Within-wingbeat damping: dynamics of continuous free-flight yaw turns in *Manduca sexta*

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Free-flight body dynamics and wing kinematics were collected from recordings of continuous, low-speed, multi-wingbeat yaw turns in hawkmoths (*Manduca sexta*) using stereo videography. These data were used to examine the effects of rotational damping arising from interactions between the body rotation and flapping motion (flapping counter-torque, FCT) on continuous turning. The moths were found to accelerate during downstroke, then decelerate during upstroke by an amount consistent with FCT damping. Wing kinematics related to turning were then analysed in a simulation of hawkmoth flight; results were consistent with the observed acceleration–deceleration pattern. However, an alternative wing kinematic which produced more continuous and less damped accelerations was found in the simulation. These findings demonstrate that (i) FCT damping is detectable in the dynamics of continuously turning animals and (ii) FCT-reducing kinematics do exist but were not employed by turning moths, possibly because within-wingbeat damping simplifies control of turning by allowing control systems to target angular velocity rather than acceleration.

Keywords: flight; control; dynamics; turning

1. INTRODUCTION

Flying animals appear to effortlessly solve an array of difficult control problems while both stabilizing themselves against external perturbation and manoeuvring, all without the use of dedicated control surfaces found in human-designed flying vehicles. A recent study of low speed yaw turns in a wide variety of flying animals found that these capabilities might be aided by rotational damping arising from an interaction between wing flapping motions and whole-body rotational velocity, termed flapping counter-torque (FCT) (Hedrick *et al.* 2009). In FCT-dominated flight dynamics, internally generated or externally imposed yaw velocities decay rapidly under conditions of symmetric flapping, i.e. deceleration does not require specific wing kinematics. These effects were first

isolated in the deceleration phase of a complete turn, but also probably influence the body dynamics of animals in other phases of a turn. Here we examine continuous, free-flight, multi-wingbeat yaw turns in the hawkmoth *Manduca sexta*, investigating whether FCT damping is detectable during continuous yaw manoeuvres and examining the implications of its presence for the type of wing kinematic asymmetry used to generate yaw turns in this species.

While FCT damping might lead to many different turning patterns, we initially developed two different hypothetical turning strategies for an animal flying with damped rotational dynamics—periodic and continuous turns (figure 1). The FCT model predicts a damping half-life of less than a wingbeat for *M. sexta*, suggesting that periods of little or no manoeuvring torque generation would lead to observable decreases in yaw velocity. For example, figure 1*a* shows a flapping pattern where torque is generated only in downstroke, allowing damping to slow the moth during upstroke. Alternatively, if the moth produced manoeuvring torque continuously or substantially reduced the magnitude of the damping coefficient, observable deceleration on a half-wingbeat time scale would occur only at the end of the turn when the animal ceased manoeuvring torque production (figure 1*a*). These two possibilities, periodic or continuous torque generation, carry different implications for control of movement. In the case of the former, the correlation between applied torque and body velocity is strengthened relative to the correlation between torque and body acceleration (figure 1). This potentially simplifies the per-wingbeat control model for movement, converting it from a second order to a first order system (e.g. Cowan & Fortune 2007) and thereby reducing the rate at which flying animals must acquire and process information to stay aloft. If torque is produced continuously or damping is minimized, the locomotor dynamics model remains second order. For this reason, and owing to their large FCT damping coefficients in symmetric flapping, we expected the hawkmoths studied here would use periodic turns.

2. MATERIAL AND METHODS

Sixteen male hawkmoths (*M. sexta*) were gathered as pupae from the domestic colony maintained in the University of North Carolina Department of Biology. Beginning four days after eclosion, the moths were trained to feed on sugar water presented in an artificial flower. Following training, yaw turns were elicited from the moths by presenting them with the artificial flower and moving it in an arc around the moth. These recordings were gathered in a 71 × 71 × 74 cm glass-walled flight chamber dimly illuminated in the visible spectrum and brightly illuminated in the near-infrared (680 nm) by light emitting diodes (Roithner LaserTechnik GmbH, Austria). Trials were filmed at 1000 Hz with three cameras (two Phantom v7.1 and one Phantom v5.1; Vision Research, Wayne, NJ), which were calibrated using direct linear transformation (Hedrick 2008), allowing three-dimensional reconstruction of the flight kinematics. Trials from four of the sixteen moths were selected for further analysis based on visual inspection to assess (i) duration of continuous turning, (ii) absence of contact between the moth and flower and (iii) absence of large changes in roll or pitch (these events were rare). The selected trials were then digitized: the three-dimensional positions of four markers on the moth's body were recorded along with the wing tips and the notches at the trailing edge intersection of the fore and hind wings. These locations were recorded at four phases during each wingbeat: the start, middle and end of the downstroke and the middle of the upstroke. Roll, pitch and yaw angles were then extracted from the four body points and roll, pitch and yaw time-derivatives calculated from a quintic smoothing spline which assumed a 0.75° error in each recorded angular position; this error rate was estimated by repeated digitizing of the same

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Figure 1. Turning against flapping counter torque of the form $\dot{\omega} = (T - k\omega)I^{-1}$. A conceptual figure showing the relationship between torque (T), angular acceleration ($\dot{\omega}$) and angular velocity (ω) in conditions of (a) periodic torque production (i) with strong damping and (b) continuous but reduced torque production (i) and damping. In (a), damping causes velocity to decline in the absence of active torque production (ii), disrupting the correlation between torque and acceleration over a complete wingbeat (iii), but strengthening the correlation between torque and velocity (iv). In (b), the correlation between applied torque and acceleration (iii) is much greater than the correlation between torque and velocity (iv). Terms I and k represent moment of inertia and a damping constant, respectively. Shading indicates the downstroke phase of a wingbeat.

trial. Euler angle derivatives were then transformed back to the body coordinate system (Stengel 2004). Finally, a mean angular velocity for each wingbeat was computed as the average of each set of start of downstroke, middle of downstroke, end of downstroke and middle of upstroke points. All calculations were carried out in MATLAB r2008b (The Mathworks, Natick, MA). Additionally, the effects of the measured wing kinematics were investigated using a blade-element simulation of hawkmoth flight (Hedrick & Daniel 2006).

3. RESULTS

The analysed trials had a duration of 0.59 ± 0.09 s (mean $\pm$ s.d.), during which the moths rotated by $91 \pm 23^\circ$ at a whole-recording angular velocity of $159 \pm 57^\circ \text{ s}^{-1}$. Maximum instantaneous yaw rates within each trial ranged from 723 to 306° s^{-1} . Mean linear velocity during the trials was $0.37 \pm 0.14 \text{ m s}^{-1}$.

The moths exhibited a regular pattern of within-wingbeat changes in yaw rate, with the angular velocity at the end of downstroke greater than the angular velocity at the end of the following upstroke (figure 2a). Considered across all wingbeats collected in this study (figure 2b), the pattern was statistically significant ($p < 0.0001$) and the ratio of the velocity at the end of upstroke to velocity at the end of the preceding downstroke was found to be 0.70 ± 0.06 (figure 2c, model II regression slope $\pm$ s.e.), i.e. the moths accelerated in downstroke and decelerated in upstroke. To see whether this result was consistent with FCT damping of a passive upstroke following an active downstroke, we used the FCT model to predict the upstroke to downstroke velocity ratio. Since FCT shows that an exponential decay model predicts angular deceleration in yaw turns, the FCT half-life and event duration are all that is required to predict the amount of deceleration. We used the previously reported FCT half-life for *M. sexta* (28.4 ms, Hedrick *et al.* 2009) and the duration of upstroke, found to be

17.3 ± 2.2 ms (mean $\pm$ s.d.) for these data, resulting in a predicted ratio of:

$$\left. \begin{aligned} \omega_{\text{final}} &= \omega_{\text{initial}} \left(\frac{1}{2} \right)^{17.3/28.4} \\ \text{and } \frac{\omega_{\text{final}}}{\omega_{\text{initial}}} &\cong 0.66. \end{aligned} \right\} \quad (1.1)$$

The predicted ratio is within the 95% CI for the ratio determined from the data, 0.59–0.82.

Wing kinematic measures associated with yaw turns were similar to those described for banked yaw turns in the forward flight of the hawkmoth species *Agrius convolvuli* (Wang *et al.* 2008). As in that study, the relative positions of the left and right wing at the end of the downstroke (i.e. at the time of ventral stroke reversal) were significant predictors of the mean yaw velocity for the wing stroke in question, with an R^2 of 0.58 and $p < 0.0001$ for the relationship between sweep angle (ϕ) differences and velocity rate and an R^2 of 0.50 and $p < 0.0001$ for elevation angle (θ) differences relating to yaw velocity (see the electronic supplementary material, figure S1). The correlations were such that yaw to the right was associated with the right wing reaching a greater elevation angle than the left wing at the end of the downstroke and also with the right wing ending with a lesser sweep angle than the left wing. Neither of these wing kinematic measurements was associated with body acceleration to a statistically significant ($p < 0.05$) degree.

The effects of the measured kinematic pattern were examined by recreating them in a simulation of hawkmoth flight (Hedrick & Daniel 2006). A flapping pattern which created a -12.5° right–left difference in wing elevation angle and 10° difference in wing sweep angle at the end of the downstroke, the approximate

Figure 2. (a) Yaw velocity through time for a single trial, with end of downstroke and upstroke points marked. (b) Aggregate data comparing end of downstroke and end of upstroke yaw velocities for all trials and wingbeats along with model II regression results. (c) The data in (b) were analysed using a mixed model multiple regression across all wingbeats from all individuals. The model included logistic effects for individual moths and a least-squares term for the effect of end of downstroke yaw. None of the individual effects in this model were significant ($p > 0.05$), permitting reanalysis of the data using a model II (i.e. major axis) regression to account for the similar error ranges and identical units of the independent and dependent variables. All statistical calculations were performed in R 2.1 (R Core Development Team 2009). (d) Simulation results of the biological and alternative kinematics and their least-squares fits to the flapping counter torque damped yaw turning equation $\dot{\omega} = (T - k\omega)I^{-1}$, where $\dot{\omega}$ is angular acceleration, T turning torque, k the FCT damping coefficient, ω is angular velocity and I moment of inertia. For the biological kinematic, $T = 8.6 \times 10^{-3}$ N m and $k = 2.9 \times 10^{-5}$ N⁻¹m⁻¹s⁻¹. In the alternative case, $T = 3.5 \times 10^{-3}$ N m and $k = 8.0 \times 10^{-6}$ N⁻¹m⁻¹s⁻¹. (a) Solid line, instantaneous yaw rate; filled black diamonds, end of downstroke; open circles, end of upstroke; (b) filled dots, all recorded wingbeats; $R^2 = 0.69$, $p < 0.00001$; $y = 0.70x - 39.73$. (d) Solid bold line, biological yaw kinematic; dashed bold line, alternative yaw kinematic; thin solid line and thin dashed line, least-squares fits to $\dot{\omega} = (T - k\omega)I^{-1}$.

midpoints of the kinematic observations (see the electronic supplementary material, figure S1) resulted in rapid yaw acceleration to the right during the downstroke followed by deceleration during the upstroke (figure 2d). Beginning from rest, the simulated moth using this biologically derived kinematic accelerated during the downstroke then decelerated during the upstroke, reaching a yaw velocity of 120° s^{-1} at the end of the first stroke, similar to that exhibited by real moths with similar kinematic deviations. However, these were not the only kinematics capable of producing yaw in the simulated moth. An alternative kinematic which modified the basic flapping motion only by increasing the mean spanwise rotation of the right wing by 10° , thus increasing wing angle of attack during the downstroke while decreasing it during the upstroke, was chosen for comparison to the biological case as the two kinematics reach similar peak yaw rates (figure 2d). This alternative kinematic produced acceleration during both

downstroke and upstroke and a yaw velocity of 320° s^{-1} after one stroke. Analysis of the simulation outputs revealed that the alternative kinematic reduced manoeuvring torque and damping by 59 and 64 per cent, respectively. Thus, continuous turn dynamics of the type hypothesized in figure 1b, and characterized by reduced but less variable torque and reduced damping, are probably feasible in flapping flight. There is no evidence that moths turn in this way, but a recent report of fruitfly yaw turning showed that those animals yaw by increasing the spanwise rotation of one wing (Bergou *et al.* 2010), the hypothetical kinematic which gave rise to more continuous turns in our simulations.

4. DISCUSSION

The regular within-stroke changes in yaw velocity reported here, as well as the match between observed yaw deceleration and that predicted by the FCT

model, confirm that FCT type damping does occur in each wingbeat of continuous, multi-flap turns and not only at the end of a sequence of turns as initially described in Hedrick *et al.* (2009). Additionally, this damping was present in a simulation of flapping flight based on the wing kinematics recorded from turning moths. However, examination of alternative kinematics in the simulation indicated that not all turning kinematics are equally subject to damping; kinematics which depend on asymmetry in wing angle can reduce the magnitude of the FCT damping coefficient. This lends support to the somewhat speculative notion that strategies which incorporate FCT or other damping modes are favoured because, from the point of view of the neuromuscular system, these kinematics convert second-order Newtonian dynamics to a first-order kinematic model, allowing neuromuscular outputs to encode body velocity rather than body acceleration. Velocity encoding at the neuromuscular level may also facilitate neurosensory to neuromuscular fusion given the well-described velocity-encoding properties of the insect visual sensory system and their linear response to a wide range of stimuli (e.g. Fry *et al.* 2009). Alternatively, kinematics that generate continuous accelerations may not be readily available to animals owing to anatomical constraints, or may have other costs such as higher power requirements.

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