high, medium, and low levels of clutter density). Based on broadcast patterns observed in previous obstacle-avoidance studies with this species (Jen and Kamada 1982), we predicted that IPIs of bats flying in high-density clutter would be shorter than those of bats flying through medium-density clutter, which would in turn be shorter than those of bats flying in low-density clutter. We also wanted to determine whether the close proximity of the nearest chains in the high-density condition challenged the bat's navigation sufficiently to force the bat to emit sounds at very short IPIs so that echoes from one sound would still be arriving when the next sound was emitted. This would cause *pulse-echo ambiguity* about which echoes were to be associated with which broadcasts, an important practical problem for radar and sonar systems (Denny 2007). We also predicted that more strobe groups would be observed in the high-density condition, where bats were at the greatest risk of colliding with numerous obstacles in close proximity for a sustained period of time, than in medium-density clutter, where the obstacles were present but farther away for the duration of the flight. We predicted IPIs in the low-density condition would resemble those used in free flight in the room essentially without obstacles.

Methods

Study animals

Four adult big brown bats, *E. fuscus* Beauvois, two females (Emma, Potter) and two males (Hoover, Snoopy), were used in the experiment. They were obtained from roosts in attics of private residences in Rhode Island. The animals were kept in individual cages of aluminum mesh in a room with controlled temperature (22°C) and humidity (60–70% relative). The light-dark cycle of the room was kept at 12 h-on:12 h-off (lights turned on at 22 30 hours and off at 10 30 hours) so the experiments could be performed on alert bats during daytime. Bats were fed mealworms (*Tenebrio* larvae) in the experiment as well as in a bowl placed in their cages. They were also provided with vitamin-infused water (using Poly-vi-sol drops). Bats were weighed daily, and their mealworm intake was adjusted to keep them within a weight range of 16–21 g. All procedures for care and use of bats were reviewed and approved by the Brown University IACUC in accordance with USDA and USPHS guidelines.

Experimental setup

The experiment was conducted in a flight room measuring 10.5 m long, 4.3 m wide, and 2.4 m high (Fig. 1). The walls and ceiling of the flight room were covered with 5-cm-thick black fireproof anechoic acoustic foam panels (Illbruck Acoustic, Minneapolis, MN, USA) that absorbed 20–25 dB of the energy of incident echolocation pulses to prevent

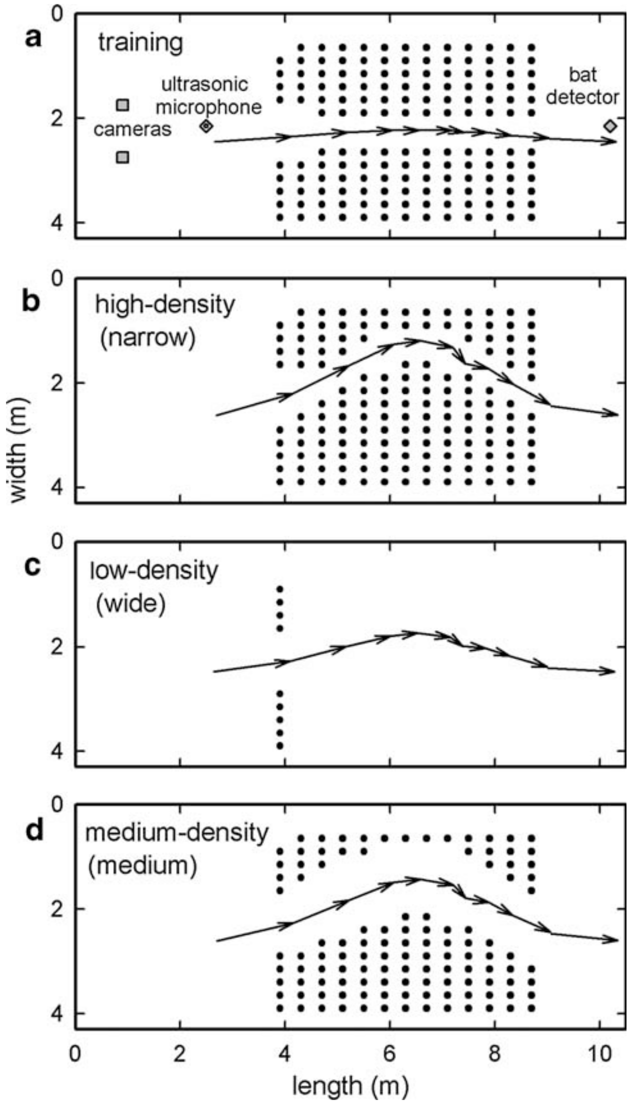


Fig. 1 Diagrams of the flight room from above, showing the chain arrays used here, with the positions of recording equipment relative to the typical release and landing locations of the bat (flight path shown by arrows). If completely filled, the array would contain 182 chains. **a** Training condition. **b** High density (*narrow corridor*). **c** Low density (*wide corridor*). **d** Medium density (*medium corridor*). Densities are shown in order of presentation

extremely strong echoes returning from the walls from affecting the bats' performance. Segments of black plastic chain 2.2 m long were hung from hooks in the ceiling to create the obstacle clutter conditions.

The lower ends of the chains were attached to metal hooks in the floor with rubber bands, which held them tense vertically, so the chains were stationary and yet capable of yielding if bats collided with them. The chains were composed of links 4.0 cm wide, 7.5 cm long, and 1.0 cm thick. Each chain, with its series of links, was a repeatable three-dimensional reflective structure for scattering incident bat sounds. Echoes from the chains are intuitively stronger and more complex than those produced from vertically stretched wires used in previous obstacle-avoidance experiments. Individual thin wires scatter incident sounds largely by specular reflection only at the point on each wire that is perpendicular to the axis of travel of the sound from the bat. When a bat flies towards the wires, its vertical position in flight varies so that this reflection point moves up and down the wire. Echoes from other points along the wire are too weak to give a clear picture of the extended nature of the wires from any of the broadcasts, which may explain why bats frequently collided with such wires (Griffin 1958) even though their overall behavior indicated that the size of the wire was adequate for detection. In contrast, each of the chains returns a succession of echoes from its component links to yield a picture of the extended nature of the obstacle it presents to the bat.

The rectangular matrix of hanging chains filled most of the flight room (Fig. 1). The front edge of the chain matrix was positioned 3 m away from the two video cameras that were used to follow bat flights, while the back edge of the matrix was located 1.8 m from the rear of the room and the wall on which bats usually landed. Approaching bat sounds were recorded from the far end of the room. The chains were arranged in 14 columns (left–right from the bats' approach) and 13 rows (front-back from the bats' approach), with a single position at the left front corner empty (to accommodate the edge of the apparatus for exhausting air from the room through a virus-screening Hepa-filter). This yielded a total of 181 possible chain positions in the matrix. Each chain column was separated from its neighbors on the left or right sides by a 25-cm gap, calibrated to be similar to the average wingspan of *E. fuscus* in flight (see Griffin 1958). Spread fully, the bat's wings extend for about 30 cm. This separation was just narrow enough to deter bats from readily flying between adjacent columns of chains. Instead, bats were channeled to fly through the larger gaps created by removing selected chains to create different clutter densities. Sequential rows of chains from front to back were separated by 40 cm gaps.

Chains were removed from selected points in different columns and rows of the matrix to create one *training-density* condition (Fig. 1a) and three experimental density conditions. The *high-density* experimental condition (Fig. 1b) with a narrow corridor was a curved path surrounded by 151 chains, and the *medium-density* condition (Fig. 1d) with a medium-width corridor was a curved path surrounded by 115 chains. The *low-density* condition (Fig. 1c) contained only the first (front) row of nine chains, to establish a direction for the bats to fly through. The training-density condition had the same width of corridor as the high-density condition but without any curvature. To ensure that the bats would not shy away from the chains in the high-density condition, we trained bats to fly through the matrix with the same high-density as the most demanding of the experimental conditions but without the curve in the path. Note that the front row, with four chains removed, gave the bats the same entry area to the matrix for all conditions.

Materials

The flight paths of the bats were recorded with a pair of thermal-imaging Indigo Merlin infrared cameras (FLIR Systems, Wilsonville, OR, USA) with 25-mm (0.5× wide-angle) lenses. The infrared spectral sensitivity of these cameras was 3–5 μm, providing for very good images of flying bats from their body heat among the visible, but much cooler, hanging chains. The cameras were located close to the wall of the flight room behind the flying bat and aimed so their fields of view converged at a point beyond the back wall of the room, allowing for stereoscopic reconstruction of three-dimensional flight paths through the chain matrix (Fig. 1). These cameras were synchronized so that corresponding left and right video frames provided a stereo indication of the bat's momentary flight position. Echolocation sounds were picked up by a Mini-3 heterodyne bat detector (Ultrasound Advice, London, UK) tuned to approximately 30 kHz and located at the back of the room. Both bat detector audio and infrared video were recorded on Hi-8 mm videotapes using two Sony GV-A500 Video Walkmans, one for each infrared camera. The bat detector output was sufficient to extract IPIs from the acoustic data. Other acoustic parameters such as duration and frequency content could have been extracted, but since they vary unpredictably with the orientation of the bat to the recording microphone as well as to any adaptive responses the bats might make, we believe that any conclusions drawn from their measurements would be unacceptably tenuous.

Experimental procedure

Each bat was trained to fly through the chain matrix after being released from the hand of an experimenter positioned in front of the matrix. Upon emergence from the back of the chain matrix, the bat would usually land on the anechoic foam of the back wall. A second experimenter then fed the bat one mealworm as a reward. The bat then was carried back to the front of the room for another flight. If bats landed in a location other than the back wall after passing through the matrix, they were retrieved (by hand or with a net) and then fed one mealworm. Bats that flew through the matrix once, failed to land and then flew unassisted through the matrix a second time were fed one mealworm once they had landed.

The entire experiment was carried out in the dark, so that the chains would not be visible to the bat. Additionally, both the links of the chains and the foam-covered ceiling and walls were black. Landing locations were visible as bright spots on the video monitor screens of the two Video Walkman recorders, which were placed well out of camera and microphone range. Small LED camping headlamps were used to search for bats after they landed.

The experiments were conducted from 12 August to 11 October 2005. The training phase of the experiment was conducted from 12 to 30 August 2005, and it consisted of flying bats through the training-density condition to acclimate them to the experimental task. All bats were then flown in the different experimental chain densities for a sufficient number of days to accumulate more than 100 flights overall for each condition. The density order high-low-medium was chosen to reduce the possibility that bats would become acclimated to the curved path in the high-density condition and then not change their behavior significantly when flying a similar, but more open path in the medium-density condition. The low-density condition provided a single row of chains for the bats to fly through, but no further path guidance after they passed through the gap. It took too long to remove and then reattach the chains for varying the density from flight-to-flight or bat-to-bat during a given day.

A "flight" consisted of a bat flying through one of the experimental chain matrix conditions, from the starting end of the room (with the cameras) to the back of the room (toward the bat detector). Bats were released by hand 1.5 m in front of the matrix, flew through the chains, and then emerged from the matrix to land on the acoustic foam covering the back wall. Occasionally, bats would not land, but would instead circle around to the front of the matrix and fly through again. These flights were included in the data. Trials in which bats failed to fly completely through the chain matrix or flew in the wrong direction were not included in the data. Following the training phase, the bats were then flown in the high-density condition for 10 days ($N = 96$ data flights), the low-density condition for 11 days ($N = 119$ data flights), and finally the medium-density condition for 7 days ($N = 117$ data flights).

Echo measurements

To characterize the stimuli reaching a bat's ears during an approaching flight, measurements of the strength of echoes reflected by successive rows in the chain matrix were taken in the training-density condition from a position 33 cm in front of the chain matrix. Bat-like FM ultrasonic sounds were projected at the chain matrix from an electrostatic loudspeaker (LTV, Inc., Model EST-2), and echoes reflected by links in the chains were recorded using a microphone system that mimicked the ears of a bat. A National Instruments PCI-6111e digital-to-analog converter board in a Pentium-III computer generated the test sound, a 1-ms long, linear FM sweep from 110 to 15 kHz. The test signal had an amplitude of 110 dB SPL (peak-to-peak) at a position 10 cm in front of the loudspeaker. Two Bruel & Kjäer Model 4136 ("¼-inch") condenser microphones separated by 3 cm recorded echoes of the test signals produced by the centrally positioned loudspeaker. Echoes picked up by the microphones were amplified 1000X and then filtered to a passband of 15–100 kHz with Wavetek-Rockland Model 442 variable bandpass filters. Echoes were digitized at a sampling rate of 500 kHz per channel through the analog-to-digital inputs of the National Instruments PCI-6111e board. Custom LabView and Matlab software windowed the data and averaged the reflected echoes from the targets for 20 repetitions of the test signal to improve the signal-to-noise ratio. In addition, on selected flights in the training configuration, an ultrasonic microphone (Titley Electronics, Ballina, NSW Australia) that was more sensitive than the B & K Model 4136 was placed between the video cameras, behind the release point, and pointed towards the far end of the chain matrix. This microphone thus was behind the bat during its flight and positioned to receive echoes of the bat's own signals from the chains while the bat made its flight.

Data analysis

Audio and video for the flights were clipped from the digital videocassettes to save only the segment of the flight where the bat was engaged in the array and then separated into AVI (video) and WAV (audio) files using Premiere Pro v.7.0. (Adobe Systems, San Jose, CA, USA). Each video file in the pair for each flight (left and right cameras) was truncated to start with the bat near the point of original release and end shortly after the bat emerged from the end of the chain matrix. A video motion-analysis software system (Motus v.8.2, Peak Performance Technologies, Centennial, CO, USA) was used to convert the bat's two-dimensional position on corresponding stereo frames of the two synchronized video recordings into a single set of points tracing the bat's flight path in three dimensions. This program computes a synthetic three-dimensional (3D) space enclosing the array of chains and the bat's zone of flight by registering the locations of a series of reference points on stereo pairs of video frames recorded by each of the video cameras. The resulting set of potential data-points inside this space is expressed in rectangular coordinates based on the measured locations of these reference points. The accuracy of reconstruction depends on the number and spacing of reference points used. The data presented in Figs. 5, 6, 7, 8 and 9 below were processed using 516 reference points, created in the video images by attaching six small metal clamps to individual chains at heights of 0.65, 0.96, 1.29, 1.64, 1.97, and 2.32 m above the floor. Of the 182 possible chains (Fig. 1), 86 chains distributed throughout the array were used to hold the reference points. The resulting reconstruction is shown in the horizontal (plan view, or left–right/front-back) plane in Fig. 2. The two camera views containing the original data depict a plane orthogonal to the view from above—in the left–right/down–up plane of an elevation view from the bottom of Fig. 2. Accuracy of reconstruction is affected primarily by the distortion caused by the wide-angle lenses; residual transformation of this distortion into the final 3D space is illustrated by the slight warping of the horizontal view in Fig. 2. The practical result is that any given point along the bat's flight path is known with respect to the nearest chains at an accuracy of about 2 cm along the left–right and down–up (original) dimensions and about 4 cm in the front–back (computed) third dimension.

The bat's position from one frame to the next was interpolated by the motion-analysis program to yield smooth lines showing the flight of each bat in two dimensions viewed from above. Bat flight paths through the chain matrix were plotted in SigmaPlot 6.0 (Systac Software, San Jose, CA, USA) as top–down views of the coordinates imported from video motion analysis files. The final data extracted from the video–audio file for each flight path was clipped for a second time, at the beginning where the bat entered the chain array at the first row of chains and at the end where it passed by the last row of chains. These truncation points were determined by careful inspection of those position plots and of bat soundtracks, which became muffled as the bat exited the matrix to approach and land on the acoustic foam of the far wall of the room. By this means, only the path positions and IPIs representing the bat's direct engagement with the chains were used to characterize the bat's behavior. For the low-density condition with only one row of chains, the imaginary position of the last row of chains present in the high-density or medium-density conditions was used as the exit reference so that all of the flights could be compared on the same spatial basis.

To determine IPIs without observer bias, these truncated echolocation soundtracks were analyzed (as WAV files) with a custom Matlab v.7.0 (Mathworks, Natick, MA, USA) program that exploited the characteristics of the bat-detector output. Because this output is at human-audible frequencies, the audio channel of each video Walkman recorder was adequate for logging acoustic data. First, the acoustic record for each flight was converted into a spectrogram of the detector's reduced-frequency version of the bats' ultrasonic signals. This display proved to be noise-resistant and very effective for marking the time-of-occurrence of successive bat sounds, because the time-frequency dispersion caused by the FM sweeps in the original sounds was removed by the bat detector. Second, the time-series signals from the individual frequency slices

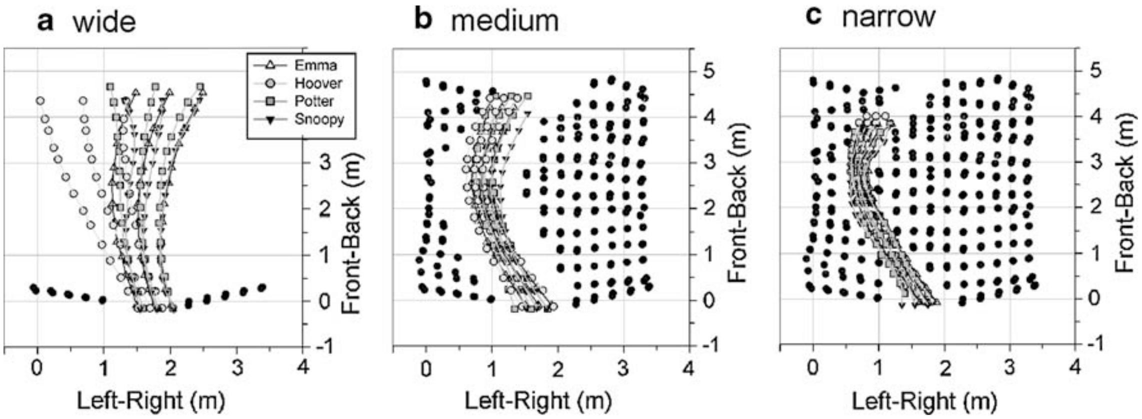


Fig. 2 Plan-view plots, derived from video 3D reconstruction, showing overlays of the mean ± 1 standard deviation for flight paths taken by four bats in the three obstacle densities. The slight warping of the rectilinear plots for the array of chains viewed from above (left–right/front–pack plane) originates in the distortion of the video images caused by the wide-angle lenses on the cameras, which have an elevation view of the scene from a plane perpendicular to this plan view (camera-view axes are left–right/down–up from the bottom of these plan views; see Fig. 1). The 3D reconstruction of the scene by the video motion-analysis programs accommodates the lens distortion in the plane of the video images, but some residual warping appears in the computed orthogonal plane shown here (see "Methods—data analysis")

of the spectrogram were full-wave rectified and summed together across frequencies to create a single spectrogram envelope across all audio frequencies in the bat-detector output for each flight. Third, this aggregate spectrogram envelope, which contained a series of peaks for successive bat sounds emitted during the flight, was smoothed with a Butterworth filter and then a moving-average filter to maximize isolation of peaks registering individual sounds from their neighboring peaks. Finally, the Matlab program produced a graph of the spectrogram envelope "function", thus creating a display of the sequence of sounds, while also computing a point-process representation that listed time-of-occurrences of the peaks to determine when each bat sound occurred and to calculate the IPIs for that flight. The timing precision for determining the occurrence of bat sounds from the spectrogram-processing program on bat-detector output was ±100 μs; this is very respectable for an automatic process considering that individual FM bat sounds are several milliseconds long. Sequences of bat sounds were characterized by the times-of-occurrence of sounds and by the IPIs between successive sounds recorded during each flight. These were plotted both as time series for the sound streams and as distributions of IPIs for each bat in each condition.

Sequences of sounds extracted for each flight were plotted and inspected for the existence of strobe groups across the three-clutter conditions. A strobe group was characterized by a long IPI (the inter-strobe-group interval) followed by one or more short IPIs (the intra-strobe-group intervals). In practice, IPIs between strobe groups tended to be 2–3 times longer than IPIs within strobe groups. To determine the significance of any difference between distributions of IPIs over the three density conditions, we also conducted pairwise comparison *t* tests.

The time series of IPIs obtained from each experimental condition were coded in terms of whether a given IPI was (1) longer than the previous IPI, (2) shorter than the previous IPI, or (3) the same as the previous IPI. The criterion for change was a lengthening or shortening of the IPI by more than half of the standard deviation (SD) for the distribution of IPIs being processed. This excluded small variations in IPI less than half the SD from consideration, so that only relatively large changes came to define the occurrence of strobe groups. These coded sequences were subjected to analysis for sequential first-order shorter-versus-longer-versus-same probability contingencies using the Markov chain method with UNCERT (Hailman and Hailman 1993).

Each IPI value (from the onset of one pulse to the onset of the next) corresponds to a time interval for which echoes from the first sound could continue to arrive from rows of chains without overlap of echoes from that sound into the period of echo reception that follows the second sound. If echoes arrive from the more distant chains at delays longer than the IPI value, then the second sound will be followed by echoes of *both* sounds, creating confusion about which broadcast (the first or the second) actually was responsible for the echoes. The first step in learning whether bats can disambiguate echoes to the corresponding broadcasts is to demonstrate that bats will allow echo delays to be longer than IPIs. Accordingly, using the delay of echoes in air (5.8 ms/m), the maximum distance, or range, of chains that would not cause pulse-echo ambiguity was determined from each IPI value in selected flights. These unambiguous pulse-echo range lines were plotted along with the ranges of all the chains in the array to determine the extent of pulse-echo ambiguity in different clutter densities.

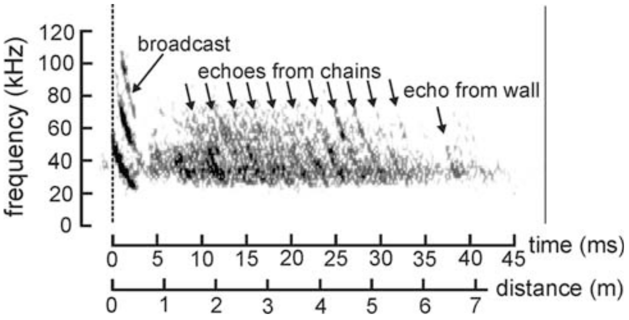


Fig. 3 Spectrogram of broadcast sound (*at left*) and echoes reflected by all rows of chains for a bat flying towards the chain array at the moment of passing the first row of chains. This recording was made by an ultrasonic microphone (Titley Electronics, Ltd) placed on a stand 1 m behind the bat. The bat's broadcast and echoes from all rows of chains are clearly visible

Results

Flight paths

All four bats (Emma, Hoover, Potter, Snoopy) learned to fly through the chain array at the training density and made the transition to the sequence of different experimental densities without incident. No collisions with any of the chains were observed during any of the experimental flights. Figure 2 shows overlays of the mean ± 1SD for all of the flight paths of the four bats in each of the three experimental conditions. In the narrow and medium conditions, the corridor through the chains constrained the bats to fly virtually identical paths overall, whereas in the wide condition, the flight paths of the bats diverged slightly after they had passed the initial row of chains. Flight velocities were 3.8 ± 0.99 m/s (mean ± 1SD) in the high-density array, 4.9 ± 1.2 m/s in the medium-density array, and 4.7 ± 0.65 m/s in the low-density array. Pairs of velocities were significantly different in t tests between the high-density condition and either the medium-density or the low-density condition, ($P < 0.001$), but the medium-density and low-density conditions were not different ($P = 0.43$). The bats thus flew more slowly in the high-density array, while they flew at the same velocity in the medium- and low-density arrays. Video recordings showed the bats making 11–12 wingbeats/s in representative flights.

Strength of chain echoes

Recordings of echoes from the chains received by the ultrasonic microphone located behind the bat and pointed in the direction of flight registered strong echoes from all of the rows of chains while the bat moved through the array (Fig. 3). The bat's broadcast, with its first, second, and third harmonic sweeps clearly visible, was followed in time by reflections off the floor at 5 ms and then from each of the 11 rows of chains in the array that were in front of the bat this point in its flight (the bat already had passed the first row and was located approximately at the gap in the second row). Less well-organized signals in the spectrogram at delays of 7–10 ms were returned from several of the chains in the first few rows that were off to the bat's left and right sides. Since they were near the bat as well as the microphone, their reflections overlapped.

The echoes returned by the chains for the incident "artificial bat" FM test signal were very strong. Figure 4 shows the sound pressure of echoes from chains at different distances in comparison with the sound pressure of echoes from several types of targets—an ideal sphere (Lawrence and Simmons 1982), real plastic spheres from 3.2 to 19.1 mm in diameter (Simmons and Chen 1989), and mealworms at different orientations (Simmons and Chen 1989). Estimated echo-detection thresholds for *E. fuscus* are plotted on the same graph (Kick 1982; Kick and Simmons 1984). For the nominally 110-dB SPL broadcast, the amplitude of echoes returning from the chains in the first four rows was 87–97 dB SPL. As might be expected because each chain is an extended target, not a point target, echo strength declined only slightly for increases in the distance to the chains from 20 to 140 cm. Compared to the other experimental targets, the structure of the chain matrix creates echoes that do not decrease as much in sound pressure at increasing distances. Useable echoes were returned to the flying bat by all rows of the matrix. We calculated that these echoes were well above detection thresholds at the distances where the bats encountered them, indicating that acoustic conditions favorable to pulse-echo ambiguity existed in the chain flights.

Interpulse intervals

The bats emitted continuous sequences of echolocation sounds on all flights through the chain arrays. All of the bat sounds were registered on the audio tracks of the video tapes with high signal-to-noise ratios. A total of 7,650 IPIs were analyzed from sound records obtained in 332 flights by the four bats. The bats emitted their sounds in a pattern that depended on the density of the array. Figure 5 shows the timing of sonar pulses for six representative flights by one bat (Hoover) in each of the experimental conditions. All of the acoustic data for the chain-array flights has the format shown in this illustration. During flights through the narrow corridor of the high-density array, bats emitted many more sounds and sounds at shorter IPIs than in the

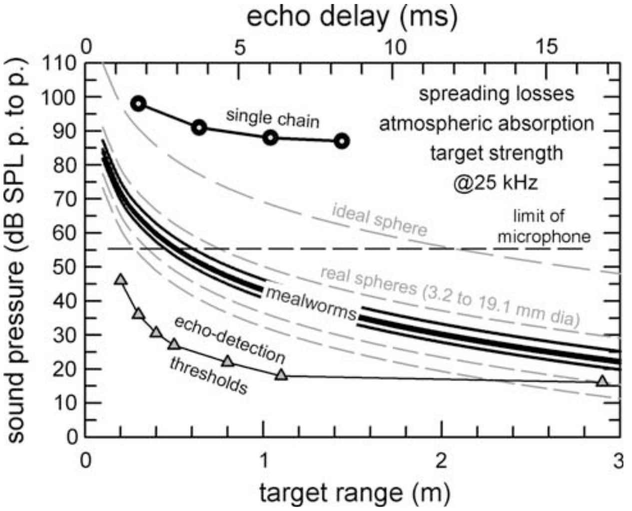


Fig. 4 The relative strength of echoes reflected a single chain in the array at distances from 0.23 to 1.42 m (*black circles*) for comparison with the strengths of echoes reflected by other objects used in experiments with bats. First, for reference, an ideal sphere having no loss due to target strength, just distance (*gray long-dash curve*) (Lawrence and Simmons 1982); second, a series of real spheres with diameters from 19.1 down to 3.2 mm (*gray short-dash curves*); and, third, a mealworm suspended on a fine wire (*solid black curves*) (Simmons and Chen 1989). Triangular gray data-points show echo-detection thresholds for big brown bats estimated or measured in several experiments (Kick 1982; Kick and Simmons 1984; Simmons et al. 1992)

medium-width, medium-density or wide, low-density arrays (Fig. 6). Moreover, nearly all of the sounds emitted during flights through the high-density condition were organized into strobe groups—doublets or triplets of sounds separated by short IPIs, with longer IPIs between strobe groups (see representative example in Fig. 5). Strobe groups were present, too, in the sound patterns for flights in the medium- and low-density conditions, but they did not dominate the results.

The overall mean IPI for the high-density condition ($n = 3{,}259$ IPIs) was 41.7 ± 19.7 ms. The mean for the medium-density condition ($n = 1{,}878$ IPIs) was 74.9 ± 56.4 ms. The mean for the low-density condition ($n = 2{,}513$ IPIs) was 56.0 ± 28.9 ms. *T* tests for pairwise comparisons of the three means revealed that the difference between each pair of means was highly significant ($P < 0.0001$), but, of course, the number of total measurements ($n = 7{,}650$) was very large. These mean IPI values and the statistical significance of their differences are misleading, since sounds occurred in sequences that had a complex organization with regard to IPIs. Combining IPIs across flights to represent each flight, each bat, or each condition by a single value (the mean) assumes that the distribution of IPIs is unimodal and reasonably symmetrical, but the occurrence of strobe groups may produce bimodal distributions composed of short IPIs within strobe groups and long IPIs between strobe groups.

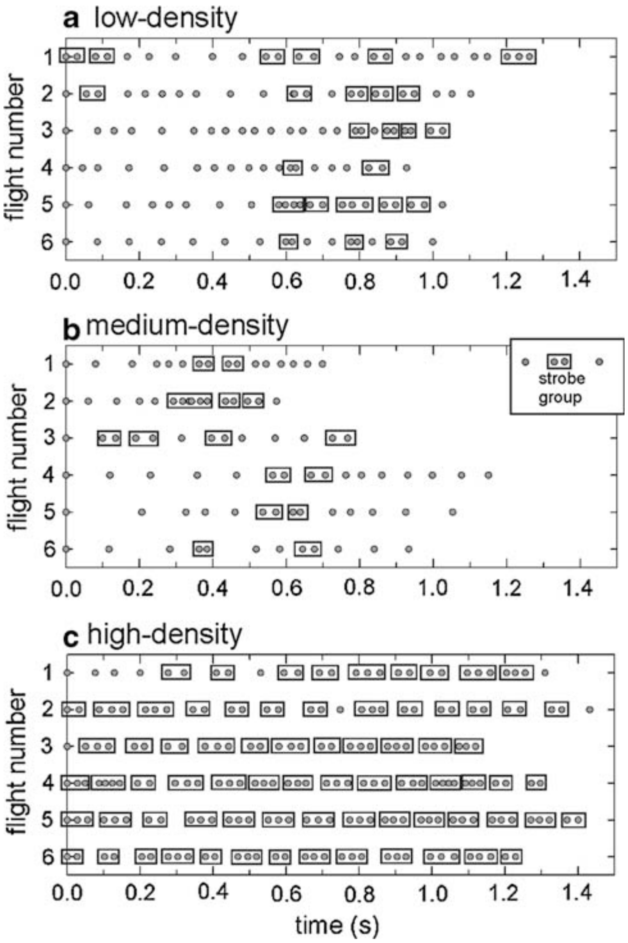


Fig. 5 Times-of-occurrence of sonar broadcasts during six flights by one bat (Hoover) in each of the three obstacle densities. Strobe groups (pairs or triplets of sounds grouped together at short IPIs) are outlined by *rectangles*

The order of presentation of the experimental conditions was high-low-medium for all of the bats, and it is possible that the progression of mean IPIs from long to short in this same order is a consequence of bats' becoming accustomed to the task as the experiment progressed. When we inspect the time history of the experiment (Fig. 6), we see an increase in the mean IPI from one experimental condition to the next condition, as tested above, but there does not appear to be a pattern of increasing IPIs across time *within* each condition. Across flights, the scatter of mean IPI values remains within the span of 1SD across the means. It thus is unlikely that the increasing mean IPIs *across* conditions are merely due to the bats' becoming experienced. Instead, changing the clutter density caused a step change in the mean IPI due to some aspect of the experimental conditions.

Figure 7 shows histograms for the distribution of IPIs for and the number of sounds emitted by each bat in each experimental condition. Individually, each bat emitted shorter and more tightly clustered IPIs in the high-density condition than in the medium- or low-density conditions.

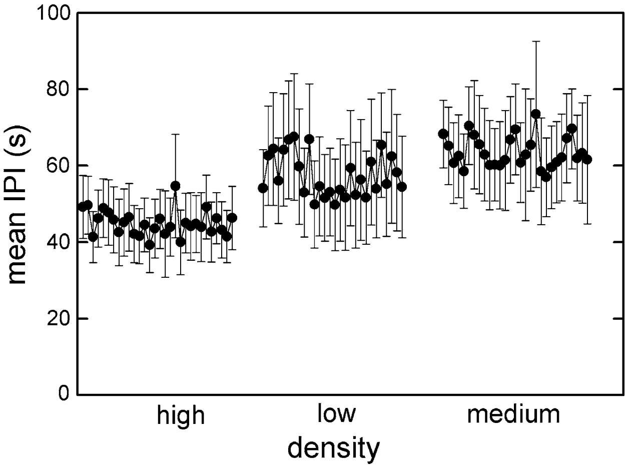


Fig. 6 Plot of mean IPIs ± 1 standard deviation for successive flights combined across all four bats in the three obstacle densities. From *left* to *right*, the sequence of data-points is for successive flights in the order of occurrence and conditions in the order of presentation. The overall trend of increase is stepwise between conditions rather than smoothly from flight-to-flight within each condition

The four bats behaved about the same, making the experimental conditions, not the individual bats, the focus of our data analysis.

Figure 8 shows the distribution of IPIs for each chain-array condition combined across all four bats. On average, the bats used fewer sounds per flight (1,878/117 = 16) in the medium-density condition than the high-density (3,259/96 = 34) or low-density (2,513/119 = 21) conditions. From these proportional distributions, it is apparent that the pattern of broadcasts is qualitatively very different in the high-density condition than in the medium- and low-density conditions. In the high-density array, the distribution of IPIs is tight and unimodal with a peak at about 30 ms, whereas in the other conditions the distributions are broader and bimodal. In both the medium-density and low-density conditions, the shorter-interval peak is at about 40–50 ms and the longer-interval peak is at about 80–90 ms. Additional data on IPIs used by *E. fuscus* during free flight along a 4-m path in the same room (309 measured IPIs from 25 separate flights for a mean of 12 sounds per flight) by two bats making 25 flights (Saillant et al. 2007) was analyzed (Fig. 8), and also contained two peaks located at 50 and 90 ms, which further illustrates the unique nature of the bats' echolocation behavior when flying in the high-density array.

Strobe groups

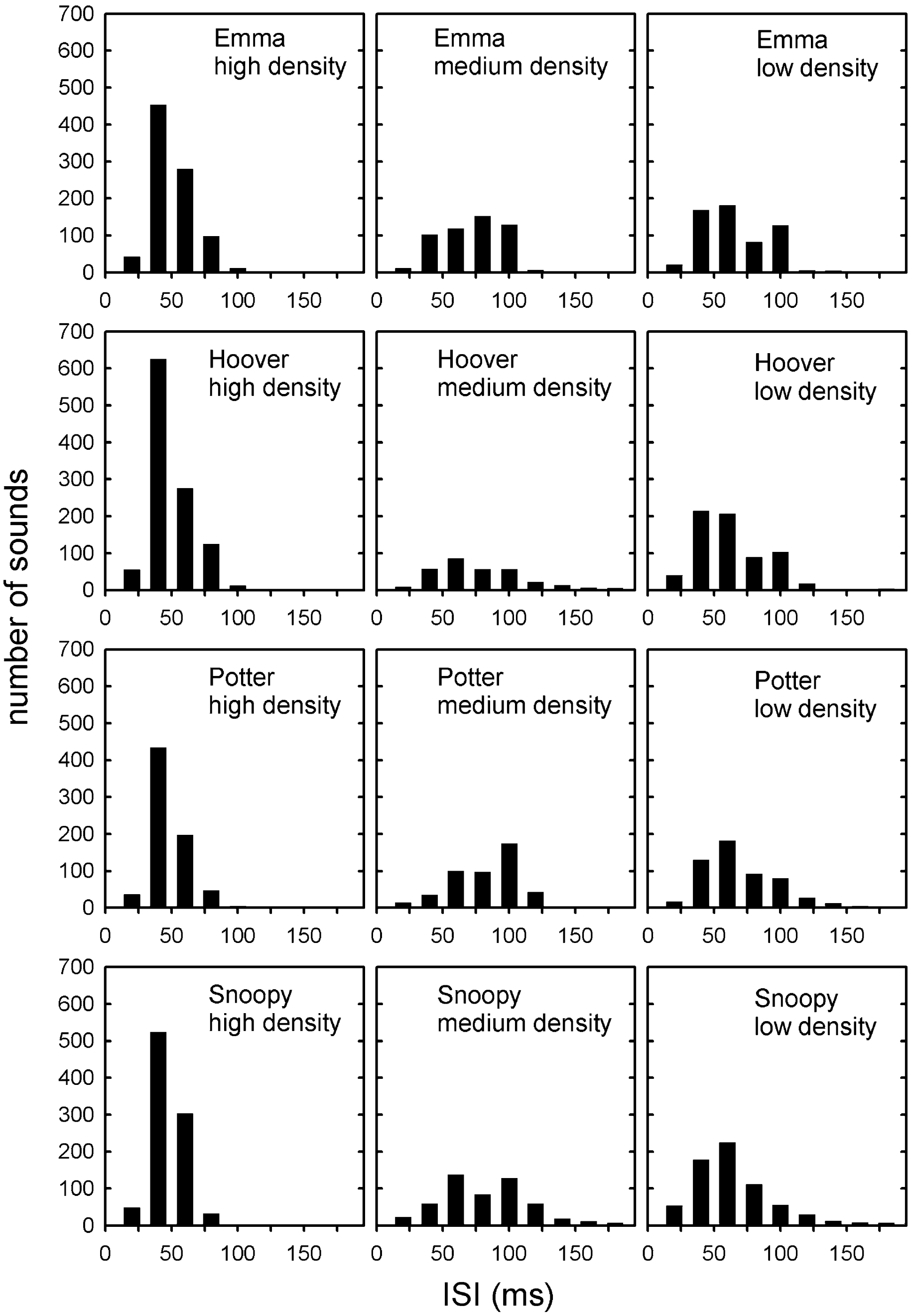
In the examples of pulse timing shown in Fig. 5, IPIs within well-defined strobe groups were only 25–35 ms long, whereas IPIs between strobe groups were about 50 ms (consistently, in the high density condition) or even up to 100 ms (irregularly, in the low density and high density conditions). Using our definition of a strobe group (a longer IPI followed by one or more shorter IPIs, with change considered as greater than half the SD of the IPI distribution), the entire dataset was processed using a first-order Markov chain analysis to determine the probability of alternating long and short IPIs in each of the three experimental conditions. Table 1 gives the probabilities of shorter–longer-same IPIs conditioned on whether the initial IPI was itself shorter, longer, or the same as its predecessor. On average, the occurrence of strobe groups would be manifested by sequences of IPIs that alternate between being longer and shorter. In the high-density condition, IPIs that have just become longer (the *longer* preceding IPI) are highly likely to be followed by IPIs that are *shorter* ($P = 0.880$). They are unlikely to be followed by even longer IPIs ($P = 0.019$) or by IPIs of the same length ($P = 0.101$). In our sample bat soundtrack (Fig. 5), virtually all of the sounds were arranged in strobe groups, so that a single long IPI was bounded by two or more short IPIs in the preceding and following strobe groups. So, two successive long IPIs occurred rarely. IPIs that have just become shorter are more likely to be followed by IPIs that are longer ($P = 0.603$). This signifies a strobe group comprised of two closely spaced sounds, a doublet. If a particular strobe group begins with the transition from a longer IPI to a shorter IPI and contains three closely spaced sounds in succession (a triplet), the initial shorter IPI will be followed by an IPI of similar length ($P = 0.367$). It is less likely to be followed by an even shorter IPI because intra-strobe-group intervals already are very short ($P = 0.030$). In the high-density condition, more than 90% of the sounds were emitted in strobe groups (Table 1a). That same alternation of lengthening or shortening occurs in the medium-density or low-density conditions for roughly half of the sounds (Table 1b, c). However, we observed relatively few IPIs shorter than 50 ms, and even fewer as short as 25–35 ms (Fig. 8) (IPIs that serve as the signature for strobe groups). The proportion of IPIs in the range of 25–35 ms is about 0.44 in the high-density condition (where strobe groups dominate), about 0.073 in the medium-density condition, and about 0.18 in the low-density condition. There are not nearly enough of these short intervals for the alternation probabilities shown in Table 1b and c to come from strobe groups. Instead, most of the alternations are between the much longer IPIs associated with the peaks at 40–50 ms and 80–100 ms in the distributions.

Discussion

The chain-array task

Intense reflections were returned to the ultrasonic microphone by all of the columns of chains in response to the bats' broadcasts during flights. Echoes from the chains are

Fig. 7 Distributions of IPIs from all flights for each bat in the three obstacle densities. *Bars* show the absolute number of sounds within a range of IPI values in each histogram bin



70 dB or more higher compared to the echo-detection thresholds of *E. fuscus* (Fig. 4), so they would have been very audible to the bat during the entire flight. As might be expected for such strong targets, during flights through the array, the bats did not collide with any of the chains, even when passing through the narrow corridor in the high-density condition (Fig. 1b). Screens of vegetation are strikingly similar to this chain array in reflecting strong echoes from leaves and branches that are broadly distributed in depth and direction (Müller and Kuc 1997; Grunwald et al. 2004; Yovel et al. 2008). When probed with bat-like FM sounds, different kinds of plants reflect dense clusters of echoes that overlap to varying degrees, creating patterns of delays and spectral interference notches that prior research has established to be the basis for single-object perception by *E. fuscus* (Simmons et al. 1990). This same distributed acoustic backscatter was observed from the chains (Fig. 3), with each major element of the reflections attributable to a row of chains. In acoustic terms, the chain matrix is a realistically complex clutter stimulus for testing bats because the depth of virtually the entire array can be sensed by bats as they enter the clutter zone.

It is tempting to compare the chain array with the row of vertical wires used in obstacle-avoidance tests (Griffin

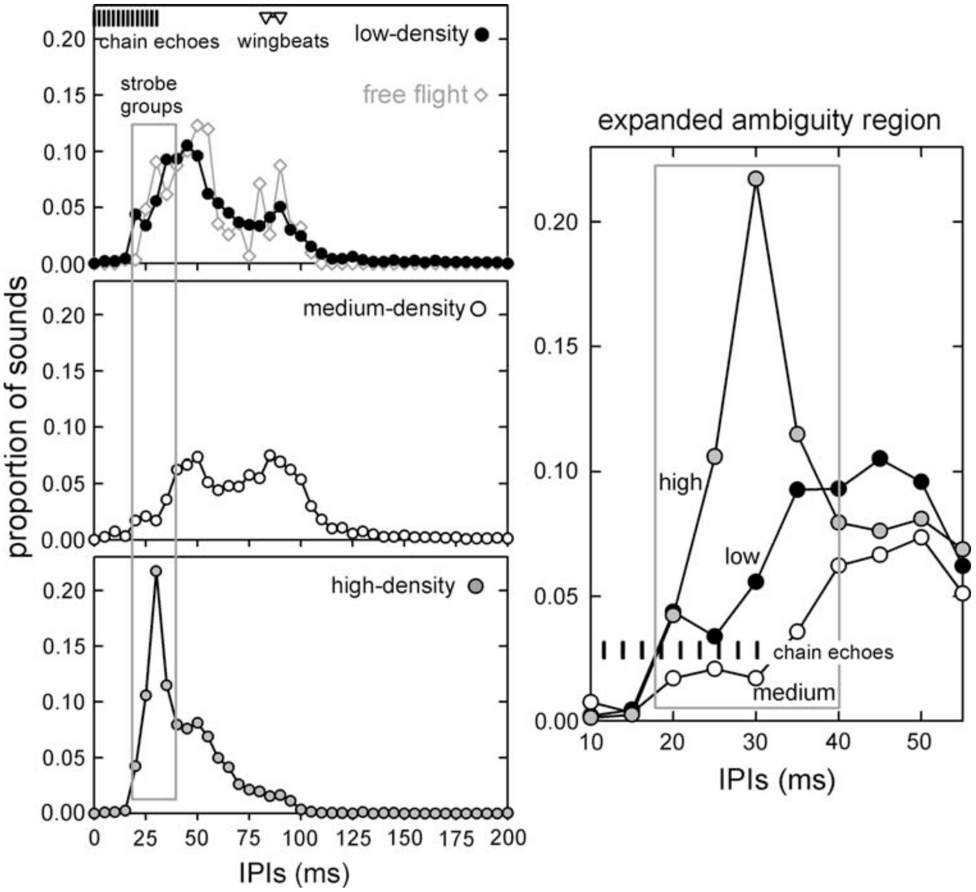


Fig. 8 Combined distributions of IPIs for all flights in low, medium, and high densities. Data are plotted as proportions to compensate for differences in the absolute number of sounds used by different bats in different conditions. The expanded plot (*right*) shows the region of IPIs most sensitive to pulse-echo ambiguities. The *horizontal row of vertical tic-marks* shows the span of chain echoes. *Inverted white triangles* depict the range of wingbeat intervals. Proportion of IPIs emitted in free flight in the flight room are shown by the *gray line* with *gray diamonds*

Table 1 Probabilities that IPIs representing given transitions will be followed by longer IPIs, shorter IPIs, or IPIs of about the same length

Preceding IPI	Following IPI		
	Longer	Shorter	Same
a. High density			
Longer	0.019	**0.880**	0.101
Shorter	**0.603**	0.030	0.367
Same	0.457	0.148	0.394
b. Medium density			
Longer	0.210	**0.510**	0.280
Shorter	**0.578**	0.224	0.198
Same	0.238	0.364	0.398
c. Low density			
Longer	0.175	**0.559**	0.265
Shorter	**0.549**	0.169	0.282
Same	0.320	0.337	0.343

Probabilities of alternating IPI lengths (shorter IPIs being followed by longer IPIs or vice versa) are in bold

1958; Grinnell and Griffin 1958; Jen and McCarty 1978; Jen and Kamada 1982). However, obstacle-avoidance tests with wires were not designed to explore the bat's reactions to clutter; instead, they were intended to determine how the bat's echolocation behavior reflected the bat's sensitivity to objects as they approached. The whole point was to *reduce* the strength of reflections by decreasing the diameter of the wires to assess how far away the bat would react. In contrast, the point of the chains was to minimize the dependence of the strength of echoes on distance so that individual objects would be detected across a wide span of distances. The bats flying in the chain array received a barrage of strong, clearly detectable echoes extending in time over 30–35 ms (Figs. 3, 4) corresponding to chains extending in space over 5–6 m. As discussed below, the bats exhibited reactions to the chains that covered perceived spaces out to 5 m or so, whereas in obstacle-avoidance tests with wires, distances of reaction rarely exceeded 1 m and were often shorter.

Interpulse interval patterns

The echolocation behavior of the bats flying in the chain array is consistent with hypotheses based on the density of the arrays, with one seeming exception—the significantly longer mean IPI value for the medium-density condition. But that observation actually confirms these expectations by revealing the bats' perception of the clutter depth itself. When a bat was just passing through the gap in the first row of chains, echoes continued to arrive from successive rows of chains for up to 30 ms following each broadcast (Fig. 3); the tic-marks in Fig. 8 align this period of echo arrival with the IPI distributions themselves. Second, echolocation sounds usually are emitted in rough synchrony with a flying bat's wingbeats (Schnitzler 1971; Suthers et al. 1972; Kalko 1994; Wong and Waters 2001; Moss et al. 2006), so we have indicated the period of the wingbeat frequency (11–12 Hz) estimated from the videos (Fig. 8). The two main peaks in the IPI distributions for the low-density and medium-density conditions do indeed correspond to intervals between sounds of 1 per wingbeat (80–90 ms) or 2 per wingbeat (40–50 ms). In contrast, the distribution for the high-density condition has a peak sharply localized at 30 ms, which, although not far from an average of three sounds per wingbeat, is a misleading index of wingbeat synchrony, because the distribution is skewed by the large number of short IPIs within strobe groups. IPIs predominantly alternate between short and long in the high-density condition (Table 1a), so a better index is to combine the roughly 30-ms interval for within a strobe group with the longer 50-ms interval that follows a strobe group to obtain a total interval of 80 ms, which now does correspond to a single wingbeat period. For our six sample flights (Fig. 5c), on average, 11–13 strobe groups occurred in 1 s of flight, so a rough synchrony of sonar emissions to wingbeats may occur for all three clutter densities.

Echolocation in different clutter densities

Our primary finding involves the big brown bat's echolocation strategy for coping with perception of the clutter while maneuvering to fly through the array. The pattern of emission of sonar sounds in the low-density array, with only the initial, entry row of chains (Fig. 8), is similar to the pattern used by bats freely flying along the length of the room (compare curves with black circles and gray diamonds in the plot for the low-density condition). We expected this, because both conditions involved an open space comprising most of the room. With one crucial difference (see below), the pattern of sonar emissions in the medium-density condition was similar, too. The distributions for both low-density and medium-density clutter were bimodal with peaks around 40–50 and 80–90 ms. In the low-density and medium-density conditions, the bats' flight velocities were similar, too. In the low-density condition, there were no chains to impede the bat's flight once it passed the single row of chains that served to align its entry into the space normally occupied by the rest of the chain array. However, in the medium-density condition, there was only a corridor created by removing chains from four to five rows in a curved path; all of the other chains were present. When the bat flew along the center of this corridor (Fig. 2b), the distance to the nearest chains on the left and right was about 100–120 cm. As bats flew into the turn in the corridor, they briefly approached to within about 80 cm from the nearest chains to their left and front. These distances are 3–4 times larger than the bat's maximum wingspan of roughly 30 cm. Nevertheless, from the overall similarity of the IPI distributions in the low-density and medium-density conditions (Fig. 8), the bats treated these two conditions as perceptually similar, at least in the context of the ongoing action—flying through the array. In effect, the presence of numerous chains located as close as 100 cm and densely arrayed over distances as far as 5 m (the chains in the medium-density condition) did not evoke a radical change in the pattern of pulse emissions compared to the low-density, or free-flight condition, with only the wall located 3–5 m away in the bat's path.

In striking contrast, in the high-density array, the bats' echolocation behavior was radically different even though their actions were the same. Here, during flight, bats were 60–70 cm or less away from the nearest chains on the left and right. As they turned along the corridor, the bats actually approached to within 30–35 cm of the nearest chains (Fig. 2c), which is about the breadth of their wingspan. The bats' flight velocities were also significantly slower than in the other conditions. High-density IPI distributions had completely different shapes. Nearly all of the sounds emitted during flights through the high-density array occurred with IPIs shorter than 50–60 ms, and even less than 35 ms, whereas few sounds were emitted with such short IPIs in the medium- and low-density conditions (Fig. 8).

The region of greatest difference across the distributions was for IPIs between 20 and 40 ms (Fig. 8). The righthand plot in Fig. 8 shows an expanded region (of ambiguity; see below) with the low-, medium-, and high-density IPI distributions superimposed. When we concentrate on this region, the effects of clutter density are magnified, and it is clearer to discern several aspects of bat behavior. The proportion of IPIs in the range of 20–40 ms is about 0.56 in the high-density condition, about 0.15 in the medium-density condition, and about 0.32 in the low-density condition. This proportion is so high in the high-density condition, and the shape of the distribution is so compressed, that the high-density condition apparently belongs to a different regime of echolocation behavior.

A detailed comparison of the high-density condition with the medium-density and low-density distributions illustrates what we mean by that assertion. As predicted, the mean IPI in the high-density condition (41.7 ± 19.7 ms) was significantly shorter than those in the medium-density (74.9 ± 56.4 ms) or low-density conditions (56.0 ± 28.9 ms), and strobe groups dominated the recordings (Fig. 5). In dense clutter, the difficult task of perception and action is manifested by the use of sustained rapid emissions of echolocation sounds at the short IPIs within strobe groups, which reflects the need for close-in obstacle avoidance, alternating with the longer IPIs between strobe groups, which reflects the need to probe farther away for long-range path planning. In medium-density and low-density clutter, the need for long-range planning remains, but the requirements for close-in maneuvering evidently are relaxed enough to permit the use of much slower pulse repetition rates (40–100 ms instead of 25–50 ms). In addition, although-the low density and medium-density IPI distributions are similar in overall shape—both in the aggregate (Fig. 8) and taken one bat at a time (Fig. 7), the mean IPI in the medium-density condition is significantly longer than the mean in the low-density condition. Both aspects of the results are contrary to the prediction that mean IPIs should be related quantitatively to clutter density (the higher the density, the shorter the IPIs). Instead, the bats transformed abruptly from one pattern of short IPI echolocation in the high-density condition to a qualitatively different pattern of longer, variable IPI echolocation used in the low-density and medium-density conditions. Also, they used anomalously long IPIs in the medium-density condition compared to the low-density condition. Looking into this latter discrepancy reveals subtle aspects of the bat's reaction to the clutter.

The *difference* in the proportions of sounds at IPIs of 20–40 ms between the low-density and the medium-density conditions is about 0.17 (Fig. 8). The region of long IPIs from 80 to 100 ms is insignificant in the distribution from the high-density condition, but that region contains the second major peak in the distributions from both low-density and medium-density conditions. The proportion of IPIs at 80–100 ms in the low-density condition is about 0.31, while that proportion in the medium-density condition is about 0.18. The difference between these proportions is about 0.13. Thus, the deficit of IPIs in the 20–40 ms range in the medium-density condition is about the same as the increase in the proportion at 80–100 ms, which accounts for the mean IPI being so anomalously long in the medium-density condition (74.9 ms) compared to the low-density condition (56.0 ms). Moving a differential proportion of 0.15 of the IPIs from the short 20 to 40-ms range to the long 80 to 100-ms range effectively converts the medium-density distribution into the low-density distribution. The row of tic-marks that delineates the span of delays for echoes from the chains in Fig. 8 indicates why the bats made this shift. In the medium-density condition, the distribution of IPIs does not begin until about 35–40 ms, which is longer than the 32-ms delay span of chain echoes. In the medium-density condition, before emitting each new broadcast, the flying bat waits until all of the echoes from the chains have arrived. The 4 to 5-row width of the corridor appears sufficient to give bats "elbow room" to maneuver without having to update their images of the scene as rapidly as they have to in the high-density condition, where the corridor is only 2–3 rows wide.

Pulse-echo ambiguity

We predicted that bats in the high-density condition would emit more strobe groups than in the low- or medium-density conditions, based on evidence that they use that emission pattern when faced with challenging echolocation tasks, for example, when actively seeking prey near clutter (Moss and Surlykke 2001; Moss et al. 2006). In fact, in contrast to the other conditions, nearly all of the sounds emitted by the bats while flying through the high-density array were arranged in strobe groups (see Table 1; Fig. 5).

The functional interpretation is that use of short IPIs within strobe groups gave bats rapid updates of perception for objects that were close and possibly dangerous, while use of longer IPIs between strobe groups gave bats the opportunity to probe farther into their surroundings to plan their future course. The slower velocity and consistent use of short IPIs in the high-density array demonstrate that flying bats manipulate their IPIs not only to regulate rapid acquisition of new information in dynamically changing situations, but also to create a depth-of-field for longer-range probing. Bats using strobe groups seem to be alternatively echolocating at two different spatial scales (Moss and Surlykke 2001); they use short IPI pulse emissions to perform obstacle avoidance, as well as long IPI pulse emissions to perform large-scale navigation, such as to find their way to the end of the room and the food reward. While this latter possibility has been considered likely for some time (see Schnitzler and Kalko 2001; Schnitzler et al. 2003), our results offer direct experimental confirmation, because the bats waited for all echoes to return before emitting the next sound.

By using strobe groups, the bats may be addressing the problem of pulse-to-pulse echo ambiguity created when they emit successive sounds at very short IPIs within each strobe group. Figure 9 illustrates what happens when a bat emits two successive sounds so close together that echoes of the first sound are still returning when the second sound is sent out. For a period of perhaps 5–10 ms following the second sound, echoes of the first sound will arrive mixed together with echoes of the second sound. Since two successive pulses by the same bat will have very similar FM waveforms, the bat theoretically should be unable to assign echoes unambiguously to their corresponding broadcasts. Improper assignment of echoes would create spurious echo-delay estimates and introduce phantom objects into the bat's delay images. The longer IPI that follows each strobe group gives the bat an opportunity to gather all of the echoes from one sound before emitting the next sound, thus

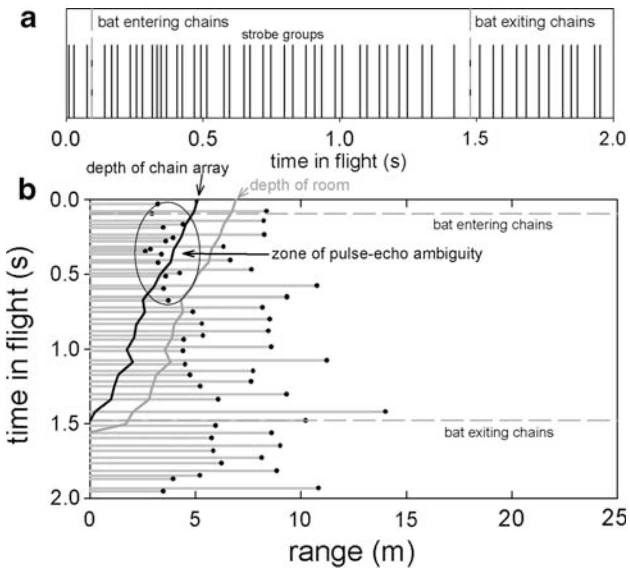


Fig. 9 The relationship between target ranges and IPIs that cause pulse-echo ambiguity during a representative flight (by 1 bat, Emma) in high density clutter. **a** Sequence of echolocation sounds emitted during a 2-s flight. In this example, nearly all bat sounds are arranged in strobe groups. Time passes from *left* to *right*. **b** The depth of the chain array at each point in the bat's flight path in terms of the range to the last row of chains (*black irregular sloping line*), and depth of the room in terms of the range to the back wall (*gray irregular sloping line*). The bat's entry and exit from the array are shown by *horizontal gray dashed lines*. Time passes from *top* to *bottom*. For each IPI value, the target range with an echo delay matching the time that elapses between sounds is shown by a *horizontal gray line* terminating in a *black circle*. The zone of pulse-echo ambiguity is indicated by a *black ellipse*

eliminating the potential for pulse-echo ambiguity. As the bat flies along the corridor through the chains, eventually it passes far enough that all of the echoes from the rest of the array *do* fit into the short IPIs of strobe groups (Fig. 9), and the problem of pulse-echo ambiguity no longer occurs on that flight. The question remains to be investigated of just how similar two successive FM sounds in a strobe group actually are when the bat is at different locations along the flight path.

A phenomenon similar to strobe groups has been observed in cetacean sonar and is related to creating pulse-echo ambiguity (Au 1993). Turl and Penner (1989) termed the organized combinations of stable-interval clicks emitted by beluga whales (*Delphinapterus leucas*) as "packets". They observed several patterns of click trains during behavioral tasks in which the beluga was echolocating towards a particular target. In one type of click train, two or three sounds were emitted in quick succession, followed by a longer time interval to the next group of sounds. Beluga sound packets were further analyzed by Rutenko and Vishnyakov (2006), and found to occur during searching for objects, along with head-tilting and full-body flipping, possibility to obtain better acoustic representations of targets. However, beluga whales also emitted sound packets when searching for objects at longer distances; the authors speculate that this might aid in large-scale overviews of the environment, but no detailed explanation has been provided for this behavior.

Comparing emission patterns of different species, each of which is known to prefer either open spaces or cluttered spaces—is problematic because the pattern of sound emission is not the only adaptation of bats to clutter. The bat's reaction to clutter is dominated by its assessment of the obstacles represented by the clutter. Two species of bats with different maneuvering capabilities might be equally able to distinguish a target from the background, but their respective biomechanical limitations would give the incorrect impression from their flight that only one of them actually perceives the target. As with most other behavioral comparisons among different bat species, the importance of clutter in relation to echolocation has to be considered in the context of a broader range of characters than just perception (Aldridge and Rautenbach 1987; Fenton 1994; Jones 1999; Neuweiler 2000). Overall size, wing aspect ratio, prey size, feeding ecology, and echolocation signal characteristics may prove to scale together with the ability to cope with clutter, but finding the exact constellation of those features will require applying a standardized, quantifiable test of clutter performance to different species of bats.

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