

Acoustic scanning of natural scenes by echolocation in the big brown bat, *Eptesicus fuscus*

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SUMMARY

Echolocation allows bats to orient and localize prey in complete darkness. The sonar beam of the big brown bat, *Eptesicus fuscus*, is directional but broad enough to provide audible echo information from within a 60–90 deg. cone. This suggests that the big brown bat could interrogate a natural scene without fixating each important object separately. We tested this idea by measuring the directional aim and duration of the bat's sonar beam as it performed in a dual task, obstacle avoidance and insect capture. Bats were trained to fly through one of two openings in a fine net to take a tethered insect at variable distances behind the net. The bats sequentially scanned the edges of the net opening and the prey by centering the axis of their sonar beam with an accuracy of ~5 deg. The bats also shifted the duration of their sonar calls, revealing sequential sampling along the range axis. Changes in duration and directional aim were correlated, showing that the bat first inspected the hole, and then shifted its gaze to the more distant insect, before flying through the net opening. Contrary to expectation based on the sonar beam width, big brown bats encountering a complex environment accurately pointed and shifted their sonar gaze to sequentially inspect closely spaced objects in a manner similar to visual animals using saccades and fixations to scan a scene. The findings presented here from a specialized orientation system, echolocation, offer insights into general principles of active sensing across sensory modalities for the perception of natural scenes.

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Key words: echolocation, bat, active sensing, directionality, visual scanning, scene analysis.

INTRODUCTION

Animal sensory systems are continuously bombarded by environmental input, which must be selectively processed to enable effective use of information for species-specific behaviors in complex and noisy environments. Sensory information may be filtered already at the receptor level in simple systems (e.g. Nilsson et al., 2005) or by bottom up and top down processes in the central nervous system (Bartels and Zeki, 1998; Mitchinson et al., 2007). Visually dominant animals tend to sequentially sample information by moving their eyes or head to selectively fixate stimuli at the fovea or visual streak (Liversedge and Findlay, 2000; Eckmeier et al., 2008).

The echolocating bat presents an excellent animal model for exploring whether sequential stimulus sampling extends to modalities beyond vision. Bats produce ultrasonic vocalizations, and use information carried by sonar echoes to forage and avoid obstacles (Popper and Fay, 1995). Moreover, bats adaptively control the features of the sonar sounds they use to probe the environment, and these signals can be quantitatively analyzed to measure and model changes tied to perception. Previous studies of echolocation in an open environment show that the big brown bat locks its sonar beam onto a prey item hundreds of milliseconds before capture (Ghose and Moss, 2003). The present study extended this work to measure the big brown bat's sonar beam-directing behavior in a more complex environment that included both obstacles and prey.

When an echolocating bat seeks insect prey in the proximity of vegetation, because of the broadness of the sonar beam, each vocalization results in a cascade of echoes, arriving from different

directions and at different delays. Field observations document that echolocating bats cope with acoustic clutter by adapting the spectro-temporal characteristics of sonar signals to decrease the duration and broaden the bandwidth of individual calls and increase the repetition rate in groups of calls (Schnitzler et al., 2003; Surlykke and Moss, 2000). These vocal-motor strategies are assumed to sharpen information about the features and location of prey and to segregate prey echoes from clutter echoes. In humans, sound frequency and pitch are particularly important for parsing an auditory scene (Bregman, 1990), but such cues may not be as useful for the echolocating bat, as its sonar calls constrain the echo frequency information, and ambiguous spectral information can arise from the overlap of echoes from multiple closely spaced objects. Thus, we hypothesize that spatial cues about object direction and distance play a prominent role in the big brown bat's analysis of auditory scenes. Furthermore, we hypothesize that the big brown bat's perception of a complex environment depends on its active control over sonar vocalizations to enhance spatial information about the direction and distance of multiple objects. This is the focus of the present study.

In the experiments reported here, we required echolocating bats to perform a dual task, obstacle avoidance and prey capture. Using high-speed stereo videography and synchronized sound recordings with a microphone array, we measured the directional aim of the big brown bat's sonar beam pattern in the free-flying animal. The big brown bat's sonar beam is wide enough to generate audible echoes simultaneously from multiple objects, and we conducted this

study to determine whether the animal's beam-directing behavior is consistent with sequential or simultaneous sampling of sonar targets. Studies of eye movements reveal that humans sequentially foveate parts of a visual scene, even when features, such as those of a face, may be closely spaced (Land and Hayhoe, 2001; Kumar et al., 2005). The width of the sonar beam suggests that the big brown bat does not need to scan closely spaced objects sequentially, because all objects within as much as 30 deg. off the beam axis return echoes of comparable strength.

We report here, however, that the big brown bat does sample the environment sequentially with its sonar, adjusting the direction and distance of its acoustic gaze to closely spaced objects in a complex environment. This is an important finding, because it indicates that sequential scanning offers the animal an advantage that would not be predicted from the characteristics of the sonar beam and implies higher spatial resolution along the midline of the sonar receiver.

MATERIALS AND METHODS

General behavioral methods

Four big brown bats, *Eptesicus fuscus* Beauvois 1796, served as subjects in these experiments, two males and two females. The animals were collected from private homes in Maryland (Department of Natural Resources scientific collecting permit 41213) and housed in the University of Maryland bat vivarium. Bats were exposed to a reversed 12 h dark:12 h light cycle and given free access to water. Bats were maintained at 80% of their *ad lib* feeding weight and normally fed mealworms only during experiments. Animal care and experimental procedures were approved by the University of Maryland Institutional Care and Use Committee.

We conducted studies of the flight path and sonar signals used by *E. fuscus* as it performed a task that required both obstacle avoidance and target localization. Experiments were carried out in a large flight room (Fig. 1), lined with acoustic foam (Sonex, Illbruck, Minneapolis, MN, USA). Low level long wavelength lighting excluded the big brown bat's use of vision (Hope and Bhatnagar, 1979), but still allowed for high-speed video recording and 3-D reconstruction of the animal's flight path. In this experiment, the bat had to detect and localize a tethered insect behind one of two openings in a mist net that divided the flight room. The positioning of the food reward was randomized from trial to trial. The back end of the room was divided further by a partition net, requiring the bat to select the correct opening to obtain its food. The mist net was made of 0.1 mm threads, arranged in a grid and spaced 25 mm apart. The net was moved every day to prevent the subjects from memorizing the positions of the openings. The openings were circular, *ca.* 40 cm in diameter, requiring the bats to maneuver quite accurately to fly through. *E. fuscus* could detect the mist net and the two openings using echolocation, but would occasionally crash into it, presumably because the weak echo returns from this obstacle were difficult to detect and localize.

After preliminary training, the four bats performed a total of 141 trials with between 16 and 67 trials per animal (Table 1), depending on their health and motivation to perform the task. Food rewards, tethered mealworms, were suspended at a height of about 1.5 m above the floor, at different distances in front of and behind the net. The database only includes the trials in which the bats attempted to capture the prey. For analysis, we pooled the trials into four groups according to worm-net separations: far front (worm more than 10 cm in front of the net), close front (worm between 10 and 0 cm in front of the net), close behind (worm between 0 and 10 cm behind the net) and far behind (worm between 10 and 110 cm behind the net). The trials

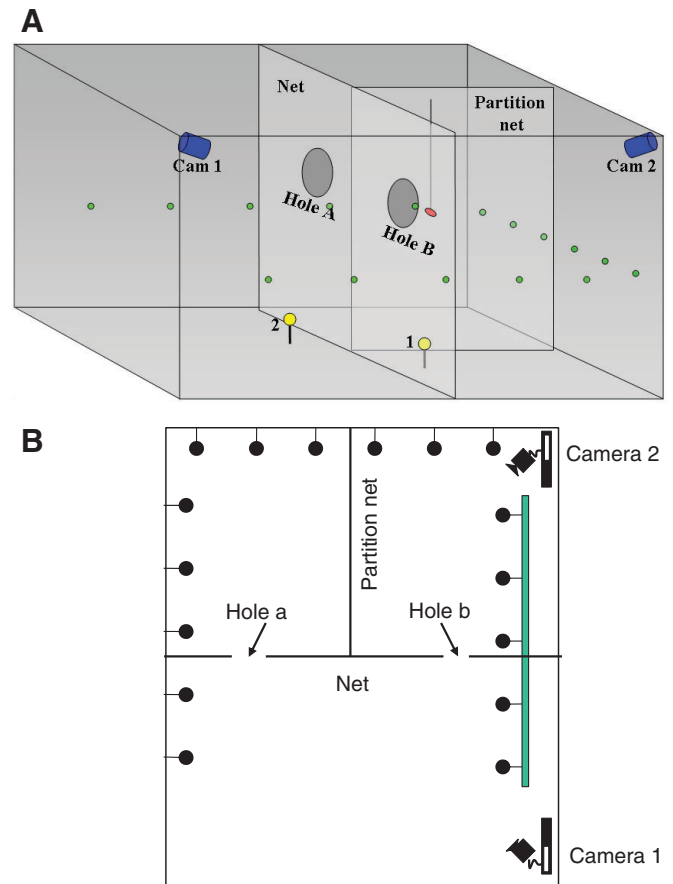


Fig. 1. Schematic 3-D (A) and top view (B) of the flight room (7 m × 8 m × 2 m) and experimental set-up for the dual task. A net is stretched across the flight room and one of two openings (hole a or b) allows the bat access to a food reward (tethered insect; red oval) on the other side of the net. The bat's task is to find the tethered insect behind one of these openings and fly through it to access the food. A partition net divides the back end of the room to allow the bat access to the food reward only if it flies through the correct opening. Two high-speed video cameras (Cam 1 and Cam 2) were used to reconstruct the 3-D flight path of the bat and positions of other objects in the room. Full bandwidth recordings of the bat's echolocation calls were taken with two microphones (1 and 2) positioned on the floor. A 16 microphone array (green circles in A, black circles along the inside perimeter of the inner box in B) positioned along three walls was used to reconstruct the beam pattern of each sonar emission.

with the tethered mealworm far behind the net were sub-divided into 'on-axis' and 'off-axis', where the mealworm hung either directly behind the hole or at an angle of 45 deg. or more from behind the hole. We ran 37 on-axis and 14 off-axis trials in total.

Echo measurements

To characterize the echo levels experienced by the big brown bat in this task, we measured echoes from the worm and the net. Using Tucker-Davis-Technologies System 2 (Alachua, FL, USA; hardware and software), amplified, filtered (Stanford Research Systems, Sunnyvale, CA, USA), frequency modulated (FM) sounds were generated and broadcast through a speaker [Tweeter LT800, frequency response flat (± 3 dB) up to 100 kHz] powered with Krone-Hite DC amplifier (Brockton, MA, USA). Echoes were picked up with a GRAS 1/4 in microphone (40BF, GRAS, Holte, Denmark)

amplified 40 dB by a Larsen-Davis amplifier/power supply (Provo, UT, USA), filtered by a WaveTech filter (Karachi, Pakistan; band-pass filtered 10 kHz–100 kHz) and digitized on-line with a Wavebook (IOtech, Cleveland, OH, USA), using a sampling rate of 500 kHz. The broadcast signal was 1 ms in duration and consisted of a downward linear FM sweep, from 90 kHz to 20 kHz, shaped by a Hanning window function. The source level from the speaker was 77 dB peSPL (peak equivalent sound pressure level) at 10 cm. The signal was repeated every 50 ms. The speaker and the microphone pointed towards the same position on the target, but the microphone was placed 10 cm closer to the target than the speaker to maximize the signal to noise ratio. The speaker was placed 50 cm from the target. With a signal duration of 1 ms, there was no overlap between the outgoing sound and returning echo. We measured the target strength of the net at two angles, 90 and 45 deg., between the net and the sound beam. Target strength of the mealworm was measured from the side. All target strength calculations are referenced to 10 cm such that the target strength was measured in dB as the echo level 10 cm from the target relative to the incoming sound level at the target. The target strength of the net measured at an angle of 90 deg. was -26 dB, whereas the target strength measured at an angle of 45 deg. was -22 dB. The target strength of the tethered worm was -16 dB. All sound levels are given in dB SPL re. 0.0002 Pa r.m.s. The microphones were calibrated using a Brüel and Kjær sound level calibrator (4231, Nærum, Denmark).

Video and sound recordings

Two frame-synchronized, high-speed video cameras (Kodak MotionCorder, 240 Hz, San Diego, CA, USA) were positioned in the upper corners of the flight room. A calibration frame (Peak Performance, Boulder, CO, USA) was placed in the room and filmed by both cameras prior to each recording session. The video cameras were used to record the positions of the microphones, net and holes, and the target, bat flight path and capture behavior.

Full bandwidth echolocation signal recordings were taken by two ultrasonic transducers placed on the floor within the calibrated space, and recorded digitally on an IOtech Wavebook (sample rate 250 kHz per channel).

Sonar beam measurements in free-flying bats

The echolocating bat controls not only the spectral-temporal features of its echolocation cries but also the aim and directional characteristics of its sonar beam. *Eptesicus fuscus* is an oral emitter, and the sonar beam is aligned with the head. A linear microphone array was used to record the big brown bat's sonar signals at 16 different locations in the flight room. For each video frame in which a vocalization was detected, the normalized beam intensity at each microphone was computed. *E. fuscus* emits a broad band FM call with a first harmonic sweeping down from *ca.* 60 to 25 kHz. The original signal was decomposed into three sub-bands (20–30 kHz, 30–40 kHz, 40–50 kHz) and the intensities computed in each sub-band for every vocalization. Using standard tables (ISO 9613-1) a scaling factor correcting for the sound absorption due to air was computed for each frequency band (see Lawrence and Simmons, 1982). Finally, the intensities in each band were corrected for spherical loss and summed to yield a normalized intensity for each vocalization in the direction of each microphone. Vectors were drawn from the bat to each microphone. The length of each vector was made proportional to the normalized intensity at the corresponding microphone. Based on these vectors we constructed a normalized shading pattern such that the peak intensity has a value of 1.0 and is colored black. Lighter colors denote progressively lower

intensities. The resultant shading pattern displays an estimate of the big brown bat's 2-D beam pattern. The resultant vector provides an estimate of the bat's beam axis, and the angular separation between the beam axis and an object of interest (obstacle or prey) defines the tracking angle (for details, see Ghose and Moss, 2003). A third video camera was placed below the hole for close-up recordings in selected trials at the start of the experiment to verify that the beam axis accurately represented the aim of the bat's head.

The duration and pulse interval (time from start to start of pulses) defines the pulse-echo separation. These time measurements were recalculated to distance (m) using a velocity of sound of 340 m s^{-1} at room temperature and humidity, and depicted along the range axis (lower panel of Fig. 2). Plots of pulse duration, measured in meters, along with the distance from bat to net and bat to insect, respectively, revealed how the big brown bat, by decreasing the pulse duration, prevented overlap between its sonar vocalization and net or insect echoes.

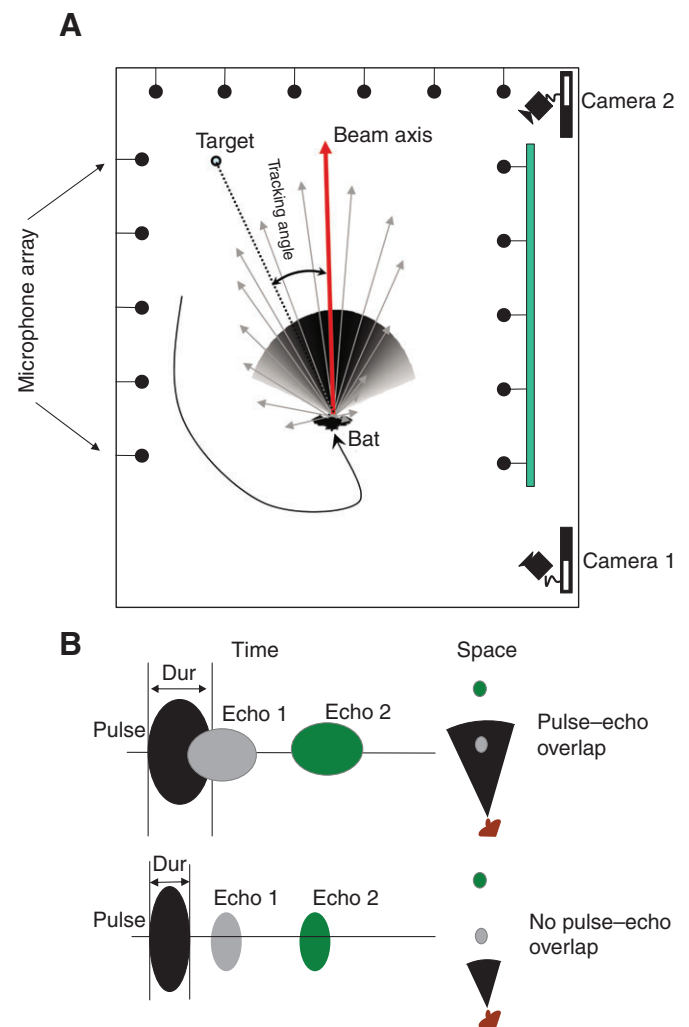


Fig. 2. (A) Schematic illustration of the method used to calculate the direction of the big brown bat's sonar beam axis and the tracking angle from microphone array recordings. (B) Temporal relationship of pulse and echo(es) from the bat's perspective. The pulse duration (Dur) defines the distance in front of the bat where the echo from an object will overlap with the outgoing pulse. Decreasing the pulse duration can prevent overlap between the bat's sonar vocalization and the echo. If there are several objects at different ranges, the bat may experience overlap with echoes from closer objects and avoid overlap with more distant objects.

RESULTS

The big brown bat, *Eptesicus fuscus*, actively controls the features and directional aim of its sonar calls to probe the environment. We studied each bat's vocal behavior, along with its performance. We reconstructed the 3-D flight path, and correlated to echolocation behavior, to quantify the vocal control and flight strategies it employed to negotiate a dual task, requiring both obstacle avoidance and prey capture. Fig. 3 shows two typical strategies, when the prey is far behind the hole. The bat may either fly directly towards the prey after passing the hole or it may first negotiate the hole and then make a U-turn to take the tethered insect, in particular when the prey is far off-axis with respect to the middle of the hole.

Success rates

All bats achieved close to 100% success rates when capturing tethered mealworms in an open room, but introduction of the fine mist net in this experiment reduced the bats' overall success rates to between 50 and 82%, indicating how difficult the task was (Table 1). It has been shown that grouping of pulses or 'strobing' occurs when bats are required to operate in acoustically complex environments (Moss et al., 2006). In all net trials, pulse interval (PI) plots showed that bats produced sonar sound groups for extended periods of time, indicating how challenging this task was for the big brown bat. The plots show that sonar strobing started well before (0.5–1 s) the bat crossed the net (Fig. 3). With the worm in front of the net, the task was comparable to prey capture in clutter and, accordingly, the bats' performance rates were comparable to those observed in an earlier experiment requiring the bats to take tethered insects between 40 and 10 cm from an artificial plant (Moss et al., 2006). As in clutter experiments, the success was lower the closer the prey was to the net.

All bats were reluctant to fly through the hole at first, in particular bats W24, HP2 and BL52, and therefore it was only possible to collect a limited data set from these animals in the two behind net conditions (Table 1). Trials where the bats did not attempt to capture the prey were not included. HP4, on the other hand, learned quickly, and flew through the net to take insects as far as 110 cm behind the net. For these reasons, different numbers of trials were run for the four bats under the different conditions.

The bats' success dropped drastically as the reward was moved from positions in front of the net to positions behind the net. With

the worm behind the net the task became more difficult because the bats faced two challenges: negotiating the net and capturing the insect prey. This task required the bats to maneuver through the (correct) hole before seizing the prey. We did not include trials with the target far behind the net if the bats did not attempt to fly through, as the primary goal of this study was to quantify the bat's sonar behavior in solving the task, rather than its success rate. The bats typically started by flying two or three rounds on the starting side of the net, where they approached the holes while emitting a series of high repetition rate pulses, inspection trains, presumably to decide which hole to fly through for capture.

When the worm was close behind the net many failures were misses, where the bat neither captured nor touched the worm. When the worm was far behind the net, many failures were due to the bat choosing to fly through the wrong hole (Table 1). In all trials, the echo from the worm, regardless of its position behind the net, was well above the bat's detection threshold when it flew within 1 m of the net before crossing it.

When the reward was far behind the net, it could either be on-axis with the hole, i.e. on a straight line perpendicular to the net, starting approximately in the middle of the hole, or off-axis, i.e. at an angle of 45 deg. or more with respect to that line. The success in on-axis trials was not higher than in off-axis trials (on-axis, 57%; off-axis, 56%; $P > 90\%$, Chi-square). Thus, the results for on- and off-axis trials were pooled into one category: far behind.

Echo measurements

Target strength measurements were used to estimate detection distances assuming sonar calls with a source level of 110 dB SPL and 30–35 kHz as the dominant frequency (Surlykke and Moss, 2000), and a detection threshold of 20 dB in the cluttered lab. These estimates indicate that the net echoes would be detectable by the bat at a maximum distance of 3.1 m when ensonified at 90 deg. and at 3.8 m when ensonified at 45 deg. The target strength of the mealworm was stronger, indicating that it would be detected by the bat at distances up to 4.8 m, greater than those encountered by the bat in this study.

Directional adjustments in sonar calls

The acoustic behavior of all big brown bats revealed distinctly sequential sampling of echo information from the net and the worm. The changes in beam angle clearly illustrate the sequential

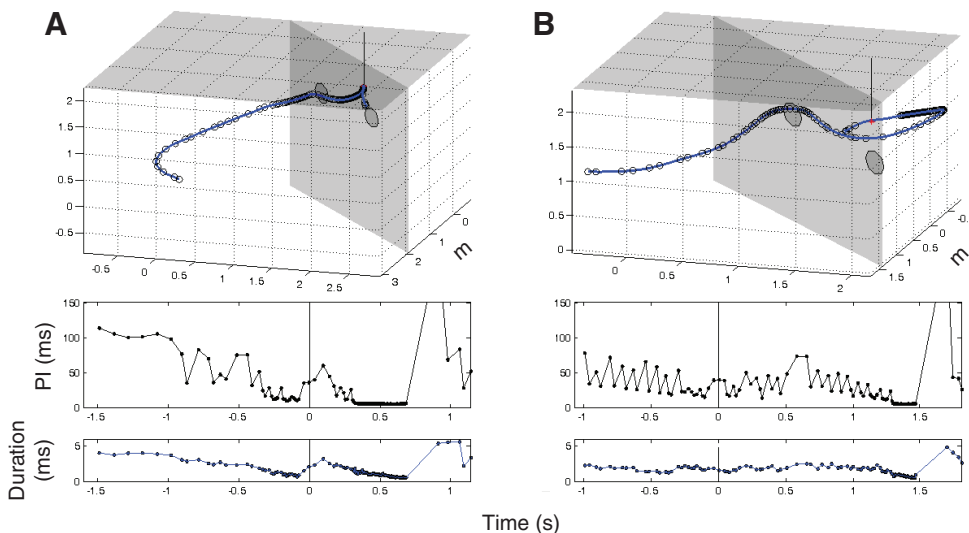


Fig. 3. The two panels show 3-D plots (axes, m) aligned with plots of pulse interval (PI) and pulse duration. Time=0 s is when the bat flies through the hole. In A the worm was 58 cm behind the hole, on-axis, and the bat flew straight from the hole to seize the prey. In B the worm was 56 cm behind the hole, off-axis, and the bat made a 'U-turn' before capture. When the bat approached the net, the pulse interval and duration were reduced, as shown in the lower panels.

Table 1. Success rate (%) for the four bats at the four positions of the reward

Bat	Far in front (max. -10 cm)		Close in front (-10 to 0 cm)		Close behind (0 to +10 cm)			Far behind (+10 cm to max.)			Overall	
	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	<i>W</i>	%	<i>N</i>	<i>W</i>	%	<i>N</i>
BL51	100	7	84.2	19	83.3	6		0	2		82.4	34
HP2	100	2	80	10	66.7	3		–	0		81.3	16
HP4	–	0	100	2	60	5	1	60	60	16	61.2	67
W24	–	0	–	0	50	8	2	42.9	14	2	50	24
All bats	100	9	88.1	31	65	22	3	34.5	76	18	68.7	141

Far in front, more than 10 cm in front of the net; Close in front, 0–10 cm in front of the net; Close behind, 0–10 cm behind the plane of the net; and Far behind, more than 10 cm behind the net. *N*, number of trials; –, no data available. When the reward was behind the net, the bat might miss it, by flying through the wrong hole. The number of this type of miss is given under *W* (wrong hole).

processing. The bat directed its beam back and forth between the left and right edges of the net hole until around 100–300 ms before flying through the net opening, when the beam axis was shifted from the edges and directed through the hole towards the worm (Fig. 4). The scanning between the left and right edge shows that the bat did not sample all elements of the auditory scene simultaneously, but shifted its focus from object to object sequentially. Animations of the bat's dynamic adjustments of the beam pattern as it performed in this task can be found at <http://www.bsos.umd.edu/psyc/batlab/nethole/beamaim/>.

We measured the angular difference between the beam axis and the edges of the net hole and the insect prey to quantify its directional 'gaze' at the time of each vocalization across trials.

The precision with which the big brown bat aligned its head with a target is far greater than needed to maintain a strong, audible echo.

Indeed, this bat species' sonar beam is sufficiently broad to yield detectable echoes 30–60 deg. off-axis (Ghose and Moss, 2003). The big brown bat's accurate directional aim of the sonar beam axis at obstacles and prey may be driven by requirements for higher spatial resolution along the auditory midline. This observation leads us to infer that the directional aim of the sonar beam axis is related to target localization and selection.

The directional aim data in Fig. 4 show sequential scanning of obstacles (right and left edges of the net hole) and prey in all trials. When the bats were far from the hole, the angles to the edges and the prey were so close it was difficult to determine precisely where they were directing the sonar beam axis, but when they came closer to the net, the data revealed that they directed the sonar beam axis to the left or to the right edge of the hole, or to the prey, but not to all of these objects simultaneously. They scanned back and forth

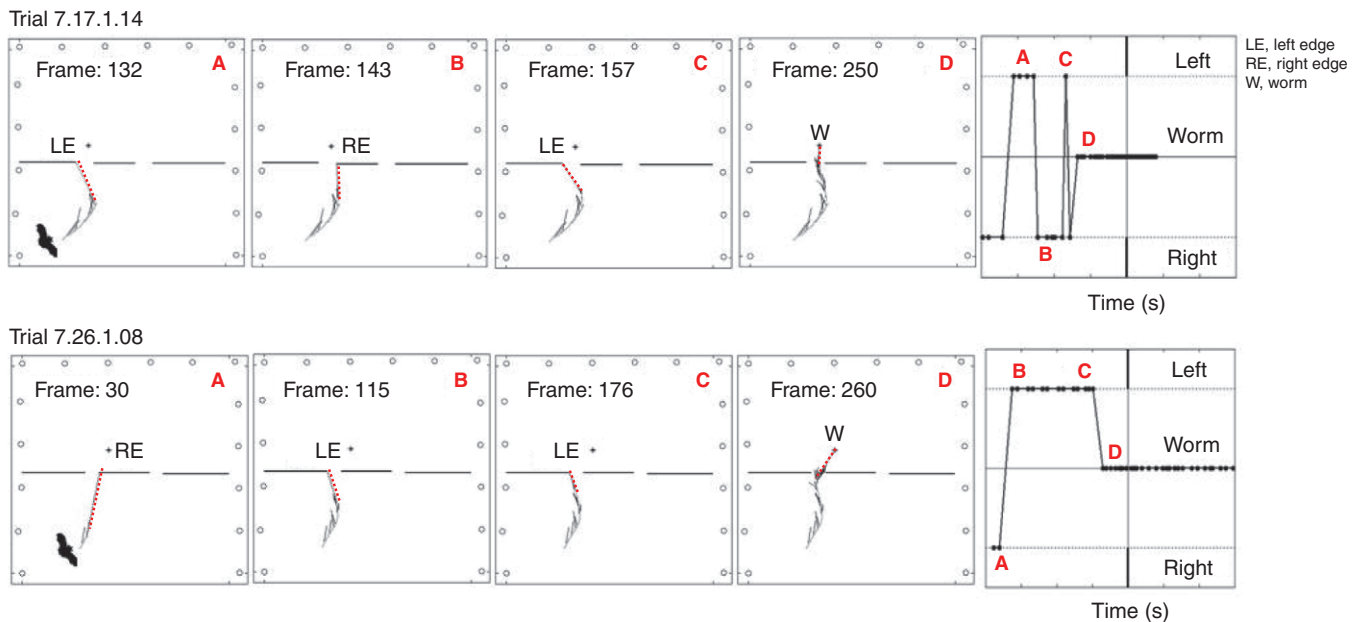


Fig. 4. Data from two selected trials, when the big brown bat flew towards and through the net hole and captured the insect on the other side. The four panels (A–D) for the two trials show beam directing data up to selected video frames (number displayed in each panel). The dashed red line extends the beam axis of the last call displayed in each panel, illustrating how the beam was directed at either the right edge (RE) or the left edge (LE) of the hole, until the bat shifted its beam axis to the more distant worm (W). The plots on the right summarize schematically the bat's beam-directing behavior in the two selected trials. The edges of the holes are shown as horizontal lines, with LE as the upper line and RE as the lower line. Each call is represented by a filled black circle on either of these lines, according to beam axis. The red letters (A–D) refer to the corresponding panels. The plots show how the bat scanned sequentially back and forth between the left and right edges of the hole until 200–300 ms before crossing the net, when it shifted its beam direction towards the worm on the other side of the net. In trial 7.17.1.14 the bat took a 'quick look' at the left edge with one call (in frame 157 of C).

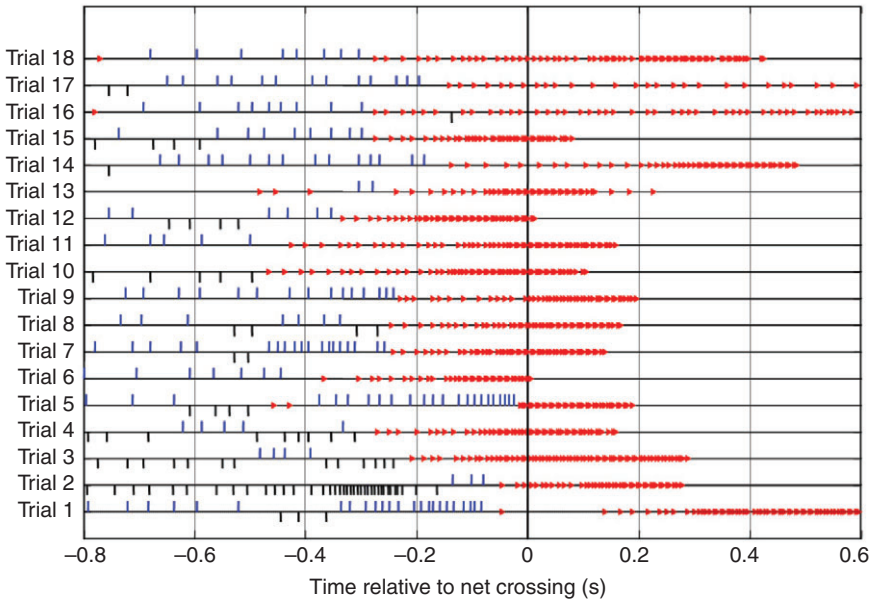


Fig. 5. Summary of the beam aim of the calls produced by the big brown bat, subject HP4, as it approached the net and flew through the hole to get the insect in 18 successful trials with the insect far behind the net. Beam aim for each sonar call is displayed as a function of time, with all trials aligned with respect to the time when the bat flew through the net hole (zero on the abscissa). Blue line segments above the time axis for each trial show vocalizations directed at the left edge of the net hole, and black line segments below the time axis show vocalizations directed at the right edge of the net hole. Vocalizations directed at the mealworm are shown with red triangles pointing to the right. Beam-directing behavior was taken from the beam axis measurement, ± 5 deg. The plots illustrate how the bat scanned back and forth between the edges of the hole. Well before crossing the net hole (time zero) the bat shifted its gaze to the more distant prey (red triangles).

between these objects, a behavior that shows parallels with saccadic eye movements. The tracking angle revealed that well before crossing the net, the beam axis shifted from the edges of the hole to the worm on the other side of the net.

The bat's sequential acoustic scanning between the left/right edge of the hole and the tethered worm was prominent over the entire sequence of trials in this experiment, as illustrated in Fig. 5, which summarizes 18 successful trials with bat HP4. Vocal data for each trial are displayed as a function of time, and they are aligned with respect to the time when the bat flew through the net hole (zero on the abscissa). Blue line segments above the time axis for each trial show vocalizations directed at the left edge of the net hole, and black line segments below the time axis show vocalizations directed at the right edge of the net hole. Vocalizations directed at the mealworm are shown with red triangles pointing to the right. These plots display the sequential shifts in beam aim between closely spaced objects as the bat approached and crossed the net opening. Also shown for each trial is the shift in the bat's beam aim to the worm long before it crossed the net at time zero.

In some trials the subjects interspersed sonar beam fixations at the edges of the hole with fixations at the worm, but in most trials the bats did not direct any cries towards the insect until initiating their final approaches to the hole. Presumably, the bats did not need updated information on the insect's position, because during inspections earlier in the trial they had already found the worm, which guided the choice of which hole to fly through. The bats typically flew several rounds on the starting side of the room before flying through the net hole to retrieve a food reward. Our data collection was ended triggered after capture of the insect, and the buffer size (video and sound recording) was limited to 8 s, which is much shorter than the total duration of most trials.

While scanning the edges of the net hole, the bat directed the beam axis to one edge of the net opening over a number of successive sonar calls. Earlier experiments (Ghose and Moss, 2003) in an open room showed that the big brown bat fixated the beam axis on the worm *ca.* 300 ms before capture with an angular offset close to zero (± 3 deg.). In the experiments reported here, locking the beam axis at an object with high accuracy started much earlier with respect to the time of capture. In trials with the tethered worm ≥ 50 cm behind

the net, the bat started directing the beam at the edges of the hole around 500–800 ms before crossing the net, and the worm was captured between 100 and 600 ms after passing through the hole (Fig. 5). Directing the beam axis on the net edges was at least as accurate (± 5 deg.) as directing it on the worm, even though the flying bat changed its position from call to call. The directional aim of calls to objects in the environment was assigned by two independent observers who used beam axis measurements and beam aim animations to score data for each trial. Inter-observer reliability was greater than 0.9, and any trial segments in question were scored by a third observer. The directional aim data reported here are based on the agreement of at least two observers. Tracking angle distributions for the left and right edges of the net hole, as well as the worm, are presented for bat HP4 in Fig. 6. The criterion for assigning where the bat directed its sonar beam before it crossed the net was a tracking angle of ≤ 15 deg. relative to the net hole edges or the worm. The few vocalizations that did not fall within this range were not assigned to any object.

The sequential fixation on either the left or right edges of the net hole indicated that the big brown bat did not sample sonar information about the two sides of the net hole (auditory objects) simultaneously. Another indication that the bat sequentially sampled closely spaced objects comes from the beam aim behavior in certain trials (see Fig. 4), which showed that the bat directed one call, a 'quick look', to the opposite edge of the hole it was inspecting with several successive sonar calls. The sonar pulse interval was short as the bat was close to crossing the net when these quick looks occurred. Analysis of two such examples, when the bat interspersed one call to one edge of the hole in between a series of calls directed at the opposite edge, revealed pulse intervals of 22 and 33 ms when directing the beam to one edge of the net opening and only 18 ms when directing the beam axis back, yielding a total duration of these quick looks of around 50 ms (see Fig. 4). Such fast motor control likely did not result from immediate feedback from each sonar call, but probably required planning over several calls. The bat's sonar pulse interval when it was changing beam aim from the left to right edge of the net opening had a similar duration, and it was seldom that bats emitted any calls 'in transition', i.e. producing calls in between shifts of the beam

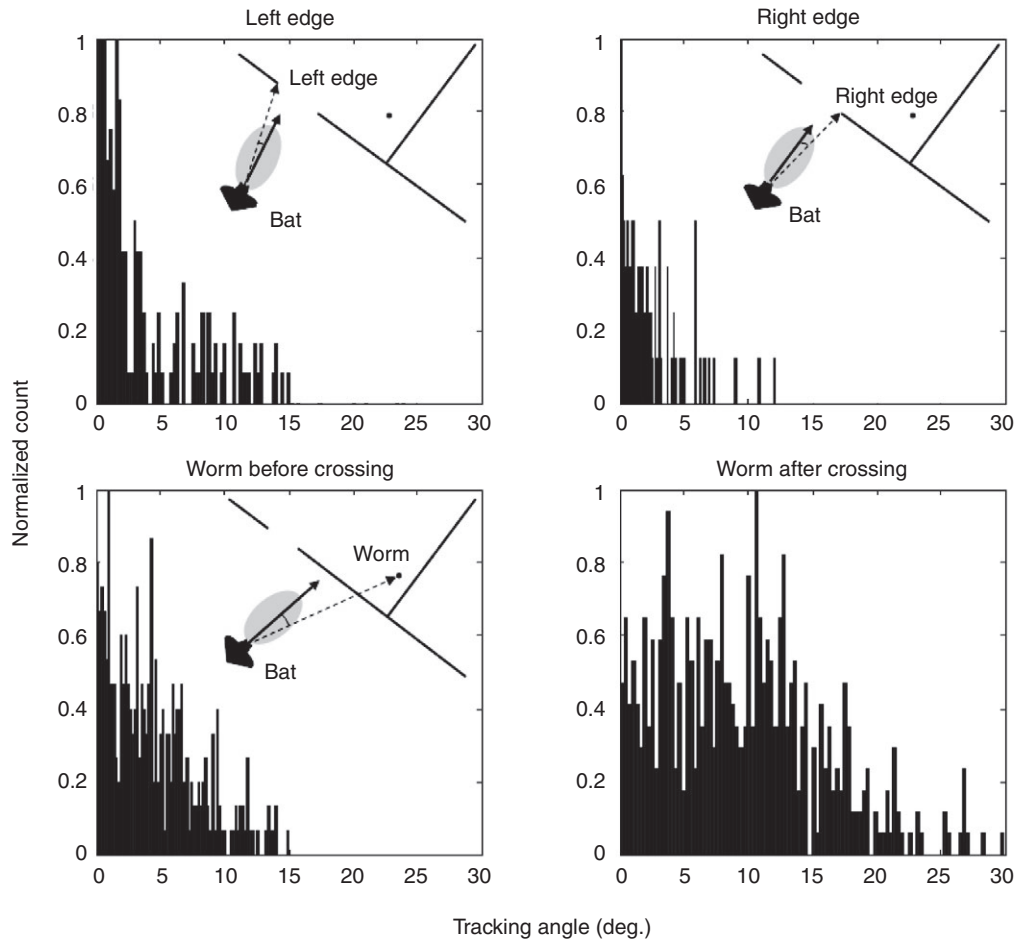


Fig. 6. The plots show tracking angle distributions for sonar calls directed at the left and right edges of the net, as well as the worm before and after passing the net. Sonar beam tracking angles ≤ 15 deg. were assigned to the left or right edges of the net hole or the worm. The few vocalizations that did not fall within this range were not assigned to any object. Data in this figure include vocalizations that were produced by the bat in both successful and unsuccessful trials.

direction from one edge of the net hole to the other or at the prey. In 18 successful trials where bat HP4 captured the prey far behind the net, it directed its beam to either the left or the right edge in 325 calls, at the worm in 332 calls, and only in between these objects in 4 calls. This summary includes only sonar calls before the final insect capture buzz in the 18 trials. Thus, the data demonstrate that bats were able to shift the directional aim of the sonar beam in a very short time interval.

Temporal adjustments in sonar calls

The results from measurements of temporal features of the sonar calls confirmed the results of the beam aim data because pulse duration and repetition rate also showed that the bats sampled the acoustic objects sequentially. When echolocating bats home in on a prey item, they adjust the duration and timing of their sonar signals to temporally isolate the prey echoes in a pulse–echo overlap-free window. In these experiments bats adapted their acoustic behavior in a similar manner. Pulse duration and PI decreased when the bat approached the net opening, although not by as much as in a typical terminal buzz before prey capture. Pulse duration decreased monotonically such that there was no overlap between the outgoing sonar signal and the echo return from the net, until around 100–300 ms before the bat flew through the net opening, when pulse duration increased (Fig. 7). As the bat approached the net, the decrease in pulse duration served to prevent overlap between its vocalizations and net echoes. When the call duration was increased before the bat crossed the net, the beam extended well beyond the net towards the worm on the other side. The results suggest that the

increase in pulse duration, allowing for overlap between sonar vocalizations and net echoes, marks the point in time when the bat shifted its gaze along the range axis from the net to the more distant worm.

Concurrent with the increase in duration observed before crossing the net, PI often increased, although not all trials revealed this pattern distinctly. Subsequently, pulse duration and PI decreased again until capture of the insect. In the final attack of the insect, the PI and duration values were characteristic of a typical terminal buzz for *E. fuscus* (Surlykke and Moss, 2000).

Comparison of pulse duration with beam aim (dashed red line in Fig. 7A) further illustrates that the time when the bat shifted its gaze from the edges of the net opening to the worm (taken from tracking angle data) corresponds well with the time when the bat increased pulse duration, allowing overlap between net echo and pulse. The bottom panel of Fig. 7A shows how the pulse duration (measured as distance; blue curve) changed in relation to the distances between the bat and worm (black) and between the bat and net (magenta). Hence, both independent measurements, beam angle and pulse duration, showed that the bat shifted its sonar gaze from net hole to prey well before it flew through the hole. Furthermore, these shifts in beam direction and call duration co-occurred. On average, the shift in sonar beam axis to the prey occurred 220 ± 140 ms before crossing the net, and the increase in pulse duration resulting in overlap with the net echo occurred 219 ± 79 ms before crossing the net. The correlation between the time of the shift of beam axis and the time of increase in pulse duration (Fig. 7B) was statistically significant, $R^2=0.59$ ($P<0.01$). The shift in gaze from net hole to

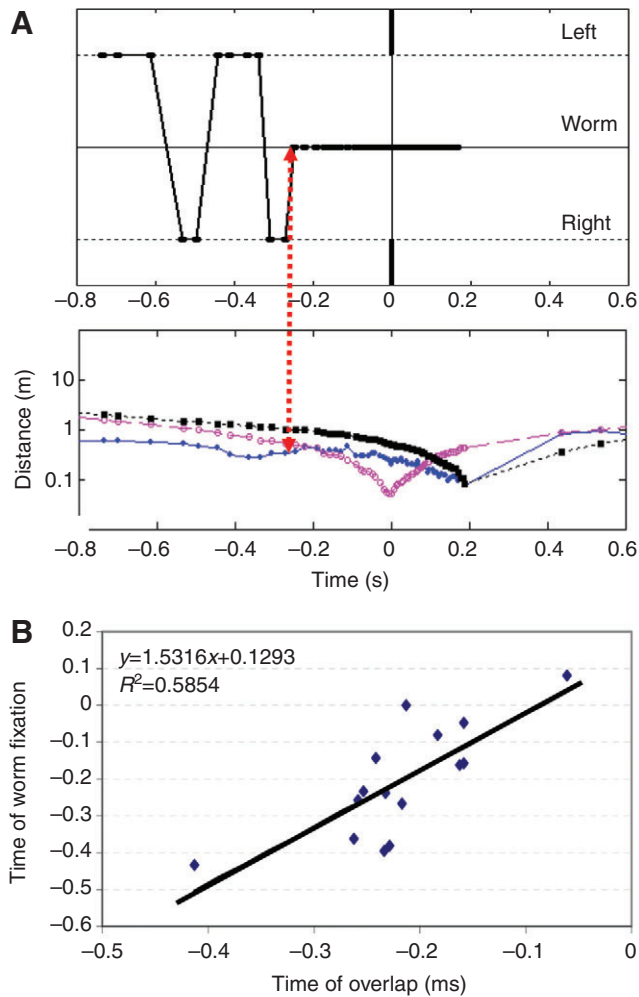


Fig. 7. (A) Top, schematic illustration of the beam-directing behavior in a selected trial (see also Fig. 4). The big brown bat scanned back and forth between the left and right edges of the hole until ca. 250 ms before flying through the hole, when the beam axis shifted to the worm. Bottom, duration of sonar calls from the same trial, converted to distance (blue curve), plotted as a function of time relative to net crossing (time zero). The magenta curve shows the distance between the bat and net, with a minimum at time zero, when the bat flew through the hole. The black curve shows the distance between the bat and worm. Sonar signal duration (blue) decreased as the bat approached the net, but started increasing approximately 300 ms before it crossed the net, creating overlap between call and net echoes around -250 ms, corresponding with the shift of beam aim to the worm (red dashed double-headed arrow). (B) Time of worm fixation (Y-axis) plotted against time of pulse–echo overlap (X-axis) over 16 trials.

worm may indicate the time when the bat had localized the hole with enough accuracy to fly through, and started planning its attack of the insect.

DISCUSSION

How do animals process, organize and utilize information from a rich and complex environment? Furthermore, how is this information integrated with motor programs to support perceptually guided behavior? To pursue these questions we analyzed in detail the big brown bat's active control over its sonar signals as it performed a spatial task that required both obstacle avoidance and target interception.

Echolocation, like other active sensing systems, involves feedback between action and perception: the bat produces ultrasonic vocalizations and processes echo information to guide vocal-motor adjustments to further probe the environment. Similar to active visual scanning of the environment by eye movement, fixation and accommodation, the big brown bat scans the environment acoustically by directional control of the sonar beam (through movement and fixation of the head aim), coupled with range-dependent adaptive changes in sonar call duration and pulse interval. Measurement of the directional aim and features of the big brown bat's sonar cries allows us direct access to the signals that drive its behavior.

Sequential sampling of spatial information

The results of our study demonstrate that the big brown bat sequentially samples the environment with its sonar vocalizations, adjusting the direction and distance of its acoustic gaze, in a manner analogous to sequential visual fixation of objects within a complex visual scene. Due to the broad directionality of the emitted beam (Ghose and Moss, 2003), almost equal sound energy impinges on objects within a wide angle ahead of the bat. The sonar beam of the big brown bat is sufficiently broad (>120 deg. at 6 dB down from the peak) (Hartley and Suthers, 1989) to return concurrent audible echoes from the closely spaced opening in the net and the tethered worm. If the big brown bat was to simultaneously sample echo information from the obstacle and prey in this task, we would expect the animal to maintain its beam axis in the general direction of all these objects. However, we found that the big brown bat points its sonar beam axis sequentially at the edges of the net opening and prey, often scanning back and forth between these objects. This behavior pattern resembles visual scanning of objects in a natural scene by humans (Land and Hayhoe, 2001).

The big brown bat's sequential acoustic scanning of the obstacle and prey is consistent with findings reported by Barber and colleagues, who showed that the gleaning pallid bat, *Antrozous pallidus*, cannot process two streams of auditory information simultaneously (Barber et al., 2003). However, in Barber and colleagues' experiments, the two streams of information were obtained through echolocation and passive listening. The central auditory system of the pallid bat appears to have evolved to segregate the processing of echolocation and prey-generated sounds into two separate populations of neurons in the inferior colliculus (Fuzessery, 1994). Here, all streams of acoustic information, from both prey and obstacles, were obtained through echolocation. As the bat sequentially adjusted the direction and duration of the sonar beam to inspect the obstacle and prey, we infer that directional and temporal cues are the most important acoustic parameters to this animal for the segregation of auditory objects in the scene. This indicates that the big brown bat's adaptive control of the beam aim and pulse duration is key to its success in complex, cluttered environments. Insectivorous bats of different species exploit a wide variety of habitats ranging from very cluttered space to completely open air. It is hard to imagine that it will be possible in the future to measure and track the beam aim of a bat hunting in the wild. However, the fine correlation between beam aim and temporal call features demonstrated by this study indicates that changes in temporal parameters correlated to a bat's position with respect to background may allow one to infer which objects in the natural environment the bat was sampling along the range axis. Thus, future field studies may reveal whether other bat species with different habitat preferences also sample auditory objects sequentially to segregate streams in a complex natural habitat.

In visual animals, eye movements during scanning of a scene consist of a series of fixations interspersed by saccades to move the eye from one point to the next. Birds move the whole head to fixate the eyes (Eckmeier et al., 2008). In primate vision, behavioral (Rizzolatti et al., 1987) and neurophysiological studies (Kustov and Robinson, 1996) suggest a tight coupling between eye movement and attention systems. In the echolocating bat, we suggest that beam axis direction may correspond to its attention to different objects in the scene. Any listening animal will turn its head toward a sound of interest, exploiting the maximum directional acuity of hearing along the midline, which, for example, has been demonstrated elegantly in a thorough series of experiments with barn owls (Konishi, 1993). Echolocating bats can take advantage of the added directionality of the outgoing sound to reduce echo intensity from an off-axis object by controlling the aim of the sonar beam.

In vision, fixation points are related to the behavioral task (e.g. Yarbus, 1961). Pertinent to our study are look-ahead fixations. Numerous studies of humans engaged in natural tasks that require multiple, visually guided sequential behaviors have shown that reaching for an object is preceded by fixations at the object up to a few seconds in advance (e.g. Hayhoe et al., 2003). These look-ahead fixations are thought to contribute to task planning (Hodgson et al., 2000). A study of humans stepping over an obstacle (Patla and Vickers, 1997) showed that subjects fixated on the obstacle before, but not during, the period in which they navigated the obstacle. In our study we observed sonar beam fixations by the big brown bat on the edges of the net hole before but not when getting close to the time of net crossing, suggesting a link between perception and action planning also in the echolocation system.

Accuracy of sonar beam fixations

Sonar fixations serve to lock the beam axis onto an object over successive sounds, just as visual fixations lock the fovea accurately onto a target until the next saccade. We measured the accuracy with which the big brown bat directed its sonar beam aim at obstacles, and compared these measurements with the accuracy of its beam aim at prey (Ghose and Moss, 2003). In the present study, the big brown bat directed its sonar beam at the obstacle with high accuracy, locking the beam axis onto the edges of the net opening over successive vocalizations with deviations of less than 5 deg., even though the angle of the object with respect to the bat continuously changed as it flew. Ghose and Moss (Ghose and Moss, 2006) proposed that this accurate locking of the sonar beam during prey interception serves to simplify steering towards and, finally, interception of the prey. As the results here show that the big brown bat's accuracy of directing the sonar beam axis to the obstacles it must avoid is as high as that to the prey, we infer that centering the beam axis also serves perceptual functions related to scene analysis. This implies that receiver width may be much narrower than the transmitted beam pattern.

The big brown bat's beam-directing behavior is much more precise than required for target echo detection. In a variety of species, localization accuracy is highest along the midline, falling off in the periphery [humans (Mills, 1958); monkey (Brown et al., 1982); cat (Heffner and Heffner, 1988)]. For example, the minimum audible angle in humans is about 1 deg. along the midline, increasing to 7.5 deg. at a test azimuth of 70 deg. As the echolocating bat's auditory system follows a general mammalian plan (Covey and Casseday, 1995), we hypothesize that its localization accuracy is also highest along the midline and falls off with azimuth, which is corroborated by the accurate directional control of the sonar beam in flight. When

sitting on a platform, the big brown bat can track a target even more accurately, i.e. approximately 1 deg. (Masters et al., 1985). Enhanced processing of echoes along the midline shares some of the functional advantages of a fovea or visual streak in the retina, but without morphological specializations at the receptor level.

Rapid transitions between sonar fixations

The sequential scanning of the echolocating bat resembles results from vision studies showing that humans and other primates sample information from a complex display by a series of fixations, interrupted by saccadic eye movements. The latency to make a visual saccade is typically longer than 200 ms (Liversedge and Findlay, 2000). When planning ahead, saccade latencies may be substantially shorter (Fischer and Weber, 1993), but still far greater than the big brown bat's latency of 20–50 ms to re-direct its sonar beam between the net opening and prey in this dual task.

Suppression of visual sensitivity during saccades gives rise to the perception of a continuous and stable retinal image, in spite of the retinal smear created by high velocity eye movements (Dodge, 1905; Volkman et al., 1978). The echolocating bat rarely produced sonar calls during the transition from beam directing at one object to another. Instead of actively suppressing sensory input during high velocity head movements, the big brown bat appears to minimize auditory smear by reducing echo input when its head is turning. Thus, this bat species reduces information processing demands on the receiving auditory system through its vocal-motor control of the signal output.

Acoustic gaze along the range axis

When the echolocating bat shifts the direction of its sonar beam from obstacle to obstacle it also makes range-dependent adjustments in the duration of sonar calls to avoid pulse–echo overlap, suggesting accommodation to objects at different distances. If the big brown bat encounters objects at different distances, it typically shortens its calls to avoid pulse–echo overlap with the closest object. Therefore, the duration of this bat species' vocalizations provides an index of its acoustic gaze along the range axis. When a bat tolerates overlap between its pulse and the echo from a closer object, we infer that it has shifted its acoustic gaze to a more distant object. This shift in acoustic gaze occurred regularly in this dual task: after the bat found the net opening, it shifted its acoustic gaze to the worm behind the obstacle, tolerating overlap between its sonar calls and net echoes, sometimes for as long as 350 ms. In vision, shifts in fixation between targets that lie in different directions and at varying depths also require a combination of saccadic and vergence movements (Kumar et al., 2005).

Conclusions

Our results show that the big brown bat sequentially samples spatial information from closely spaced objects in a complex acoustic scene, even though shifts up to 30 deg. in the directional aim of its sonar beam axis should yield echoes of similar strength, due to the broad width of the beam (Ghose and Moss, 2003; Hartley and Suthers, 1989). Ghose and Moss (Ghose and Moss, 2006) demonstrated a correlation between the big brown bat's head direction and its flight control and suggested that this bat species uses its head orientation to set up a common reference frame for sensorimotor integration, as it converts its sonar information into flight motor commands. The results of the present study extend this interpretation to suggest that the big brown bat's accurate beam-directing behavior also plays a role in spatial localization and attention. In particular, the big brown bat's active control of sequential beam fixations to obstacles and

prey may reflect its higher spatial resolution and allocation of perceptual resources along the auditory midline.

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