A Behavior-Based Model of Foraging Nectarivorous Echolocating Bats

Thinh H. Nguyen(✉) and Dieter Vanderelst

University of Cincinnati, Cincinnati, USA
{nguye2t7,vanderdt}@mail.uc.edu

Abstract. We propose a simulation-based model of flower finding in echolocating nectarivorous bats. In particular, we propose a behavior-based model that uses two sensorimotor loops to dock with flowers. The EchoVr, as we have termed our echo simulator, uses a bank of echoes collected by ensonifying real objects with a physical (bat-like) sonar device. Using the EchoVr, we built a 2D environment consisting of simulated objects. We trained a neural network to activate the correct sensorimotor loop based on the echoes received by the simulated bat. The model guides the simulated bat to dock successfully with the flower opening (95% success rate) by computing control commands solely from echoic inputs.

Keywords: Nectarivorous bats · Echolocation · Sonar · Behavior-based

1 Introduction

More than 500 species in 67 plant families depend on bats as their primary pollinators [4]. Certain flower species have been shown experimentally to be approached by bats using sonar [5,7,8,18], and many others are believed to be located using echolocation. Several studies have investigated the acoustic cues bats use to approach flowers [8,16,18], but no sensorimotor model has been proposed or tested to explain how bats exploit these cues.

Previously, we argued [13,14,22] that behavior-based control architectures [2,11] offer promising models to understand bat sonar-based behavior. These architectures assume minimal reliance on internal representations, which are challenging to infer from echo data. Using sensorimotor loops that directly connect sensory input to actions should allow bats to react effectively in real-time situations [1], regardless of environmental complexity.

In this paper, we set out to build a model of the sensorimotor behavior that guides echolocating bats to the opening of flowers while avoiding obstacles. In particular, we present a behavior-based model that uses separate sensorimotor loops to complete the task. Our model uses two sensorimotor loops: an approach loop and an avoid loop. The approach loop uses acoustic cues from echoes to guide the bat toward a target, while the avoid loop steers the bat away from potential obstacles. The simulated bat will learn to activate an appropriate loop on the currently received echoes.

© The Author(s), under exclusive license to Springer Nature Switzerland AG 2025
O. Brock and J. Krichmar (Eds.): SAB 2024, LNAI 14993, pp. 51–62, 2025.
https://doi.org/10.1007/978-3-031-71533-4_4

2 Methods

2.1 Targets and Arena

We set up a foraging task in a virtual arena for a simulated echolocating bat. The goal is for the bat to navigate to flower openings while avoiding collisions with flower sides and arena walls. In the current work, we reuse our previously developed method to simulate the echoes received by an echolocating bat, termed EchoVR, [14]. This simulator uses a bank of echoes collected by ensonifying real objects with a physical (bat-like) sonar device. The sonar device comprises a single ultrasonic emitter and two microphones embedded in 3D-printed bat pinnae.

The EchoVR allows one to build a 2D environment consisting of the ensonified objects and calculates the binaural echoes for arbitrary positions and orientations of the simulated bat in the environment. Note that by feeding the EchoVR a large set of echoes collected from real objects, the environment also incorporates sources of noise, i.e., the noise inherent in the physical devices used to collect the echo data. For example, the EchoVR models variations in the echo that occur even if the same object is ensonified by the bat from the same position and orientation. As the signal-to-noise ratio of the physical ensonficiation devices is lower than that of the bat's sonar system, the noise produced by the EchoVR can be seen as a worst-case scenario when modeling bat echolocation [3].

The EchoVR takes into account the head-related transfer function of the bat, as its echo database was collected using microphones embedded in 3D printed pinnae of the bat *Micronycteris microtis* [20]). It also accounts for the acoustic phenomena of spreading and atmospherical attenuation that weaken the echoes as distance increases and interference between echoes. The EchoVr also includes a model of the auditory periphery of bats [24]. This model converts simulated echoes to a representation that is a proxy of the bat's cochlear activation pattern. This model returns a low-passed, logarithmically compressed envelope of the received echoes (an example is shown in Fig. 1). Therefore, the cochlear model reduces the temporal resolution of the echoes but accentuates weaker echoes. More details on the EchoVR can be found in [14].

For the present work, we ensonified two objects: a plant and a cardboard pole. These two objects vary greatly in geometric complexity. The plant consists of many stochastically oriented surfaces that result in complex echoes, typical of vegetation, e.g., [23,27]. In contrast, the cardboard pole has a basic geometry, resulting in a simple echo. The echoes of the two objects are depicted in detail in [14].

The bat is modeled as emitting narrowband calls with a frequency of 42 kHz and a duration of about 2 ms. These parameters are determined by the ensonification device used to collect the physical echoes from the pole and the plant, as detailed in [14]. Furthermore, we model the bat as emitting 40 calls per second. This emission rate is biologically plausible and corresponds to the approximate call rate used by Nectarivorous bats approaching targets [5,6].

Without access to the echoes of real flowers visited by bats, we used the two objects to construct target flowers for the simulated bat. In doing so, we attempted to create a target to test the hypothesis that a behavior-based model can be trained to approach a complex target (returning complex echoes) from a range of appropriate angles. We constructed a proxy for a flower composed of one plant and two poles. The poles are spaced at a distance of 30 cm from the center of the plant, creating an opening with an angular span of 60°. The opening of the flower defines the successful docking zone. This arrangement recreates the typical bilateral symmetry of flowers. The diameter of 30 cm of the proxy flower is larger than for the real flowers visited by nectarivorous bats [16]. However, by making the flower larger, we compensate for our simulated bat's (current) lack of spectral information (see Discussion for details).

The arena walls, which the bat should avoid, are made of plants arranged in a rectangle. Figure 1 shows the arrangement of the flower and the arena. Note that this arrangement of the flower results in considerably complex echoes (see Fig. 1c for an example). The plant is a complex reflector in itself. The two poles add two more strong reflectors to this. Furthermore, the relative strength and time of arrival of the echoes of the plants and poles are determined by the position and orientation of the bat in the arena.

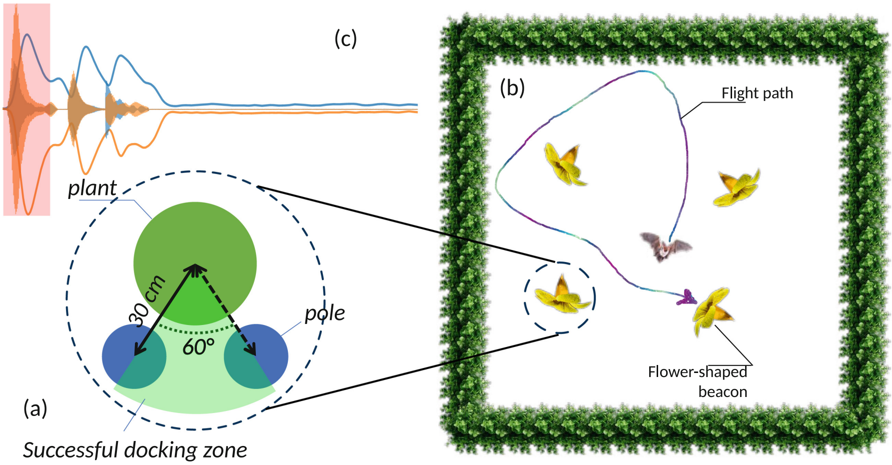

Fig. 1. (a) The arrangement of the proxy for a flower used in this paper. The arrangement consists of a central plant and two symmetrically placed cardboard poles. (b) The arena (16×16 m^2) in which we test our simulated bat. The walls of the arena consist of plants. (c) An example of echoes received by the bat from the flower in the left (orange) and right (blue) ears. The envelopes extracted using the cochlear model are also depicted (the envelope for the left ear is plotted inverted for clarity). The highlighted part of the waveforms is the bat's emission. These are followed by a complex echo (consisting of multiple copies of the emitted pulse). (Color figure online)

2.2 Sensorimotor Loops

In this paper, we propose that bats can find flowers using only two sensorimotor loops: an approach loop and an avoid sensorimotor loop. By activating the correct loop at each point in time, the bat can approach targets (i.e., the flower's docking zone) or avoid objects (i.e., the walls and parts of the flower outside the allowed docking zone). In the following, we introduce these control loops. Next, we explain how we trained the model to activate the correct loop based on the current echoes.

Approach Loop. The approach sensorimotor loop uses two acoustic cues extracted from the echoes: the delay in the onset of the echo t_o and the Interaural Level Difference (ILD) ΔI. In the following, we explain how these cues are used to set the linear velocity ν and the angular velocity ω when the approach sensorimotor loop is active.

Following each call generated by the bat, the echo onset delay t_o is extracted from the simulated echoes by determining the time at which the response of the cochlear model crosses a threshold. Therefore, the delay in the echo t_o gives the delay between the generation of the call and the arrival of the first (sufficiently strong) echo. The echo onset delay t_o is related to the distance d_o of the object that returns the echo as $t_o = 2d_o/c$ with c the speed of sound in air (here set to 343 m/s).

The ILD ΔI is obtained by integrating the response of the cochlear model for the left and right ears, starting at t_o for the duration of the echo (i.e., until the response drops below a threshold). This results in the echo intensity I_L and I_R for the left and right ears, respectively. This assumes that the auditory system of a bat functions approximately as an energy integrator [25]. Next, the ILD ΔI is calculated as follows,

$$\Delta I = 10 \times \log_{10} \frac{I_L}{I_R} \tag{1}$$

A positive (negative) ILD indicates that the echo reaching the left (right) ear is louder. Indeed, the ILD inherently contains azimuthal position information about the object from which the echo is returned, e.g., [21].

After extracting the ILD ΔI and the onset delay t_o, we use these parameters to calculate the control commands, that is, the linear velocity ν and the angular velocity ω. The equation (derived from tau-based control principles [10]) for the linear velocity ν is,

$$\nu = (\nu_{\max} - \nu_{\min})[1 - (1 - K \times A \times (d_o))^{\frac{1}{K}-1}] \tag{2}$$

with K set to 0.1 and A representing the braking coefficient, determining the rate at which the slowing occurs. We set $\nu_{\min} = 1$ m/s, $\nu_{\max} = 4$ m/s, and $A = 1$ m/s^2 as conservative flight speeds and acceleration for nectarivorous bats [26]. Equation 2 results in a non-linear deacceleration of the bat as it approaches the target. After calculating the linear velocity, we calculate the bat's angular velocity as follows,

$$\omega = \nu / R_{\text{trn}} \tag{3}$$

with R_{trn}, the bat's turn radius, given as,

$$R_{\text{trn}} = -\text{sign}(\Delta I)\big(\log(|\Delta I|) - R_{\text{min}}\big) \tag{4}$$

Eqs. 3 and 4 allow the bat to steer towards a target. The bat must minimize the difference in loudness between the left and right ears to approach the source of the returning echo. In other words, ΔI should be regulated to zero. When $\Delta I > 0$ ($\Delta I < 0$), the echo source is left (right) of the bat and the turning radius R_{trn} should be set to a positive (negative) value to turn left (right). Moreover, when the magnitude of the ILD ($|\Delta I|$) is large, the source of the echo is further away from the central azimuth, and the bat must make a sharper turn. In contrast, when the magnitude of the ILD ($|\Delta I|$) is smaller, the bat will make a smaller correction turn to gradually guide itself towards the source of the returning echo. When $|\Delta I| = 0$, the turning radius R_{trn} is infinite and the bat flies straight. In Eq. 4, R_{min} is the minimum allowed turning radius, which is determined based on the bat's current velocity ν,

$$R_{\text{min}} = \nu^2/a \tag{5}$$

to allow us to restrict the angular velocity of the bat to a biologically realistic range. Holderied [9] reported that the flight speed determines the smallest turning radius of different species of bats. In particular, he suggested that bats' turning radii are limited such that the g-force they experience is (most often) below about 3g. Hence, in Eq. 5, we set $a = 3$.

In summary, the approach sensorimotor loop controls the angular and linear velocity of the simulated bat. It turns the bat towards the source of the echo and reduces its speed as it approaches the target. The angular and linear velocities and the acceleration are limited to biologically plausible values, resulting in realistic dynamics.

Avoid Loop. When activated, the avoid sensorimotor loop steers the bat away from obstacles. In this section, we describe how this loop is implemented. Similarly to the approach sensorimotor loop, the avoid sensorimotor loop uses the onset distance d_o and ILD ΔI to set the linear velocity ν and the angular velocity ω when activated. When using the avoid sensorimotor loop, the linear velocity ν is calculated in the same way as when using the approach loop.

The main difference between the approach and avoid loops lies in how the angular velocity is set. Equation 6 sets the turning radius R_{trn} when the avoid loop is activated. The turning radius depends on the distance to the object that returns the echo (and not on the magnitude of the ILD as in the approach loop). If the distance d_o is smaller, the bat is more likely to collide with the object and should perform a sharper turn (that is, employ a smaller turning radius). Equation 6 implements this logic.

$$R_{\text{trn}} = \text{sign}(\Delta I)[\log(1 - \frac{d_o}{d_{0,\max}}) - R_{\text{min}}] \tag{6}$$

In Eq. 6, $d_{0,\max}$ is the maximium detection delay (distance), here set to 3 m. The turn radius is converted to angular velocity using Eq. 3. Moreover, the minimum turning radius $R_{\min}$ is, as for the approach loop, set using Eq. 5.

In summary, the avoid loop sets the bat's linear velocity in the same way as the approach loop. Nearer to obstacles, the linear velocity is reduced but kept within biologically realistic bounds. The angular velocity is set so that closer to obstacles the bat takes sharper turns.

2.3 Training the Bat

Having specified the sensorimotor loops, we now explain how we train a neural network to select the correct loop to activate based on current echoes. Since the network takes the current binaural echoes (after cochlear processing) as input and returns a selected loop to be activated, the network converts the echoes into suitable motor commands by activating the right loop.

To train the neural network, we need to collect echoes from the arena and label each echo with the suitable sensorimotor loop to be activated. We design a *teacher model* to allow us to automate the echo labeling task. Although training can be set up in a reinforcement learning framework (see [12,14] for our previous work using reinforcement learning to train artificial echolocators), the current approach allows us to avoid the complexity of using reinforcement learning by leveraging heuristics about the problem. In the following, we explain the functioning of the *teacher model* before describing how the *teacher model* was used to train the neural network.

Teacher Model. The *teacher model* takes the bat's current pose and the spatial arrangement of the walls and flowers to determine the appropriate sensorimotor loop for this spatial arrangement. This sets the *teacher model* apart from the final neural network that controls the bat. The bat's control neural network will only receive the echoes as input and is not provided with any information about the bat's current pose and spatial arrangement of objects.

The *teacher model* operates as follows. First, it assesses the proximity of the bat to the arena walls. If the bat is within 1.5 m of a wall and is oriented toward it, the *teacher model* returns the avoid loop as the appropriate loop to activate. If the bat is not within 1.5 m of a wall or is not oriented toward it, the *teacher model* lists all flowers in the arena in order of their distance from the bat. Next, the *teacher model* assesses the relative position between the bat and the closest flower. It feeds this relative pose to a Support Vector Machine classifier (SVM). This classifier tries to predict the outcome of activating the approach loop for a given relative pose between a bat and a flower. More details on training the SVM classifier will be discussed in the following section.

If the SVM classifier suggests that the approach loop would lead to a *dock* (i.e., a successful outcome), the *teacher model* returns the approach sensorimotor loop as appropriate to activate. If the SVM predicts that the approach loop would result in a *hit* with the non-opening side of the flower, the avoid sensorimotor loop is selected. When activating the approach loop is not predicted to result in contact with the flower (*dock* or *hit*), the SVM classifies the outcome at that pose to be *miss*. If the classifier returns a *miss* output, the *teacher model* proceeds to evaluate the next flower, farther away. The avoid loop is returned if no *dock* is predicted after the *teacher model* has evaluated the four closest flowers.

Support Vector Machine Classifier. As mentioned in the previous section, the *teacher model* used to scaffold the training of the neural network controlling the bat contains an SVM that suggests which sensorimotor loop to use based on the pose of the bat and the configuration of the arena. In this section, we explain how this SVM was trained.

To gather training data, we performed a simulation in which a single flower is placed in the center of the arena, and a bat is spawned in a random pose within a range of 10 m around the flower. The bat uses the approach sensorimotor loop until one of three outcomes occurs: (i) the bat successfully arrives at the proxy flower opening, (ii) the bat collides with the flower outside the docking zone, or (iii) the bat moves beyond the 10-m radius around the circle. We refer to these outcomes as *dock*, *hit*, and *miss*, respectively.

Running 200,000 trials starting from randomized poses, we observed that 5,659 poses result in *docking*, 29,421 poses result in *hitting*, and the remaining 164,920 poses result in *miss*. The poses leading to the three outcomes are shown in Fig. 2. This figure shows that most poses pointing toward the flower opening guide the bat to the flower opening (panel a).

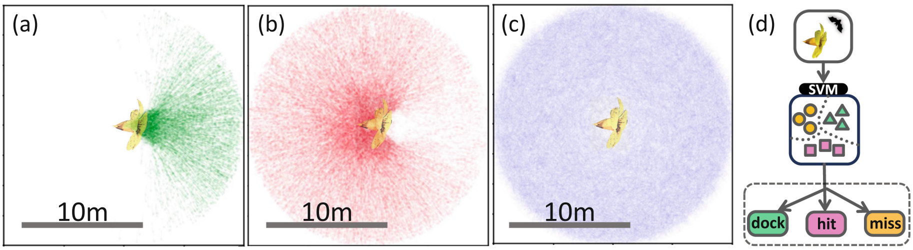

Fig. 2. Results of 200,000 trials in which the bat ran the approach sensorimotor loop starting from random poses with respect to the flower. Each data point in panels a-c represents a different pose of the bat (location and orientation). (a) Poses that lead to *docking*. (b) Poses that lead to *hits*. (c) Poses that lead to *misses*. The poses in panels a-c are used to train an SVM classifier (d) to predict the outcome if the approach loop is used at a given pose.

Using the data generated using the 200,000 runs, we fitted an SVM capable of classifying the current pose as one of the three outcomes based on the echoes received at that pose. Due to a disproportionally large number of *miss* poses, we impose a limit of 100,000 *miss* poses within our data set. This results to a data

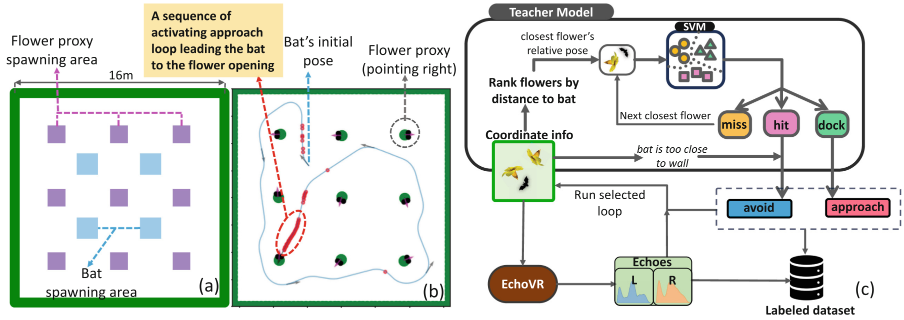

Fig. 3. (a) schematic layout of the environment used to train the neural network. The arena measured 16 × 16 m and contained 9 zones in which a flower was placed (the flower's center was jittered) with a random orientation. The bat spawned in one of four areas with a random orientation. (a) One example run used to collect the training data for the neural network. (c) *teacher model* architecture and how it is used to collect a data set of echoes labeled with sensorimotor loops.

set consisting of 135,080 poses with 4% *dock* poses, 22% *hit* poses, and 74% *miss* poses.

The SVM (Figs. 2d and 3c) was trained on these data using a regularization parameter $C = 0.1$ and a kernel of the radial basis function (RBF), using a kernel coefficient $\gamma = 10$. We adopted an 80/20 train-test split for evaluating the model's performance. After training, the SVM classifier could correctly classify 91% of poses as leading to *dock*, *hit*, or *miss* when using the approach loop.

Training the Neural Network. In this section, we explain how the *teacher model* presented in the previous sections was used to train the bat's controller: a neural network that takes the binaural echoes and activates one of two sensorimotor loops.

We created a setup featuring nine flowers in a 16 × 16 m arena surrounded by walls consisting of plants (Fig. 3). The flowers are placed in nine square regions. The bat spawns in one of four regions. At each step of the simulation, the *teacher model* is used to select the approach or the avoid sensorimotor loop. Figure 3b shows one run that ends with the bat docking with a flower. Using the *teacher model*, we collected 5000 runs ending in the bat docking with the flower. For each step of each run, we recorded the binaural echoes as received by the bat and the sensorimotor loop suggested by the *teacher model*. Therefore, we constructed a large data set of echoes labeled with the sensorimotor actions suggested by the *teacher model*. The data set consisted of 2,156,782 binaural echoes. Approximately 22% of these were associated with the approach loop. The remaining 78% were associated with the avoid loop. We partitioned the data set into an 80:20 train-test split. This data set was used to train a neural network that directly converted the echoes to a selected sensorimotor loop.

We used a fully connected neural network model that features six hidden layers with sizes of 128, 256, 256, 128, 64, and 16, each using ReLU activation. The output layer has a softmax function applied over one-hot vector the size of 2 corresponding to the two sensorimotor loops. Training is done using the Adam optimizer with a learning rate of 5×10^{-5} and weight decay of 5×10^{-5}. The network input layer receives the echo envelopes. The output layer consists of two units that assess the probability associated with each sensorimotor loop for a given echoic input. We trained the model for 200 epochs using the Adam optimizer and a mini-batch size of 2048. The model converges to 84% accuracy.

3 Results

We evaluated the bat's performance controlled by the neural network for 1000 episodes, during which the simulated bat autonomously determined the sensorimotor loop to execute at each step solely based on the echoic input from the scene. It is important to note that while the *teacher model* had access to the bat's relative position to the flowers and the walls, the neural network only used the echoes as input. An evaluation episode is run for 2000 steps (50 s at 40 calls per second) (*miss* outcome), or until the bat arrives at a flower opening (*dock* outcome) or collides with a wall or the side of a flower (*dock* outcome). We compared our 'trained bat' with a 'baseline bat' that randomly selected a new sensorimotor loop at each simulation step.

The trained bat using the neural network for sensorimotor loop selection outperforms the 'baseline bat' selecting sensorimotor loops randomly (Fig. 4g). The trained model yields a *dock* rate of 93%. On average, the trained model takes around 600 steps (or 15 s at 40 calls per second) to collide with an object (either *dock* or *miss*), which is approximately 2.5 times longer than the duration that the random model takes (see Fig. 4h). We show examples of each outcome in Fig. 4 a-f.

Dock outcomes occur when the bat recognizes it is in a favorable position (based on the echoes) to approach the flower opening and engage the approach loop. In both Figs. 4a and 4b, the bat turns on the approach loop when facing the opening of flower C to *dock*. In contrast, the bat tends to turn away if it comes close to a non-opening side of the flower (as depicted with flower B in Fig. 4a). When the bat is not facing any particular object, it consistently opts for the avoid loop, as observed at the beginning of the episode in Fig. 4b.

The most common scenario resulting in a *hit* outcome is when the bat becomes trapped in the corner of the arena (see Fig. 4c). Other occurrences of the *hit* outcome, happening at a rate of 0.5%, are when the bat collides with a non-opening part of a flower (see Fig. 4d). As the bat attempts to navigate the arena while looking for the front of a flower, there are instances where it *bounces around* until the time limit expires. One of these *miss* episodes is illustrated in Figs. 4e.

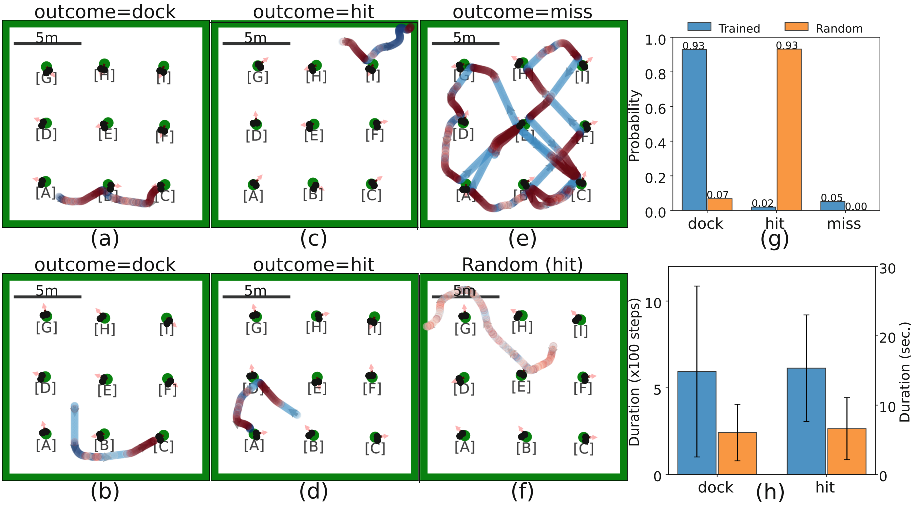

Fig. 4. Examples of runs where the bat is guided by the trained neural network, resulting in outcomes categorized as *dock* (a-b), *hit* (c-d), and *miss* (e). The network chooses between the avoid and approach sensorimotor loop at each step based on the echoes. Avoidance steps are shown in shades of blue, while approach steps are shown in shades of red, with darker shades indicating higher confidence. An example where the bat is guided by a random policy is shown in (f). (g) The likelihood of each outcome for the trained neural network and the random policy. (h) The duration of each outcome for both the trained and random models.

4 Discussion

We developed a behavior-based reactive navigation model trained to guide a bat in foraging flowers using narrowband echolocation calls as input. The model demonstrates high success rates in this task, approaching flowers closely and veering away if the bat nears the non-opening side of a flower while continuing to approach if facing the flower opening. This strategy effectively prevents collisions with walls or the non-opening sides of flowers. However, a notable inefficiency arises: when the bat veers away from the non-opening side of a flower, it misses the opportunity to investigate the other side, resulting in the *miss* outcome. In the future, we will explore an additional sensorimotor loop that allows the bat to focus on a single flower target to improve efficiency.

Our model introduces several simplifications. The flowers were modeled as composite objects, and the bat operated only in 2D. Furthermore, the environment was simpler than the environment typically faced by nectarivorous bats. Nevertheless, the model demonstrates the feasibility of modeling the complex task of approaching flowers at the correct angle using sensorimotor loops activated under the correct conditions and justifies further expanding our work. We are working on a more elaborate model that includes more realistic flower echoes and a more sophisticated arbitration approach to select the appropriate sensorimotor loop. Future iterations of the model could also include more specific behavior observed in bats. For example, bats are capable of selecting flowers to approach based on their size [17] or morphology [7].

Previous explanations of foraging in nectarivorous bats suggested that bats use the spectral content of the echoes to find and approach flowers (see [7, 16–18] for example). Our current model does not use spectral cues, nor does it have access to them, as the echoes were narrowband signals. Instead, the current model solves the problem in the time domain using the time-intensity profiles of the echoes. To allow the use of temporal cues, our proxy flower had a diameter larger than is typical for flowers (here: 30 cm; see [19] for examples of real flowers). Hence, in our model, we trade spectral information for temporal information (see, for example, [15] for a discussion about the relationship between spectral and temporal information in echolocating bats). In the future, collecting broadband echoic data to populate the EchoVR would enable us to create a model that exploits the spectral cues presumably used by bats.

Acknowledgments. This work was funded by NSF grant 2034885, Principles of intelligent sensorimotor behavior under informational constraints.

References

1. Arkin, R.C.: Behavior-Based Robotics. Intelligent Robotics and Autonomous Agents, 3rd ed, 2000 edn.. The MIT Press (1998). http://gen.lib.rus.ec/book/index.php?md5=bdd0766feef0ca8774ea8cf6646add72
2. Brooks, R.A.: Cambrian Intelligence: The Early History of the New AI. MIT Press (1999)
3. Chitradurga Achutha, A., Peremans, H., Firzlaff, U., Vanderelst, D.: Efficient encoding of spectrotemporal information for bat echolocation. PLoS Comput. Biol. **17**(6), e1009052 (2021)
4. Fleming, T.H., Geiselman, C., Kress, W.J.: The evolution of bat pollination: a phylogenetic perspective. Ann. Bot. **104**(6), 1017–1043 (2009)
5. Gonzalez-Terrazas, T.P., et al.: How nectar-feeding bats localize their food: echolocation behavior of Leptonycteris yerbabuenae approaching cactus flowers. PLoS ONE **11**(9), 1–18 (2016). https://doi.org/10.1371/journal.pone.0163492
6. Gonzalez-Terrazas, T.P., Martel, C., Milet-Pinheiro, P., Ayasse, M., Kalko, E.K.V., Tschapka, M.: Finding flowers in the dark: nectar-feeding bats integrate olfaction and echolocation while foraging for nectar. Roy. Soc. Open Sci. **3**(8) (2016). https://doi.org/10.1098/rsos.160199
7. Helversen, D.V., Helversen, O.V.: Object recognition by echolocation: a nectar-feeding bat exploiting the flowers of a rain forest vine. J. Comparat. Physiol. Neuroethol. Sens. Neural Beh. Physiol. **189**(5), 327–36 (2003)
8. von Helversen, D., von Helversen, O.: Acoustic guide in bat-pollinated flower. Nature **398**(6730), 759–760 (1999). https://doi.org/10.1038/19648
9. Holderied, M.W.: Akustische Flugbahnverfolgung von Fledermäusen: Artvergleich des Verhaltens beim Suchflug und Richtcharakteristik der Schallabstrahlung. Ph.D. thesis, Friedrich-Alexander-Universität Erlangen-Nürnberg (2001)
10. Lee, D.N., Reddish, P.E., Rand, D.T.: Aerial docking by hummingbirds. Naturwissenschaften **78**(11), 526–527 (1991). https://doi.org/10.1007/BF01131406

11. Mataric, M., Michaud, F.: Behavior-based systems. In: Siciliano, B., Khatib, O. (eds.) Springer Handbook of Robotics, pp. 891–909. Springer, Heidelberg (2008). https://doi.org/10.1007/978-3-540-30301-5_39
12. Mohan, A.V., Vanderelst, D.: Training a simulated bat: Modeling sonar-based obstacle avoidance using deep-reinforcement learning. In: 2020 IEEE Symposium Series on Computational Intelligence (SSCI), pp. 2241–2249 (2020). https://doi.org/10.1109/SSCI47803.2020.9308555
13. Nguyen, T., Vanderelst, D., Peremans, H.: Sensorimotor behavior under informational constraints: a robotic model of prey localization in the bat micronycteris microtis. In: ALIFE 2021: The 2021 Conference on Artificial Life. MIT Press (2021)
14. Nguyen, T.H., Vanderelst, D.: Toward behavior-based models of bat echolocation. In: 2022 IEEE Symposium Series on Computational Intelligence (SSCI), pp. 1529–1536 (2022). https://doi.org/10.1109/SSCI51031.2022.10022100
15. Schmidt, S.: Perception of structured phantom targets in the echolocating bat, Megaderma lyra. J. Acoust. Soc. Am. **91**(4), 2203–2223 (1992). https://doi.org/10.1121/1.403654
16. Simon, R., et al.: Acoustic traits of bat-pollinated flowers compared to flowers of other pollination syndromes and their echo-based classification using convolutional neural networks. PLoS Comput. Biol. **17**(12), e1009706 (2021)
17. Simon, R., Holderied, M.W., von Helversen, O.: Size discrimination of hollow hemispheres by echolocation in a nectar feeding bat. J. Exp. Biol. **209**(18), 3599–3609 (2006)
18. Simon, R., Holderied, M.W., Koch, C.U., von Helversen, O.: Floral acoustics: conspicuous echoes of a dish-shaped leaf attract bat pollinators. Science **333**(6042), 631–633 (2011)
19. Simon, R., Rupitsch, S., Baumann, M., Wu, H., Peremans, H., Steckel, J.: Bioinspired sonar reflectors as guiding beacons for autonomous navigation. Proc. Nat. Acad. Sci. **117**(3), 1367–1374 (2020). https://doi.org/10.1073/pnas.1909890117
20. Vanderelst, D., De Mey, F., Peremans, H., Geipel, I., Kalko, E., Firzlaff, U.: What noseleaves do for FM bats depends on their degree of sensorial specialization. PLoS ONE **5**(8), e11893 (2010)
21. Vanderelst, D., Holderied, M.W., Peremans, H.: Sensorimotor model of obstacle avoidance in echolocating bats. PLoS Comput. Biol. **11**(10), e1004484 (2015)
22. Vanderelst, D., Peremans, H.: A computational model of mapping in echolocating bats. Anim. Behav. **131**, 73–88 (2017)
23. Vanderelst, D., Steckel, J., Boen, A., Peremans, H., Holderied, M.W.: Place recognition using batlike sonar. Elife **5**, e14188 (2016)
24. Wiegrebe, L.: An autocorrelation model of bat sonar. Biol. Cybern. **98**(6), 587–595 (2008)
25. Wiegrebe, L., Schmidt, S.: Temporal integration in the echolocating bat, megaderma lyra. Hear. Res. **102**(1), 35–42 (1996)
26. Winter, Y.: Flight speed and body mass of nectar-feeding bats (glossophaginae) during foraging. J. Exp. Biol. **202**(14), 1917–1930 (1999)
27. Yovel, Y., Franz, M.O., Stilz, P., Schnitzler, H.U.: Plant classification from bat-like echolocation signals. PLoS Comput. Biol. **4**(3) (2008). https://doi.org/10.1371/journal.pcbi.1000032