Supplementary information

0.1 Equation of motion

We began with the general equations of motion for velocity-squared damping during rotational movement

$$\frac{F_m}{T} = I\ddot{\phi}(t) + \Gamma|\dot{\phi}(t)|\dot{\phi}(t) + \frac{k_l}{T^2}\phi(t), \tag{1}$$

where F_m is the force from flight muscles, I is wing inertia, Γ is the aerodynamic damping parameter, k_l is thoracic linear stiffness, and T is the transmission ratio.

0.2 Inertia

The term $I\ddot{\phi}(t)$ is an inertial term, parameterized by a lumped wing inertia I. Following the derivations of (*1*), we calculate I as the sum of inertia due to wing mass (I_w) and added mass (I_a):

$$I_w = r_2^2(m)m_wR^2, \quad \text{and} \quad I_a = vr_2^2(v)R^2, \tag{2}$$

The added mass (v) is defined as the following:

$$v = \frac{2\rho\pi\hat{v}R^3}{\text{Æ}^2} \tag{3}$$

All terms are defined in Table 1.

0.3 Aerodynamic damping

The term $\Gamma|\dot{\phi}(t)|\dot{\phi}(t)$ is an aerodynamic damping term, parameterized by a single aerodynamic paramter Γ. We calculate this aerodynamic parameter by following the work of Whitney & Wood (*2*). The quasi-steady drag force (F_D) on insect wings over a single wingstroke can be modeled as

$$F_D = \frac{1}{2}\rho\tilde{C}_DA_w\hat{r}_2^2(s)R^2\dot{\phi}^2. \tag{4}$$

Setting the drag torque $\tau_D = F_D l_{cp}$ and $\tau_D = \Gamma\dot{\phi}^2$, where l_{cp} is the center of pressure (*3*), yields the velocity-squared damping coefficient (Γ) as

$$\Gamma = \frac{1}{2}\rho\tilde{C}_D A_w \hat{r}_2^2(s) R^2 l_{cp} \tag{5}$$

0.4 Thorax elasticity and the wing hinge

The term $\frac{k_l}{T^2}\phi(t)$ is an elastic term, parameterized by a spring constant k_l and a transmission ratio T. We take the linear spring constant from (*4*), making a correction to account for the contribution of active flight muscle. We calculate the active stiffness of the DLM from (*5*), double it to account for potential contributions from the DVM as well, and add it to the thoracic stiffness. This is possible because the flight muscle is in parallel with the thoracic spring. This method likely overshoots the contribution of active muscle, therefore demonstrating that our conclusion is robust to any reasonable active muscle stiffness.

The insect flight system converts a linear displacement of muscle and the thoracic spring to a large, angular displacement of the wings. This is accomplished through the complex, three-dimensional deformation of the wing hinge. Mathematically, we reduce the wing hinge to a linear transmission parameterized by a single quantity T, which we term the transmission ratio and define as the ratio of peak-to-peak wingstroke amplitude to peak-to-peak muscle displacement amplitude. T is mathematically equivalent to the reciprocal of the length of the moment arm through which the muscle acts on the wing, and therefore has units of m^{-1}. We can take muscle strain and wingstroke amplitude from the literature to make the following calculation

$$T = \frac{\phi_o}{X_o} \tag{6}$$

where ϕ_o is the peak-to-peak wingstroke amplitude and X_o is the peak-to-peak muscle displacement amplitude. From here, we can equate the energy stored in the linear thoracic spring and the overall rotational spring to solve for the rotational spring stiffness in terms of known parameters.

$$k_l X_o^2 = k_\tau \phi_o^2 \tag{7}$$

Manipulating this equation algebraically and substituting in the definition of T, we arrive at an expression for rotational stiffness as a function of linear stiffness and transmission ratio:

$$k_\tau = \frac{k_l}{T^2} \tag{8}$$

This rotational stiffness is the coefficient of $\phi(t)$ in the dynamics equation.

0.5 Validation of model

As a simple step of validation, we calculate the ratio of peak elastic to peak inertial power using our lumped parameters and compare it to previous estimates of elastic energy return in the hawkmoth thorax. Peak elastic and inertial powers can be found by integrating the elastic and inertial torques respectively over a half-stroke and multiplying it by the frequency of oscillation:

$$P_{elastic} = \omega \int_0^{\frac{\phi_o}{2}} \frac{k}{T^2} \phi d\phi = \frac{k\phi_o^2 \omega}{8T^2} \tag{9}$$

$$P_{inertial} = \omega \int_0^{\frac{\phi_o}{2}} I\omega^2 \phi d\phi = \frac{I\phi_o^2 \omega^3}{8} \tag{10}$$

The ratio of these two quantities yields 37-58% depending on which value of thorax elasticity is used (with without muscle), which is in agreement with previous estimates of thorax elastic energy exchange (*4*). Therefore, our model quantitatively captures the dynamic contributions of elasticity to spring-wing mechanics.

$$\frac{P_{elastic}}{P_{inertial}} = \frac{k}{T^2 I \omega^2} = 37 - 58\% \tag{11}$$

0.6 Muscle forcing

The left-hand-side of the spring-wing equation is the muscle forcing term. We use a simple, phenomenological model of muscle, modeling the force as a purely sinusoidal forcing with amplitude F_o and frequency $\omega = 25$ Hz, matching Manduca's wingbeat frequency. Since the units of this term must match torque units, we also divide by the transmission ratio, so the complete left-hand-side is given by:

$$\tau_m = \frac{F_o}{T} \sin(\omega t) \tag{12}$$

As discussed in the maintext, we began with a F_o of 0.5 N, matching results from isolated Manduca DLM work loop experiments (*5*). Due to the extremely low and unrealistic wingbeat amplitudes that resulted, we increased F_o to an adjusted value of $F_o^* = 2.25$ N, which resulted in wingbeat amplitudes that match real Manduca data.

0.7 Numerical methods

To solve the equation of motion, we used Python's differential equation solver solve ivp to numerically calculate the emergent wingstroke amplitude ϕ_o over a range of frequencies from 1 to 50 Hz. At each frequency, we simulated wingbeats over a period of 3 seconds starting from zero initial conditions. The emergent wingbeat amplitude was extracted from wingbeats only

Table 1: Variable definitions and values

variable	value	description
k_l	4078 ± 510 N m^{-1} (*4, 5*)	thoracic stiffness with muscle
k_{thorax}	2582 ± 510 N m^{-1} (*4*)	thoracic stiffness
I	5.69± 0.34 E-8 kg m^2	wing inertia
T	2230 ± 110 m^{-1}	transmission ratio
Γ	3.69 ± 0.33 E-8 kg m^2	damping coefficient
$r_2(m)$	0.383 ± 0.003 (*6*)	nondimensional 2nd moment of wing area
$r_2(v)$	0.482 ± 0.001 (*6*)	nondimensional 2nd moment of added mass
$r_2(s)$	0.518 ± 0.001 (*6*)	nondimensional 2nd moment of wing shape
m_w	0.092 g (*6*)	wing mass (both wings)
$\hat{v}$	1.08 (*6*)	added mass
ρ	1.225 kg m^{-3}	air density
A_w	1881 mm^2 (*6*)	wing area (both wings)
Æ	5.53 ± 0.04 (*6*)	wing aspect ratio (both wings)
R	51 mm (*6*)	wing length
$\tilde{C}_D$	1.5 (*3*)	drag coefficient
l_{cp}	30.6 mm (*3*)	aerodynamic center of pressure
ϕ_o	117 ± 6° (*6*)	peak-to-peak wingstroke amp
X_o	0.46 ±0.02 mm (*5*)	peak-to-peak muscle displacement amp
F_o	0.5 N (*5*)	zero-to-peak muscle force amp
F_o^*	2.25 N	adjusted zero-to-peak muscle force amp

after steady-state has been reached. We then plot this amplitude as a function of frequency, and find the frequency that resulted in the highest amplitude; this is the resonant frequency.

To run the sensitivity analysis, we modified one of our lumped parameters at a time so they were their 0.5th percentile value and re-generated the resonance curve. We repeated this process with the 99.5th percentile values for each parameter. To find the necessary parameter values for resonance to be achieved, we varied each parameter one at a time and generated the system resonance curve. We continued iterating this process until the resonant and wingbeat frequencies matched, until the parameter hit zero, or we saw no further change in resonance frequency by changing the parameter value.

References

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