Paper

Nonlinear dynamics in free flight of an echolocating bat

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Abstract: A mathematical model is proposed to describe the nonlinear dynamics of the echolocation behavior of a bat during free flight in an enclosed chamber. In the model, a bat dynamically controls its flight and pulse directions ($\phi_f$ and $\phi_p$ respectively), to avoid collision with multiple walls of the chamber; namely, the bat varies $\phi_f$ and $\phi_p$ repulsively from the closest wall, minimizing the difference between $\phi_f$ and $\phi_p$. Numerical simulation of the model with specific parameter values demonstrates that the bat can successfully fly in the chamber while emitting pulses along the inner periphery of an eight-shaped flight path, which is consistent with the results of a behavioral experiment conducted by using a Japanese house bat (\textit{Pipistrellus abramus}).

Key Words: bats, echolocation dynamics, flight dynamics, free flight, modeling

1. Introduction
Animals use various sensory systems to recognize their surrounding objects, and these sensory systems are considerably diverse due to the variety of animal species and their habitats. For example, many species of diurnal animals such as human beings and birds mainly rely on vision whereas certain nocturnal animals rely on hearing; frogs vocalize calls by inflating and deflating their vocal sacs and hear the calls of other individual frogs through their eardrums [1, 2]. Based on the information obtained through their sensory systems, animals dynamically control their motions; human beings maneuver the steering wheel by following their visual line when driving a car [3]; dragonflies directly fly towards the point of interception of a moving prey by steering to minimize the movement of the image of the prey on their retina [4, 5].

Bats are unique animals that use auditory information to recognize their surrounding objects [6]; they emit ultrasound pulses and subsequently detect the echoes reflected from obstacles and prey. While bats emit directional pulses through their noses or mouths, they receive echoes via their ears. Hence, the echoes detected by bats are also directional.

Previous experimental studies have revealed that bats dynamically change their flight and pulse
directions during prey-capture flights in a laboratory chamber and also during natural foraging in a field [7, 8]. To quantitatively examine the performance of such complex echolocation behaviors of bats, theoretical studies based on a mathematical model can be useful. We have previously proposed a mathematical model describing the flight dynamics of bats during prey pursuit, and the estimated parameters of the model have revealed that Japanese horseshoe bats (*Rhinolophus ferrumequinum nippon*) choose effective flight paths for successful prey capture [9]. The present study proposes a novel mathematical model that describes the nonlinear dynamics involved in both changes in the flight and pulse directions of bats flying in a space enclosed by walls.

2. Mathematical modeling of an echolocating bat during free flight

In this section, we propose a mathematical model to describe the flight and pulse-emission dynamics of an echolocating bat during free flight in a defined space. First, a fundamental model is proposed for the case that a flying bat avoids collision with a single large wall (Section 2.1). Second, the model is extended to describe the obstacle-avoidance behavior of a bat during its flight in a limited space enclosed by four static walls whose structure can be considered as a simulation of the flight chamber used in our previous experiments (Section 2.2).

2.1 Collision avoidance with a single large wall

Laboratory experiments have revealed that the change in a bat’s position in the flight chamber is considerably greater in the horizontal plane than in the vertical plane [7, 10]. Therefore, we focus on the flight and pulse-emission dynamics in the horizontal plane for simple modeling. As shown in Fig. 1A, the flight angle of the bat is described as $\phi_f(t)$, and the angle to which the bat emits a pulse is described as $\phi_p(t)$. $\phi_f(t)$ and $\phi_p(t)$ are defined as variables ranging from $-\pi$ to $+\pi$. Using $\phi_f(t)$, the dynamics of the bat’s position is described as follows:

$$\frac{d}{dt} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = v \begin{pmatrix} \cos \phi_f(t) \\ \sin \phi_f(t) \end{pmatrix}, \quad (1)$$

where $(x(t), y(t))$ represent the position of the bat in the horizontal plane, and $v$ denotes a positive parameter describing the flight velocity of the bat.

Then, we model a simple case in which the bat flies by controlling $\phi_f(t)$ and $\phi_p(t)$ to avoid collision with a single large static wall as follows:

$$\frac{d\phi_f(t)}{dt} = F_f(\phi_p(t) - \phi_f(t)) + G_f(r_w(t))H_f(\phi_w(t) - \phi_f(t)), \quad (2)$$

$$\frac{d\phi_p(t)}{dt} = F_p(\phi_f(t) - \phi_p(t)) + G_p(r_w(t))H_p(\phi_w(t) - \phi_p(t)), \quad (3)$$

where $r_w(t)$ and $\phi_w(t)$ represent the distance and angle from the bat to the wall in the perpendicular direction as shown in Fig. 1A, respectively. $\phi_w(t)$ is defined as a variable from $-\pi$ to $+\pi$. Under the situation of Fig. 1A, $\phi_w(t)$ is always equal to $\pi/2$, because the wall is horizontally placed in the 2-dimensional space. In this model, we assume that the obstacle wall is always located within the echolocation range of the flying bat.

We then discuss the mechanisms of the echolocation of a flying bat, so as to explain how the bat estimates $r_w(t)$ and $\phi_w(t)$ in the present model. For example, when a bat pursues a small target such as prey like moth and mosquito, the bat can obtain the information about the distance and angle to the target via echolocation. Namely, a bat can estimate the distance to the target by using time interval between pulse-emission and echo-arrival, while the bat can estimate the angle to the target by detecting the time and sound-intensity differences of the echo between two ears [6]. Therefore, a bat can localize such a small target on the basis of the distance and angle obtained via echolocation. In contrast, our model describes the situation that a bat avoids the collision with a continuous large wall (see Fig. 1A and B), so that the simulated bat is assumed to detect continuous echo reflected from the continuous wall. Even when the echolocation range does not include the point of the wall positioned
in the perpendicular direction as shown in Fig. 1A and B, the bat can still estimate the distance and angle to the nearest point of the wall in its echolocation range (corresponding to \( r_{\text{near}}(t) \) and \( \phi_{\text{near}}(t) \) in Fig. 1B) by using the onset of the continuous echo. Moreover, the bat seems to estimate the wall plane in its echolocation range (corresponding to \( \theta_{\text{line}} \) in Fig. 1B) by using the continuous echo arriving at various latencies and sound-intensities that include the information about the positions of different points of the wall. Consequently, we assume that the simulated bat can estimate \( r_w(t) \) and \( \phi_w(t) \) as \( r_w(t) = |r_{\text{near}}(t)\sin(\phi_{\text{near}}(t) - \theta_{\text{line}})| \) and \( \phi_w(t) = \pi/2 + \theta_{\text{line}} \) from \( r_{\text{near}}(t) \) and \( \phi_{\text{near}}(t) \) and \( \theta_{\text{line}} \). Note that, when the echolocation range includes the point of the wall in the perpendicular direction, the bat can directly estimate \( r_w(t) \) and \( \phi_w(t) \) as \( r_w(t) = r_{\text{near}}(t) \) and \( \phi_w(t) = \phi_{\text{near}}(t) \) by just using the onset of the continuous echo.

Fig. 1. Schematic diagram of the present mathematical model described by Eqs. (1)–(3). (A) Collision avoidance with a wall by controlling flight and pulse angles. \( \phi_f(t) \) represents the flight angle of the bat, and \( \phi_p(t) \) represents the pulse angle. We first assume that a single large wall is located within the echolocation range of the bat. Then, \( r_w(t) \) and \( \phi_w(t) \) represent the distance and angle to the wall in the perpendicular direction, respectively. On the basis of \( r_w(t) \) and \( \phi_w(t) \), the bat dynamically varies \( \phi_f(t) \) and \( \phi_p(t) \) to avoid collision with the wall. (B) Estimation of \( r_w(t) \) and \( \phi_w(t) \) due to echolocation. Since a continuous wall is considered in the present model, a bat is assumed to detect continuous echo reflected from the continuous wall. While the bat can estimate \( r_{\text{near}}(t) \) and \( \phi_{\text{near}}(t) \) by using the onset of the echo, the bat can estimate \( \theta_{\text{line}} \) by using the continuous echo arriving at various latencies and sound-intensities that include the information about the positions of different points of the wall. Subsequently, we assume that the simulated bat can estimate \( r_w(t) \) and \( \phi_w(t) \) as \( r_w(t) = |r_{\text{near}}(t)\sin(\phi_{\text{near}}(t) - \theta_{\text{line}})| \) and \( \phi_w(t) = \pi/2 + \theta_{\text{line}} \) from \( r_{\text{near}}(t) \), \( \phi_{\text{near}}(t) \) and \( \theta_{\text{line}} \), even when the echolocation range does not include the point of the wall in the perpendicular direction.

As shown in Eqs. (2) and (3), our model consists of six functions \( F_f(\phi_p(t) - \phi_f(t)) \), \( F_p(\phi_f(t) - \phi_p(t)) \), \( G_f(r_w(t)) \), \( G_p(r_w(t)) \), \( H_f(\phi_w(t) - \phi_f(t)) \) and \( H_p(\phi_w(t) - \phi_p(t)) \). We then discuss the behavioral meanings of these functions.

The functions \( F_f(\phi_p(t) - \phi_f(t)) \) and \( F_p(\phi_f(t) - \phi_p(t)) \) represent the interactions between \( \phi_f(t) \) and \( \phi_p(t) \). Here, the phase difference \( \phi_f(t) - \phi_p(t) \) is defined as a \( 2\pi \)-periodic variable ranging from \(-\pi \) to \( \pi \). Subsequently, we assume that these functions \( F_f(\phi_p(t) - \phi_f(t)) \) and \( F_p(\phi_f(t) - \phi_p(t)) \) are \( 2\pi \)-periodic. Previous experimental studies have shown that a bat usually emits ultrasound pulses towards the direction related to its own flight direction with a small difference [11]. Therefore, \( F_f(\phi_p(t) - \phi_f(t)) \) and \( F_p(\phi_f(t) - \phi_p(t)) \) need to be modeled as the functions minimizing the difference between \( \phi_f(t) \) and \( \phi_p(t) \).

Then, the functions \( G_f(r_w(t)) \) and \( G_p(r_w(t)) \) represent the risk of the bat in colliding with the wall; when the distance to the wall \( r_w(t) \) is small, the bat must quickly change \( \phi_f(t) \) and \( \phi_p(t) \) to avoid collision. Consequently, we assume that the functions \( G_f(r_w(t)) \) and \( G_p(r_w(t)) \) satisfy the following conditions:
The functions $H_f(\phi_w(t) - \phi_f(t))$ and $H_p(\phi_w(t) - \phi_p(t))$ represent suitable turn directions for collision avoidance, which is based on the direction in which the bat approaches the wall. A clockwise (or counterclockwise) turn is required while the wall is located to the left side (or right side) from bat’s flight and pulse directions, as shown in Fig. 2. Therefore, we assume that $H_f(\phi_w(t) - \phi_f(t))$ and $H_p(\phi_w(t) - \phi_p(t))$ satisfy the following conditions:

\begin{align}
G_f(r_w(t)) > 0 \quad &\text{and} \quad \frac{dG_f(r_w(t))}{dr_w(t)} < 0, \\
G_p(r_w(t)) > 0 \quad &\text{and} \quad \frac{dG_p(r_w(t))}{dr_w(t)} < 0.
\end{align}

(4)

(5)

Note that $\phi_w(t) - \phi_p(t)$ and $\phi_p(t) - \phi_w(t)$ are calculated as variables ranging from $-\pi$ to $+\pi$, respectively. The conditions $0 \leq \phi_w(t) - \phi_f(t) < \pi$ and $0 \leq \phi_w(t) - \phi_p(t) < \pi$ in Eqs. (6) and (8) correspond to the case in which the wall is located to the left side of the bat’s flight and pulse directions, while the conditions $-\pi \leq \phi_w(t) - \phi_f(t) < 0$ and $-\pi \leq \phi_w(t) - \phi_p(t) < 0$ in Eqs. (7) and (9) correspond to the case in which the wall is located to the right side.

A.

Wall

Clockwise turn

B.

Wall

Counterclockwise turn

Fig. 2. Schematic diagram of turn directions required for collision avoidance in the present model expressed by Eqs. (2) and (3). When the wall is located to the left side of the bat’s flight and pulse directions, a clockwise turn is required. In contrast, when the wall is located to the right side, a counterclockwise turn is required. The functions $H_f(\phi_w(t) - \phi_f(t))$ and $H_p(\phi_w(t) - \phi_p(t))$ satisfying Eqs. (6)–(9) realize such required turn directions.

2.2 Free flight in a chamber

We next model the situation that the bat flies within a chamber of length $L_x$ and width $L_y$ (see Fig. 3), enclosed by four static walls. In this model, the bat is assumed to detect the walls located within its echolocation range of $\theta_x$ that is defined as a positive parameter from 0 to $2\pi$. The bat then determines the closest one among the four surrounding walls by comparing the normalized distances $r_{w(i)}(t)/D_{w(i)}$: $r_{w(i)}(t)$ represents the distance from the bat to respective walls in the echolocation range, while $D_{w(i)}$ represents the distance from one wall to the opposite wall, i.e., $D_{w(i)} = L_x$ or $L_y$ (see Fig. 3). Since the experimental data presented in this study were recorded after a bat flew one or two laps in the chamber (see Sec.4), the bat was likely to have mapped the chamber before
settling into a stable flight path. Based on this speculation, we assume that the bat knows $L_x$ and $L_y$ in advance and can use them to calculate the normalized distances, for simplicity. The validity and implication of this assumption is further discussed in Sec. 5. Subsequently, the bat pays its attention to the closest wall with the smallest $r_{w(i)}(t)/D_{w(i)}$; namely, the distance and direction to the closest wall are used as $r_w(t)$ and $\phi_w(t)$ in Eqs. (2) and (3), and the distance from the closest wall to the opposite wall is used as $D_w$. Note that $\phi_w(t)$ can take four different values $0$, $\pi/2$, $\pi$ and $-\pi/2$ in this situation surrounded by four walls, which correspond to the angles to Wall 1, Wall 2, Wall 3 and Wall 4, respectively.

![Fig. 3. Schematic diagram of the rule for determining the closest wall from the bat. In this model, the bat is assumed to detect the walls that are located within its echolocation range of $\theta_e$. The bat subsequently determines the closest wall by comparing the normalized distances $r_{w(i)}(t)/D_{w(i)}$, where $r_{w(i)}(t)$ represents the distance to respective walls within the echolocation range, and $D_{w(i)}$ represents the distance from one wall to the opposite wall, i.e., $D_{w(i)} = L_x$ or $L_y$. It is then assumed that the bat pays its attention to the closest wall with the smallest $r_{w(i)}(t)/D_{w(i)}$; namely, the distance and direction to the closest wall are used as $r_w(t)$ and $\phi_w(t)$ in Eqs. (2) and (3), and the distance from the closest wall to the opposite wall is used as $D_w$ in Eqs. (12) and (13).](image)

Then, we define the functions of Eqs. (2) and (3) to qualitatively satisfy the conditions mentioned in Sec. 2.1. The functions $F_f(\phi_p(t) - \phi_f(t))$ and $F_p(\phi_f(t) - \phi_p(t))$ are modeled as follows:

$$F_f(\phi_p(t) - \phi_f(t)) = \alpha_f \sin(\phi_p(t) - \phi_f(t)),$$

$$F_p(\phi_f(t) - \phi_p(t)) = \alpha_p \sin(\phi_f(t) - \phi_p(t)),$$

where $\alpha_f$ and $\alpha_p$ are positive weighting parameters for $F_f(\phi_p(t) - \phi_f(t))$ and $F_p(\phi_f(t) - \phi_p(t))$, respectively. We use the sinusoidal functions in this model as the first-order approximation of the Fourier expansions of the $2\pi$-periodic functions $F_f(\phi_p(t) - \phi_f(t))$ and $F_p(\phi_f(t) - \phi_p(t))$. This approximation is inspired by Kuramoto model [12], and therefore the absolute value of the phase difference $|\phi_p(t) - \phi_f(t)|$ is expected to be minimized.

To satisfy the conditions of Eqs. (4) and (5) by using the normalized distance to the closest wall, the functions $G_f(r_w(t))$ and $G_p(r_w(t))$ are modeled as follows:

$$G_f(r_w(t)) = \frac{\beta_f}{r_w(t)/D_w},$$

$$G_p(r_w(t)) = \frac{\beta_p}{r_w(t)/D_w}.$$
where \( \beta_f \) and \( \beta_p \) denote positive weighting parameters for \( G_f(r_w(t)) \) and \( G_p(r_w(t)) \), respectively.

To satisfy the conditions of Eqs. (6)–(9), the functions \( H_f(\phi_w(t) - \phi_f(t)) \) and \( H_p(\phi_w(t) - \phi_p(t)) \) are then modeled as follows:

\[
H_f(\phi_w(t) - \phi_f(t)) = \begin{cases} 
\pi^{-1}(\phi_w(t) - \phi_f(t) - \pi) & (0 \leq \phi_w(t) - \phi_f(t) < \pi), \\
\pi^{-1}(\phi_w(t) - \phi_f(t) + \pi) & (-\pi \leq \phi_w(t) - \phi_f(t) < 0),
\end{cases}
\]  

(14)

and

\[
H_p(\phi_w(t) - \phi_p(t)) = \begin{cases} 
\pi^{-1}(\phi_w(t) - \phi_p(t) - \pi) & (0 \leq \phi_w(t) - \phi_p(t) < \pi), \\
\pi^{-1}(\phi_w(t) - \phi_p(t) + \pi) & (-\pi \leq \phi_w(t) - \phi_p(t) < 0).
\end{cases}
\]

(15)

\( H_f(\phi_w(t) - \phi_f(t)) \) and \( H_p(\phi_w(t) - \phi_p(t)) \) are also related to the risk of collision as well as \( G_f(r_w(t)) \) and \( G_p(r_w(t)) \). The bat is required to perform a quick turn for collision avoidance when \( |\phi_w(t) - \phi_f(t)| \) and \( |\phi_w(t) - \phi_p(t)| \) are small, which corresponds to the situation that the bat flies towards the closest wall almost perpendicularly. Therefore, it is assumed that \( |H_f(\phi_w(t) - \phi_f(t))| \) and \( |H_p(\phi_w(t) - \phi_p(t))| \) of Eqs. (14) and (15) take the maximum values at \( \phi_w(t) - \phi_f(t) = 0 \) and \( \phi_w(t) - \phi_p(t) = 0 \), respectively. \( H_f(\phi_w(t) - \phi_f(t)) \) and \( H_p(\phi_w(t) - \phi_p(t)) \) are normalized from \(-1\) to \(1\) by dividing them by the factor \( \pi \), for simplicity.

3. Numerical simulation of the mathematical model

We perform numerical simulation to examine a stable flight path appearing in the present model described by Eqs. (1)–(3) and (10)–(15). Certain parameters of the model are fixed at particular values on the basis of behavioral experiments conducted by using Japanese house bats in a laboratory flight chamber [11]. The size of the flight chamber is set as \( L_x = 7 \) m and \( L_y = 3 \) m for the simulation, corresponding to the size of the actual chamber used in the behavioral experiments. The parameter \( v \) in Eq. (1) is set as \( v = 3 \) m/s using the mean horizontal flight velocity during the behavioral experiments. By measuring the sound pressure level of the ultrasounds emitted by the bats, their echolocation range \( \theta_e \) is estimated to be \( \frac{100\pi}{180} \) rad [11].

The other four parameters \( \alpha_f, \alpha_p, \beta_f, \) and \( \beta_p \) are then varied. Because \( H_f(\phi_w(t) - \phi_f(t)) \) and \( H_p(\phi_w(t) - \phi_p(t)) \) of Eqs. (14) and (15) are normalized from \(-1\) to \(1\), the parameters \( \beta_f \) and \( \beta_p \) can be considered as the weighting factors to the second terms in the right sides of Eqs. (2) and (3), respectively. Then, the summation of each parameter set is constrained as \( \alpha_f + \alpha_p = \alpha \) and \( \beta_f + \beta_p = \beta \) where \( \alpha \) and \( \beta \) are positive parameters. Consequently, \( \alpha_f, \alpha_p, \beta_f, \) and \( \beta_p \) are described as follows:

\[
\alpha_f = \gamma \alpha, 
\]

(16)

\[
\alpha_p = (1 - \gamma) \alpha, 
\]

(17)

\[
\beta_f = \delta \beta, 
\]

(18)

\[
\beta_p = (1 - \delta) \beta, 
\]

(19)

where \( \gamma \) and \( \delta \) denote positive parameters ranging from \(0\) to \(1\), and represent the usage ratios of \( (\alpha_f, \alpha_p) \) and \( (\beta_f, \beta_p) \), respectively. The parameters \( \alpha \) and \( \beta \) are first fixed as \(1\) for simplicity, and are then varied so as to compare the effects of the first and second terms in the right sides of Eqs. (2) and (3).

Figure 4 shows a stable flight path obtained from numerical simulation under the constraint of \( (\alpha, \beta) = (1, 1) \), assuming \( (\alpha_f, \alpha_p) = (0.4, 0.6) \), \( (\beta_f, \beta_p) = (0.4, 0.6) \), \( L_x = 7 \) m, \( L_y = 3 \) m, \( v = 3 \) m/s, and \( \theta_e = \frac{100\pi}{180} \) rad. The initial conditions are set as \( x(t = 0) = 1.0, y(t = 0) = 1.5, \phi_f(t = 0) = \pi/3, \) and \( \phi_p(t = 0) = \pi/3 - \pi/10 \). The green bars represent the pulse angle \( \phi_p(t) \). An eight-shaped path is consistently observed in this simulation.

We then examine the suitable conditions for successful collision avoidance in the present model by varying the two parameters \( \gamma \) and \( \delta \) from \(0\) to \(1\) at the interval of \(0.01\) under the constraint of \( (\alpha, \beta) = (1, 1) \). The other parameters and initial conditions are all fixed at the values described above.

Figure 5 represents the collision-free flight time of the bat. A collision is determined to have occurred
Fig. 4. Numerical simulation of a stable flight path observed in the present model of Eqs. (1)–(3) and (10)–(15). The parameter values of the model are fixed as \((\alpha_f, \alpha_p) = (0.4, 0.6), (\beta_f, \beta_p) = (0.4, 0.6), L_x = 7 \text{ m}, L_y = 3 \text{ m},\) \(v = 3 \text{ m/s, and } \theta_e = \frac{180}{\pi} \text{ rad.}\) The initial conditions are set as \(x(t = 0) = 1.0, y(t = 0) = 1.5, \phi_f(t = 0) = \pi/3, \) and \(\phi_p(t = 0) = \pi/3 - \pi/10.\) Green bars represent the pulse angle \(\phi_p(t).\) The data shown here is obtained from the numerical simulation from 44.1 to 50.0 s under the above conditions. The bat successfully flies in the chamber without collision during this simulation, and a consistent eight-shaped path is observed. Black arrows represent the turn direction of the bat. Note that \(\phi_p(t)\) is plotted at the intervals of 0.1 s in this figure, in order to clearly display the pulse angles without overlaps. When the distance from the bat to the wall reduces to less than 5 cm, which corresponds to the body length of Japanese house bats. In contrast, if the simulated bat continues to fly for 50 s without collision, such an instance is considered as successful collision avoidance. The yellow region in Fig. 5 represents suitable parameter values for successful collision avoidance, which is found to lie in the ranges of \(0 \leq \gamma \leq 1\) and \(0.35 < \delta < 0.65.\) As shown in Fig. 4, a consistent eight-shaped path can be observed in the present model. To investigate the consistency of such an eight-shaped path, we calculate the averages of \(\frac{d\phi_f}{dt}\) and \(|\frac{d\phi_f}{dt}|\) for each parameter set of \((\gamma, \delta)\) with which the bat succeeds in collision avoidance for 50 s, as follows:

\[
\frac{d\phi_f}{dt} = \frac{1}{T} \int_0^T \frac{d\phi_f}{dt} \, dt,
\]

\[
\left|\frac{d\phi_f}{dt}\right| = \frac{1}{T} \int_0^T \left|\frac{d\phi_f}{dt}\right| \, dt,
\]

where \(T\) denotes a positive parameter representing the collision-free flight time of the bat, which is set at the maximum value 50 s in this study. We next detect the occurrence of the eight-shaped path on the basis of \(\frac{d\phi_f}{dt}/\left|\frac{d\phi_f}{dt}\right|\). When the bat flies in a circular path, the turn direction is fixed as either clockwise or counterclockwise. Therefore, \(\frac{d\phi_f}{dt}/\left|\frac{d\phi_f}{dt}\right|\) is maintained at either +1 or −1. On the other hand, if the bat flies along an eight-shaped path as shown in Fig. 4, the bat turns both clockwise and counterclockwise with the similar ratio, indicating that \(\frac{d\phi_f}{dt}/\left|\frac{d\phi_f}{dt}\right|\) is close to 0. Figure 6 shows the values of \(\frac{d\phi_f}{dt}/\left|\frac{d\phi_f}{dt}\right|\) during the successful collision-avoidance flights that are marked as the yellow region in Fig. 5. The simulation demonstrates that \(\frac{d\phi_f}{dt}/\left|\frac{d\phi_f}{dt}\right|\) is close to 0 (ranging from −0.024 to 0.038) in the parameter region of \(0 \leq \gamma \leq 1\) and \(0.35 < \delta < 0.65,\) showing that an eight-shaped path is consistently observed through the wide parameter region of the present model. Experimental studies have demonstrated that echolocating bats emit pulses as slightly preceding their flight directions (i.e., along the inner peripheries of the flight directions) during free flights in a chamber, suggesting that the bats search the space that they will pass immediately after the pulse emissions [11]. To examine such sensing strategies based on the controls of pulse directions, we calculate the average of \(\frac{d\phi_f}{dt}(\phi_p - \phi_f)\) as follows:

\[
\]
Note that $\phi_p - \phi_f$ is defined as a variable ranging from $-\pi$ to $+\pi$. $\frac{d\phi_f}{dt}(\phi_p - \phi_f)$ takes a positive value when the bat emits a pulse along the inner periphery of its flight direction (see Fig. 7A), whereas $\frac{d\phi_f}{dt}(\phi_p - \phi_f)$ takes a negative value when the bat emits a pulse along the outer periphery of its flight direction (see Fig. 7B). Figure 7C shows that $\frac{d\phi_f}{dt}(\phi_p - \phi_f)$ can be both positive and negative depending on the value of $\delta$ under the constraint of $(\alpha, \beta) = (1, 1)$; namely, $\frac{d\phi_f}{dt}(\phi_p - \phi_f)$ is positive in the region of $0.35 < \delta < 0.5$, and $\frac{d\phi_f}{dt}(\phi_p - \phi_f)$ is negative in the region of $0.5 < \delta < 0.65$.

Numerical simulation shown in Figs. 5 and 6 indicates that an eight-shaped path is consistently observed in the present model. To further examine the robustness of this result, another parameter and initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied. We carefully analyzed the flight paths obtained from behavioral experiments using Japanese house bats [11], and confirmed that the flight velocity varied almost between 2 and 4 m/s around the mean value of 3 m/s. On the other hand, the initial conditions should be varied.
Numerical simulation of \( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \) for the cases of successful collision avoidance that are marked as the yellow region in Fig. 5. For a bat flying along an eight-shaped path as shown in Fig. 4, its turn direction is almost equally distributed between both clockwise and counterclockwise, indicating that \( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \) is close to 0. The simulation demonstrates that \( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \) is always close to 0 (ranging from −0.024 to 0.038) in the parameter region of 0 \( \leq \gamma \leq 1 \) and 0.35 \( < \delta < 0.65 \) under the constraint of \((\alpha, \beta) = (1, 1)\).

Numerical simulation of \( \frac{d\phi_p}{dt}(\phi_p - \phi_f) \) for the cases of successful collision avoidance that are represented by the yellow region in Fig. 5. (A, B) Schematic diagram illustrating whether a bat emits a pulse along the inner or outer periphery of its flight direction. A positive value of \( \frac{d\phi_p}{dt}(\phi_p - \phi_f) \) means that a bat emits a pulse along the inner periphery of its flight direction (see Fig. 7A). In contrast, a negative value of \( \frac{d\phi_p}{dt}(\phi_p - \phi_f) \) indicates that the bat emits the pulse along the outer periphery of its flight direction (see Fig. 7B). (C) \( \frac{d\phi_p}{dt}(\phi_p - \phi_f) \) calculated for successful flight cases under the constraint of \((\alpha, \beta) = (1, 1)\). While \( \frac{d\phi_p}{dt}(\phi_p - \phi_f) \) is positive in the region of 0.35 \( < \delta < 0.5 \), \( \frac{d\phi_p}{dt}(\phi_p - \phi_f) \) is negative in the region of 0.5 \( < \delta < 0.65 \).

Also demonstrates that \( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \) rarely takes much larger or less value than 0. The inset of Fig. 8 shows a representative flight path of such a rare case that \( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \) takes the minimum value −0.48 among the simulation. Although the flight path does not have an intersection, it is still similar to an
Fig. 8. Numerical simulation of \( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \) for various values of flight velocity and initial conditions. While the flight velocity \( v \) in Eq. (1) is varied from 2 to 4 m/s, the initial conditions of the flight and pulse angles are varied among \( (\phi_f(t = 0), \phi_p(t = 0)) = (\pi/3, \pi/3-\pi/10), (\pi/3, \pi/3+\pi/10), (\pi/6, \pi/6-\pi/10) \) and \( (\pi/6, \pi/6+\pi/10) \). Other parameters and initial conditions are fixed as the same values with those of Figs. 5, 6 and 7. The simulation demonstrates that \( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \) is distributed around 0, meaning that an eight-shaped path is consistently observed. The simulation also demonstrates that \( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \rarely takes much larger or less value than 0. The inset shows a representative path of such a rare case that\( \frac{d\phi_f}{dt} / \left| \frac{d\phi_f}{dt} \right| \) takes the minimum value \(-0.48\) among the simulation. Although the representative path does not have an intersection, it is still similar to an eight-shaped path rather than a circular path.

The present model is based on two behavioral aspects of echolocating bats, i.e., the interactions between \( \phi_f(t) \) and \( \phi_p(t) \), and the repulsive controls of \( \phi_f(t) \) and \( \phi_p(t) \) from the closest wall. While the first terms on the right sides of Eqs. (2) and (3) describe the interactions between \( \phi_f(t) \) and \( \phi_p(t) \), the second terms describe the repulsive controls from the closest wall. To determine which term is more important for successful collision-free flights, we examine two representative cases of \( \alpha \) and \( \beta \) satisfying \( \beta > \alpha = 1 \) or \( \alpha > \beta = 1 \). Note that \( \alpha \) and \( \beta \) constrain the summations of \( (\alpha_f, \alpha_p) \) and \( (\beta_f, \beta_p) \) as shown in Eqs. (16)–(19). Figure 9 represents the result of numerical simulation on the assumption of \( (\alpha, \beta) = (1, 1.5) \) or \( (1.5, 1) \). Other parameters and initial conditions are fixed as the same values with those of Figs. 5, 6 and 7. The parameter range suitable for the collision-free flight is wider when assuming \( (\alpha, \beta) = (1.5, 1) \) (see left panels of Fig. 9). In contrast, other properties are the similar with the case of \( (\alpha, \beta) = (1, 1) \); an eight-shaped path is consistently observed (see middle panels of Fig. 9); the bat emits pulses along the outer or inner periphery of the flight direction depending on the value of \( \delta \) (see right panels of Fig. 9).
A.  
\[ \alpha = 1, \beta = 1.5 \]

\[ \frac{d\phi_f}{dt} (\phi_p - \phi_f) \]  
for different parameter sets of (\(\alpha, \beta\)) that constrain the summations of (\(\alpha_f, \alpha_p\)) and (\(\beta_f, \beta_p\)), respectively. (A, B) Results of the simulation assuming (\(\alpha, \beta\)) = (1, 1.5) or (1.5, 1). The other parameters and initial conditions are fixed as the same values with those of Figs. 5, 6 and 7. The simulation demonstrates that the parameter range suitable for collision-free flights is wider when assuming (\(\alpha, \beta\)) = (1.5, 1) (see left panels). In contrast, other properties are the similar with the case of (\(\alpha, \beta\)) = (1, 1); an eight-shaped path is consistently observed (see middle panels); the bat emits pulses along the outer or inner periphery of the flight direction depending on the value of \(\delta\) (see right panels).

B.  
\[ \alpha = 1.5, \beta = 1 \]

\[ \frac{d\phi_f}{dt} (\phi_p - \phi_f) \]  

Fig. 9. Numerical simulation of the collision-free flight time, \(\frac{d\phi_f}{dt} / \left| \frac{d\phi}{dt} \right|\) and \(\frac{d\phi_f}{dt} (\phi_p - \phi_f)\) for different parameter sets of (\(\alpha, \beta\)) that constrain the summations of (\(\alpha_f, \alpha_p\)) and (\(\beta_f, \beta_p\)), respectively. (A, B) Results of the simulation assuming (\(\alpha, \beta\)) = (1, 1.5) or (1.5, 1). The other parameters and initial conditions are fixed as the same values with those of Figs. 5, 6 and 7. The simulation demonstrates that the parameter range suitable for collision-free flights is wider when assuming (\(\alpha, \beta\)) = (1.5, 1) (see left panels). In contrast, other properties are the similar with the case of (\(\alpha, \beta\)) = (1, 1); an eight-shaped path is consistently observed (see middle panels); the bat emits pulses along the outer or inner periphery of the flight direction depending on the value of \(\delta\) (see right panels).

4. Laboratory experiment conducted by using a Japanese house bat

We compare the results of the numerical simulation with those of laboratory experiment conducted by using a Japanese house bat [11]. In the experiment, the bat flew freely in the chamber, and the ultrasound pulses emitted by the bat were recorded with a microphone-array system. By analyzing the differences in the sound pressure level between individual microphones, the pulse angles were measured. The flight path of the bat was captured by using two high-speed video cameras operating at a rate of 125 frames per second.

Figure 10 shows two consecutive flight paths of the bat in the horizontal plane. Both paths are eight-shaped, which is consistent with the results of the numerical simulation shown in Figs. 4, 6, 8 and 9. Note that these data were recorded after a bat flew one or two laps in the chamber, respectively.

Figure 11 shows the histogram of \(\frac{d\phi_f}{dt} (\phi_p - \phi_f)\) estimated from the experimental data of Fig. 10. The value of \(\frac{d\phi_f}{dt} (\phi_p - \phi_f)\) was obtained at each pulse-emission time instant. The distribution of positive \(\frac{d\phi_f}{dt} (\phi_p - \phi_f)\) is dominant, indicating that the bat more frequently emitted ultrasound pulses along the inner periphery of its flight direction during the behavioral experiment. As shown in Figs. 7 and 9, such inner-periphery pulse emissions can be observed in the parameter range realizing \(\frac{d\phi_f}{dt} (\phi_p - \phi_f) > 0\)
5. Discussion

In this study, a mathematical model is proposed to describe the flight and pulse-emission dynamics of an echolocating bat during free flight in a space enclosed by obstacle walls. To theoretically examine the performance of collision avoidance flight, we first focus on the parameters $\gamma$ and $\delta$ representing the usage ratios of $(\alpha_f, \alpha_p)$ and $(\beta_f, \beta_p)$ by constraining the summation of each parameter set as 1. The parameters $(\alpha_f, \alpha_p)$ weight the interactive controls between $\phi_f(t)$ and $\phi_p(t)$ (see Eqs. (10) and (11)), and the parameters $(\beta_f, \beta_p)$ weight the repulsive controls of $\phi_f(t)$ and $\phi_p(t)$ from the closest wall (see Eqs. (12) and (13)). Our numerical simulation demonstrates that a bat flying along an eight-shaped path succeeds in avoiding collisions with the walls when the parameters $\gamma$ and $\delta$ are in the ranges of $0 \leq \gamma \leq 1$ and $0.35 < \delta < 0.65$, respectively (see Figs. 5 and 6); the simulation also shows that pulse emission along the inner periphery of the path is consistently observed in the region of $0 \leq \gamma \leq 1$ and $0.35 < \delta < 0.5$ (see Fig. 7). Furthermore, our behavioral experiment revealed that a Japanese house bat flew without collision along an eight-shaped path, and also revealed that the
Fig. 11. Experimental data on the distribution of $\frac{d\phi_f}{dt}(\phi_p - \phi_f)$. This histogram was obtained from the two consecutive flights shown in Fig. 10. The histogram demonstrates that the distribution of positive $\frac{d\phi_f}{dt}(\phi_p - \phi_f)$ is dominant, indicating that the bat more frequently emitted ultrasound pulses along the inner periphery of its flight direction during this behavioral experiment.

Bat more frequently emitted pulses along the inner periphery of its flight direction (see Figs. 10 and 11) [11]. Consequently, both of the eight-shaped flight paths and the inner-periphery pulse emissions are qualitatively explained by the present model with specific parameter ranges of $0 \leq \gamma \leq 1$ and $0.35 < \delta < 0.5$ under the constraint of $(\alpha, \beta) = (1, 1)$ (see Eqs. (16)–(19)). This consistency indicates that control of $\delta$ (i.e., $\beta_f$ and $\beta_p$) is crucial for the collision avoidance in this model, and also suggests that the bat’s successful flight can be understood as the optimization of these parameter values. To confirm the robustness of these results, we conduct additional simulations by changing the flight velocity $v$, the initial conditions $(\phi_f(t=0), \phi_p(t=0))$, and the parameters $(\alpha, \beta)$. The simulations demonstrate that an eight-shaped path is consistently observed (see Figs. 8 and 9), and also demonstrate that the value of $\alpha$ weighting the first terms in the right sides of Eqs. (2) and (3) needs to be larger for increasing the suitable parameter range of successful collision-free flights (see Fig. 9).

In our mathematical model, the conditions of Eqs. (12) and (13) assume that a bat adaptively controls its behavioral parameters depending on the size of the flight chamber, because Eqs. (12) and (13) are rewritten as $G_f(r_w(t)) = D_w/\beta_f r_w(t)$ and $G_p(r_w(t)) = D_w/\beta_p r_w(t)$ where $D_w$ is a parameter describing the size of the flight chamber, i.e., $D_w = L_x$ or $L_y$. This assumption is partially supported by behavioral experiments demonstrating that a bat can adapt its behavioral parameters (e.g., flight velocity and inter-pulse interval) to different sizes of their flight spaces [13].

On the other hand, we define $F_f(\phi_p(t) - \phi_f(t))$, $F_p(\phi_f(t) - \phi_p(t))$, $G_f(r_w(t))$, $G_p(r_w(t))$, $H_f(\phi_w(t) - \phi_f(t))$, and $H_p(\phi_w(t) - \phi_p(t))$ of Eqs. (2) and (3) as satisfying the conditions mentioned in Sec.2.1. Numerical simulation then shows that the present model qualitatively explains the experimental results. However, there are many variations in these functions such as linear functions and various types of nonlinear functions. Our future plans include the estimations of these functions from experimental data. In particular, field experiments demonstrate that hunting strategies of echolocating bats including acoustic properties of ultrasounds and flight velocities are considerably diverse depending on species and their habitats (e.g., forests, caves and open-spaces) [14]. By comparing the model func-
Fig. 12. Numerical simulation of the collision-free flight time of the bat, when assuming Eqs. (23) and (24) instead of Eqs. (12) and (13). The parameters and initial conditions are fixed as the same values with those used in the simulation shown in Figs. 5, 6, and 7. The result of the simulation indicates that the bat always collides with a wall within 3 s of flight time, showing that the collision-free flight cannot be consistently achieved under these conditions. Therefore, the assumption of normalized distances is necessary for the present model to qualitatively explain the successful collision-free flight observed during the behavioral experiment.

The parameters estimated from various experiments, we would be able to mathematically examine the differences of their echolocation and flight strategies.

In the present model, we assume that the bat pays its attention to the closest wall by comparing the normalized distances of \( r_w(t) / D_w \). To examine whether this assumption is necessary for explaining the collision-free flights of a bat, additional simulation is conducted. Figure 12 represents the collision-free flight time when neglecting the effect of the normalized distances by replacing \( G_f(r_w(t)) \) and \( G_p(r_w(t)) \) of Eqs. (12) and (13) with the following functions, respectively:

\[
G_f(r_w(t)) = \frac{\beta_f}{r_w(t)}, \tag{23}
\]

\[
G_p(r_w(t)) = \frac{\beta_p}{r_w(t)}. \tag{24}
\]

The parameters and initial conditions are fixed as the same values with those used in Figs. 5, 6, and 7. The simulation with these functions shows that a bat always collides with a wall within 3 s (see Fig. 12). This result indicates that the assumption of normalized distances is necessary to qualitatively explain the successful collision avoidance observed during the behavioral experiment, because the model with the functions of Eqs. (12) and (13) assumes that the bat knows \( L_x \) and \( L_y \) in advance and can use them to calculate the normalized distances. Comparison of the two cases with and without the calculation of the normalized distances is suggestive. The calculation of the normalized distances is likely to make it possible for the bat to recognize every wall with similar frequencies. To maximize the success rate of collision avoidance, it would be important for the bat to design its flight path by using the information of multiple obstacles. This speculation is partially supported by our behavioral experiments using more obstacles in the flight chamber [11]; namely, bats tend to emit pulses towards several obstacles during collision avoidance. However, the validity of the assumption about the normalized distances should be further examined both theoretically and experimentally, because the bat may not perform such normalization.

On the other hand, Japanese house bats sometimes flew with circular paths in a laboratory cham-
Fig. 13. Numerical simulation of a stable flight path observed in the present model of Eqs. (1)–(3) and (10)–(15), when assuming a square-shaped flight chamber described by $L_x = L_y = 7$ m. The other parameters and initial conditions are fixed as the same values with those of Fig. 4. A circular flight path is observed at this specific condition. However, a circular path is not observed when assuming $(L_x, L_y) = (7, 3)$ that is consistent with the size of an actual chamber (see Figs. 5, 6, 8 and 9).

To explain the occurrence of such circular paths based on the present model of Eqs. (1)–(3) and (10)–(15), we need to assume a square-shaped chamber as shown in Fig. 13. While various theoretical problems still remain including bifurcation analysis of the changes between circular and eight-shaped paths by varying the chamber size, further modification of the model may be required. For example, the acoustic dynamics of the pulse emissions can be taken into consideration for the modification of the model. It is well known that echolocating bats actively vary inter-pulse intervals depending on their distances from the objects such as obstacles and prey [6]; namely, the bats emit pulses more frequently when approaching objects. Based on such dynamic control of the spatial and temporal sampling period of acoustical sensing accompanied with flight speed, bats can sense surrounding objects located at different distances and angles. The extension of the present model based on such pulse-emission dynamics may explain the variety of observed flight paths. Because bats consume energy when flying with emitting pulses, efficient control of their flight and acoustic directions is important from the viewpoint of minimum energy loss and high-performance navigation.

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