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Modeling bat prey capture in echolocating bats: The feasibility of reactive pursuit

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Abstract

Echolocating bats are the only mammals engaging in airborne pursuit. In this paper, we implement a reactive model of sonar based prey pursuit in bats. Our simulations include a realistic prey localization mechanism as well as a model of the bat's motor behavior. Critically, in contrast to previous work, our model incorporates bats' ability to execute rapid saccadic scanning motions keeping the prey within its field of view. Decoupling the flight direction from the gaze direction allows our model to capture erratically moving prey using reactive control. We conclude that the rapid shifts in gaze direction allow bats to deal with the narrow field of view provided by their sonar system.

Keywords:

1. Introduction

Pursuit is an essential skill for many flying animals [52]. Echolocating bats are the only mammals engaging in airborne pursuit. In contrast to insects [e.g., 50, 51, 46, 39] and birds [36], these animals uniquely rely on bio-sonar [22, 23], rather than vision. In this paper, we implement a model of prey pursuit in echolocating bats. The objective of this effort is twofold.

First, an integrated model allows testing whether the various piecemeal sensorimotor loops that have been hypothesized to underlie prey pursuit are sufficient to explain successful prey capture [17, 19, 18, 11, 20]. Indeed, more than fifty years of research [22] have yielded substantial information on the prey capture behavior of bats. Owing to their active sonar, bats' flight paths can be reconstructed with high precision, both in the lab [e.g., 47, 66] and the field [e.g., 29, 27]. Moreover, their use of pulsed active bio-sonar allows assessing their echolocation behavior in great detail [e.g., 70, 17, 7, 63]. Also, various studies have evaluated the cues used by bats to localize prey [71, 58, 7, 53]. Finally, the aerodynamics of bat flight is an active topic of research [2, 5, 54, 48, 15].

Prey capture in bats has been modeled before [38, 44, 10]. Masters [44] modeled bats capturing targets thrown up in the air based on a 2D model (vertical plane), an experimental situation studied empirically by Cahlander and Webster [6]. In a later study, Kuc [38] presented a sensorimotor model of prey capture. He modeled prey approach using the interaural level difference to correct the yaw of the bat. The pitch of the bat was determined by comparing

the echo amplitude between the fundamental and the overtone, the direction of which was determined using a theoretical model. The prey was assumed to move randomly, and different prey flight speeds were tested. Finally, Erwin et al. [10] modeled the approach of stationary targets. These authors modeled both the localization of the prey and the aerodynamics of the bat in more detail than either [38] and [44]. However, in this study, only static prey was considered. In spite of this simplification, Erwin et al. [10] concluded that a predictive strategy was necessary to capture the prey. In more recent work, Aihara et al. [1] modeled the pursuit of moving prey. However, these authors did not model the target localization process. The position of the prey was directly accessible to the model. Therefore, their model did not account for limitations in target localization performance, which has been shown to be important in determining a bats approach to a target [4]. These last two studies also modeled prey capture in 2D (horizontal plane) only.

The lack of integrated models including all that is known about 3D sonar-based pursuit of flying prey by bats represents a gap in our understanding of flight based pursuit in animals. In particular, as bats, by virtue of using echolocation, face different sensorial constraints than the better-studied insects and birds. Compared to vision, sonar has a field of view that is less broad unless for small distances (see Fig. 2) [62], has a lower angular resolution and a more limited range [60]. A complete mathematical model of sonar-based pursuit can help in elucidating how bats deal with these unique constraints. To the best of our knowledge, Kuc [38] is the only author to have modeled

both the perception and acquisition of moving prey. His work suggests that prey capture can be supported by reactive control loops. The current paper builds on this earlier work by proposing a reactive model of prey capture that both incorporates recent findings [17, 18, 19, 20] on prey capture behavior in bats as well as a realistic model of prey localization [53, 10].

Models, being entirely specified, allow identifying gaps in our knowledge [41]. Model assumptions that can not be justified based on experimental data reveal limitations in our current understanding of the phenomenon. Limits to our understanding are also revealed by quantitative and qualitative differences between the simulated and observed behavior. Therefore, the second objective of this paper is to identify hiatuses in our understanding and knowledge of sonar-based prey capture in bats and to suggest foci for future empirical research.

2. Model

2.1. Prey model

We chose to simulate a prey that is flying erratically, but randomly relative to the behavior of the bat, akin to an ear-less insect that does not engage in evasive manoeuvres. To generate realistically curved flight paths like the ones shown in Ghose et al. [19, 20], we simulated the paths of target insects as consisting of a sequence of sections with different angular velocities. Each section had a duration of d , drawn from an exponential distribution with scale parameter λ set to 1 second.

At the start of each section, the insect was assigned new rotational yaw and pitch velocities drawn randomly from the intervals $[-180^\circ/\text{s}, +180^\circ/\text{s}]$ and $[-90^\circ/\text{s}, +90^\circ/\text{s}]$, respectively. In addition, the flight speed of the insect during this section of the simulated flight was drawn from a uniform distribution ranging from 0.5 m/s to 2 m/s. The angular velocities and the flight speed of the insect were maintained for d seconds, after which a new section with randomly selected parameters was initiated.

The insect's flight path was constrained to start at a distance of 2 meters from the bat [10]. Indeed, bats usually change from the search to an approach phase only at distances of 1 to 2 m from the target, even though detection may well occur before [59]. In addition, the azimuth ϕ_i and elevation θ_i position of the insect relative to the bat were randomly drawn from $[-30^\circ, 30^\circ]$ and $[0^\circ, -30^\circ]$, respectively. This ensured that the insect was located within the sonar beam of the bat. The initial flight direction of the insect was randomly picked from the range $[-180^\circ, 180^\circ]$ and $[-45^\circ, 45^\circ]$ for yaw and pitch, respectively.

2.2. Bat model

The proposed bat model consists of a perception model and a motor control model itself consisting of three separate control loops. The perception model uses the binaural output of a functional model of the cochlear processing of

a sonar echo to detect the prey (comparison with hearing threshold) and determine the prey direction relative to the head (comparison with a memorized set of spectral templates). The distance to the prey is only indirectly used in the pursuit behavior by determining the call rate. Prey classification is not modelled. The first control loop in the motor control model uses the perception model output to steer the head such that the new gaze direction coincides with the last perceived prey direction by the time the next call is emitted. The second control loop steers the flight direction to align with the gaze direction but only after a delay. To avoid the bat overtaking the prey, the third control loop lowers the flight speed as the gaze direction (tracking the prey direction) differs more from the flight direction.

Referring to the terminology used by Wei et al. [69] the control strategy we propose is most similar to the Classical Pursuit Strategy (CP). However, there are some important differences. First, it should be noted that different from the strategies analyzed by these authors we allow the bat to continuously adapt its speed to the motion of the prey. Second, we separately control the bat's gaze direction and its flight direction. So, while the gaze is controlled to reactively orient towards the prey, the flight direction shows a delayed convergence onto the gaze direction. Consequently, the flight paths of the bat resulting from the proposed control strategy differ systematically from those generated by CP.

2.2.1. Acoustics and Prey Localization

In line with typical echolocation behavior observed in bats [e.g., 70, 17, 7, 63], the simulated interpulse interval (IPI) was modeled as dependent on the distance to the prey. Based on data reported by Saillant et al. [56] for the big brown bats, *Eptesicus fuscus*, we modeled the pulse interval to change linearly from 100 to 20 ms for distances of 300 to 75 cm from the prey (see Fig. 4a). We limited the minimum IPI value to 20 ms as this is the minimum reaction time of the bats reported in [16]. For every simulated call, the echo strength S_e was calculated (see [60]) as follows,

$$S_e = 120 - 40 * \log_{10} \frac{d_p}{0.1} + 2\alpha_f \cdot d_p + C \quad (1)$$

Equation 1 gives the echo strength S_e , in decibel SPL, arriving at the bat (before being filtered by the head related transfer function, see below). The call strength is taken to be 120 dB at a reference distance of 10cm. The distance to the prey is denoted by d_p . The parameter C determines the target strength. We set $C = -20\text{dB}$, i.e. the value reported by [60] for the target strength of a spherical reflector (diameter 4cm) at the same reference distance of 10cm. Equation 1 assumes two-way spherical spreading. This assumption has been shown to be justified both for the outgoing waves [24] and the returning echoes [60].

In equation 1, α_f denotes the frequency dependent at-

Figure 1: Simulated directionality (combining the emission and the hearing directionality) in the frontal hemisphere for *Phyllostomus discolor* (data from De Mey et al. [9], Vanderelst et al. [65]). The depicted directionality is for the left ear. The depicted frequencies correspond to those used for modeling the localization process and were obtained using equation 2.

mospheric attenuation of the echo. We approximated the attenuation for the broadband call using a single attenuation value for 70 kHz, lying halfway between the lowest and highest frequency of the modeled call (50-90 kHz, see below). Hence, α_f was set to -2.63 dB/m.

De Mey et al. [9] and Vanderelst et al. [65] simulated the hearing and emission directionality of *Phyllostomus discolor*, respectively. Using these data, we obtained a realistic directionality of a representative bat sonar system by combining simulations of the emission directionality and the hearing directionality of the left ear. Next, we interpolated the combined directionality of the sonar system in 1° steps from -90° to 90° in both azimuth and elevation. The directionality was normalized such that the maximum value across all frequencies and all azimuth and elevation directions was 0 dB. Note that through this procedure we remove the possible gain of the bat's pinnae [13] resulting in a conservative estimate of the bat's detection threshold. We obtained the corresponding directionality for the right ear by mirroring the left ear data.

Bats are thought to localize prey in azimuth and elevation using predominantly binaural and spectral cues from their sonar [71, 58, 7, 40]. We propose a target localization, i.e. target direction estimation, mechanism based on binaural spectral cues that is very similar to the one proposed in Erwin et al. [10] and is a simplified version of the model we presented in detail elsewhere [53]. In summary, due to the directionality of the sonar system, echoes returning from specific directions will have different spectral contents. By comparing the actual spectral content of the echo with the set of expected spectra, one for every (azimuth, elevation)-pair, derived from the directionality we estimate the azimuth and elevation of the prey.

To extract these spectral cues we propose a highly simplified functional model of the processing in the bats cochlea keeping the overall model as general as possible. Hence, we limit the characterization of the echo spectrum to the set of responses of a minimum number of frequency channels using the concept of rectangular bandpass filters with Equivalent Rectangular Bandwidths (ERB). This concept was introduced by Glasberg and Moore [21] as a convenient approximate psychophysical model for peripheral filtering in human hearing. The frequency range from 50 to 90 kHz, i.e. the frequency band *P. discolor* emits most energy in [65], can be covered by choosing 5 non-

overlapping rectangular bandpass filters with central frequencies f_k , $k = 1 \dots 5$ shown in Fig 1 and corresponding bandwidths $ERB(f_k)$, $k = 1 \dots 5$ given by the formula proposed by Glasberg and Moore [21],

$$ERB(f) = 24.7 \cdot (4.37 \cdot \frac{f}{1000} + 1). \quad (2)$$

Note that this formula was derived for humans for the frequency range $f = 100\text{Hz}-10\text{kHz}$. Hence, we do not intend to claim that this is a realistic approximation of the bat's peripheral frequency selectivity but we consider it a lower boundary of the spectral information extracted from the echo. Furthermore, using such a model allows treating the noise in the various frequency channels as independent, again simplifying further processing.

Prey localization in the simulation is then performed as follows. For each simulated call, the spectral template $\vec{t}_{\phi, \theta}$ closest to azimuth ϕ_p and elevation θ_p is extracted from the directionality and combined with the echo strength value calculated before

$$\vec{t}_{\phi_p, \theta_p} = [L_{\phi_p, \theta_p, f1} \dots L_{\phi_p, \theta_p, f5}, R_{\phi_p, \theta_p, f1} \dots R_{\phi_p, \theta_p, f5}] + S_e \quad (3)$$

with $L_{\phi, \theta, fi}$ and $R_{\phi, \theta, fi}$ denoting the directionality dependent gains for the five frequency channels for the left and right ear, respectively (depicted in Fig. 1). Independent noise is then applied to each of the values in $\vec{t}_{\phi_p, \theta_p}$ resulting in the simulated measurement corrupted by noise,

$$\vec{t}_{\phi, \theta} = \vec{t}_{\phi_p, \theta_p} + \mathcal{N}(0, \Sigma) \quad (4)$$

with Σ a diagonal matrix. The values in $\vec{t}_{\phi, \theta}$ smaller than 20dB are fixed at 20dB to model the information loss in frequency channels that fall below the noise level. The value of 20dB SPL is widely used as the functional detection threshold of the bat when hunting in the wild [60]. Finally, the perceived azimuth and elevation position, $\hat{\phi}_p$ and $\hat{\theta}_p$, of the prey were determined by finding the template corresponding with an echo from ϕ and θ for which $\|\vec{t}_{\phi, \theta} - \vec{t}'_{\phi, \theta}\|$ is smallest

$$(\hat{\phi}_p, \hat{\theta}_p) = \text{Min}_{(\phi, \theta)} \{\|\vec{t}_{\phi, \theta} - \vec{t}'_{\phi, \theta}\|\} \quad (5)$$

Figure 2 depicts the resulting localization performance of the simulated bat as a function of the azimuth and elevation of the prey, ϕ_p and θ_p , and the distance to the prey d_p . It can be seen that accuracy of prey localization decreases rapidly for peripheral positions with increasing prey distance.

2.2.2. Motor behavior: Rotation

Both nasal [65] and mouth emitters [64, 30] emit highly directional sonar beams. The ears further increase the directionality of the sonar system [65, 49, see also figure 1]. As a result, peripheral reflectors return weaker echoes and are localized with less precision [53, 71, see also figure 2].

Figure 2: Simulated prey localization errors (in degrees) in azimuth and elevation as a function of the position in the frontal hemisphere and distance. These plots confirm the intuition that localization should be better around 0° azimuth and elevation than in the periphery. Also, this figure shows that prey localization is impossible at distances beyond 5m.

This suggests that a bat tracking prey should benefit from keeping the target in the center of its beam. There is ample evidence confirming that this is what bats do. For example, Ghose and Moss [17] observed the behavior of *Eptesicus fuscus* performing captures of tethered insects in the lab. These authors reported the bats centered their beam on the target. During the last 300 ms of a capture, sequence bats locked their beam onto the target with a standard deviation of about 3 degrees. Further evidence suggests that tracking of targets is accomplished purely reactively. The bat seems to update its gaze direction based on the last perceived position of the prey [43]. Based on these findings, we modeled the change in the bat's gaze after the reception of each echo by assuming constant head rotation speeds given by,

$$\dot{\phi}_g = \frac{\hat{\phi}_p}{\text{IPI}}, \quad \dot{\theta}_g = \frac{\hat{\theta}_p}{\text{IPI}} \quad (6)$$

with the estimated prey direction $\hat{\phi}_p, \hat{\theta}_p$ given by Eq.(5) and IPI denoting the inter pulse interval. This guarantees that by the time the next call is emitted the bat's gaze direction will point towards the last estimated prey direction.

To limit the head orientation relative to the body to feasible values we imposed constraints on the gaze directions ϕ_g and θ_g . We assumed the bat could rotate its head in azimuth from -90° to 90° . In elevation, we assumed θ_g could range from -45° to 45° . Both the roll of the head (with respect to the body) and that of the body (with respect to the world frame) were limited to 30° and 60° , respectively. Seibert et al. [57] reported on the scanning behavior of *Pipistrellus pipistrellus* during flight. These authors found that *Pipistrellus pipistrellus* moved its acoustic gaze by maximally 40° between subsequent calls with average interpulse interval varying from 86 to 97 ms. Hence, the maximum observed head rotation velocity in their study was about $400^\circ/\text{sec}$. Therefore, we limited both rotation speeds $\dot{\phi}_g$ and $\dot{\theta}_g$ to the range $[-400^\circ/\text{s}, 400^\circ/\text{s}]$. Finally, we also limited the maximum acceleration of the head to $5000^\circ/\text{s}^2$ based on the data from [61], see figure 4d)-e).

Ghose and Moss [18] and Falk et al. [11] found that the flight path of bats is linked to its gaze direction by a Delayed Linear Adaptive Law. In line with the model they propose to capture this behavior, we modeled the change in yaw and pitch ($\dot{Y}_b$ and $\dot{P}_b$, respectively) as given by equations 7 and 8,

$$\dot{Y}_b(t + \tau) = k \cdot \phi_g(t) \quad (7)$$

$$\dot{P}_b(t + \tau) = k \cdot \theta_g(t) \quad (8)$$

In these equations, $\dot{Y}_b$ and $\dot{P}_b$ denote the rotational velocities of the bat at time $t + \tau$. In other words, these equations denote the change in flight direction (see Fig. 3). The terms ϕ_g and θ_g denote the gaze direction (with

Figure 3: (a) Reference frames fixed to the world XYZ_W , the body XYZ_B and the head XYZ_H . Gaze direction ($=X_H$) relative to the body frame. (b) Prey direction relative to the head frame.

Table 1: List of values for τ (in ms) and k observed by Ghose and Moss [18] and Falk et al. [11] in flight room experiments for *Eptesicus fuscus* capturing tethered insects.

Reference	Condition	Stage	τ	k
Falk et al. [11]	Open	Search	108	3.27
Falk et al. [11]	Forest	Search	112	2.93
Falk et al. [11]	Open	Buzz	52	9.17
Falk et al. [11]	Forest	Buzz	128	7.33
Ghose and Moss [18]		Search	148	3.21
Ghose and Moss [18]		Buzz	96	6.26
Ghose and Moss [18]		Tracking	128	4.24

respect to the body frame, fig. 3) while k is a gain parameter. The parameters k and τ that best describe the behavior of the bat have been found to vary across conditions and stage of prey capture [18, 11] (see table 1). In this paper, we ran simulations using the values of $k = 3$ and $\tau = 150\text{ms}$, i.e. values appropriate when modelling the Search/Approach phase of the hunt. We chose to model this phase (IPI > 20 ms [11]) as it is not clear to what extent the bat can still adapt its flight path to the information received during the Buzz phase.

Falk et al. [12] had *Eptesicus fuscus* execute tight turns between passages in two closely spaced mist nets. The bats approached the second passage using climb rates of about 30° . Assuming that descend rate should be at least equal to the achievable climbing rate, we limited the pitch $\mathcal{P}_b$ to the range $[-30^\circ, +30^\circ]$.

Aerodynamic constraints limit the maximum turning rate of a bat [3]. In particular, the maximum turning rate is inversely related to the flight speed [25]. In this paper, we limited the yaw turning rate $\dot{Y}_b$ based on the flight paths of *Myotis daubentonii* as recorded by Jones and Rayner [31]. We fitted a linear model to the logarithm of the speed and angular velocity data (see 4b). For simulated bat velocities below the range of the data covered by Jones and Rayner [31], we fixed the angular velocity to the maximum fitted value. The turning rates thus obtained are more conservative than those reported by Holderied and Jones [25] (see 4b). In the absence of separate data on yaw and pitch rotations, we imposed the same limitation on the pitch rotational velocity $\dot{\mathcal{P}}$.

2.2.3. Motor behavior: Speed control

Bats adjust their speed while pursuing prey [e.g., 19, 31]. In our simulations, the bat slows down as the gaze angles ϕ_g and θ_g become larger. The rationale for this assumption is that large gaze angles indicate that the bat is overtaking the insect prey. In effect, it indicates that the bat is trying to look over its shoulder to keep the insect within the beam and drive ϕ_p and θ_p to zero. Specifically, we calculate the desired speed of the bat v_b^* as,

$$v_b^* = \min[\cos(\phi_g), \cos(2 \cdot \theta_g)]^2 \cdot v_{max} \quad (9)$$

making the desired speed of the bat at each point in the simulation equal to the maximum velocity if the bat looks straight ahead, i.e. $\phi_g = \theta_g = 0$. The desired speed is reduced to zero if either $\phi_g = \pm 90$ or $\theta_g = \pm 45$ (i.e., the maximum allowed gaze angles).

Some additional constraints were imposed on the actual speed v_b of the bat. First, the minimum allowed velocity was 0.5 m/s. Also, the acceleration and deceleration of the bat were limited to 4 m/s^2 and 10 m/s^2 , respectively. These correspond to values observed by Jones and Rayner [31, 32]. Finally, the maximum velocity v_{max} of the bat was limited to 5 m/s. This constraint was derived from inspecting the flight speed profiles as reported by Ghose et al. [19]. The simulations were started with the bat flying at the maximally allowed speed.

2.3. Prey capture

The mouths of echolocation bats have small diameters, i.e., typically less than 10 mm [e.g., 37, 30]. Therefore, catching insects using only the mouth would require bats to approach bats with an accuracy of less than 1 cm. However, bats often use their flight membranes as a way to increase the catching volume [e.g., 35, 34, 68, 23]. Using either the wings or the interfemoral membrane, they pouch the insect and transfer it to the mouth. Gardiner et al. [14] list the wingspan of 89 species of insectivorous bats (see fig. 4c)). Based on their data and the finding that the tip of the wing can be used to catch prey [68], we consider the insect to be captured if the simulated bat approaches it to within 10 cm. Alternatively, a simulated trial is ended after 15 seconds or whenever (1) the distance between the bat and prey comes to exceed 5 m or (2) the insect is no longer detected by the bat. In our model, at 5 m distance, localization of the insect is impossible due to the low echo strength (Fig. 2) and the bat is assumed to have lost track of the prey.

2.4. The Constant Absolute Target Direction Strategy

Bats have been suggested to follow a time-optimal strategy to prey capture [19, 20], the so-called Constant Absolute Target Direction Strategy (CATD). This strategy is a mathematically optimal strategy in case the target moves unpredictably. The CATD dictates the flight corrections a pursuer should make in response to the pursued target. Adhering to the CATD guarantees the shortest interception time [33]. The CATD has also been suggested to underlie the pursuit behavior of hoverflies, dragonflies [50] and hawks [36] (but see Mischiati et al. [46]).

In this paper, we do not explicitly implement the CATD. Hence, we wish to evaluate how closely the simulated flight paths adhere to the CATD. Two criteria have been used to quantify how well animals adhere to the CATD. First, the Gamma statistic γ has been used [e.g., 20, 19, 46]. This statistic is calculated as follows

$$\gamma_t = \cos(\alpha) \quad (10)$$

Figure 4: (a) Plot depicting the modeled inter pulse interval as a function of the distance to the prey target. The bat data was taken from Saillant et al. [56]. (b) Modeled constraints on the angular velocity of the bat. Data from Jones and Rayner [31]. The grey band depicts the maximum angular velocities observed by Holderied [26] for 13 species of bat. (c) Distribution of the wingspan of echolocating bats as reported by [14]. (d-e) Data from Sumiya et al. [61, fig.2d therein] showing the changes in the gaze direction of *Pipistrellus abramus* during two consecutive prey captures. The red bands in (d) indicate regions we were unable to extract data for. (e) Distribution of the head acceleration calculated based on the data depicted in (d).

Figure 5: (a) The angles ϕ_e , ϕ , ϕ' (see text) as defined in the xy-plane. (b) The angle between the vector $\vec{x}$ pointing from the bat to the prey and its derivative $\dot{\vec{x}}$ (represented by its discrete approximation) is denoted by α .

with α the angle between the vector $\vec{x}$ from the bat to the prey and its time derivative $\dot{\vec{x}}$, see fig. 5. If $\gamma = -1$, the motion of the bat relative to the prey is along the vector $\vec{x}$.

The second criterion that has been used is the error angle ϕ_e , with $\phi_e = \phi - \phi'$, see fig. 5. This is the difference between the angle ϕ' , defined as the angle between the vector $\vec{x}$ connecting the bat and the prey and the direction of flight of the bat, and the value of the angle ϕ as prescribed by CATD and given by equation 11, see [19]

$$\phi = \sin^{-1} \frac{v_p \sin \beta}{v_b} \quad (11)$$

with v_b and v_p the speed of the bat and the prey respectively and the angle β defined as the angle between the vector $\vec{x}$ connecting the bat and the prey and the direction of flight of the prey. As shown in [19], the bat maneuvers to reduce ϕ_e to zero during pursuit according to the law

$$\frac{d\phi_e}{dt} = k_e \phi_e (t - \tau_e)$$

with k_e a negative gain parameter and τ_e a combination of delays in various subsystems. It can be shown [19] that when the stability constraint $k\tau_e > -\pi/2$ is met ϕ_e will converge to zero.

We will calculate these same measures for the flight paths generated by our model and compare the statistics with empirical observations reported by Ghose et al. [19], [20]. This will allow us to assess how closely our modeled bat follows the CATD.

3. Results

To evaluate the impact on the pursuit behavior of a number of modelling choices we made, three conditions were studied, each representing a different setting for the parameters controlling the pursuit behavior.

- Condition 1: Maximum head acceleration is $5000^\circ/s^2$, $k = 3$ and $\tau = 150$ ms, variable speed according to Eq.(9).
- Condition 2: Head is fixed to body, $k = 3$ and $\tau = 150$ ms, variable speed according to Eq.(9).
- Condition 3: Maximum head acceleration is $5000^\circ/s^2$, $k = 3$ and $\tau = 150$ ms, fixed speed $v_b = 2.5$ m/s.

Condition 1 is the reference condition including all control loops described above. Condition 2 is introduced as it allows to judge the impact of an independently controlled head on the pursuit behavior by comparing conditions 1 and 2. To implement condition 2 we modeled the change in yaw and pitch ($\dot{Y}_b$ and $\dot{P}_b$, respectively) as driven by the perceived azimuth ($\hat{\phi}_p$) and elevation ($\hat{\theta}_p$) of the prey (compare to equations 7 and 8),

$$\dot{Y}_b(t + \tau) = k \cdot \hat{\phi}_p(t) \quad (12)$$

$$\dot{P}_b(t + \tau) = k \cdot \hat{\theta}_p(t) \quad (13)$$

and kept the gaze direction equal to the flight direction. Condition 3 allows to judge the impact of the velocity control loop introduced in the model. The speed value chosen was set to half the highest speed.

For each condition, we ran 100 trials. Figure 6 collects basic statistics about the flight paths for each of the three conditions. Figures 7 and 8 show exemplary flight paths obtained for each of the three conditions. Visualizations of all simulated trajectories are provided as supplementary material. Capture success and duration varied significantly across conditions. The simulated bat was able to catch the insect in about 75 percent of trials in condition 1. When fixing the head the capture probability is reduced to about 35 percent, whereas fixing the speed at 2.5 m/s reduces the capture probability even more to about 25 percent. Statistics in the remainder of the paper only pertain to the trials in which capture was successful.

Comparing the trajectories shown in Figures 7 and 8 for condition 1 shows that while CATD-like trajectories can clearly arise from a reactive controller this is not guaranteed to be the case (the paths for all replications are provided as supplementary material). The paths for condition 2 are simpler, i.e. contain less loops, when compared to those for conditions 1 and 3, as also confirmed by the shorter average duration of the condition 2 paths that lead to capture (see Fig. 6). Comparing the paths for condition 3 with those for conditions 1 and 2 it can be seen that the radius of curvature for the loops is larger for condition 3. For conditions 1 and 2 the controller will typically reduce the speed when turning as both the turning and the speed reduction are caused by the prey moving towards the periphery of the field of view. This speed reduction will result in a tighter turn than is possible with a constant speed of 2.5 m/s as is the case for condition 3.

Figure 9 shows the mean value of γ as a function of time for the last second before capture. The figure compares the simulation results with the average γ as observed by Ghose et al. [20]. The figures reveal that for all conditions the simulated bat trajectories tend to converge to $\gamma = -1$ close to capture in accordance with the evidence from the real bat experiments. However, close to capture, the gamma values obtained in the simulations tend to be somewhat higher than those reported by Ghose et al. [20].

Figure 10 depicts the error angle ϕ_e as a function of time over the last second before capture. As for the γ criterion, the simulated data are compared with empirical data. Ghose et al. [20] reported the ϕ_e for a number of capture trials. Here, we have extracted the envelope of the error traces reported by Ghose et al. [20]. We extracted, for each instance the largest positive and negative value for $\mathcal{Y}_e$ from the reported traces. In this case, the simulated values of ϕ_e for condition 1 remain contained the most within the empirical error envelope [20], in particular when close to target, but the differences with the results for conditions 2 and 3 are small.

Figure 11 depicts for the three conditions the fit to the data of the delayed differential model for the error

angle ϕ_e proposed in [19]. For all three conditions the value of the product $k_e\tau_e$, respectively given by -0.36, -0.17 and -0.48, all comply with the stability constraint $k_e\tau_e > -\pi/2$. The value $\tau_e = 120$ ms extracted from the experimental data in [19] falls in between the delays τ_e for conditions 1 and 2, the gain $k_e = -3.55$ extracted from the experimental data is higher than the corresponding values for all conditions. Overall the values for condition 1 match the experimentally observed ones the best.

4. Discussion

To the best of our knowledge, we present the first model to decouple the head rotation from the body rotation by implementing the adaptive control law as proposed by Ghose and Moss [18] and Falk et al. [11]. Our results show, that in combination with reactive beam aiming [43], this mechanism is sufficient to support capture of erratically moving prey. As in the work of Kuc [38], Masters [44] and Bar et al. [4], our model consists entirely of reactive (non-predictive) loops. Erwin et al. [10] conducted experimental trials with real bats to calibrate their model. In these experiments, bats often flew past the prey, looped around, and returned to capture the prey. This lead them to adapt their model to include a predictive mechanism to initiate this looping. In our model, such a mechanism is absent. Nevertheless, we observed (qualitatively) similar behavior: simulated bats that missed the target looped around coming in for another attempt. This behavior is a direct result of the decoupling of the gaze direction and the flight direction, as commonly observed in bats [17, 57, 17, 20]. Indeed, contrary to the assumption made by the prey pursuit models proposed so far [10, 38, 44, 4], flight and gaze directions can (and often do) differ. Our results indicate that this divergence between flight direction and gaze direction allows both our model and the real bat to fly past the prey while still focusing on it. The time delayed coupling then describes how the flight direction 'catches up' with the gaze direction.

The advantages for a bat of decoupling gaze and flight direction derive from the considerably different response times of the body and the head. The head has low inertia and short response time. In contrast, the body (determining the flight direction) has higher inertia and longer response time. The difference in responsiveness between the two systems can be appreciated by evaluating the histograms of the instantaneous angular accelerations of both the head and the body (Fig. 12). The distributions of the angular accelerations of the body are localized around zero degrees per second. In contrast in conditions 1 and 3, the angular accelerations of the head are more uniformly distributed and correspond with the maximum values much more often indicating that the controller makes extensive use of the higher responsiveness of the head. It should be pointed out that these extreme values mostly occur together with short interpulse interval values, resulting in small actual head/gaze angle corrections. Note that in

Figure 6: Basic statistics about the flight paths for each of the three conditions. (a) Capture success rate, (b) Boxplot of average velocities across trials (only trials in which the bat captured the prey are included), (c) Boxplots of flight durations across trials (only trials in which the bat captured the prey are included). P-values above each panel refer to the results of a Kruskal-Wallis H-tests for independent samples.

Figure 7: Example flight trajectories resembling the paths resulting from the CATD for each of the three conditions: (left) condition 1, (middle) condition 2, (right) condition 3. Top row: top views. Bottom row: Side views.

Figure 8: Example flight trajectories different from the paths resulting from the CATD for each of the three conditions: (left) condition 1, (middle) condition 2, (right) condition 3. Top row: top views. Bottom row: Side views.

Figure 9: Plots of the distribution of γ_t (eq. 10) as a function of time to capture. In each panel, the heat map depicts the distribution of γ_t for the current simulations. The overlaid curves show the data from behavioral experiments reported by Ghose et al. [20] and the mean and median values of γ_t for the simulations.

Figure 10: Plots of the distribution of ϕ_e (eq. 11) as a function of time to capture. In each panel, the heat map depicts the distribution of ϕ_e for the current simulations. The overlaid curves show the data from behavioral experiments reported by Ghose et al. [20] and the mean and median values of ϕ_e for the simulations.

Figure 11: Fitting the evolution in time of ϕ_e by the delayed differential equation $\frac{d\phi_e}{dt} = k_e\phi_e(t - \tau_e)$ as proposed in [19].

Figure 12: Distribution of the angular accelerations of the head and body in the different conditions. Top row: yaw, bottom row: pitch.

condition 2 the head is fixed and this extra degree of freedom can not be exploited by the controller.

In summary, our simulations suggest that the high responsiveness of the gaze direction together with its partly uncoupled nature from the flight direction, allows bats to pursue and capture insects using reactive control. Rapid gaze shifts seem to be a bat's way of coping with unpredictable prey behavior and the limited field of view sonar provides [62]. Modeling the gaze direction as fixed with respect to the body could explain why previous modeling studies reported low capture rates using reactive pursuit strategies. Indeed, as shown in figure 6, fixing the head to the body has a detrimental effect on the success rate. This confirms that, at least in our simulations, decoupling the head and the body is critical for successful capture.

We did not explicitly model the CATD. Nevertheless, we found that the error angles ϕ_e and their evolution in time as well as the γ -statistic corresponded largely to the values reported by Ghose et al. [19, 20]. In particular, the median and average values for ϕ_e were close to 0 (fig. 10). In addition, γ approached -1 close to capture (fig. 9). Although, the values for gamma, close to capture, were found to be larger than those reported by Ghose et al. [20] and the numerical values of the parameters k_e and τ_e differed from the ones experimentally derived by Ghose et al. [19]. Looking at the trajectories in our simulated hunting sequences, we notice that some trials resemble the behavior

reported by Ghose et al. [19, 20] very closely while others are clearly different. Therefore, we conclude that flight paths resembling those predicted by the CATD can arise from different control strategies, e.g. the one proposed in this paper, provided the right conditions, i.e. initial prey position and flight direction relative to the bat, are present.

So far, the CATD has only been demonstrated in two studies on the same species of bat (*Eptesicus fuscus*). Therefore, it remains to be seen how wide-spread this strategy is across species and environmental conditions. Indeed, the flight paths reported by Corcoran and Conner [8] of *Myotis volans* chasing moths seem to indicate that the CATD might not be used by all species of bat in all situations. Given our finding that CATD-like paths can result from other pursuit strategies and the limited evidence on the CATD across species and conditions, we suggest that further studies are needed to elucidate when bats use the CATD.

Evasive responses elicited by bat calls have been documented in a range of insect prey [28]. Several authors have assessed the evasive behavior of moths [55, 67] and other prey [e.g. 45, 42, 20]. Nevertheless, only limited data on the actual flight paths of insect prey showing evasive behavior are available [8, 20]. Data on the flight paths of unresponsive prey, i.e. insects showing no evasive behavior, are even more scarce. Hence, we reverted to modelling prey as executing random trajectories. A similar approach was taken by Kuc [38]. However, as the behavior of the real bat is driven by the motion of the prey, the dynamics of the prey's flight will determine which strategies are feasible and optimal [52]. Hence, as an alternative to the CATD hypothesis proposed by Ghose et al. [19, 20], we conjecture that CATD-like paths observed in real bats when confronted with real prey are an emergent phenomenon arising from the interaction of a reactive pursuit strategy with real prey flight dynamics. At this moment however, insufficient data on the flight behavior of real prey is available to decide between these two alternative hypotheses. We conclude that prey behavior represents an important hiatus in our current understanding of sonar based prey capture

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