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Importance of body rotation during the flight of a butterfly

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In nature the body motion of a butterfly is clearly observed to involve periodic rotation and varied flight modes. The maneuvers of a butterfly in flight are unique. Based on the flight motion of butterflies (*Kallima inachus*) recorded in free flight, a numerical model of a butterfly is created to study how its flight relates to body pose; the body motion in a simulation is prescribed and tested with varied initial body angle and rotational amplitude. A butterfly rotates its body to control the direction of the vortex rings generated during flapping flight; the flight modes are found to be closely related to the body motion of a butterfly. When the initial body angle increases, the forward displacement decreases, but the upward displacement increases within a stroke. With increased rotational amplitudes, the jet flows generated by a butterfly eject more downward and further enhance the generation of upward force, according to which a butterfly executes a vertical *jump* at the end of the downstroke. During this jumping stage, the air relative to the butterfly is moving downward; the butterfly pitches up its body to be parallel to the flow and to decrease the projected area so as to avoid further downward force generated. Our results indicate the importance of the body motion of a butterfly in flight. The inspiration of flight controlled with body motion from the flight of a butterfly might yield an alternative way to control future flight vehicles.

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I. INTRODUCTION

Insects are the most ancient flyers alive; they have evolved with a sophisticated flying structure and flight performance that adapts to their environments. Rapidly flapping their wings in the air, insects fly with complicated aerodynamic interactions and enhance their flight performance with several transient flight mechanisms. The prospective benefits of flapping wings may inspire ways to create and to design a microscale aerial vehicle (MAV) with effective maneuverability. A MAV refers to a flying machine with a limited wing span and flight speed, and is suitable for special tasks such as surveillance, rescue, or flying in a limited space [1]. Mechanically mimicking the flight dynamic of an insect is challenging; the power density of a current man-made actuator is limited, and such a large flapping frequency with a size as tiny as an insect body is difficult to achieve; operating with flapping at a large frequency could lead to fracture of a mechanical structure and the wings of the vehicles. Flyers with a small flapping frequency thus become a more nearly ideal model for the design of a MAV. Understanding the mechanism of flight and the maneuvering tactics of an insect with a small flapping frequency might yield valuable insight into creating future flight vehicles for human beings.

Among flying insects, butterflies fly with a small flapping frequency and great maneuverability. The flapping frequency of butterflies is only about 10 Hz, or perhaps even smaller in some larger subjects [2]. A butterfly enhances its flight performance in nature with manifold salient flight features, for example, wake capture, a *clap-and-fling* mechanism, and leading-edge vortices (LEVs) [3]. The wings of a butterfly are structurally flexible, which enhances the efficiency of its lift production [4] and the stability of its flight [5]. When a butterfly flaps with broad wings, the pressure generated instantaneously at the forewing tip is ten times that of the wing loading, which empowers it with an ability to alter its flight direction in a few flapping cycles [6]. In nature, butterflies perform with great maneuverability, flying with an unpredictable flight trajectory from predators [7]. A phenomenon observed in real flight is that many butterflies fly with an oscillatory body motion [8]. Unlike most insects that fly with a constant body angle, a butterfly rotates its body periodically. Assaying the flight of a hawk moth tethered in a variable-speed wind tunnel, Ellington *et al.* [9] claimed that, for most insects, the body angle altered only when they intended to alter their flight speed, for example, from hovering to forward flight; the body angle was greater when an insect was hovering, and gradually decreased when the forward speed increased, even though the sample was constrained and vertical translation was excluded from their experiment. The alteration of the body angle might also produce a variation of the vertical speed. The body motion of a butterfly is transient and rotates continually, even when it is in the same flight mode. A small bird was observed to have a similar body mechanism during hovering [10]; it periodically opens its tail to capture the downward flow generated by the wings. The flow acting on the tail yields the recovering torque of the bird and stabilizes its vision during hovering, but a butterfly controls its body angle differently: It actively folds its abdomen and transfers the moment to the thorax, which produces an additional torque of the butterfly's body, and a deviation of the body angle and stroke plane. Theoretically investigating a butterfly taking off, Sunada *et al.* [11] noted that a butterfly alters its body angle with the moment generated by aerodynamic forces and abdominal motion, and produces an inclination of the stroke plane. A butterfly flaps its wings downward or backward by the rotation of the body, and generates the resultant aerodynamic forces into usable directions. Their concept offers a basic explanation of the effect of the body motion of a butterfly, but the discussion was based on the motion of butterfly in takeoff; detailed discussion of the connection between the flight modes and the body motion was thus lacking from their investigation. Recently authors have investigated the flight

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dynamics of butterflies in free flight [12,13]; controlling the mass and the length of the abdomen of a butterfly, the authors of both papers stated that the body angle and the abdominal motion are essential for the stability of the butterfly's flight. Clarifying a relation between the body motion and the flight mode of a butterfly is essential to revealing the flight maneuver. Various body motions of a butterfly are observed when it performs flight modes of varied types; a butterfly is believed to be able consciously to manipulate its body motion to achieve varied flight modes, but preceding authors focused more on the discussion of a specific flight mode, especially hovering, forward flight, and ascent; the translation in these motions is constrained to only one degree of freedom (1 dof) or even neglected. Also, the wing and body kinematics were measured from the flight of butterflies fixed or tethered in a wind tunnel; the behaviors of a butterfly—such as transient flight speed, and wing and body kinematics—under those conditions might differ from those of an insect in free flight [12–14]. The flight translation of a butterfly in multiple directions is rarely discussed, leaving unclear our understanding of the flight maneuver strategy.

The aim of this work is to investigate the flight maneuverability of a butterfly in relation to its body posture in a transient condition. Because the variation of the flight speed of a butterfly is larger than that of other insects, the flight dynamics of a butterfly are less stable, which makes difficult the analysis of its flight maneuver. To investigate precisely the flight dynamics of a butterfly, including the transient translation, in a discussion of butterfly flight is essential [15]; we thus created a numerical model of a butterfly based on the wing and body kinematics recorded from butterflies in free flight. In a simulation model with transient vertical and horizontal translations, a butterfly is able to move freely in the air. The flow field, flight trajectory, and flight mode of a butterfly with varied body posture are compared and discussed at length in the following sections. How does a butterfly manipulate the motion of its body to achieve various flight modes? On the basis of the simulation results, we answer that question; the implications might provide a scheme to control the flight of future MAVs with a small flapping frequency.

II. METHOD

A. Measurement of wing and body kinematics of a butterfly in real forward flight

Most of the authors of previous works recorded the wing kinematics of butterflies with an insect tethered in a wind tunnel; the transient flight speed was neglected and the behavior recorded from their method might differ from that of an insect in free flight. We therefore recorded experimentally the wing and body motions and transient speeds of butterflies during free flight; a similar method of measurement was applied in our preceding work [15–17]. Fourteen leaf butterflies (*Kallima inachus*) were captured within our campus and fed with fruit in the laboratory. The motion and postures of the Indian leaf butterfly were characterized and analyzed during flight in a transparent experimental chamber ($70 \times 50 \times 70\,\mathrm{cm}^3$). The wings and body motion of a butterfly were recorded with two synchronized high-speed cameras (Phantom v7.3 and Phantom v310). The cameras were aligned orthogonally and operated at 1000 frames per second with pixel resolution 1024 × 1024. In free flight, the wing and body kinematics varied with the flight mode of a butterfly. Because recording the precise forward flight of a butterfly in the laboratory experiment is difficult, we redefined the forward flight as when the ratio between the vertical translation and horizontal translation within a cycle is smaller than 0.2. The wing and body kinematics of 40 individual flight cycles that butterflies executed in forward flight were recreated with our programs (developed in house in MATLAB).

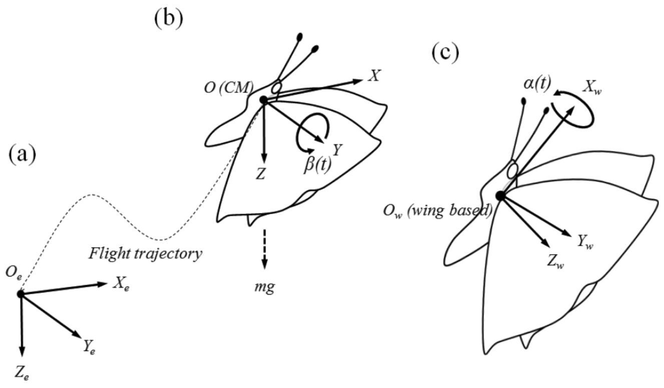

FIG. 1. Coordinate systems to describe the motion of a butterfly in flight. The butterfly body rotates along axis Y and the wing flaps along axis X_w.

B. Definition of coordinate systems and the flight motion

Three coordinate systems were adopted to describe the wing and body kinematics of a butterfly in free flight. The relations among the coordinate systems used in this work are shown in Fig. 1. First, the global coordinate system ($X_e Y_e Z_e$) is a Cartesian system fixed in the laboratory [Fig. 1(a)]; Z_e is the same as the direction of gravitational force and is defined positive downward. Second, the coordinate (XYZ) translates parallel to the global coordinate system, with the origin at the center of mass of the butterfly (CM) set at the midpoint between the two wings [18] [Fig. 1(b)]. Third, the coordinate system ($X_w Y_w Z_w$) is attached to the base of the wing that rotates and translates with the butterfly body [Fig. 1(c)].

Figure 2 shows the wing and body kinematics of a butterfly recorded from the forward flight. The flight motions of a butterfly couple mainly with the rotation of the body and the flapping of the wings; two parameters serve to describe these two motions—flapping angle $\alpha(t)$ and body angle $\beta(t)$, respectively. The body angle is the rotation of the body along axis Y; the body angle is considered to be the angle between the center line of the thorax and the horizontal plane [Fig. 1(b)]. The body angle is 90° when the butterfly body is vertical and 0° when horizontal. The wings of a butterfly rotate about axis X_w. The butterfly's wings clap together at the beginning of a downstroke; the flapping angle is thus defined as 0° at this time, and increases when the wings open. In Fig. 2, T is the flapping period; t/T is normalized time. The line with squares denotes the flapping angle of wings, $\alpha(t)$; the line with circles denotes the body angle of the body, $\beta(t)$. The error bars in

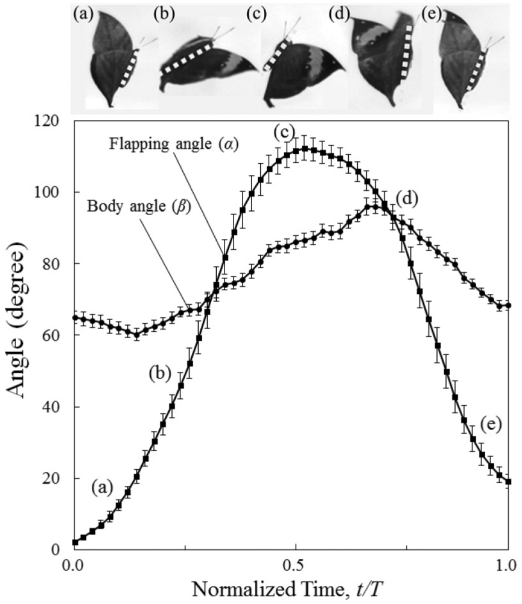

FIG. 2. Wing and body kinematics of butterflies recorded in free flight.

the figure are means of the standard deviation (SEM). In the real flight of a butterfly, the flight motion is transient and uncontrollable, which leads to the wings and body kinematics being not exactly periodic functions. The rotational motion of a wing along axes Y_w and Z_w, respectively, however, is smaller than the flapping and body angles in a butterfly flight. These minor wing kinematics that we recorded fluctuated in separate observations and had large standard deviations; these angles can hence not be identified from the free-flight experiment. The effects of these two angles were hence neglected in the simulation model. The wing and body motions recorded from experiment were input into the simulation; the flight speed calculated from the simulation was then verified with the flight speed recorded from experiment.

C. Simulation model of a butterfly in transient flight

During experimental observation, the body motion of a butterfly was found to vary with the flight mode; experimental analysis of the relation between the flight mode and the body posture was, however, difficult as we were unable to mandate a butterfly to fly in a specific flight mode in the laboratory. To investigate the connection between the body dynamics and the flight modes of butterflies, we created a simulation model of a butterfly in flight to investigate the complicated behavior. A similar numerical model was established in our preceding work [15], which focused on a discussion of the interaction between the transient flight speed and the wing motion of a butterfly in forward flight, neglecting the vertical translation. In this work, we improved the model by including both vertical and horizontal translations in the simulation, which is more similar to the natural flight of a butterfly. We created a physical model of a butterfly in the simulation based on the real size of a leaf butterfly with average wing span (S) 6.2 cm and mass (m) 0.40 g. The fore and hind wings moved simultaneously during flight and were simplified as one broad wing; the thorax and abdomen of butterflies were simplified as one body. The wings and body were considered to act as rigid bodies in the simulation. The butterfly in the model was bounded with air in a large cylinder divided into a tetrahedral grid with total mesh number 5×10^7; the boundaries of the cylinder were set as pressure outlets (Fig. 3). The flow field was calculated numerically with commercial software (ANSYS FLUENT 14.5). The governing equations of the flow field include the incompressible continuity equation and the Navier-Stokes equation, expressed as

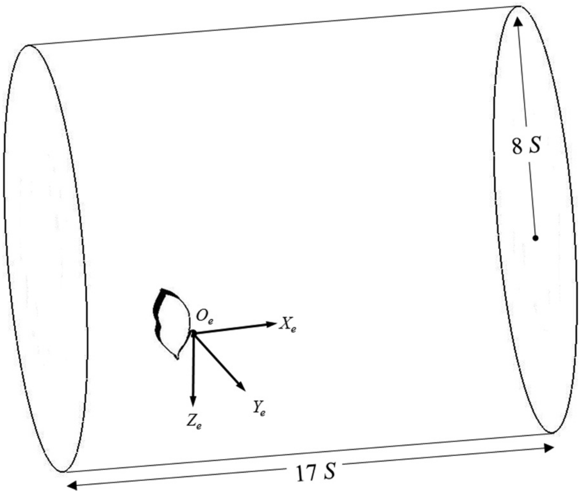

FIG. 3. Physical model of a butterfly in flight; S in the figure denotes the wing span of a butterfly.

$$\nabla \cdot \mathbf{u} = 0, \tag{1}$$

$$\rho_f \frac{D\mathbf{u}}{Dt} = -\nabla p + \mu \nabla^2 \mathbf{u} + \mathbf{f}, \tag{2}$$

in which t denotes time, $\mathbf{u}$ velocity vector, $\mathbf{f}$ body force vector, and p pressure; for air at 25 °C, density $\rho_f = 1.225\,\mathrm{kg\,m^{-3}}$, and viscosity $\mu = 1.789 \times 10^{-5}\,\mathrm{kg\,m^{-1}\,s^{-1}}$. The flow solver was set as laminar based on a finite-volume method; a semi-implicit method for a pressure-linked equation (SIMPLE) with a second-order upwind scheme was applied to solve Eqs. (1) and (2). A flapping cycle was divided into 400 time steps in the calculation. A local remeshing skill was adopted for the moving surface of a butterfly during a simulation.

D. Wings and body kinematics of a butterfly

Figure 4 shows the variations of the flapping and body angles of a butterfly in the simulation. Two trigonometric functions [Eqs. (3) and (4)] that served to approach the two angles recorded from experiment are expressed as

$$a(t) = \frac{A_f}{2} - \frac{A_f}{2}\cos(2\pi f t), \tag{3}$$

$$\beta(t) = \beta_0 - \Delta\beta \sin(2\pi f t), \tag{4}$$

in which A_f is the stroke amplitude of the flapping angle; $\Delta\beta$ is the rotational amplitude of the body angle, and β_0 is the initial body angle of a butterfly body; f is the flapping and rotating frequency of the butterfly. In the simulation, we

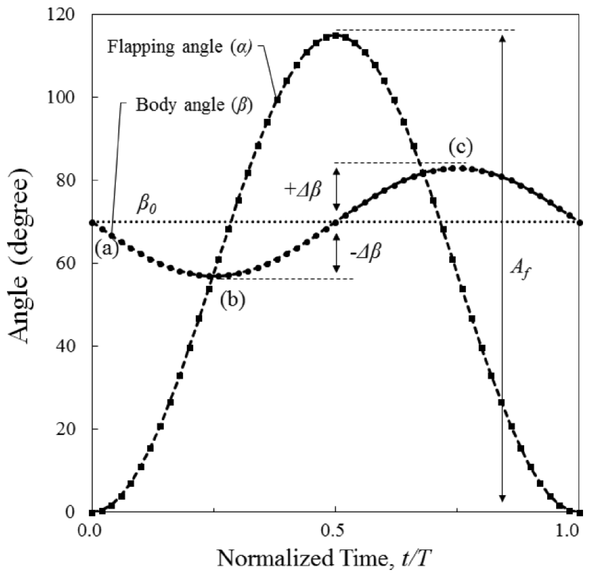

FIG. 4. Flight kinematics, flapping angle $\alpha(t)$, and body angle $\beta(t)$ of a butterfly in the simulation.

used 10 Hz to represent the flapping frequency of this species, which is slightly smaller than the average flapping frequency recorded from the experiment, 10.79 Hz. A flapping cycle is divisible into four stages: $t/T = 0$–0.25 is the first half of the downstroke, $t/T = 0.25$–0.50 is the second half of the downstroke, $t/T = 0.50$–0.75 is the first half of the upstroke, and $t/T = 0.75$–1.00 is the second half of the upstroke (Fig. 4). The flapping angle was set the same for all simulation cases with stroke amplitude 115°, as in this work we focus on the effect of the rotational motion of the body on the flight of a butterfly; two parameters of the body—initial body angle β_0 and rotational amplitude $\Delta\beta$—were controlled with varied values in the simulation. The initial body angle is defined as the angle between the body and the horizon at the beginning of the stroke [Fig. 5(a)]. The body would oscillate symmetrically between the initial body angle with amplitude $\Delta\beta$: The body attains a minimum $\beta_0 - \Delta\beta$ at $t/T = 0.25$ and a maximum $\beta_0 + \Delta\beta$ at $t/T = 0.75$ [Figs. 5(b) and 5(c)]. In the simulation, the initial body angle was tested from 70° to 90°, and the rotational amplitude of the body was tested from 25° to 40°; the body rotates slightly with a small rotational amplitude, and the rotation becomes evident when the rotational amplitude increases. The rotation of the body leads to the plane of the wing stroke inclining periodically during a butterfly flight.

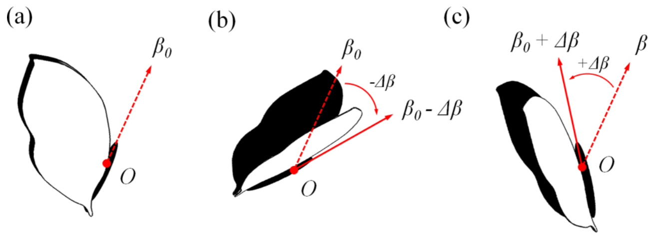

FIG. 5. Definitions of initial body angle and rotational amplitude; the motions in (a–c) refer to the posture at the instant labeled in Fig. 4.

The fore and hind quarters of a butterfly are held together during the flight; also, the wings partly overlap onto their body. Unlike for many other insects that rotate their wings relative to the flow by feathering [19], the wing base of a butterfly can hardly perform a feathering motion due to its structure [7,20]. The flight of a butterfly in our current model is considered based on a body rotation. The elevation angle was also neglected in this model as it leads to the tail of the wings touching each other, which creates a problem during a simulation. In considering the wing area to be constant, the elevation angle has, however, little effect on the generation of aerodynamic forces, but has a great influence on the generation of aerodynamic torque [unpublished results]. Even the elevation angle is thus neglected; flight trajectories presented in this work are precise because the body motion is prescribed.

The coordinate system used is described in Fig. 1. The coordinate (XYZ) translates parallel to the global coordinate system. The relation between two coordinates is expressed as

$$\begin{bmatrix} X \\ Y \\ Z \end{bmatrix} = \begin{bmatrix} X_e \\ Y_e \\ Z_e \end{bmatrix} + \begin{bmatrix} \Delta x \\ 0 \\ \Delta z \end{bmatrix}, \tag{5}$$

in which Δx and Δz are the horizontal and vertical translations, respectively. The displacement in the lateral direction was neglected in the simulation model. Two coordinates are the same at the beginning of flight as the translation is zero. More details about the calculation of the position and translations of the butterfly appear in the next section. The body rotates about axis Y by the body angle; the wing then rotates about axis X_w by the flapping angle. Therefore, the wing axis angular rates are based on the frame (XYZ) and are calculated by successive rotations, and are expressed as

$$\begin{aligned} \Omega_X &= \dot{\alpha}(t)\cos\beta(t), \\ \Omega_Y &= \dot{\beta}(t), \\ \Omega_Z &= -\dot{\alpha}(t)\sin\beta(t), \end{aligned} \tag{6}$$

in which $\dot{\alpha}(t)$ and $\dot{\beta}(t)$ are the angular velocities of $\alpha(t)$ and $\beta(t)$. This transformation is based on the coordinate of the right wing; the motion of the left wing was treated with the same procedure but with $-\alpha(t)$ in Eq. (6), as the direction of rotation is opposite that of the right wing. According to this process, the body angle and flapping angle are transferred to three angular velocities; the flight motion is then readily described with these three components in the simulation. The flight motion in the simulation is in accordance with the real flight of a butterfly, as shown in our video in the Supplemental Material [21].

E. Calculation of transient flight speeds

With broad wings and a small flapping frequency, a butterfly flies with an inconstant speed and an erratic trajectory. The speed of the butterfly relative to the surrounding fluid is transient and varies with direction; including the transient translation in the discussion is hence necessary in an investigation of the real flight of a butterfly. A two-way coupling of fluid and rigid dynamics of a butterfly was applied to determine the transient flight speed and CM of a butterfly in the simulation.

The flight speed and position of a butterfly were updated at each time step. The flight speed of a butterfly was calculated as follows. We first integrated the aerodynamic forces acting on a butterfly. The total force $\mathbf{F}_{\mathbf{total}}$ is contributed by pressure force $\mathbf{F}_{\mathbf{P}}$ and viscous force $\mathbf{F}_{\mathbf{v}}$ acting on the surface of the butterfly. The pressure force is normal to the surface of a butterfly; viscous force is the tangential force on the surface. Two forces are obtained by summation over the cells on the butterfly surfaces,

$$\mathbf{F}_{\mathbf{total}} = \mathbf{F}_{\mathbf{p}} + \mathbf{F}_{\mathbf{v}} = -\sum_{i=1}^{N} p_i \mathbf{n}_i \Delta s_i + \sum_{i=1}^{N} \tau_{\mathbf{w},i}\ \Delta s_i, \qquad (7)$$

in which p_i and $\tau_{\mathbf{w},i}$ are the pressure and the wall shear vector at the ith cell center; N is the total number of cells on the butterfly surface; Δs_i is the area of the ith cell; $\mathbf{n}_i$ is the normal vector of the ith cell. The wall shear stress is defined by the normal velocity gradient at the wall in a laminar flow. Both the p and $\tau_{\mathbf{w}}$ vary around the surfaces of the butterfly. The total force is decomposable further into vertical and horizontal directions, and becomes expressed as

$$\mathbf{F}_{\mathbf{total}} = F_H \mathbf{i} + F_V \mathbf{k}, \qquad (8)$$

where $\mathbf{i}$ and $\mathbf{k}$ are unit vectors in directions X_e and Z_e; F_H is the magnitude of horizontal force; F_V is the magnitude of vertical force. As the geometry and flight motion of the butterfly is symmetrical to plane XZ, the lateral forces in direction Y cancel and are neglected. The acceleration vector of the butterfly was calculated according to Newton's second law as

$$\mathbf{a} = a_X \mathbf{i} + a_Z \mathbf{k} = \left(\frac{F_H}{m}\right)\mathbf{i} + \left(\frac{F_V}{m} + g\right)\mathbf{k}, \qquad (9)$$

in which g is the acceleration of gravity; a_x and a_z are the magnitudes of horizontal and vertical acceleration of a butterfly. The velocity vector of the insect is an integral of the acceleration:

$$\mathbf{U} = V_X \mathbf{i} + V_Z \mathbf{k} = \left(\int_0^t a_x dt\right)\mathbf{i} + \left(\int_0^t a_z dt\right)\mathbf{k}. \qquad (10)$$

From the definition of the global coordinate system, V_x is the forward flight speed and $-V_Z$ is the upward flight speed. The flight speed of a butterfly was set as stationary at the beginning of the calculation, and gradually affected by the gravity force, wing motion, and body motion. The flight speed was calculated with Eq. (10) in each time step and was then returned to the solver for the calculation of the next time step. The CM and flight speed of a butterfly are obtained according to this calculation; a butterfly can move freely on plane $X_e Z_e$. The above physical functions were then programmed in language C and linked to the solver FLUENT.

III. RESULTS AND DISCUSSION

A. Comparison of flight in simulation and experiment

Figure 6(a) indicates the variation of upward and forward flight speeds in the free-flight simulation with initial body angle 70° and rotational amplitude 27°; the butterfly with this motion can perform forward flight in the simulation. At the beginning of the flight, the mean forward speed is small and the net negative horizontal force is smaller than the positive horizontal force generated by a butterfly. The forward speed gradually increases through the motion of the butterfly. After the flight speed increases, the negative horizontal force and positive horizontal force acting on the butterfly are balanced; the flight speed becomes periodic after a few strokes [Fig. 6(a)]. The butterfly is unable to generate sufficient upward force against gravity at the beginning of a flight ($t/T = 0$–2); the elevation of the butterfly decreases slightly during this period. When the forward speed gradually increases, the generation of upward force is enhanced by the flight speed and is able to support the body weight of the butterfly in the succeeding strokes. The upward force and the gravity force are balanced—the butterfly flies almost horizontally. Flying with broad wings, butterflies beginning from a stationary condition can attain a stable flight within five flapping strokes.

To verify the accuracy of our simulation model, we further compared the flight speeds in the simulation and in the experimental record of a butterfly in forward flight. Figure 6(b)

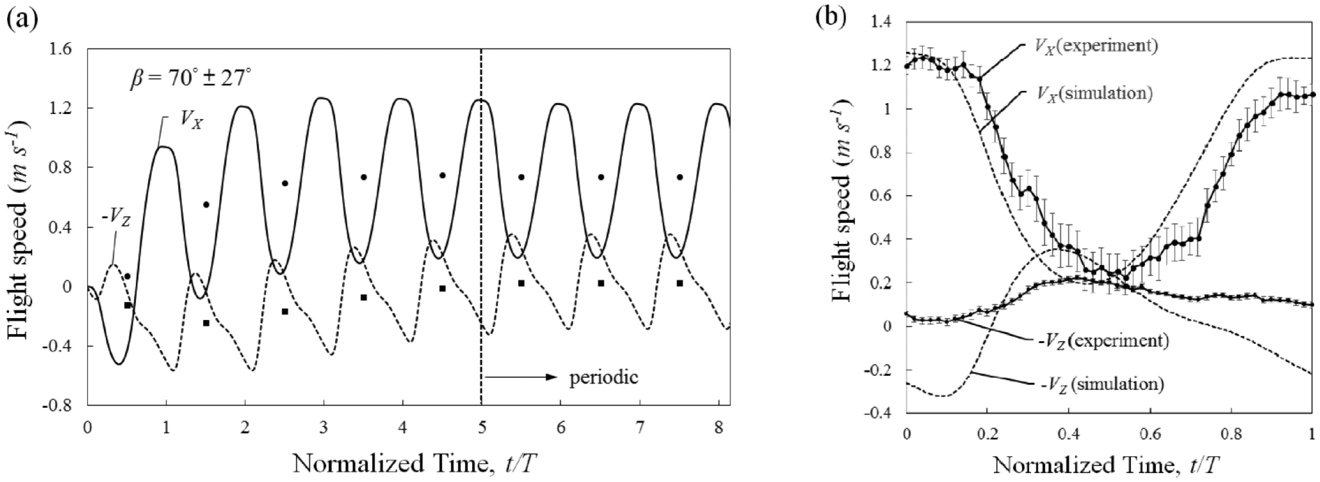

FIG. 6. (a) Upward and forward speeds of a butterfly in forward flight tested in a free-flight simulation. The butterfly can perform forward flight with the body motion, $\beta = 70^\circ \pm 27^\circ$. (The circles and squares are the mean forward speed and upward speed within a cycle.) (b) Comparison of flight speeds of a butterfly in forward flight between simulation and real flight.

TABLE I. Comparison between simulation and experiment for a butterfly in forward flight.

	Simulation	Experiment (averaged ± SEM)
Flight mode	Forward flight	Forward flight
Mass of butterfly	0.40 g	0.40 ± 0.06 g
Flapping frequency	10.00 Hz	10.79 ± 0.25 Hz
Stroke amplitude	115.0°	115.2° ± 3.4°
Initial body angle	70.0°	68.4° ± 1.8°
Rotational amplitude	27.0°	18.9° ± 2.7°
Average forward speed	$0.74\,\mathrm{m\,s^{-1}}$	$0.72 \pm 0.06\,\mathrm{m\,s^{-1}}$
Average upward speed	$0.03\,\mathrm{m\,s^{-1}}$	$0.13 \pm 0.01\,\mathrm{m\,s^{-1}}$

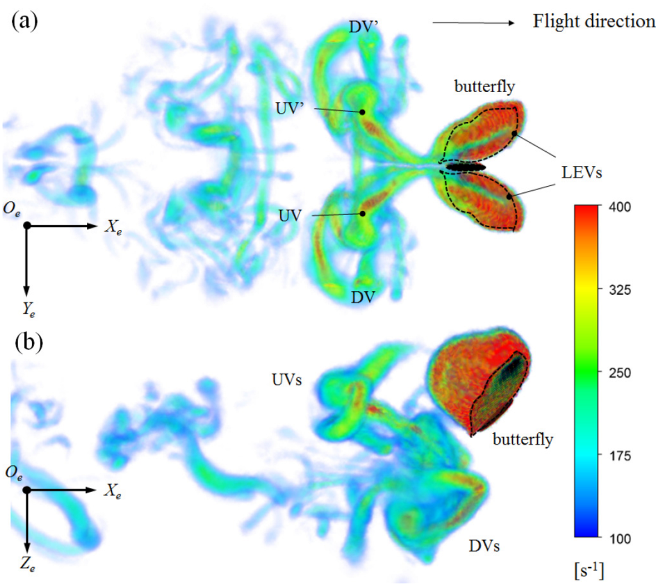

FIG. 7. Vorticity magnitude for the butterfly in forward flight from (a) top view and (b) side view. In the figures, DV and DV′ refer to downstroke vortex rings; UV and UV′ refer to upstroke vortex rings.

shows the upward ($-V_Z$) and forward flight (V_X) speeds in experiment and simulation; these curves of flight speeds are similar. The mean forward speed in the simulation is $0.74\,\mathrm{m\,s^{-1}}$, almost the same as that recorded in experiment, $0.72\,\mathrm{m\,s^{-1}}$. In contrast, the variation of the upward speed in the simulation model is slightly smaller than that recorded in the experiment; the mean upward speeds in the simulation and experiment are 0.03 and $0.13\,\mathrm{m\,s^{-1}}$. Table I summarizes the flight and physical parameters in simulation and for a real butterfly. To perform forward flight in the simulation, the rotational amplitude is 27°, slightly larger than that recorded in the experiment. Possible reasons include that the flapping frequency (10 Hz) of a butterfly in the simulation model is slightly less than the flapping frequency of the real butterfly (10.79 Hz); also, the wings of the current model were considered rigid and the feathering motion was neglected. A butterfly thus increased the rotational amplitude in the simulation to generate a greater upward force so as to be able to support its body weight. Overall, the simulation model is consistent with the experimental data, which indicates that the simulation model can accurately reflect the flight of a real butterfly in nature.

Figure 7 indicates the vorticity magnitude generated by a butterfly in forward flight in the simulation; the butterfly translates by successively generating vortex rings into the wake. The forward speed has a maximum value of $1.2\,\mathrm{m\,s^{-1}}$ at the beginning of a downstroke. The leading-edge vortices (LEVs) attach to the surface of the upper wings at the beginning of this stroke and can create a low pressure on the upper wing surface, which yields a large pressure difference between the upper and lower wing surfaces [22]. Butterflies generate an upward force and a backward force during this period; the forward speed decreases to a minimum of $0.2\,\mathrm{m\,s^{-1}}$, and the upward speed gradually increases to a maximum of about $0.40\,\mathrm{m\,s^{-1}}$ during the middle of the stroke. The body motion begins to recover from the least point after $t/T = 0.25$; the vortices gradually shed from the wings and form two separate vortex rings (DV and DV′) individually beneath the butterfly (Fig. 7). During the upstroke, the wings and body move backward; vortices are generated at the opposite surfaces of the wings. The body becomes vertical and the wings clap together at the end of the stroke; the two vortex rings (UV and UV′) merge and form an intense vortex structure behind the butterfly. The butterfly is thus pushed forward by the backward jet; the forward speed attains a maximum at the end of the upstroke. During that upstroke, the butterfly generates scarcely any vertical force; the upward speed then decreases to a negative value with the body force at the end of the upstroke.

B. Flight trajectories and body rotational motion

Because the flight speed has large variations, the flight trajectory of a butterfly is erratic and difficult to define. To characterize the flight modes of a butterfly, we quantified the four types of flight modes of that were observed in the free flight of butterflies as forward flight, oblique flight, vertical flight, and falling. First, when the forward translation is appreciably larger than the vertical translation ($-\Delta z/\Delta x < 0.2$), the flight motion is treated as *forward flight*. Second, when the forward and upward translations are comparable ($0.2 < -\Delta z/\Delta x < 5.0$), the flight mode is defined as *oblique flight*. When the upward translation is significantly larger than the forward translation ($-\Delta z/\Delta x > 5.0$), the flight motion is defined as *vertical flight*. When the butterfly moves downward and cannot maintain its altitude, the flight motion is defined as *falling*.

Figure 8 shows the flight trajectories of a butterfly in relation to varied initial body angles (β_0) and rotational amplitudes ($\Delta\beta$) within a cycle after the flight speeds become periodic. The four regions in the figure correlate with the various flight modes defined above. When the initial body angle is 70° [Fig. 8(a)] the horizontal displacements of five cases are almost the same, about 0.070 m, which indicates that the rotational amplitude has little effect on the horizontal translation. In contrast, the upward displacement is much affected by the rotational amplitude. For a small rotational amplitude ($\Delta\beta = 25°$), the upward force generation cannot support the weight; the butterfly in its flight trajectory descends. When the rotational amplitude increases slightly to 27°, the upward force generated is almost equal to the body weight; the net

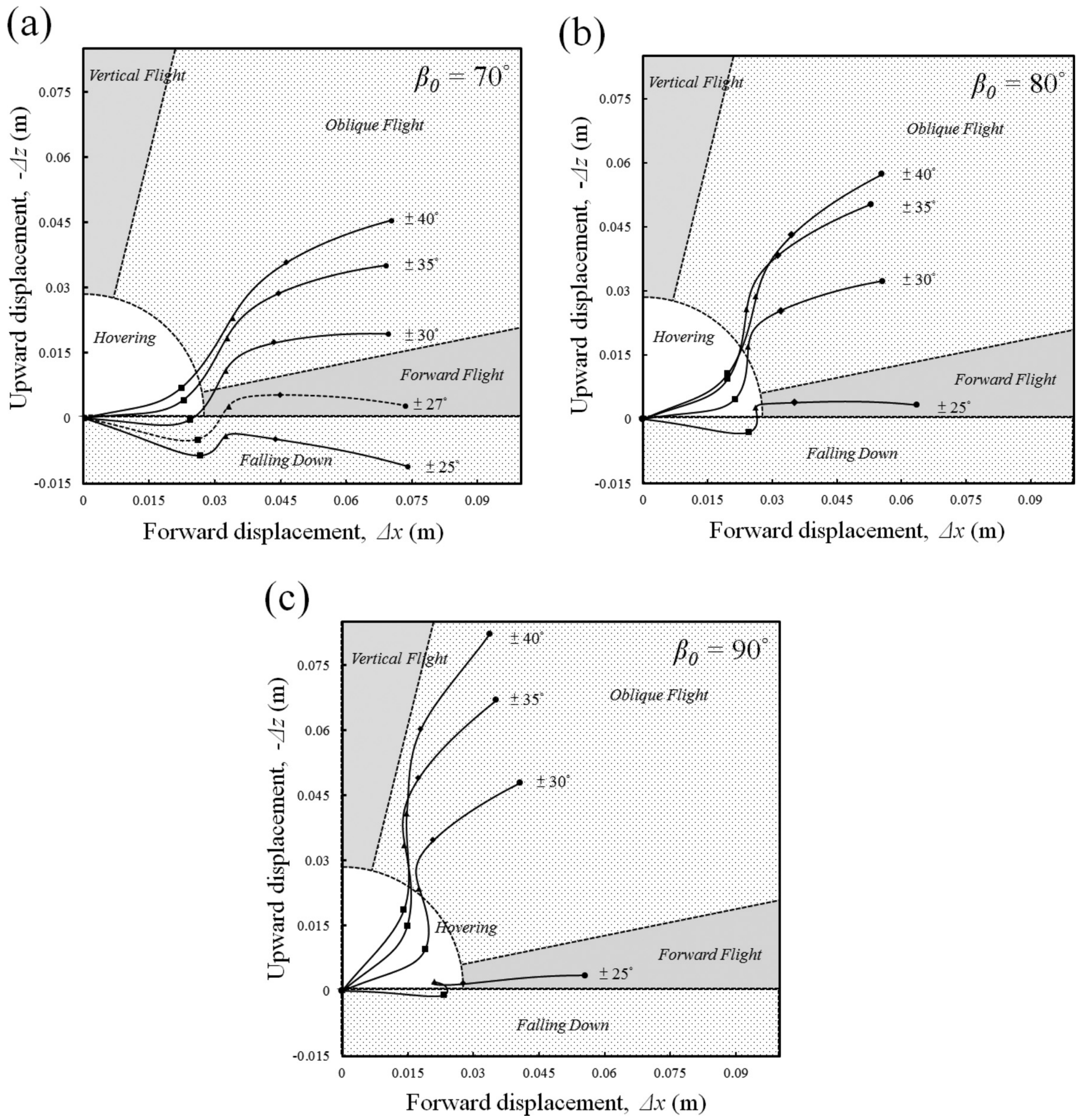

FIG. 8. Flight trajectories within a cycle with varied rotational amplitude and initial body angle (a) $\beta_0 = 70^\circ$, (b) $\beta_0 = 80^\circ$, and (c) $\beta_0 = 90^\circ$ [23]. The squares, triangles, diamonds, and circles on the lines represent the body positions at $t/T = 0.25$, 0.5, 0.75, and 1.00, respectively.

vertical displacement is almost zero and the butterfly can perform forward flight. As the rotational amplitude continues to increase, the amount of upward displacement significantly increases; the flight mode becomes oblique flight. The upward displacements are 0.017, 0.033, and 0.046 m when the rotational amplitudes are 30°, 35°, and 40°, respectively. When the initial body angle attains 80° [Fig. 8(b)], the horizontal displacement of the four cases decreases to about 0.060 m. With rotational amplitude 25°, the upward force generated and the body weight are balanced; a butterfly is able to perform the forward flight mode. Similar to the case with initial body angle 70°, the upward displacement increases when the rotational amplitude increases. When the body becomes initially vertical [Fig. 8(c)], the horizontal displacement decreases; the upward displacement significantly increases. The flight trajectories are more sensitive to the rotational amplitude when the body is vertical; the upward displacement is significantly enhanced with larger rotational amplitude, but the horizontal displacement slightly decreases. When the rotational amplitude is 25°, the butterfly still performs forward flight but with a decreased forward speed. When the rotational amplitude increases to 30°, the upward displacement is almost equal to the forward displacement, with values 0.046 and 0.044 m, respectively. When the rotational amplitude is 35°, the upward displacement increases to 0.068 m and the forward displacement decreases to 0.035 m. When the rotational amplitude is 40°, the upward displacement is 0.079 m and is twice the forward displacement, 0.038 m. The flight mode with this motion is nearly vertical and is similar to the butterfly in takeoff. The tendency of body motion and flight modes was also observed in the flight of

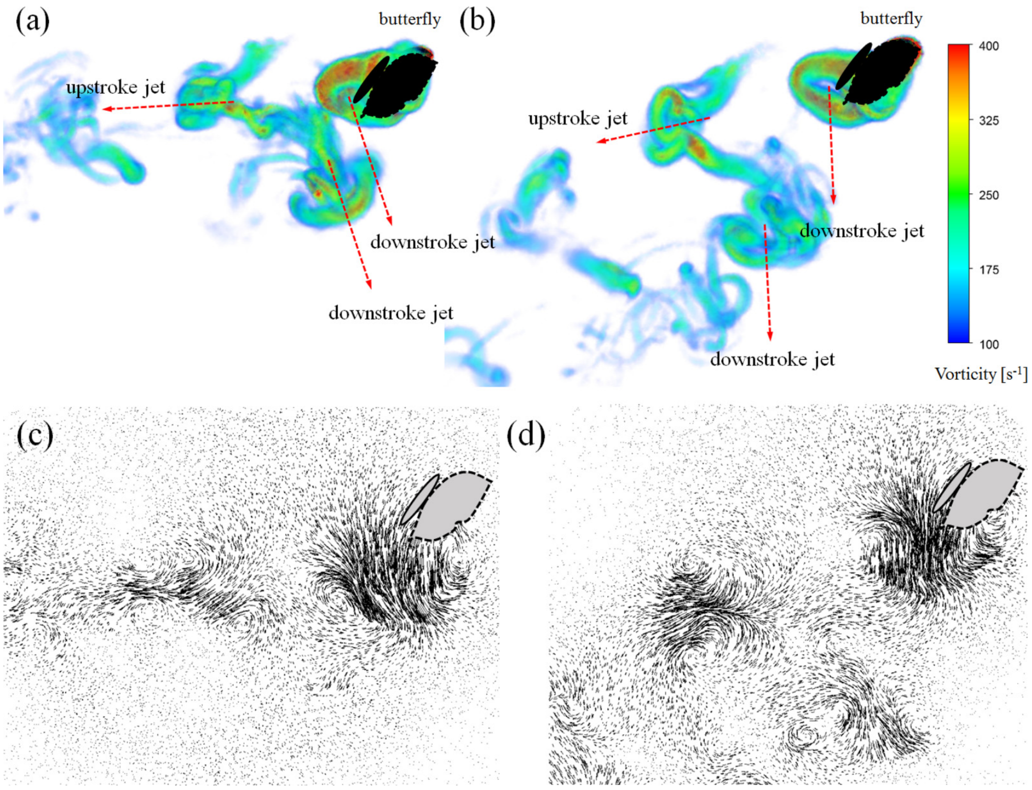

FIG. 9. Vorticity magnitude and vectors of the flow field at $t/T = 0.50$ for a butterfly with rotational amplitudes (a,c) $\Delta\beta = 27^\circ$, and (b,d) $\Delta\beta = 40^\circ$ when the initial body angle is 70°.

other butterflies in experiment. The vibrational amplitude of the thorax angle is recorded at about 40° for the butterflies *Pieris melete* and *P. protenor* in takeoff [6,11]. The variation of the thorax angle of chestnut tiger butterflies (*Parantica sita*) in forward flight in a wind tunnel at a fixed speed is about 15° [13], and about 20° in our butterfly (*Kallima inachus*) in free forward flight.

According to the above analysis, the results indicate that both rotational amplitude and initial body angle play important roles for the flight modes of a butterfly. A butterfly flies with rotational amplitude about 25°–27° to stay aloft. When the initial body angle increases, the forward displacement decreases (the forward flight speed decreases). These results, in accordance with previous work, indicate that the insect can control the forward speed by varying the body angle [9]. Preceding authors claimed that, when the body angle is small, an insect can decrease the pressure drag generated by the wings and body and increase the forward flight speed. On considering the two-dimensional translation in our research, we indicate further that the body angle also has much affect on the vertical translation of a butterfly flight. When the body is vertical, the butterfly is able to generate greater upward force and tends to translate with a greater upward displacement; the flight trajectory is sensitive also to the rotational amplitude when the body is vertical. According to our analysis, no matter how a butterfly manipulates its body motion, it still flies with an appreciable horizontal translation. The reason involves the *clap-and-fling* mechanism, which is a unique feature of a butterfly [23]. In our simulation model, the two wings of a butterfly approach each other at the end of the upstroke; the fluid squeezed from between the two wings creates an additional horizontal force upon them. The unsymmetrical flapping motion of wings leads to an uneven force generated in downstroke and upstroke, and leads further to the butterfly flying forward. To perform flight modes of these kinds, further control of the flapping motion of the wings is necessary.

C. Controlling the direction of the jet flow with body rotation

As mentioned above, the butterfly generates greater upward displacements with greater rotational amplitudes. Figures 9(a) and 9(b) illustrate the wake structure generated by a butterfly with the same initial body angle 70° but varied rotational amplitudes 27° and 40°, for which the butterflies are in forward flight and oblique flight modes, respectively. Figures 9(c) and 9(d) show further the vectors of the flow field on a cross plane near the wing tip. A butterfly generates successively the vortices downward and backward when in the downstroke and the upstroke during flight. At the center of the vortex ring is an intense jet flow [24]; this downward jet flow produces an upward force, and the backward jet flow yields a horizontal force on the butterfly. Compared to the case with rotational amplitude 27°, the downstroke jet flows with rotational amplitude 40° are significantly twisted to become more downward. The butterfly is thus able to generate a greater upward force and to execute a *jump* at the end of the downstroke. The upstroke jet flow is also generated back and slightly downward. The butterfly generates upward and forward force in the upstroke with a large rotational amplitude. The wake structure generated by a butterfly explains that a rotation of the body can significantly affect the direction of the resultant force generation. A rotation of the body leads to the wing stroke plane varying during flight; in comparison, for a butterfly flying without body rotation, the stroke plane is fixed and the aerodynamic forces generated in downstroke and upstroke are opposite; a butterfly scarcely generates upward and forward and is unable to maintain its altitude without body rotation. In controlling the direction of the jet flow, the butterfly can control the flight direction with the body rotation. The unsteady flight motion with a significant body motion of a butterfly was previously considered not an optimal model for the design of a MAV, but our results reveal that this mechanism adopted by a butterfly can deflect the jet flow toward a useful direction. A butterfly can further achieve various flight modes by manipulating the rotation of its body.

With greater rotational amplitude, a butterfly is able to generate a greater vertical force, and to create greater vertical translation during flight. The vertical component is extremely sensitive to the rotational amplitude when the rotational amplitudes are 25°–27°, which are appropriate for the butterfly to perform forward flight. About this range, even a small difference of the rotational amplitudes can yield large variations of a flight trajectory (Fig. 8). The upward speed increases with the greater rotational amplitude, but, with a greater upward speed, the vertical force generation decreases during flight; the effect of increasing the rotational amplitude then becomes minor. The flight trajectories are similar with large rotational amplitudes, for example, $\Delta\beta = 35^\circ$ and 40° (Fig. 8); the upward displacement could scarcely be further enhanced on increasing the rotational amplitudes beyond 40°.

D. Interaction of the body motion and the erratic flight path

The flight path of a butterfly is irregular during free flight (Fig. 8); the causes arise from the intrinsic features of a butterfly—flying with a small flapping frequency and broad wings [1]. A butterfly generates large aerodynamic forces with broad wings in each flap but with a larger time scale for body response. Combining the two effects, the flight trajectory of a butterfly is erratic; the flight speed varies greatly during the free flight of a butterfly: the interaction between the flow and the butterfly is complicated. The flow relative to the butterfly is not constant and involves varied directions.

In forward flight, because of the horizontal force generated in the preceding upstroke, a butterfly translates forwardly during $t/T = 0$–0.25. When the wings open, the butterfly creates upward and backward forces; the flight trajectory slightly ascends and with little horizontal displacement during $t/T = 0.25$–0.50. The wings move back after the downstroke, and the horizontal displacement begins to increase again during $t/T = 0.50$–0.75. At the end of the upstroke, the forward speed becomes large and a butterfly flies with much horizontal displacement. For comparison, in the case of a large rotational amplitude, because of the large upward force generated in the downstroke, the flight trajectory ascends instantaneously during the middle of the stroke; a butterfly executes a *jump* at this time; the flight trajectory has a Z shape. Figure 10 illustrates the flight trajectory and body motion of a butterfly within a cycle. At the beginning of the stroke ($t/T = 0$–0.25), the flow relative to the butterfly moves from right to left [Fig. 10(a)]. At this time, the body angle of a butterfly is small, which decreases the projected area and further decreases the negative horizontal force generation. During the jumping stage, the wings of a butterfly are fully open; the butterfly translates mainly vertically, and the relative flow moves from up to down [Fig. 10(b)]. At this time, a butterfly manipulates its body to become vertical and parallel to the flow, which again decreases the projected area and avoids the generation of a downward force. If a butterfly moved upward with a shallow body angle, the flow would impinge on the top surfaces of the wings, and create a large downward force thereon. Including the transient flight in the discussion, the results indicate that the rotation of the body of a butterfly not only controls its flight mode but also interacts in a complicated manner with its irregular flight path, which is a clever way to avoid the generation of downward forces during a transient translation.

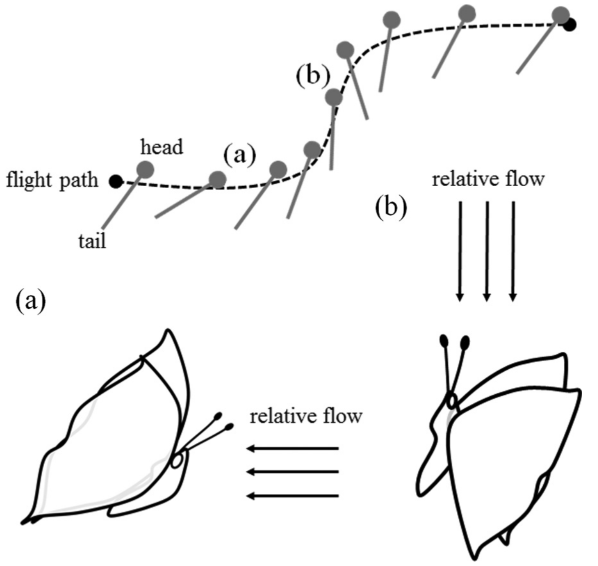

FIG. 10. The upper figure is a simplified diagram of the body motion and an irregular flight trajectory of a butterfly within a cycle. Lower figures (a,b) illustrate the flow, relative to a butterfly, and the flight postures at the moment labeled in the upper figure.

Through including the horizontal and vertical translations in a discussion of the flight of a butterfly in free flight, our results indicate the importance of the mechanism of body rotation for flight control and the aerodynamic effect. The flight maneuver of a butterfly is based on the rotation of the body, which leads to the stroke plane varying during flight. A butterfly's body skillfully interacts with its erratic flight trajectory and avoids a downward force generated in the middle of a stroke. Different from most insects that intricately control at least 2-dof wing motion at the wing base to achieve various flight modes, a butterfly separates its flight kinematics into two 1-dof motions, which are a simple flapping motion and a body rotation motion. A butterfly generates enough upward and forward forces for flight even without the wing rotation; moreover, it can modulate its flight by altering the body angle. Considering the limited power density of a current man-made actuator and the material of a mechanical structure, the small flapping frequency and the particular way that a butterfly maneuvers its flight are easier and more achievable from an engineering perspective. The investigation of the flight maneuver of a butterfly provides an alternative way to design a future MAV. An insufficiency of our current model is that the body angle is prescribed, which is unlike the real flight of a butterfly that controls its body angle with its wings and abdomen. To achieve a varied body angle as described in our article, a specific control between the wing motion and abdominal motion—for example, the lead-lag angle of the wings, amplitudes of the abdomen, or even the phase between the wing and the abdomen—is thus necessary. This complicated question remains unclear, and leaves room for future exploration.

IV. CONCLUSIONS

A butterfly is observed to rotate periodically with a body motion that alters with its flight mode. The way that a butterfly maneuvers its flight differs from that of other insects. To study the relation between the flight maneuver and body motion, we created a simulation model of butterflies in transient flight based on the real flight motion of a butterfly. The speed of a butterfly in forward flight in the simulation is in accordance with that recorded from the experiment. Two parameters of body motion—the initial body angle and the rotational amplitude—are tested from 70° to 90° and 25° to 40°, respectively. On including the vertical and horizontal translations in the analysis, the results indicate that the body motion of a butterfly affects not only the horizontal translation but also the vertical translation, which was generally neglected in preceding research. The butterfly performs forward flight with a rotational amplitude about 25°–27°. When the initial body angle increases, the forward speed of the butterfly decreases and the upward speed increases; the butterfly tends to fly vertically. In contrast, with increased rotational amplitude, a butterfly alters the aerodynamic jet to a more downward direction, and creates a greater upward force. The upward displacement is significantly increased during the middle of the stroke, and executes a *jump* motion at this time. During this jumping phase, the butterfly manipulates its body motion to be parallel to the relative flow, which decreases its projected area and minimizes the pressure drag. This unique body motion of a butterfly skillfully interacts with its erratic flight trajectory, and avoids the downward forces generated. Instead of controlling its flight with a complicated wing motion, a butterfly can achieve various flight modes via a simple body motion. The way that a butterfly maneuvers its flight revealed in this work yields insight into the creation of a MAV with effective maneuverability.

ACKNOWLEDGMENT

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