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Mathematical modeling of flight and acoustic dynamics of an echolocating bat during multiple-prey pursuit

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Abstract Bats emit ultrasound through their mouths or nostrils, and localize various objects such as obstacles and prey by analyzing the echoes. This localization ability is called echolocation. Japanese house bats (*Pipistrellus abramus*) are known to successively capture multiple insects within a short time interval of around one second by dynamically changing their flight paths and pulse directions. This suggests that echolocating bats combine flight dynamics and acoustic sensing for effective foraging. This study proposes a new mathematical model describing the nonlinear dynamics of the flight and pulse directions of an echolocating bat approaching two successive targets. In the model, a bat is assumed to control its flight and pulse directions depending on the directions to the targets. Numerical simulation of the present model shows that the model bat successfully captures both targets within a short time interval without losing them from its sonar beam, at specific parameter values. The simulation also suggests that the successive prey capture is completed especially when the echolocation pulses are directed to the subsequent target before capturing the immediate target. Such a relationship between the flight and acoustic sensing can be also observed in the behavioral data of wild bats.

1. Introduction

Nonlinear dynamics of mobile entities (e.g., animals, macromolecules, and robots) attracts a great deal of attention in physics, mathematics, and biology [1]. Theoretical and experimental studies on such spatial dynamics are required to reveal the sophisticated mechanisms of motion control of living beings.

Hunting behavior is essential for animals to survive in the wild, because they need to maximize their sensing ability to approach target prey with higher spatial resolution. In particular, bats are unique animals as they detect and capture targets by active sensing using ultrasound. Bats can recognize the physical attributes of their environment with great accuracy by comparing emitted pulses to returning echoes. Using the echolocation strategy, bats can successively capture multiple small moving insects. For example, Japanese house bats (*Pipistrellus abramus*) fly in large open spaces and capture a few hundred insects per night. It is important for them to sense multiple small insects in order to capture them in a short time interval. Our previous study revealed that bats achieve successive captures in a short time interval of around one second by dynamically changing their flight paths and the acoustic properties of their echolocation sounds [2-4], indicating that bats combine flight and acoustic sensing to capture multiple targets. To reveal the sonar strategy of bats, we need to investigate the relationship between flight and acoustic sensing.

The purpose of this study is to examine the nonlinear dynamics inherent in the controls of a bat's flight and pulse directions while approaching successive targets. To achieve this, we propose a mathematical model describing the dynamics of the flight and pulse directions, and then perform numerical simulation to demonstrate that our model can qualitatively explain successive prey captures of an echolocating bat.

2. Mathematical modeling of flight and acoustic dynamics

In our previous study, we proposed a mathematical model describing the flight dynamics of a bat while approaching a single target in a flight chamber [5]. An extension of the model is required to further examine the mechanism of the pursuit behavior for multiple targets in the field.

In this study, we take into account two points: the bat's flight dynamics and pulse-emission dynamics. Experimental studies using a custom-made microphone array showed that the changes in the flight and pulse directions in the vertical plane are much narrower than in the horizontal plane [4]. Hence, we focus on the flight and pulse-emission dynamics in the horizontal plane, as in our previous study [5]. First, the dynamics of the bat's position is modeled as follows [5]:

$$\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix} x_{\mathrm{b}}(t) \\ y_{\mathrm{b}}(t) \end{pmatrix} = v_{\mathrm{b}}\begin{pmatrix} \cos\phi_{\mathrm{f}}(t) \\ \sin\phi_{\mathrm{f}}(t) \end{pmatrix}, \qquad (1)$$

where $(x_{\mathrm{b}}(t), y_{\mathrm{b}}(t))$ represents the position of the bat in the horizontal plane, and $\phi_{\mathrm{f}}(t)$ is the flight direction of the bat in the same plane (see Fig. 1A). We define $\phi_{\mathrm{f}}(t)$ as a variable ranging from $-\pi$ to $+\pi$ rad. Parameter v_{b} is the flight velocity of the bat.

Next, we model the situation that a bat approaches two targets while changing both flight and pulse directions. In this model, $\phi_p(t)$ represents the horizontal pulse direction, and $\phi_{bt1}(t)$ and $\phi_{bt2}(t)$ represent the directions from the bat to Target 1 and Target 2, respectively (see Fig. 1A). We assume that the bat can estimate $\phi_{bt1}(t)$ and $\phi_{bt2}(t)$ as long as the respective targets are positioned within the beam of the pulse because the real bats localize their targets by using binaural cues from echoes [6]. We defined $\phi_p(t)$, $\phi_{bt1}(t)$ and $\phi_{bt2}(t)$ as variables ranging from −π to +π rad. The dynamics of the bat's flight direction $\phi_f(t)$ and pulse direction $\phi_p(t)$ is modeled as follows:

$$\frac{d\phi_f(t)}{dt} = \frac{1}{\delta_f}\left[\alpha_f \sin(\phi_{bt1}(t) - \phi_f(t)) + \beta_f \sin(\phi_{bt2}(t) - \phi_f(t))\right], \quad (2)$$

$$\frac{d\phi_p(t)}{dt} = \frac{1}{\delta_a}\left[\alpha_a \sin(\phi_{bt1}(t) - \phi_p(t)) + \beta_a \sin(\phi_{bt2}(t) - \phi_p(t))\right], \quad (3)$$

where δ_f and δ_a are positive weighting factors, and α_f and β_f (or α_a and β_a) are the parameters minimizing the angular differences between $\phi_f(t)$ and the target directions (or between $\phi_p(t)$ and the target directions) [5]. Here, α_f, β_f can be understood as the parameters describing *flight attention* to the targets, while α_a, β_a can be understood as the parameters of *acoustic attention* to the targets. For example, the model bat shifts $\phi_f(t)$ (or $\phi_p(t)$) to Target 1 when α_f (or α_a) takes a positive value [5]. Note that the model of Eqs. (2) and (3) can be extended to the model describing the flight and acoustic dynamics for more than two targets by adding another term of sinusoidal function on the right sides.

To study the suitable ratio of *flight attention* and *acoustic attention* for successful prey capture, we constrain (α_f, β_f) and (α_a, β_a) as follows:

$$\alpha_f^2 + \beta_f^2 = 1, \quad (4)$$

$$\alpha_a^2 + \beta_a^2 = 1. \quad (5)$$

Consequently, these parameters are described by using two parameters γ_f and γ_a, ranging from −π to π as follows:

$$\alpha_f = \sin\gamma_f, \quad (6)$$

$$\beta_f = \cos\gamma_f, \quad (7)$$

$$\alpha_a = \sin\gamma_a, \quad (8)$$

$$\beta_a = \cos\gamma_a. \quad (9)$$

The bat's sonar beam is then modeled as a circular piston oscillating in an infinite baffle based on the previous study [7,9]. The maximum search range (R_{max}, Fig. 1B) was set as 5 m [2,7].

3. Results

3.1. Numerical simulation of the changes in flight and pulse direction

The dynamics of the horizontal flight direction $\phi_f(t)$ and pulse direction $\phi_p(t)$ was numerically calculated based on the present mathematical model of Eqs. (1)–(9).

3.1.1. Initial conditions

The initial position and flight direction of the bat was set as $(x_b(t=0), y_b(t=0)) = (0, 0)$ and $\phi_f(t=0) = 0$. In our previous study, the initial positions of prey 1 (Target 1) and prey 2 (Target 2) were randomly determined in every trial in the echolocation distances ranging from 1.2 m to 5.0 m [7]. Further analysis of experimental data showed that the distances from the bat to the immediate target (Target 1) and the subsequent target (Target 2) were around 2 m and 4 m, respectively, at the start point when approaching the immediate target. Therefore, the initial distances from the bat to Target 1 and Target 2 (i.e., $R_{bt1}(t=0)$ and $R_{bt2}(t=0)$ in Fig. 1B) were set as 2 m and 4 m, respectively. Furthermore, the initial directions of the two targets relative to the pulse direction (i.e., $\phi_{pt1}(t=0)$ and $\phi_{pt2}(t=0)$ in Fig. 1B) were randomly determined within a range of ±60π/180 rad that was estimated as possible echolocation range on the basis of the −6 dB beam width of the directivity patterns of the echolocation pulses of Japanese house bats (i.e., *P. abramus*) [4]. The targets such as small insects fly sufficiently slower than the bats [2-4], so that two targets are assumed to stay at each initial position in this numerical simulation. Consequently, the horizontal positions of the two targets (x_{t1}, y_{t1}) and (x_{t2}, y_{t2}) are fixed as follows:

$$\begin{pmatrix} x_{t1} \\ y_{t1} \end{pmatrix} = R_{bt1}(t=0)\begin{pmatrix} \cos(\phi_{pt1}(t=0) + \phi_p(t=0)) \\ \sin(\phi_{pt1}(t=0) + \phi_p(t=0)) \end{pmatrix}, \quad (10)$$

$$\begin{pmatrix} x_{t2} \\ y_{t2} \end{pmatrix} = R_{bt2}(t=0)\begin{pmatrix} \cos(\phi_{pt2}(t=0) + \phi_p(t=0)) \\ \sin(\phi_{pt2}(t=0) + \phi_p(t=0)) \end{pmatrix}, \quad (11)$$

where the initial pulse direction of the bat (i.e., $\phi_p(t=0)$) was set as 0.1 rad, for simplicity. The flight velocity of the bat v_b was set as 5 m/s on the basis of experimental results using *P. abramus* [2,7].

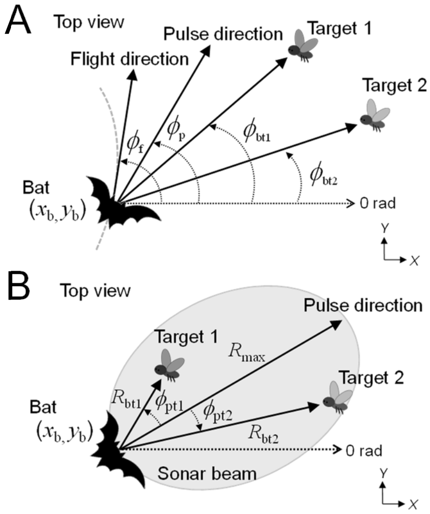

Fig. 1 Schematic diagram of the present mathematical model described by Eqs. (1)–(3). (A) The relationships between the bat and two targets in the horizontal plane. The model bat controls its flight and pulse directions ($\phi_f(t)$ and $\phi_p(t)$) by sensing the directions from itself to the targets ($\phi_{bt1}(t)$ and $\phi_{bt2}(t)$). (B) Schematic diagram of the sonar beam of the bat. The sonar beam is modeled as a circular piston oscillating in an infinite baffle with a range of 5 m (i.e., R_{max} = 5 m).

3.1.2 Conditions of prey capture

Successful target capture was defined as a case that the distance from the bat to the targets becomes less than 10 cm without losing the locations of the targets from the bat's echolocation range. Note that the distance 10 cm corresponds to the wing length of *P. abramus* [8].

3.1.3 Simulation results

Figures 2A and B show the results of our numerical simulation representing the successful examples of two consecutive captures by a model bat. The gray line describes the flight path of the model bat. The black thin arrows represent the pulse directions $\phi_p(t)$. All four variables in this model (i.e., $x_b(t)$, $y_b(t)$, $\phi_f(t)$, and $\phi_p(t)$) were calculated by using the fourth-order Runge–Kutta method with a time step of 0.001 s.

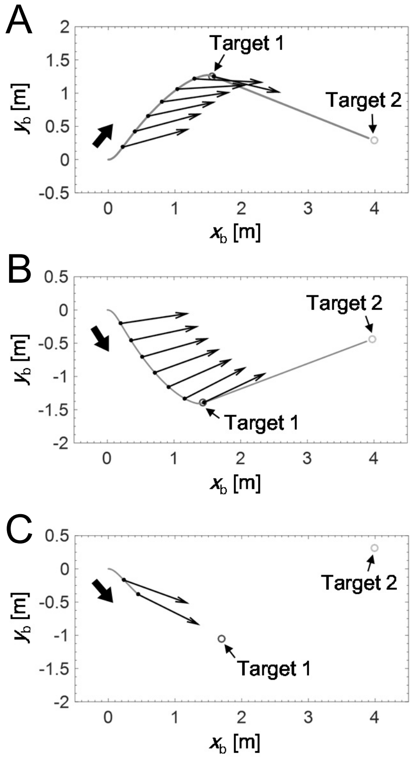

Fig. 2 Representative cases of the flight path and pulse direction calculated from the present model of Eqs. (1)–(9). The parameter values of the model were fixed as (γ_f, γ_a) = (0.6π, 0.2π) (A), (γ_f, γ_a) = (0.6π, -0.1π) (B) or (γ_f, γ_a) = (0.6π, 0.5π) (C), with (δ_f, δ_a) = (0.01, 0.05) and v_b = 5 m/s. Gray lines show the flight path of the bat. Black filled arrows show the flight direction. Open circles show the positions of Target 1 and Target 2. The pulse direction $\phi_p(t)$ showed with black thin arrows is plotted at the intervals of 0.06 s in this figure, to clearly show $\phi_p(t)$ without overlap. In (A) and (B), the model bat successfully captured both the two targets. In (C), the model bat lost Target 2 from the sonar beam on the approach to Target 1. We judged such a case of losing a target from the echolocation range as a failure to capture in our simulation.

Numerical simulation shows that the model bat successfully captured both of the targets, without losing them from its echolocation range, when the model bat directed $\phi_p(t)$ to Target 2 rather than Target 1 (i.e., $\gamma_a = 0.2\pi$ or -0.1π; see Figs. 2A and B). In contrast, the model bat could not capture the two targets when $\phi_p(t)$ was directed only to Target 1 (i.e., $\gamma_a = 0.5\pi$; see Fig. 2C).

These results at specific parameter values suggest that, for successive prey captures in a short time interval, it is important to emit pulses toward the subsequent target before capturing the immediate target.

3.2. Field measurement

3.2.1. Large-scale 3D microphone array

Recent studies of *biosonar* (e.g., in bats and dolphins) have developed in tandem with the microphone-array measurement technology for tracking animal movements based on sound recordings in the field [2,3,4,10]. In this section, we show the results of the field measurement of the sonar behaviors of the Japanese house bats *Pipistrellus abramus* (Vespertilionidae, 10–15 cm wingspan, 5–8 g body mass) [2-4]. During natural foraging, *P. abramus* emit relatively long pulses (9–11 ms) of shallow swept frequency modulated (FM) signals with the energy concentrated in the terminal sweep frequency of the fundamental component at around 40 kHz [11]. The echolocation sounds of *P. abramus* were recorded by using a large-scale 3D microphone array with 500 kHz sampling rate (Fig. 3A) at a stream near the campus of Doshisha University in southern Kyoto Prefecture, Japan, from the early summer to the fall during the evenings [4]. The 3D locations of the bats were obtained using time difference of arrival (TDOA) between a reference and three other microphones (which were separated by 1.3 ± 0.01 m in the Y-shaped array, as shown in Fig. 3B) [12]. The locations where the bats captured the targets were determined based on the occurrence of feeding buzzes (i.e., the successive pulse emissions with extremely short time intervals just before capturing the focal target) [11,13].

3.2.2. Flight behavior of the bat while approaching multiple targets

Figure 3C shows an example of the top view (i.e., horizontal plane) of the 3D flight path and pulse directions of a bat during natural hunting measured by the large-scale 3D microphone array (Figs. 3A and B). In this case, the bat successively captured two insects (Targets 1 and 2) in a short time interval of 1.1 s, directing its pulses toward Target 2 before capturing Target 1 (Fig. 3C), which is consistent with the results of our previous experimental study [3] and also consistent with the results of the present numerical simulation (Figs. 2A and B).

4. Discussion

Our numerical simulation demonstrated that the present model can qualitatively explain successive prey capture with specific parameter values. In addition, it is suggested that such successive prey capture is accomplished when a model bat flies toward the immediate target while emitting pulses toward the subsequent target.

Comparison between the theoretical and experimental studies will allow us to examine the detailed mechanisms of multiple-prey capture according to the present mathematical model. For this purpose, the parameters γ_f and γ_a, which represent *flight attention* and *acoustic attention*, respectively, need to be estimated from the experimental data using the microphone-array system. We then need to conduct the numerical simulation by changing the parameter values and initial conditions, and also need to compare the experimental and theoretical results to clarify the detailed dynamics of the decision-making of the bats during natural hunting.

It remains as a future problem to compare the dynamics of the present model to that of related mathematical models. Previous modeling studies of bat's pursuit behavior suggests that bats use a functionally predictive flight strategy during chasing erratically moving insects in the flight chamber [14], whereas another modeling study suggests that bats can successfully capture insects using nonpredictive strategy [15]. In addition, the relationship between the visual line and motion control of living beings such as humans or insects is associated with the bat's sonar behavior from the viewpoint of the interaction between attention and motion control [16,17]. Comparison between our model and these related models would be helpful to investigate the validity and generality of our model.

In this study, we propose a mathematical model describing flight and pulse-emission dynamics in the horizontal plane. However, real bats fly around in 3D space, sensing their surrounding objects. An extension of the present model will be required in order to study flight and echolocation mechanisms in 3D space, such as the mechanism using descending motion during prey pursuit. In fact, we have already extended the model of bat's flight direction in horizontal plane to the model in the 3D space [7]. The pulse-emission dynamics would be extended to the 3D space by the similar approach. The extension of bat's sonar-beam shape to the 3D space is also required according to the previous studies [9,15,18].

The real bats detect the echoes from the targets with a certain time delay varying depending on the distance between the bat and the target [19]. Such a time delay would play an important role both for echolocation and motion control. The model of Eqs. (2) and (3) can be modified to take such a time-delay effect into account by replacing $\phi_{bt1}(t)$ and $\phi_{bt2}(t)$ with $\phi_{bt1}(t-\tau)$ and $\phi_{bt2}(t-\tau)$, using a variable τ representing the time delay.

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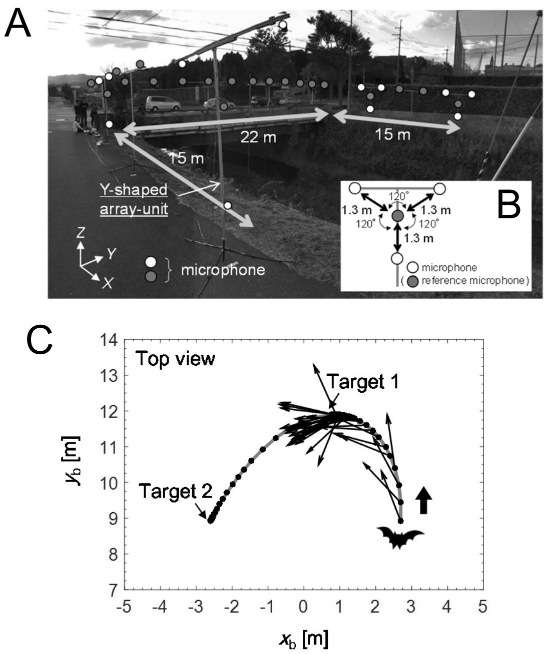

Fig. 3 (A) Photograph of the microphone array system in the field. The white circles show the microphones installed at the Y-shaped array units used to calculate the 3D sound coordinates of the bat. (B) A schematic diagram of the Y-shaped microphone array. The distance between the reference microphone (dark gray circle) and each of the three microphones (white circles) was 1.3 ± 0.01 m, and they were distributed with an angular separation of 120º. The 3D flight paths of the bats were reconstructed from differences in the arrival times of the ultrasound pulses among the microphones. (C) Representative case of the flight path (gray line) and pulse directions (black thin arrows) during successive captures of two targets. Black dots show the position where the bat emitted the pulse. Black filled arrows show the flight direction. The time interval to capture two successive targets was 1.1 s.

References

[1] Vicsek T, Zafeiris A. "Collective motion," *Phys. Rep.*, 517, pp.71–140, 2012

[2] Fujioka E, Mantani S, Hiryu S, Riquimaroux H, Watanabe Y. "Echolocation and flight strategy of Japanese house bats during natural foraging, revealed by a microphone array system," J. Acoust. Soc. Am., 129(2), pp.1081–8, 2011

[3] Fujioka E, Aihara I, Watanabe S, Sumiya M, Hiryu S, Simmons J A, et al. "Rapid shifts of sonar attention by *Pipistrellus abramus* during natural hunting for multiple prey," *J. Acoust. Soc. Am.*, 136(6), pp.3389–400, 2014

[4] Sumiya M, Fujioka E, Aihara I, Watanabe Y, Riquimaroux H, Ohta T et al. "Analysis of 3-D acoustic and flight attention of echolocating bats during attacking to multiple target preys," *ICN2014 Bat Satellite Symposium Abstract*, p.222, 2014

[5] Aihara I, Fujioka E and Hiryu S. "Qualitative and Quantitative Analyses of the Echolocation Strategies of Bats on the Basis of Mathematical Modelling and Laboratory Experiments," *PLoS One*, 8(7), e68635, 2013

[6] Aytekin M., Grassi E., Sahota M. and Moss C. F. "The bat head-related transfer function reveals binaural cues for sound localization in azimuth and elevation," *J. Acoust. Soc. Am.*, 116.6, pp.3594-3605, 2004

[7] Fujioka E, Aihara I, Watanabe S, Sumiya M, Hiryu S, Watanabe Y, et al., "Experimental and Mathematical Study on Bio-SONAR Behavior of Bats during Tracking Multiple Target Preys," *ISIMM Abstract*, p.52, 2013

[8] Hiryu S, Hagino T, Riquimaroux H, Watanabe Y., "Echo-intensity compensation in echolocating bats (*Pipistrellus abramus*) during flight measured by a telemetry microphone," *J. Acoust. Soc. Am.*, 121(3), pp.1749–57, 2007

[9] Jakobsen L and Surlykke A. "Vespertilionid bats control the width of their biosonar sound beam dynamically during prey pursuit," *PNAS*, 107(31), pp.13930–5, 2010

[10] Seibert AM, Koblitz JC, Denzinger A, Schnitzler H-U., "Scanning behavior in echolocating common pipistrelle bats (*Pipistrellus pipistrellus*)," *PLoS One*, 8(4), e60752, 2013

[11] Hiryu S, Hagino T, Fujioka E, Riquimaroux H, Watanabe Y. "Adaptive echolocation sounds of insectivorous bats, *Pipistrellus abramus*, during foraging flights in the field ," *J. Acoust. Soc. Am.*, 124(2), EL51–EL6, 2008

[12] Au W W and Herzing D L. "Echolocation signals of wild Atlantic spotted dolphin (*Stenella frontalis*),"*J. Acoust. Soc. Am.*, 113.1, pp.598-604, 2003.

[13] Kalko EK and Schnitzler H-U. "The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentoni*," *Behav. Ecol. Sociobiol*., 24(4), pp.225–38, 1989

[14] Ghose K., Horiuchi T. K., Krishnaprasad P. S. and Moss C. F. "Echolocating bats use a nearly time-optimal strategy to intercept prey," *PLoS biolo.*, 4(5), 865, 2006

[15] Kuc R. "Sensorimotor model of bat echolocation and prey capture," *J. Acoust. Soc. Am.*, 96(4), pp.1965-1978, 1994

[16] Ghose K and Moss CF. "Steering by hearing: a bat's acoustic gaze is linked to its flight motor output by a delayed, adaptive linear law," *J. Neurosci*., 26(6), pp.1704–13, 2006

[17] Land M. F. and Tatler B. W. "Steering with the head: the visual strategy of a racing driver," *Curr. Biol.*, 11(15), pp.1215–20, 2001

[18] Kuc R., "Echolocation with bat buzz emissions: Model and biomimetic sonar for elevation estimation," *J. Acoust. Soc. Am.* 131, p.561, 2012.

[19] Liang M. and Palakal M. J. "A multiple target acoustic scene representation model for bat echolocation signals," *J. Acoust. Soc. Am.*, 101(5), pp.3137-3137, 1997