# A computational sensorimotor model of bat echolocation

Harry R. Erwin[a)]
*Department of Computer Science, George Mason University, Fairfax, Virginia 22030*

Willard W. Wilson[b)] and Cynthia F. Moss[c)]
*Department of Psychology, Program in Neuroscience and Cognitive Science, University of Maryland, College Park, Maryland 20742*

A computational sensorimotor model of target capture behavior by the echolocating bat, *Eptesicus fuscus*, was developed to understand the detection, localization, tracking, and interception of insect prey in a biological sonar system. This model incorporated acoustics, target localization processes, flight aerodynamics, and target capture planning to produce model trajectories replicating those observed in behavioral insect capture trials. Estimates of target range were based on echo delay, azimuth on the relative intensity of the echo at the two ears, and elevation on the spectral pattern of the sonar return in a match/mismatch process. Flapping flight aerodynamics was used to produce realistic model trajectories. Localization in all three spatial dimensions proved necessary to control target tracking and interception for an adequate model of insect capture behavior by echolocating bats. Target capture using maneuvering flight was generally successful when the model's path was controlled by a planning process that made use of an anticipatory internal simulation, while simple homing was successful only for targets directly ahead of the model bat. © *2001 Acoustical Society of America.* [DOI: 10.1121/1.1381026]

PACS numbers: 43.80.Ka, 43.80.Lb, 43.58.Ta, 43.60.Cg, 43.60.Lq [WA]

## I. INTRODUCTION

Bats use active sensing by echolocation for spatial orientation with acoustic signals. This involves the transmission, reception, and processing of ultrasound, and yields spatial acoustic information about the environment. Animal sonar systems operate with sensorimotor feedback control, in which spatial acoustic information carried by echoes guides behavior. In echolocating bats, echo-dependent motor behaviors include adjustments in the position of the head and pinnae, in the activity of the muscle groups controlling the flight path, and in the production patterns of sonar signals. The bat's motor responses (head, pinna, and body movements; sonar vocalizations) to spatial information carried by echoes, in turn, have a direct impact on the acoustic input to its sonar receiver (Valentine and Moss, 1998). Biological sonar thus requires the coordinated operation of auditory and motor systems, and a central goal of this modeling study is to deepen our understanding of these component systems and their interactions.

Acoustic information carried by sonar reflections allows the echolocating bat to determine the three-dimensional (3D) position of a target in space. The arrival time, intensity, and spectrum of echoes at the two ears encode the location of an object in azimuth and elevation. In terrestrial animals, azimuth can be estimated from interaural time- or intensity difference (ITD or IID) cues (Blauert, 1997; Grothe and Park, 1998; Harnischpfeger, Neuweiler, and Schlegel, 1985; Shi-mozawa *et al.*, 1974; Simmons *et al.*, 1983). However, Pollak (1988) has shown that time and intensity trade off in binaural auditory neurons, which supports the alternative view that ITDs are not useful cues for localization in bats since the maximum ITDs (no greater than 55 $\mu$s in *E. fuscus*; Koay *et al.*, 1998) are much smaller than the neural latency shifts introduced by head shadowing (several ms in Jen and Chen, 1988; discussed in Moss and Schnitzler, 1995; Pollak, 1988). Elevation can be estimated from interaural differences in the return spectra generated by the structure of the pinna and tragus (Grinnell and Grinnell, 1965; Lawrence and Simmons, 1982; Wotton, Haresign, and Simmons, 1995, 1996; Wotton and Simmons, 2000) or by asymmetric movements of the pinna (Mogdans, Ostwald, and Schnitzler, 1988; Walker, Peremans, and Hallam, 1998), as seen in *Rhinolophus ferrumequinum*. In *E. fuscus*, the elevation-dependent spectral profile of the echo appears to be important, as this species' pinnae do not have the mobility seen in *R. ferrumequinum*. The third dimension, the distance between the bat and a target, can be determined from the time delay between the outgoing sound and the returning echo (Hartridge, 1945; Simmons, 1973).

To capture prey successfully, the bat must control its flight path to arrive at a location within 2–3 cm of the insect (Trappe and Schnitzler, 1982; Webster and Griffin, 1962). Often the bat positions itself above the prey item to scoop it up with its tail membrane, requiring precise information about target azimuth, elevation, and distance. Webster and Brazier (1965) discuss the accuracy of this positioning, pointing out that in wingtip captures, "the very tip of the wing is often bent over to form a catching shelf or groove about half an inch square." The bat's capture plan is ex-

---
[a)]Now at: Informatics Centre, University of Sunderland, Sunderland SR1 0DD, United Kingdom. Electronic mail: herwin@world.std.com
[b)]Now at: Tucker-Davis Technologies, 4637 NW 6th Street, Gainesville, FL 32609. Electronic mail: wwilson@tdt.com
[c)]Electronic mail: cmoss@psyc.umd.edu

pressed as adjustments in the flight path, changes in the call generation pattern, and the timing and coordination of the final capture maneuver with the wing or tail membrane. An important question is whether the bat controls this process by anticipating or predicting the future position of the target or using the current position estimate in a nonpredictive mode. This question can be fully addressed only when a moving target is present, but some insight can be derived from studies of stationary target capture, as some basic nonpredictive tactics such as simple homing are identifiable.

A second question concerns the directional components of the target's position that may be required by the bat's sonar system at various stages of insect capture. Range, azimuth, and elevation information characterize a target's position in 3D space, and can be used in any strategy. Azimuth and elevation without range can be used by simple nonpredictive strategies, such as lead pursuit (where the bat aims to fly ahead of the target), lag pursuit (where the bat aims behind the target), and simple homing (where the bat flies at the target). The bat can also triangulate a stationary target from a distance to fully localize it without using range. Azimuth and elevation need not be estimated simultaneously, but can be estimated over a series of sonar signals if the bat modulates the acoustic input to its two ears by rotating its head or flicking its ears, providing enough data to localize a nonmaneuvering target in both azimuth and elevation. This mechanism appears to be used by the bat, *R. ferrumequinum* (Mogdans *et al.*, 1988; Walker *et al.*, 1998). Whether the bat requires target range information to successfully intercept insect prey is important, as localization parameters provide the primary input to the bat's capture planning algorithm.

A third question involves the bat's control of its head aim when it pursues targets on the wing. In particular, where is the bat directing its sonar beam when it tracks and intercepts insect prey? The direction of the beam affects the values of the localization cues used by the bat to estimate azimuth and elevation and is an input to the algorithm by which those cues are extracted from the return. The bat's head aim is difficult to observe in wide-angle infrared video recordings of target capture in a laboratory flight room, but Webster and Brazier (1965) in high-speed photographic studies of insect pursuits on the wing and Masters *et al.* (1985) in a study of target tracking from a platform have reported that bats keep head aim locked to the target with an accuracy of about ±5 deg. This question can be addressed indirectly by modeling the head aim process to determine whether the model bat must turn its head to face a target to produce the localization accuracy needed for successful insect capture.

Masters (1988) and Kuc (1994) have published computational models of the prey-capture process. Masters followed up on experimental work by Webster and Brazier (1965), who had reported that bats accustomed to catching *Drosophila* in the lab showed progressive changes in their behavior when presented with mealworms projected ballistically in the air over a series of trials. At first the bats attempted to catch the mealworms by flying above them, but later modified their flight paths to approach the insects from below. These observations suggested to them that the bats

had learned the motion of the targets and were adjusting for it in their capture planning.

Masters modeled the bat's flight path as it followed three strategies: nonpredictive, predictive one sonar pulse ahead, and predictive to the path intersection. The target was modeled to follow a ballistic trajectory, and the bat's flight aerodynamics was modeled assuming a fixed minimum turning radius and a constant velocity. He showed that the curvature of the model bat's flight trajectories indicated the strategy used; he also demonstrated that a nonpredictive strategy was feasible, and observed that the bat's previous experience with the target trajectory was a potentially confounding variable.

Kuc (1994) developed his model to better understand the sensorimotor processes in prey capture by echolocating bats. He simulated a call consisting of a 25-kHz fundamental and a single 50-kHz overtone and used simple models of the beam pattern and the transfer characteristics of the bat's ear and head. The model did not perform complete localization; instead, range was used only to schedule the calls. Kuc's model controlled flight by using a simple homing strategy, zeroing the offset of the target from a center axis by measuring the difference between the return intensities at the two ears for azimuth and the difference between the intensity in the fundamental and overtone for elevation. The model homed on the target and collided with it. The model bat's reaction time was set equal to the intercall interval, which became unrealistically short during the terminal buzz. Aerodynamics was simplified, with the model bat flying at a constant speed, without banking, and with a unlimited turn rate.

Kuc's model bat captured targets using simple homing based on azimuth and elevation, and he showed that narrowband measurements of target intensity in each ear at 25 and 50 kHz were sufficient to support this. His model was successful for stationary targets, but his assumptions did not include the fine coordination of spatial acoustic information and orienting behavior that is observed in natural insect capture maneuvers by echolocating bats.

Our present paper reports the initial results from a two-phase study of bat sensorimotor integration. The first phase involved the development and calibration of a computational model of the prey-capture process and an investigation of the positional cues and motor behaviors likely to be required for the successful capture of a stationary target. This refined Kuc's approach by the inclusion of biologically realistic data on call acoustics, aerodynamics, and target localization, with the goal that the model would replicate the complex maneuvers seen during insect pursuit and capture. Empirical data were used to calibrate and validate the model, ruling out various alternative algorithms for target localization and capture planning. The second phase introduces moving targets to fully investigate whether the bat uses predictive or nonpredictive strategies to capture insect prey on the wing, and our findings from the second study will be reported in a subsequent publication.

## II. METHODS

### A. Behavioral calibration

Measurements of the flight and acoustic behavior of bats during capture of stationary targets (tethered mealworms,

*Tenebrio molitor*) in an open room were used to provide data for calibrating and validating the model. The methods used to collect and analyze these data are described in Wilson and Moss (2001) and are summarized below.

### 1. Animal subjects

The bats used in the behavioral trials were selected from a group maintained in the bat vivarium at the University of Maryland. These bats were collected (in July and August of 1997) from private homes in Maryland, housed two or three to a cage, exposed to a reversed 12:12-hour light–dark cycle, maintained at 12–16 grams body weight, and fed during experiments. Animal husbandry was carried out in accordance with guidelines established and overseen by the Institutional Animal Care and Use Committee at the University of Maryland.

### 2. Behavioral studies of echolocation behavior

Seven echolocating big brown bats (*E. fuscus*) were trained to capture tethered whole mealworms (*T. molitor*) in a large flight room (6.4×7.4×2.6 m) with the ceiling and walls lined with acoustical foam (Sonex™, Illbruck) and a carpeted floor. Insect capture data from two of the bats were used in the calibration trials, and data from the other five were used in the validation trials. Two genlocked (frame synchronized), high-speed video cameras (Kodak MotionCorder, 640×240 pixels, 240-Hz frame rate, and 1/240-s shutter speed) were positioned just below the ceiling in opposite corners of the flight room. A volume 2.2×2.2 (horizontal) ×1.6 m (vertical) within the region defined a calibrated space for reliable 3D reconstruction of the bats' flight path. A calibration frame (Peak Performance Technologies) was placed in the center of the flight room and videotaped by both cameras prior to each recording session.

Experiments were carried out using only long-wavelength (>650 nm) lighting (Plexiglas #2711, Reed Plastics, and Bogen Filter #182) to eliminate the use of vision by the bats (Hope and Bhatnagar, 1979). Mealworms were suspended at a height of about 1.0 m above the floor by monofilament line (Trilene Ultra Thin, 0.1-mm diameter) within a 5.3-m target area in the center of the room. Once each bat achieved a consistent capture rate of nearly 100%, audio and video recordings of its capture behavior began.

A small marker (Scotchlite™ reflective tape folded to present eight reflective surfaces from different angles) was glued to the bat's head and/or back where fur had been removed by depilatory cream (Nair®). This marker reflected IR back to the cameras as a bright spot that was used to help track the bat's position during subsequent reconstruction of its three-dimensional flight path.

A mealworm was suspended at a randomly selected location within the target area, and then the bat was released in a random direction to orient on the target area and find the mealworm. So that the bat would not memorize the target area, the mealworm was suspended outside the calibrated region of the room 50% of the time, and those trials were not video recorded.

The high-speed video cameras were used to record target position, bat flight path, and capture behavior. The resulting images were used in calculation of the three-dimensional positions of the bat, target, and microphones.

Echolocation signals were recorded using two ultrasonic transducers (Ultrasound Advice) placed within the calibrated space. Microphone output was amplified (Ultrasound Advice) and recorded on direct channels of a high-speed tape recorder (Racal Store-4 at 30 in. per s). An FM channel of the tape recorder was used to record TTL synch pulses corresponding to the start of each video frame and gated to the end of video acquisition.

## B. Model description

### 1. Programming

The model was developed using the C++ programming language (ISO/IEC, 1998; Stroustrup, 1997) running on a Macintosh computer. The Metrowerks Codewarrior PRO 5.0 C++ programming environment was used.

The model was a combined continuous/discrete event simulation, with the system state elements that change continuously updated at each event. It was written using both object-oriented and generic programming techniques (Austern, 1998), making use of a time-ordered queue to sequence the scheduling and execution of events, and updating the continuous components of the system state from event to event using an adaptive 4th/5th-order Runge–Kutta integration algorithm (Press *et al.*, 1988). There was an event every 1/240th second synchronous with each video frame and additional events that were scheduled asynchronously.

### 2. Model design

The model consisted of five major functions, which ran asynchronously. The target position function was responsible for maintaining and updating the target position, which in this study was held fixed. The acoustics function was responsible for scheduling and generating the call, integrating its position through space to the single target and back, and triggering sensory processing after a specified reaction time delay. The sensory processing function then used the echolocation return data to generate a measurement of the relative position of the target for updating the target state estimate. The motor planning function used the target state to plan and control the motor actions of the model, and the motor response function finally maintained and updated the state of the model bat.

### 3. Acoustics

Acoustics was modeled using the sonar equation [Eq. (1), based on Camp, 1970; Møhl, 1988; Skolnik, 1980], with the $SNR_{dB}$ being the signal to noise ratio of the return in decibels for each 1-kHz band. Target detection was assumed to occur if the total signal energy between 25 and 40 kHz exceeded an absolute detection threshold assumed to reflect both the internal noise of the bat's nervous system and sensitivity of its auditory receiver in that range of frequencies. The components of the echolocation return signal—signal level (SL), transmission losses (TL), and target strength

(TS)—were explicitly modeled. Of the noise components, noise spectral density (Nd) and noise bandwidth (BW)—the product of which is the noise power entering the receiver in the spectral frequencies to which it is sensitive—were assumed to be negligible relative to the detection threshold. The directivity of the pinnae (DI) was explicitly modeled. Model calibration indicated that a signal level corresponding to $-1$ dB was strong enough for the model bat to detect a simulated insect target at realistic ranges, and that figure was used in the study.

$$(SL-2TL+TS)-(No+BW-DI)=SNR_{dB}. \qquad (1)$$

Calibration data for the individual components of the acoustics model were taken from the literature. A realistic call pattern based on Hartley and Suthers (1989) was used with a maximum sonar transmission level of 104 dB peak-to-peak sound-pressure level at 10 cm in the frequency range of 30–33 kHz (Kick, 1982). The model applied greater attenuation to high-frequency components of the call (Hartley, 1989) as an adjustment to the transmission loss computed from the spatial divergence of the signal. The target cross-section fluctuations were based on Griffin (1967, Fig. 6, p. 291) and were modeled statistically, assuming a uniform distribution of orientations. The mean target strength (TS) was taken from data reported by Webster and Brazier (1965, their Figs. II-6 and II-7). The transfer function of the bat's ear was based on data reported by Wotton (1994) and Wotton *et al.* (1995, 1997).

For computational feasibility, the bat's call was modeled as an impulse in time (rather than the bat's FM sweep) with a spectral intensity pattern that varied in azimuth and elevation. These patterns were stored in a table, and the model interpolated linearly between tabulated points. The ear-transfer functions were stored similarly in three-dimensional tables, indexed by azimuth, elevation, and frequency. The frequency range was from 20 to 80 kHz with an interval of 1 kHz, and the azimuth and elevation were indexed corresponding to 10-deg intervals between $-70$ to $+70$ deg.

Intercall intervals changed as a function of range and were estimated from the vocalization data of the calibration trials. The interval value at long range was 66 ms, and that figure was used when the target was unlocalized or for azimuths and elevations where the model bat was not facing the target. Otherwise, the scheduling of call emissions was based on the model bat's estimate of its range to the target.

The reaction time of the bat was modeled as a constant 100-ms delay between the reception of the sonar return and the resulting update to the target state and changes to the model's behavior. This was chosen as a representative value for auditory responses in bats (Casseday and Covey, 1996) and is consistent with the reaction times reported in behavioral studies (Cahlander, McCue, and Webster, 1964; Cahlander and Webster, 1960; Kalko, 1995). Reaction times of 50-, 200-, and 400-ms were also studied.

### 4. Sensory processing

Sensory processing was responsible for maintaining the target state estimate. Range was estimated from the round-trip acoustic travel time to the target and azimuth from the intensity difference of the returns in the two ears. This algorithm was designed to produce an accurate range estimate when the model bat was approaching the target. The time associated with each measurement was the time of return receipt, rather than the time the call was reflected by the target, so that the raw range measurement had to be adjusted for potential movement of the bat model towards the target between the call generation and echo detection times. As a result, when the model bat did not approach the target, the range estimate had negative bias.

Azimuth was estimated by comparing the measured IID with a set of standard values. These were produced based on the response of the model to a set of standard spherical targets (sized to produce a target strength change of $-20$ dB at 10 cm) arrayed in azimuth at 2-m distance and 0 elevation. The algorithm for elevation treated the wideband spectral measurements as vectors in a high-dimensional vector space (Apostol, 1967, Chap. 12) and computed the elevation estimate by comparing them to a set of standard spectra generated within the model for the standard targets positioned at 2 m, at 0 azimuth and at 10-deg elevation intervals. The elevation for the best matching spectrum was used as the elevation measurement.

The model performed a state update only if the target was detected in both ears. The algorithm for determining this integrated the return signal energy in each ear in the frequency range between 25 and 40 kHz and compared that to an absolute detection threshold. If the target was detected in a single ear, the model bat turned towards that ear to increase the target intensity in the other ear. If the target was detected in both ears, the positional cue measurements were used by the model to update the target state estimate.

The position and velocity of the target, of the model bat's body center of mass, and the model's estimate of the target position were stored in Cartesian coordinates, and the bank angle of the bat was stored in radians. In the sensory processing function, these were converted into range, azimuth, and elevation by translating to the head from the body-centered coordinates and using the current direction of the head and the current bank angle to define a head-centered coordinate system. The inverse transformation was similarly handled.

Alternative models of head aim behavior were explored in the model and controlled by an input parameter, with the bat either facing forward throughout the trial or facing the target whenever it was localized in the forward hemisphere.

### 5. Motor planning

The motor planning function maintained a simple scheme of action based on when the target had been detected, the target location estimate, and the state of the model bat. The final capture maneuver was handled by having the model level out and begin straight flight at a range of 0.28 m from the target during final approach. This distance was based on experimental data from the calibration trials showing the bat leveling out and extending its tail membrane to form a pouch to capture the mealworm at about that distance.

Both simple target homing and an anticipatory algorithm making use of a predictive internal simulation of the capture

process to control the flight to the target (Rosen, 1985) were investigated for the motor planning function. The simple target homing algorithm was similar to that used by Kuc (1994) and consisted of turning the flight vector of the model bat to face the target.

The anticipatory algorithm was developed after it was noted in the calibration trials that the real bat did not simply home on the target, but often flew past, looped around, and returned to capture the insect. In this algorithm, if an internal simulation of the capture predicted that the trajectory generated by a simple homing strategy would miss the target location, additional tactics were implemented. The model first attempted to tighten its turn by slowing. If that succeeded in setting up a capture, the model bat would follow a tight circle into the target, similar to the trajectories seen in some calibration trials. If that then also failed, the capture attempt was abandoned, with the model climbing away from the target and returning for a second attempt.

### 6. Motor response

The motor response function computed a thrust, lift, and bank angle to execute the commands provided by motor planning. Those values were then used to compute the current acceleration vector and the rate of change of bank as input to a Runge–Kutta integrator to update the model state.

A simple flapping-flight model (Rayner, 1979, 1987) was used to estimate the maximum lift and thrust combinations the real bat could generate at various airspeeds and angles of attack. This was based on data from Norberg (1987, 1990) and computed the lift, thrust, and drag of the model bat flight stroke in 1/240th s increments, assuming 13.5 wingbeats per second (Wilson and Moss, 2001). Each wingbeat was modeled in ten equal spanwise increments. The model bat was assumed to have a mass of 15 g, with a 30-cm wingspan and 0.015-$m^2$ wing area, corresponding to a slightly retracted wing. Stall angle used was 1/3 radian based on von Mises (1959). Velocity at the tip of the wing was 5 m/s. Bat speed was varied from 1.0 to 4.5 m/s and the resulting lift, thrust, and drag forces were computed for 0.1-radian increments of the stroke plane angle from 0.0 to 1.0 radians. The resulting values were then fitted with a second-order polynomial approximation ($r^2 = 0.99$) to give an equation that was used in the model.

Aerodynamic limits (preferred speed and maximum tolerated acceleration) were estimated from an aerodynamic analysis (von Mises, 1959) of the calibration trial data. Behavioral data from the calibration trials showed that the bats could decelerate as quickly as 4 $m/s^2$, which was in excess of the deceleration that drag alone would produce, so the model was designed to use reversed thrust to slow.

### C. Data analysis

### 1. Video processing methods

A commercial motion analysis system (Peak Performance Technologies Motion Analysis System-Motus) was used to digitize both camera views using a Miro DC-30 Plus interface and to calculate the three-dimensional location of points marked in both camera views. Digitization was to 1/4-pixel resolution using magnification. The reflective marker placed on the bat's head and /or back was marked in each video frame where visible. The trajectory was extrapolated when the reflective marker was not visible over a segment of video frames (e.g., when concealed by a wing). The marker spanned several video pixels, and the center of the marker was estimated by eye and digitized.

The accuracy of the system was within ±0.5% over the calibrated volume. The three-dimensional space calibration frame provided 25 control points for direct linear transformation (DLT) calibration. The calibration procedure produced a mean residual error of 1.0 cm in each coordinate for the 25 control points.

The bat's velocity was estimated from the difference between position measurements separated by a time interval of 100 ms, producing a mean error of 0.245 m/s. Acceleration was estimated by measuring the change between two velocity estimates separated by a 200-m interval, resulting in a mean error of 1.73 $m/s^2$.

### 2. Audio processing methods

The model was calibrated to replicate the bat's intercall timing (onset to onset) as a function of range and orientation relative to the target. This timing was derived from recordings of the bat's sonar vocalizations processed from three channels of the Racal Store-4 reel-to-reel recorder. Sounds were played back at 1/4th the recording speed (7.5 in/s) and digitized using a National Instruments board (AT-MIO-16-1) with a sampling rate of 60 kHz per channel, resulting in an effective sampling rate of 240 kHz per channel. Custom software (LABVIEW) trimmed the digitized audio data to begin with the first and end with the last frame of video acquisition and output files were exported to a digital signal-processing program (SONA-PC, Waldmann). Using Sona-PC, a fast Fourier transform (FFT) was performed over 256 points per time step, with 16–20 points being replaced in each time step and displayed as time waveforms and spectrograms. The onset time, duration, and start- and end frequencies of the first harmonic of the emissions were marked with a cursor on the display and downloaded to a spreadsheet program (MICROSOFT EXCEL 97). Audio and video data were then merged in a single analysis file in order to associate vocal behavior with bat position at call onset.

### 3. Statistical analyses and hypothesis testing

Statistical analysis of the modeling runs was performed using the S-PLUS exploratory analysis tool (Statistical Sciences, 1995). Measurements were stored in a relational database (MICROSOFT FOXPRO), with each record containing the sample values for the independent variables, the specific group or case being studied, the time of the target capture, and a "censoring" variable indicating whether the model run was continued until capture occurred or terminated at 4 s. For comparative analysis of multiple modeling runs, these data were used as input for a statistical test consisting of a combination of the log-rank test and the Peto–Wilcoxon test

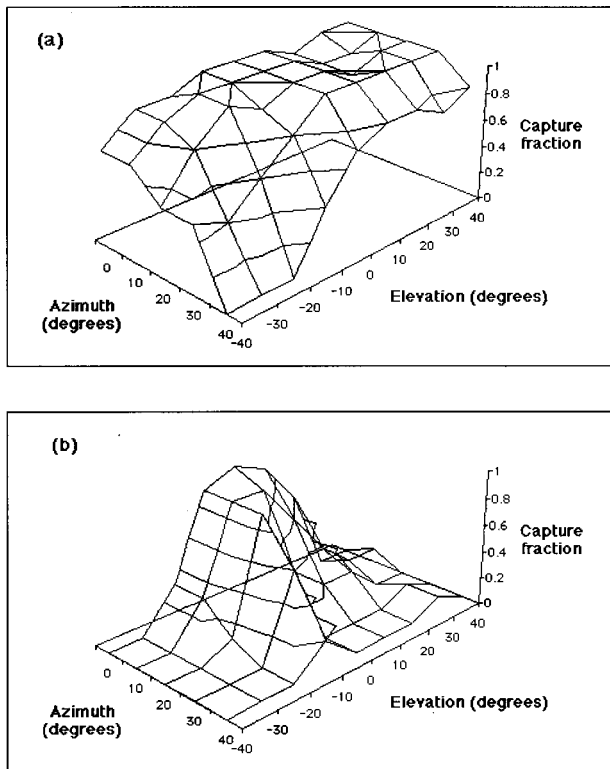Erwin *et al.*: A computational sensorimotor model of bat echolocation

FIG. 1. Capture success fraction for (a) anticipatory and (b) simple homing strategies in the right frontal half hemisphere both for a grid of target locations initially 2 m from the model bat, ten samples per position.

| Case | $\chi^2$ | $df$ | $p$ |
|---|---|---|---|
| Ear-transfer pattern | 0.1 | 1 | 0.801 |
| Call pattern | 3.4 | 1 | 0.0345 |
| Target fluctuation | 0.2 | 1 | 0.653 |
| Target spectral variation | 1.2 | 1 | 0.274 |

with an estimator approximately distributed as a chi-squared statistic with one degree of freedom (see Harrington and Fleming, 1982).

## III. RESULTS

### A. Model calibration and validation

#### 1. Calibration

The model was calibrated against the behavior seen in 16 empirical trials selected as representing typical target capture behavior in *E. Fuscus*. In these runs, the model bat was given the same initial state (body position and velocity) as the real bat and modeled in its approach to the target. (The initial state was estimated from the position of the bat at the beginning of the video recording and the velocity estimated from the positions at the beginning and 100 ms later.) The model was then calibrated by revising the algorithms of the model and input parameters incrementally until the observed behavior was replicated, much as a neural network is trained. It was then validated against an additional 15 empirical trials and finally run against a grid of standard spherical targets positioned at 2 m from the initial position of the model bat. The probability of capture of the standard targets using an anticipatory motor planning algorithm is presented in Fig. 1(a). Capture probabilities of 80% or higher were seen for initial elevations between 40 and −10 deg out to 30 deg azimuth, and for initial elevations between −20 and −30 deg out to 20 deg azimuth. Performance using the simple homing strategy was markedly poorer, with capture prob-

abilities greater than 80% occurring only within a zone that was within 20 deg of the midline and between +10 and −10 deg elevation [see Fig. 1(b)].

#### 2. Sensitivity

The sensitivity of the model to variation in the acoustical calibration data was investigated (see Table I). Only replacement of the realistic call pattern with an isotropic pattern (an unrealistic pattern with the same intensity spectrum at all azimuths and elevations) produced a statistically significant difference in the model's performance at the 5% level, with the isotropic pattern performing more poorly. The isotropic pattern eliminated information that could be used to estimate elevation, so this was unsurprising. Calibration data changes that did not affect model performance included statistical smoothing of the ear-transfer function (to smooth away local features that did not extend over more than 30% of the azimuth, elevation, or frequency range), elimination of target cross-section fluctuation (so that the target echo amplitude didn't flicker), and elimination of random target spectral intensity variation (which could have affected the elevation estimation algorithm).

The model was insensitive to maximum acceleration tolerated during maneuvering flight (a standard of 1.49 times the acceleration of gravity) and to maximum acceleration tolerated prior to target localization (a standard of 1.33 times the acceleration of gravity). It was also insensitive to preferred speed (3.32 m per second was the standard). Unrealistic performance was seen in turns when the model used steady-state aerodynamics, and it was also unrealistic when it used drag for deceleration. The model was realistic when the model used flapping-flight aerodynamics and reversed thrust for deceleration.

In those trials with an initially unlocalized target, model performance was very sensitive to the timing of when the model bat left its search pattern and began to approach the target. It was also sensitive to reaction time, detection threshold, and call timing as they affected this. The model performance when the reaction time was 200 ms or longer was particularly poor due to this sensitivity and also possibly due to lack of control.

Finally, although the exact trajectory produced in each model run was sensitive to the timing and values of the simulated sensory measurements, so that the choice of random number seed had a visible effect on the trajectory, the model was *statistically* insensitive to the choice of random number seed.

### 3. Validation

The criterion for successful replication was a capture time within 25% of the value seen in the behavioral trial requiring similar tactics. The first criterion was chosen based on the observed magnitude of the variation in bat velocity in the calibration trials at standard points—2.86 m/s with a standard deviation of 0.52 m/s at capture and of 2.70 m/s with a standard deviation of 0.59 m/s at a point 200 ms before capture. Limiting the second criterion to a similar choice of tactics was based on the observation that the tactics of the model were robust, but the exact trajectory followed by the model was dependent on the precise timing of the model's commitment to attempt capture of the target. The tactics seen in the calibration trials (produced by two bats) reappeared in the validation trials (produced by five other bats) along with some new tactics. Twelve of 15 validation trials were successfully replicated.

The most commonly observed tactic in the behavioral trials was a circling maneuver with the bat slowing to sharpen its turn while remaining near the target, a tactic the model used when it anticipated that simple homing would fail. If this tactic also failed, the model was programmed to abandon the pass and fly out to try again.

A few validation trials with novel tactics showed that the anticipatory motor planning algorithm generated simpler behavior than that actually observed. In one trial the model bat homed directly on the target in all modeling runs investigated, but the real bat flew above the target and turned and dove to capture it at the last moment. In other trials, the real bat delayed its capture of the target by 250–325 ms, usually by circling around it, while the model bat homed directly at the target. These trials—viewed in a context where the model consistently chose more direct flight paths than the real bat, even when successful—raised the question of whether the assumptions about the motor reaction time or initial target localization were in error. This led to a sensitivity study of these questions (Fig. 2) using a trial that began about 850 ms before contact. The behavior of the real bat (shown at the top) was consistent with capture using an anticipatory strategy, first slowing to sharpen its turn to compensate for a delayed start of 50–100 ms, and then homing on the target. The next four rows show various modeling runs, with different initial conditions (localized or unlocalized target), motor planning algorithms (anticipatory or simple homing), and motor reaction times (50, 100, 200, and 400 ms).

In Fig. 2, the observed bat's behavior was most similar to the pattern shown in the first row for the model, with motor reaction times of 50–200 ms. With the 400-ms reaction time, the model bat flew past the target and made a sharp turn to intercept it. The sharp turn illustrated for this model run resembled the real bat's behavior in some insect capture trials, where it performed a tight climbing turn to do a quick change of direction. The second and fourth rows show that a simple full-speed homing strategy initiated immediately after target localization would have been successful but did not match the observed trajectory. Since the real bat had probably localized the target before the start of the video recording, this suggests the bat had not *committed* to the capture at

that point; otherwise, a similar trajectory would have been expected.

### B. Localization cues and capture performance

The model computed range by measuring the echo delay between call and return time, dividing that by the speed of sound to estimate the round-trip distance, and adjusting the estimate to account for the model bat's motion towards (or away from) the target between the call emission and echo return times. This adjustment was designed to minimize the range error at the point where the model bat initiated its final capture maneuver (at a range of 0.28 m based on the distance measured in the calibration trials), and produced a systematically negative range error when the bat was not flying towards the target. The error in range varied smoothly with time for each individual trial, producing recognizable trajectories in the plots. Figure 3(a) shows the model's range localization error compared to the actual range for the validation runs, with anticipatory strategies and 100-ms reaction time. The mean value of the range localization error over 974 samples in the 15 validation runs was −1.3 mm with a standard deviation of 2.4 mm.

Errors in azimuth were produced by the linear interpolation used to estimate azimuth from the sound intensities in the two ears. Figure 3(b) shows the model's azimuth error as a function of range with a mean value of 0.2 deg and a standard deviation of 2.2 deg.

The model was designed to use spectral measurements consisting of 1-kHz narrow-band intensity samples between 20 to 80 kHz from each ear in a match/mismatch process for estimating elevation. The elevation error had two sources: a quantization error introduced by the 5-deg interval between the comparison spectra and any error in the choice of the best-matching comparison spectrum. Figure 3(c) shows the model's elevation error as a function of range with a mean value of 0.8 deg and a standard deviation of 2.0 deg. As the model bat neared the target, azimuth and elevation were able to change more rapidly, and the target was more likely to be out of the region where localization was most accurate. This produced higher angular error values when the model bat was near the target.

When the model used simple homing as its motor planning algorithm, only using range to schedule the capture maneuver, its overall capture performance was poorer than the anticipatory model for targets located off-axis. When the model used anticipatory motor planning, it functioned poorly if any of the three localization components (range, azimuth, and elevation) were missing. Azimuth and elevation were important at all stages of the model's capture process, and range was required in those trials with an anticipatory strategy where the model bat maneuvered.

The model was also modified so that the head would either aim in the direction of flight throughout the run or at the target once it was localized. In the latter case, the model bat circling a target would turn its head up to 90 deg toward the target. This had little effect when the underlying behavioral trial used a simple homing strategy, but when the model bat had to maneuver, successful interception occurred only when head aim at the target was enabled.
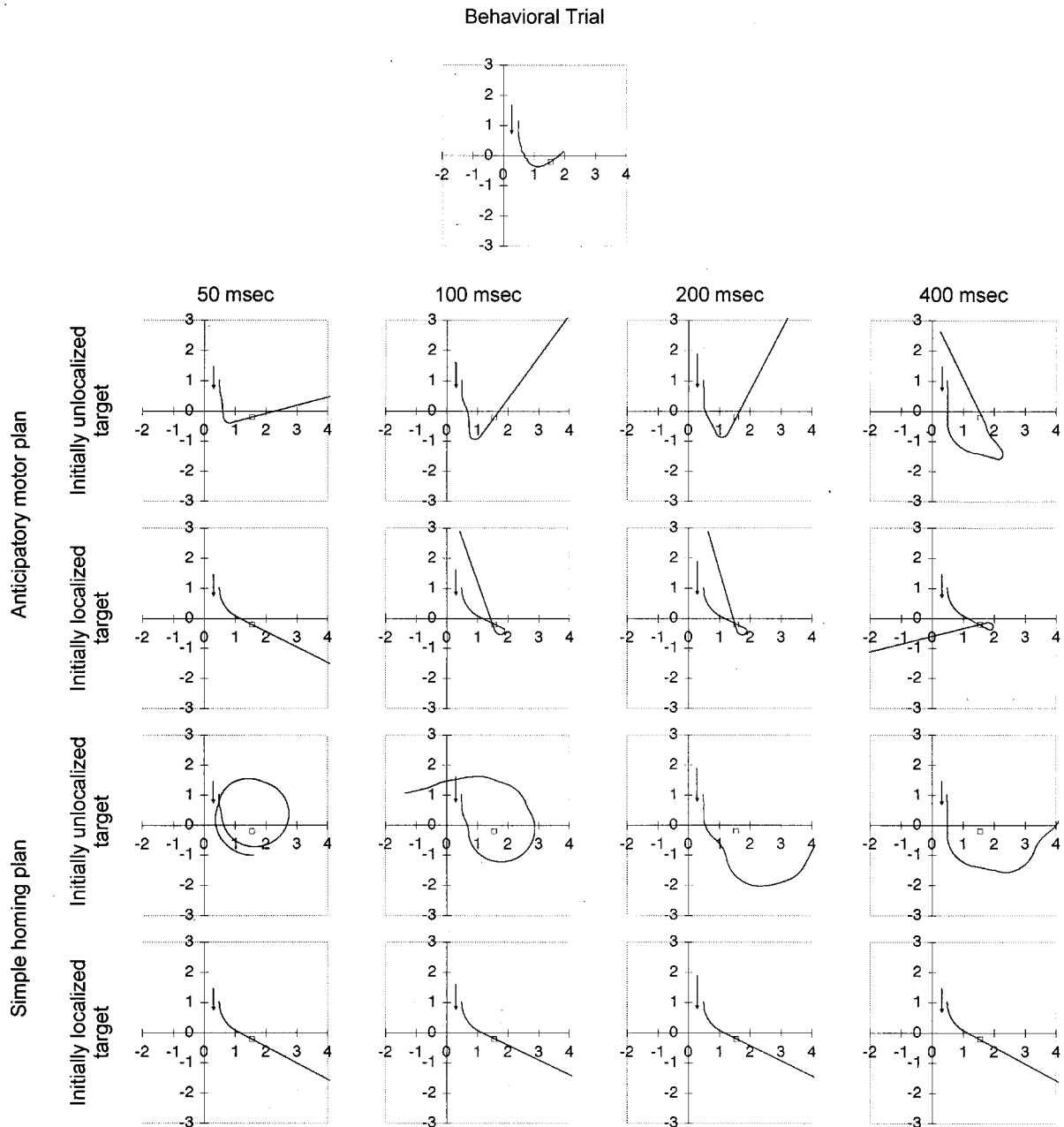
FIG. 2. Sensitivity study of a validation trial seen from above, with the reaction time and motor planning algorithm being varied. The columns show model runs with reaction times of 50, 100, 200, and 400 ms. The rows show the model bat approaching targets that were at an unknown (unlocalized) or known (localized) location at the beginning of the run, and with an anticipatory or a simple homing algorithm. Coordinates are in meters. Target location is shown by a box; bat trajectory by the line and the arrow shows direction of flight.

## IV. DISCUSSION

Webster and Brazier (1965) studied the insect capture behavior of the echolocating bat, *Myotis lucifugus*, when pursuing moths in foliage. The moths used evasive maneuvers, changing their direction of flight up to 90 deg in 200 ms. The speed of the bats' reaction to the moth maneuvers, while simultaneously avoiding branches and twigs, suggests a relatively direct translation of sensory data into motor behavior. The modeling reported here begins to provide some insight into the important parameters for successful prey interception by echolocating bats. In particular, the results of the modeling suggest that the bat anticipates when and where the

target will be at the point of interception and plans its motor behavior to position itself in 3D space to capture the prey at a specified location.

### A. Model performance

Using anticipatory motor planning, the model showed realistic capture performance for initial target positions between the acoustic axes of the ears (at ±30-deg azimuth) and with initial elevations between −10 and +40 deg. The model's spatial localization performance was about 0.8 cm at 15 cm (about the distance of a wingtip catch), which was better than the 1.5 cm estimated in three dimensions by Webster and Griffin (1962) and also better than the estimated 1.27 cm
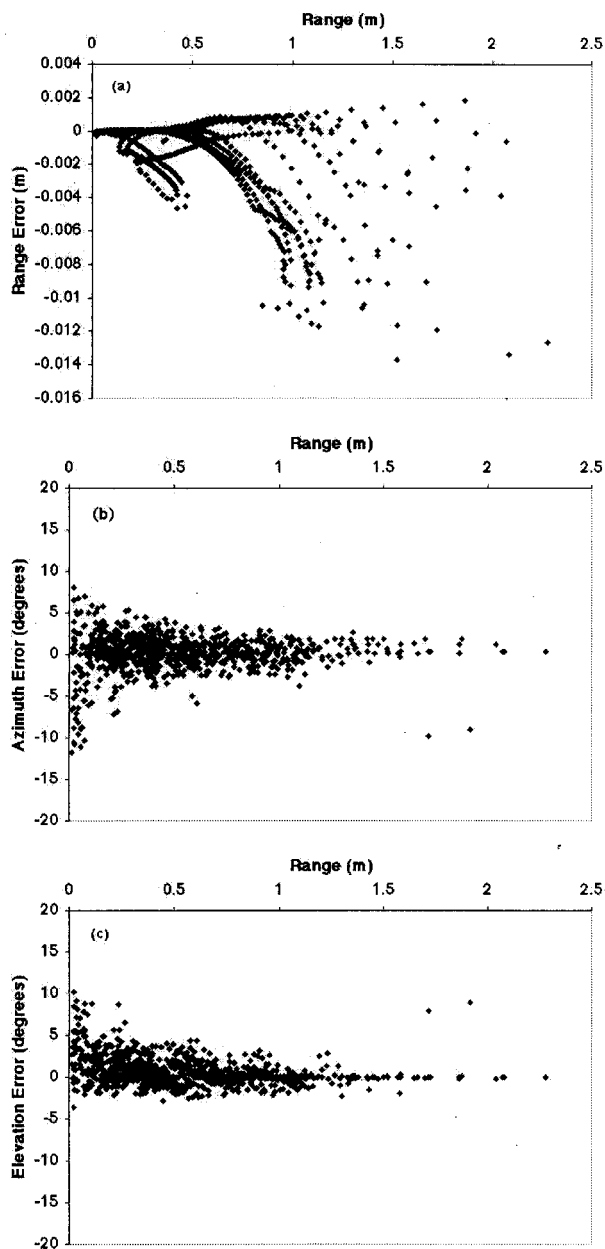
FIG. 3. (a) Range; (b) azimuth; and (c) elevation localization performance of the model during the validation runs. Each dot represents the error associated with a single call, plotted against range. There were 974 samples from 15 validation runs using anticipatory planning and 100-ms reaction time.

required for a wingtip catch reported by Webster and Brazier (1965). Standard deviations of localization accuracy were estimated to be 2.4 mm for range, 2.0 deg for azimuth, and 2.2 deg for elevation. The azimuthal localization performance was comparable with the 1.5-deg threshold for discriminating the azimuthal separations of thin rods, reported by Simmons et al. (1983) and was somewhat better than the 3.0 deg estimated for elevation by Lawrence and Simmons (1982). On the other hand, the model had markedly better performance than the minimum audible angle of about 14 deg reported in Koay et al. (1998) for passive localization in azimuth, which corresponds to about 3.5–4 cm at a 15-cm range, too large for the wingtip catch that E. fuscus is sometimes seen to make. Clearly the task demands of passive

localization are distinct from those of active echolocation, which may explain the very different behavioral estimates of localization performance.

Figure 1 shows that the model failed to capture targets when they were outside a zone defined by the acoustic axes of the ears and the upper half of the frontal hemisphere when the model bat was initially facing forward. This is interesting, given the high capture rate observed in the laboratory insect capture experiments, and evidence from laboratory and field studies that vespertilionid bats use a search cone 150–180 deg wide (Griffin, Webster, and Michael, 1960; Kalko, 1995). The general pattern of tactics used by the model in its *successful* captures—simple homing at full speed for near-zero elevations, slower homing captures above that, and multiple target passes at very high and low elevations as the model anticipated that the first pass would fail—showed no sensitivity to initial target azimuth. This suggests that the poor model performance seen at large azimuths was not due to failure to select the correct tactics, but instead might be attributed to the model bat's failure to localize the target adequately.

This model performance is consistent with acoustic studies of the combined directional characteristics of the bat's sonar emission and receiver reported in Wotton, Jenison, and Hartley (1997), and suggests that the head of E. fuscus would shadow low-elevation targets from both ears and that interaural intensity differences (IIDs) should also be ambiguous at azimuths outside the acoustic axes of the two ears. Since this bat species can capture targets with about 90% reliability in behavioral trials and often uses "pouncing" tactics to capture targets from above, the modeling is incomplete in how it handles localization. To deal with the problem of shadowing low-elevation targets, E. fuscus may face slightly downward or use scanning motions to cover the lower half of the frontal hemisphere. Recordings of echolocation calls produced by E. fuscus in the field reveal alternations in signal intensity are consistent with the proposed head-scanning behavior by bats (Surlykke and Moss, 2000).

To localize targets at large azimuths, E. fuscus may use interaural time differences (Simmons et al., 1995), to supplement intensity differences. There may also be cues hidden in the intensity spectrum, given the evidence that intensity and time differences trade off (Pollak, 1988). Alternatively, these bats may simply maneuver to bring candidate targets into the zone where they can be localized. These ideas will be explored in future modeling.

The model was used to investigate why the FM bat aims its head at the target with an estimated accuracy of about ±5 deg (M. lucifugus in Webster and Brazier, 1965). As noted above, the localization performance of the model was best when the target was initially between the two ears and above the region shadowed for both ears. This is a 60- to 80-deg cone forward of the bat, and the behavioral trial data indicate that the bat frequently captured a target using maneuvers that would take it outside that forward cone if the bat did not aim its head at the target. The trajectories followed by the bats in the behavioral trials appear to be consistent with a body orientation that would allow them to keep the target in that cone with less than 90 deg of head rotation.

Erwin *et al.*: A computational sensorimotor model of bat echolocation

## B. Comparison with other models

Kuc's (1994) model attempted to reduce to zero an elevation error signal at the two ears that was estimated as a linear combination of the target intensity in the fundamental and the overtone. The model presented here was initially designed to use that approach, but the complex pattern of biologically realistic target echoes was incompatible with the use of linear interpolation in this task. The model was therefore redesigned to compare simulated wideband spectral intensity measurements (taken every 1 kHz between 20 and 80 kHz in each ear) to calibrated standard spectra to find a nearest match. The elevation for the best-matching comparison spectrum was then used as the estimate of the elevation of the target. This approach is likely to be a simplified representation of the biological processing since it uses an impulse rather than an FM sweep as input, but it avoids having to explicitly identify an elevation-dependent notch (as discussed in Wotten *et al.*, 1996), and allows other elevation-dependent spectral cues to be used as well. This approach was successful in the model, but a realistic representation of what occurs in sonar localization by FM bats would require a fast match/mismatch in auditory processing. The modeling runs also suggest that a general change in shape of the intensity spectrum with elevation, rather than specific detection of a spectral notch, may be a robust elevation cue, since it would make more use of the information in the echo. The model showed how this approach might be calibrated to the environment, adapting to the humidity (Hartley, 1989) and the bat's current call pattern (Hartley and Suthers, 1989), which Griffin (1958, p. 184) notes can vary a great deal (see also Surlykke and Moss, 2000).

Both Masters (1988) and Kuc (1994) used simplified aerodynamics in their models. Masters assumed a fixed minimum turning radius and a fixed velocity of 5 m/s. Kuc assumed a fixed velocity of 3 m/s, no banking, and unlimited turn rate. Both sets of assumptions are inconsistent with the behavioral data, and produce flight trajectories that differ from those calculated from high-speed video recordings of insect captures by echolocating bats. Although the present model continues to use simplified aerodynamics, the banking and maneuvering it simulates interact with acoustics and motor planning in complex ways, for example, showing that target tracking requires an accurate estimate of the bat's own state, including bank, yaw, and pitch. Planning the target capture also needs this state estimate, since the bat's speed controls how quickly it can turn and what regions of the space around it can be easily accessed in an attempt to intercept the target. This suggests that further work in flight aerodynamics would provide valuable insight into the sensorimotor process underlying target capture by bats.

## C. Target capture behavior

Finally, the present model shows that three-dimensional target localization is necessary to replicate the full set of insect capture behaviors exhibited by the echolocating FM bat. For simple homing strategies, range was not needed to produce the trajectories seen in the behavioral trials, but was still required to deploy the bat's tail membrane in the final capture maneuver at the appropriate time. Azimuth and elevation were needed for all trials, which is not surprising, given that flight maneuvers cause the bat to bank, translating azimuth to elevation and elevation to azimuth.

The behavior seen in the experimental trials fell into three primary categories: captures using a simple homing strategy, delayed captures (where the bat circled or flew past the target before turning for the capture), and two-pass maneuvers to gain a position from which a simple homing capture could then be staged. Similar tactics were previously noted by Griffin *et al.* (1960), Webster and Brazier (1965), Miller and Olesen (1979), Miller (1984), Kick and Simmons (1984), Schnitzler *et al.* (1988), and Kalko (1995), but the modeling of those trials now confirms that aerodynamics and acoustics constrain the bat by limiting the points in nearby space that it can easily fly to or sample using echolocation. Selection of the most direct path to target capture does not seem to be a central factor driving the bat's behavior. The real bats rarely homed along a fast straight trajectory to the target, preferring slower homing trajectories that curved into the target, and sometimes deferred a direct capture. This has also been seen in the field and possibly reflects a strategy to maximize capture success in view of the erratic and evasive flight behavior of some insect prey (Kalko, 1995; Surlykke, 1988).

Some of the maneuvers seen in the experimental trials can now be understood as implementing a simple plan to gain a position above and aiming at the target, from which a homing capture can be attempted. Other trials suggest that the bat localized the target before committing to capture it. Execution of many of these plans appears to involve anticipatory control, since they often required starting a maneuver at some specific position relative to an already localized target.

A likely explanation of some of these delayed captures is that the bat was carefully positioning itself in 3D space to maximize its probability of successful target capture. The capture maneuver involves tight coordination of the timing of the distance-dependent vocalization patterns and positioning of the tail or wing membrane with respect to the insect to successfully intercept the prey. The bat may need to approach the insect from a specific direction and with specific timing to perform this maneuver successfully, especially if the target is moving. Different behavior may be seen when the insect is free to evade the bat, and new experiments in the lab will provide insight into this area. Studies combining sensorimotor modeling with behavioral experiments using moving targets are underway to illuminate these questions.

The two motor planning algorithms investigated were not fully satisfactory. Simple homing was effective in only part of the forward hemisphere and could not handle targets to the side that were closer than the turn radius of the bat. The anticipatory motor planning algorithm used tended to produce sharper turns than those observed in the behavioral trials and resulted in straight rather than curved trajectories toward the insect. A third algorithm ("adaptable homing") is now being explored. This estimates the maximum speed the model bat would have to fly to be able to pass through the target location using homing guidance, then adjusts to that

speed by climbing and using reverse thrust. This is expected to improve the performance of the model in future studies.

## V. CONCLUSIONS

This new sensorimotor model melds a small repertoire of motor tactics with biologically realistic acoustics and aerodynamics to replicate the echolocating FM bat's target capture behavior from experimental trials. Kuc (1994) had proposed his model as a ''small step toward understanding the power of acoustic information processing employed in nature.'' Using Kuc's work as a starting point and taking the next step of adding biological realism in selected areas, this model has shown how the elevation span for capture can be increased from 20 to 50 deg, while maintaining the same azimuthal cone. Kuc's homing model, lacking memory and using only azimuth and elevation signals to collide with the target, did not fully model how bats capture insects. The present model incorporates the use of distance information, which is required for the bat to accurately time its range-dependent vocal production patterns and to position itself at the point of intercept to collect (not collide with) the prey item.

A model using a small number of narrow-band intensity samples from each ear to estimate elevation, such as that employed by Kuc (1994), encounters difficulties when presented with echoes with realistic intensity spectra. A model that collects a spectral intensity sample over a wide band seems to be robust against noise and performs well for targets within a 60-to-80-deg cone in front of the bat.

Realistic aerodynamics constrains the bat's behavior more than was suggested in Kuc's (1994) and Masters's (1988) models. The bat has to bank to turn and is limited in the maximum accelerations that it can generate, often forcing it to maneuver to perform the target capture. Further research into the aerodynamics of echolocating bats, such as *E. fuscus*, in maneuvering flight will be valuable for understanding the role of aerodynamic constraints in defining target capture behavior.

Rapid target capture does not appear to be the preferred strategy for the bat. There is evidence that the bat does not commit immediately to target capture, instead delaying capture beyond the time simply required to maneuver to a collision with the target. The purpose of those delays is unclear, but may include target classification or maneuvers to maximize the success of target capture with a potentially long response latency. The good performance of the model with a reaction time of 100 ms suggests that anticipatory planning of tightly timed behaviors can compensate for the delay between receipt of the sensory stimulus and the corresponding motor response.

The demonstration that the model can capture targets over a wide range of elevations and azimuths, despite a reaction time of 100 ms or more, also shows that target capture algorithms need not have millisecond responsiveness. Timing seems to be important when maneuvers have to be initiated, but with accurate 3D localization of a stationary target, those maneuvers can be scheduled hundreds of milliseconds in advance of their execution. Capture of evading insects is likely to be more difficult for the bat, but once the insect commits to an escape maneuver, it limits its future ability to turn or accelerate, so that a good prediction of the insect's motion path would still allow the bat to schedule maneuvers in advance. Hence, an accurate representation of the environment that takes into account the constraints on the behavior of the objects being modeled may allow the most economical control of behavior, whether the system is concerned with making or avoiding contact with objects.

Apostol, T. (**1967**). *Calculus* (Blaisdell, Waltham), Vol. 1.

Austern, M. (**1998**). *Generic Programming and the STL* (Addison-Wesley, Reading, MA).

Blauert, J. (**1997**). *Spatial Hearing: The Psychophysics of Human Sound Localization*, revised ed., translated by J. S. Allen (MIT Press, Cambridge, MA).

Cahlander, D. A., McCue, J. J. G., and Webster, F. A. (**1964**). ''The determination of distance by echolocation,'' Nature (London) **201**, 544–546.

Cahlander, D. A., and Webster, F. A. (**1960**). *The Bat's Reaction Time* (47G-0008): MIT Lincoln Laboratory.

Camp, L. (**1970**). *Underwater Acoustics* (Wiley-Interscience, New York).

Casseday, J. H., and Covey, E. (**1996**). ''A neuroethological theory of the operation of the inferior colliculus,'' Brain Behav. Evol. **47**, 311–336.

Griffin, D. R. (**1958**). *Listening in the Dark* (Comstock, Ithaca).

Griffin, D. R. (**1967**). ''Discriminative echolocation by bats,'' in *Animal Sonar Systems*, edited by R. G. Busnel (Laboratoire de Physiologie Acoustique, Jouy-en-Josas-78).

Griffin, D. R., Webster, F. A., and Michael, C. R. (**1960**). ''The echolocation of flying insects by bats,'' Anim. Behav. **8**, 141–154.

Grinnell, A. D., and Grinnell, V. S. (**1965**). ''Neural correlates of vertical localization by echolocating bats,'' J. Physiol. (London) **181**, 830–851.

Grothe, B., and Park, T. J. (**1998**). ''Sensitivity to interaural time differences in the medial superior olive of a small mammal, the Mexican free-tailed bat,'' J. Neurosci. **18**(16), 6608–6622.

Harnischpfeger, G., Neuweiler, G., and Schlegel, P. (**1985**). ''Interaural time and intensity coding in the superior olivary complex and inferior colliculus of the echolocating bat, *Molossus ater*,'' J. Neurophysiol. **53**, 89–109.

Harrington, D. P., and Fleming, T. R. (**1982**). ''A class of rank test procedures for censored survival data,'' Biometrika **69**, 554–566.

Hartley, D. J. (**1989**). ''The effect of atmospheric sound absorption on signal bandwidth and energy and some consequences for bat echolocation,'' J. Acoust. Soc. Am. **85**, 1338–1347.

Hartley, D. J., and Suthers, R. A. (**1989**). ''The sound emission of the echolocating bat, *Eptesicus fuscus*,'' J. Acoust. Soc. Am. **85**, 1348–1351.

Hartridge, H. (**1945**). ''Acoustic control in the flight of bats,'' Nature (London) **156**, 490–494, **156**, 692–693.

Hope, G. M., and Bhatnagar, K. P. (**1979**). ''Electrical response of bat retina to spectral stimulation: Comparison of four microchiropteran species,'' Experientia **35**, 1189.

ISO/IEC. (**1998**). *Standard for the* C++ *Programming Language, ISO/IEC 14882*: ITI.

Jen, P. H. S., and Chen, D. (**1988**). ''Directionality of sound pressure transformation at the pinna of echolocating bats,'' Hear. Res. **34**, 101–108.

Kalko, E. K. V. (**1995**). ''Insect pursuit, prey capture, and echolocation in pipistrelle bats (*Microchiroptera*),'' Anim. Behav. **50**, 861–880.

Kick, S. A. (**1982**). ''Target detection by the echolocating bat, *Eptesicus fuscus*,'' J. Comp. Physiol., A **145**, 431–435.

Kick, S. A., and Simmons, J. A. (**1984**). ''Automatic gain control in the bat's sonar receiver and the neurophysiology of echolocation,'' J. Neurosci. **4**, 2725–2737.

Koay, G., Kearns, D., Heffner, H. E., and Heffner, R. S. (**1998**). ''Passive sound-localization ability of the big brown bat (*Eptesicus fuscus*),'' Hear. Res. **119**, 37–48.

Kuc, R. (**1994**). ''Sensorimotor model of bat echolocation and prey capture,'' J. Acoust. Soc. Am. **96**, 1965–1978.

Lawrence, B. D., and Simmons, J. A. (**1982**). ''Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats,'' J. Acoust. Soc. Am. **71**, 585–590.

Masters, W. M. (**1988**). ''Prey Interception: Predictive and Nonpredictive Strategies,'' in *Animal Sonar: Processes and Performance*, edited by P. E. Nachtigall and P. W. Moore (Plenum, New York), pp. 467–470.

Masters, W. M., Moffat, A. J. M., and Simmons, J. A. (**1985**). ''Sonar tracking of horizontally moving targets by the big brown bat *Eptesicus fuscus*,'' Science **228**, 1331.

Miller, L. A. (**1984**). ''Hearing in Green Lacewings and their Responses to the Cries of Bats,'' in *Biology of Chrysopidae*, edited by M. Canard, Y. Semeria, and T. R. New (Dr. W. Junk, The Hague), Vol. 27, pp. 134–149.

Miller, L. A., and Olesen, J. (**1979**). ''Avoidance behavior on green lacewings I. Behavior of free flying green lacewings to hunting bats and ultrasound,'' J. Comp. Physiol., A **131**, 113–120.

Mogdans, J., Ostwald, J., and Schnitzler, H.-U. (**1988**). ''The role of pinna movement for the localization of vertical and horizontal wire obstacles in the greater horseshoe bat, *Rhinolophus ferrumequinum*,'' J. Acoust. Soc. Am. **84**, 1676–1679.

Møhl, B. (**1988**). ''Target Detection by Echolocating Bats,'' in *Animal Sonar: Processes and Performance*, edited by P. E. Nachtigall and P. W. Moore (Plenum, New York), pp. 435–450.

Moss, C. F., and Schnitzler, H.-U. (**1995**). ''Behavioral Studies of Auditory Information Processing,'' in *Hearing by Bats*, edited by A. N. Popper and R. R. Fay (Springer, New York), Vol. 5, pp. 87–145.

Norberg, U. M. (**1987**). ''Wing Form and Flight Mode in Bats,'' in *Recent Advances in the Study of Bats*, edited by M. B. Fenton, P. Racey, and J. M. V. Rayner (Cambridge University Press, Cambridge, MA), pp. 43–56.

Norberg, U. M. (**1990**). *Vertebrate Flight* (Springer, Berlin).

Pollak, G. D. (**1988**). ''Time is traded for intensity in the bat's auditory system,'' Hear. Res. **36**, 107–124.

Press, W. H., Flannery, B. P., Teukolsky, S. A., and Vetterling, W. T. (**1988**). *Numerical Recipes in C: the Art of Scientific Computing* (Cambridge University Press, Cambridge, MA).

Rayner, J. M. V. (**1979**). ''A new approach to animal flight mechanics,'' J. Exp. Biol. **80**, 17–54.

Rayner, J. M. V. (**1987**). ''The Mechanics of Flapping Flight in Bats,'' in *Recent Advances in the Study of Bats*, edited by M. B. Fenton, P. Racey, and J. M. V. Rayner (Cambridge University Press, Cambridge, MA), pp. 23–42.

Rosen, R. (**1985**). *Life Itself: A Comprehensive Inquiry Into the Nature, Origin, and Fabrication of Life* (Columbia University Press, New York).

Schnitzler, H.-U., Kalko, E., Miller, L., and Surlykke, A. (**1988**). ''How the Bat, *Pipistrellus kuhli*, hunts for insects,'' in *Animal Sonar: Processes and Performance*, edited by P. E. Nachtigall and P. W. Moore (Plenum, New York), pp. 619–624.

Shimozawa, T., Suga, N., Hendler, P., and Schuetze, S. (**1974**). ''Directional sensitivity of echolocating system in bats producing frequency modulated signals,'' J. Exp. Biol. **60**, 53–69.

Simmons, J. A. (**1973**). '' The resolution of target range by echolocating bats,'' J. Acoust. Soc. Am. **54**, 157–173.

Simmons, J. A., Ferragamo, M. J., Saillant, P. A., Haresign, T., Wotton, J. M., Dear, S. P., and Lee, D. N. (**1995**). ''Auditory Dimensions of Acoustic Images in Echolocation,'' in *Hearing by Bats*, edited by A. N. Popper and R. R. Fay (Springer, New York), Vol. 5, pp. 146–190.

Simmons, J. A., Kick, S. A., Lawrence, B. D., Hale, C., Bard, C., and Escudiè, B. (**1983**). ''Acuity of horizontal angle discrimination in the echolocating bat, *Eptesicus fuscus*,'' J. Comp. Physiol., A **153**, 321–330.

Skolnik, M. I. (**1980**). *Introduction to Radar Systems*, 2nd ed. (McGraw-Hill, New York).

Statistical Sciences (**1995**). S-PLUS Guide to Statistical and Mathematical Analysis, Version 3.3, Seattle.

Stroustrup, B. (**1997**). *The* C++ *Programming Language* (Addison-Wesley, Reading, MA).

Surlykke, A. (**1988**). ''Interaction between echolocating bats and their prey,'' in *Animal Sonar: Processes and Performance*, edited by P. E. Nachtigall and P. W. Moore (Plenum, New York).

Surlykke, A., and Moss, C. F. (**2000**). ''Echolocation behavior of the big brown bat, *Eptesicus fuscus*, in the field and the laboratory,'' J. Acoust. Soc. Am. **108**, 2419–2429.

Trappe, M., and Schnitzler, H.-U. (**1982**). ''Doppler-shift compensation in insect-catching horseshoe bats,'' Naturwissenschaften **69**, 193–196.

Valentine, D. E., and Moss, C. F. (**1998**). ''Sensorimotor Integration in Bat Sonar,'' in *Bat Biology and Conservation*, edited by T. H. Kunz and P. A. Racey (Smithsonian Institution, Washington and London), pp. 220–230.

von Mises, R. (**1959**). *Theory of Flight* (Dover, New York).

Walker, V. A., Peremans, H., and Hallam, J. C. T. (**1998**). ''One tone, two ears, three dimensions: A robotic investigation of pinnae movements used by rhinolophid and hipposiderid bats,'' J. Acoust. Soc. Am. **104**, 569–579.

Webster, F. A., and Brazier, O. G. (**1965**). *Experimental Studies on Target Detection, Evaluation and Interception by Echolocating Bats* (Wright-Patterson Air Force Base, Dayton, OH).

Webster, F. A., and Griffin, D. R. (**1962**). ''The role of the flight membrane in insect capture by bats,'' Anim. Behav. **10**, 332–340.

Wilson, W. W., and Moss, C. F. (**2001**). ''Sensory-motor Behavior of Free-flying FM Bats during Target Capture,'' in *Advances in the Study of Echolocation in Bats and Dolphins*, edited by J. Thomas, C. F. Moss, and M. Vater (University of Chicago Press, Chicago).

Wotton, J. M. (**1994**). ''The basis for vertical sound localization of the FM bat, *Eptesicus fuscus*: Acoustical cues and behavioral validation,'' unpublished doctoral dissertation, Brown University.

Wotton, J. M., Haresign, T., and Simmons, J. A. (**1995**). ''Spatially dependent acoustic cues generated by the external ear of the big brown bat, *Eptesicus fuscus*,'' J. Acoust. Soc. Am. **98**, 1423–1445.

Wotton, J. M., Haresign, T., and Simmons, J. A. (**1996**). ''Sound source elevation and external ear cues influence the discrimination of spectral notches by the big brown bat, *Eptesicus fuscus*,'' J. Acoust. Soc. Am. **100**, 1764.

Wotton, J. M., Jenison, R. L., and Hartley, D. J. (**1997**). ''The combination of echolocation emission and ear reception enhances directional spectral cues of the big brown bat, *Eptesicus fuscus*,'' J. Acoust. Soc. Am. **101**, 1723–1733.

Wotton, J. M., and Simmons, J. A. (**2000**). ''Spectral cues and perception of the vertical position of targets by the big brown bat, *Eptesicus fuscus*,'' J. Acoust. Soc. Am. **107**, 1034–1041.