Supplementary Experimental Methods

In this section, we provide supplementary detail on the calibration of the force transducer, the morphological measurements that we made, and the methods used for frequency domain analysis.

**Force transducer calibration**

The six-axis Nano17 force transducer (ATI Industrial Automation, NC, USA) was calibrated by mounting the transducer in a range of different orientations, and measuring the effect of placing known weights on different moment arms. The magnitudes of the forces and moments that were applied were similar to those expected to be produced by the moths. A linear calibration matrix was fitted by regressing the measured voltage outputs on the applied forces and moments, and inverting. A shunt calibration was applied at the beginning of each trial to control for small changes in the electrical properties of the measurement circuit. The dynamic response of the transducer was also tested by applying a variety of dynamic loads using a precision computer-controlled rotary stage (ADRT200, Aerotech Inc, UK). The dynamic loads were applied through a high-resolution single-axis force transducer with linear response characteristics over the full dynamic range of the loads (S100, Strain Measurement Devices Ltd, UK). There was found to be negligible change in the gain and phase of the response recorded by the six-axis Nano17 force transducer, as compared to the single-axis S100 transducer over the range of frequencies discussed in this paper. We therefore used the static calibration matrix when transforming measured voltage outputs to measured forces and moments.

**Morphological measurements**

Three *Hyles lineata* (Fabricius) were killed by freezing, and photographed suspended by a light cotton thread from a variety of different hanging points. Because the centre of mass (CoM) falls directly beneath the hanging point, the point of intersection of the plumb lines for the various hanging points is an estimate of the position of the CoM. By digitally overlaying the photographs to find the intersection point of the plumb lines, the position of the CoM was found to lie in the sagittal plane, $0.45 \pm 0.01$ body lengths from the head (mean $\pm$ SE). Body length was defined as the distance from the tip of the labial palps.
to the tip of the abdomen. The position of the CoM of each moth relative to the force transducer was then estimated from photographs of the moths in the simulator. This estimate was used to transform the moments measured using the force transducer to the CoM of the moth.

We estimated the inertial properties of the body of an idealized moth with mass and length equal to the mean of the moths sampled in the experiments (Table S1). A 3D mesh of the body shape of *H. lineata* was generated from photographs of one individual and was scaled to the mean body length of all of the individuals tested. The inertial properties of the body were then calculated (Table S2) using 3D modelling software (SolidWorks, Dassault Systèmes, MA, USA) assuming a constant density distribution and a body mass equal to that of the mean of all of the moths tested. As a check on the method, we compared the position of the CoM calculated using this method with the position of the CoM estimated experimentally. The calculated CoM lay 0.47 body lengths from the head, which differed from the experimentally estimated position by just 2% of body length.

The wingbeat-averaged inertia of the wings (Table S2) was calculated by representing each wing as an infinitely thin rod with density decreasing linearly from root to tip [1]. The wing motion was assumed to be the same as that used in the published flight dynamics model on which our flight dynamics model is based [2] (i.e. a horizontal stroke plane with sinusoidal variation in stroke angle). Other measurements of wing geometry were based on measurements from one individual that were scaled by the individual’s body length relative to the mean body length of the moths tested.

**Frequency domain analysis**

We calculated the magnitude and phase characteristics of the pitch, roll, and yaw moments that the moths produced in response to the stimuli that we presented, referencing the magnitude and phase of the stimuli to the angular position of the stimulus. The frequency spectra of the forces, moments, and stimulus motion were calculated using the chirp z-transform. The chirp-z transform (CZT), or “zoom” transform, is a specialized implementation of the fast Fourier transform (FFT), which can be used to calculate the frequency spectrum of a signal over an independently specified range of frequencies, rather than at evenly-spaced intervals up to the Nyquist frequency as is the case for the usual FFT [3]. This approach is commonly used in frequency domain system identification, because of the improved resolution and accuracy that it offers over the FFT by zooming in upon a particular range of frequencies [4]. We used the CZT to identify the magnitude and phase of the signals that we measured at frequency points from
0 to 60 Hz in 0.1 Hz steps, using Welch’s method for window averaging with 80% overlapping Hanning windows of 8 s duration (see [3,4] for further explanation of these techniques). The quality of the response measurement was assessed by computing the coherence of the response [3,4] which represents, for a given frequency, the fraction of the power in the output spectrum (i.e. measurement) that can be linearly attributed to the input spectrum (i.e. stimulus).

Supplementary Flight Dynamics Analysis

In this section, we provide additional detail needed to understand how the theoretical flight dynamics model was used to predict the natural flight dynamics of H. lineata, and how it was used to predict the feedback control needed to stabilize the lateral and longitudinal flight dynamics. The flight dynamics model that we use is a rescaled version of a published theoretical model [2,5], and we refer the reader to the main text for a review of the primary literature from which it is drawn.

Dynamics of the uncontrolled system

The natural dynamics, or free dynamics, of a system are the intrinsic dynamics of the uncontrolled system. These can be approximated for an insect by assuming wingbeat-averaged forces and moments, and writing linearized time-invariant equations of rigid-body motion of the form:

\[
\dot{x}(t) = Ax(t)
\]

where \( t \) is time, where \( A \) is a system matrix with time-invariant entries, and where \( x(t) \) is the state vector. For a bilaterally symmetric system, the linearized equations of motion that describe the lateral and longitudinal flight dynamics are decoupled and can therefore be treated separately. For longitudinal motions, the state vector \( x(t) = [\delta u, \delta w, \delta q, \delta \theta]^T \) represents small disturbances from equilibrium in forward velocity (\( u \)), dorso-ventral velocity (\( w \)), pitch rate (\( q \)) and pitch angle (\( \theta \)). For lateral motions, the state vector \( x(t) = [\delta v, \delta p, \delta r, \delta \gamma]^T \) represents small disturbances from equilibrium in sideslip velocity (\( v \)), roll rate (\( p \)), yaw rate (\( r \)), and roll angle (\( \gamma \)).

Solutions to this equation are of the form:

\[
x(t) = e^{At}x(0)
\]
where $e^A$ is the matrix exponential of $A$, and where $x(0)$ are the initial conditions at $t = 0$. If the system matrix $A$ can be diagonalized, then this equation may be rewritten as:

$$x(t) = Ve^{Dt}V^{-1}x(0)$$

where $D = \text{diag}(\lambda_1, \ldots, \lambda_n)$ is a diagonal matrix whose entries are the eigenvalues of $A$, and where $V$ is a matrix whose columns are right eigenvectors of $A$. It follows that the eigenvalues and eigenvectors of the system matrix $A$ are sufficient to characterize the natural dynamics of the system completely.

The exponential matrix $e^{Dt}$ is a diagonal matrix whose entries are the exponentials $e^{\lambda_1 t}, \ldots, e^{\lambda_n t}$. The entries of the state vector $x(t)$ must therefore be linear combinations of $e^{\lambda_1 t}, \ldots, e^{\lambda_n t}$ with constant coefficients that depend only upon the initial conditions and the eigenvectors of the system matrix. Hence, the natural response of the system to an arbitrary disturbance from equilibrium is a superposition of exponentially growing or decaying modes, which are characterized by the eigenvalues and eigenvectors of the system matrix. The real part of an eigenvalue describes the damping of the mode to which it refers: if the real part is negative, then the mode is stable; if it is positive, then the mode is unstable. Eigenvalues with non-zero imaginary parts come in conjugate pairs, and correspond to oscillatory modes of motion; real eigenvalues correspond to monotonic modes. For an oscillatory mode, the magnitude of the imaginary part of the eigenvalue is the angular frequency of the oscillation. Each eigenvalue is associated with an eigenvector which characterizes the relative phase and magnitude of the different elements of the state vector in that mode.

The system matrix $A$ can be populated given knowledge of the morphological and aerodynamic properties of the system. We generated the system matrices for $H. lineata$ by using our morphological measurements of $H. lineata$ (Table S1) to redimensionalize a published theoretical model of the flight dynamics of the larger hawkmoth *Manduca sexta* (L.) [2, 5]. The aerodynamic parameters of the published model specify how the time-averaged aerodynamic forces and moments vary as functions of the instantaneous state of the system, and were computed using numerical flow simulations (see main text). For longitudinal motions, the dimensional system matrix for $H. lineata$ is:
whilst for lateral motions, the system matrix is:

\[
A_{\text{lat}} = \begin{bmatrix}
-3.533 & -0.01871 & 0.003388 & 9.81 \\
260.0 & -20.74 & 52.74 & 0 \\
-34.19 & 4.837 & -80.44 & 0 \\
0 & 1 & 0 & 0
\end{bmatrix}
\]

The numerical values of the entries in these matrices correspond to a state vector expressed in SI units. The eigenvalues and eigenvectors of these system matrices are given in Tables 2–5 of the main text, where they form the basis of the description of the natural modes of motion.

**Dynamics of the controlled system**

Subject to the assumptions made in the previous section, the dynamics of the controlled system can be written:

\[
\dot{x}(t) = Ax(t) + Bu(t)
\]

where \( B \) is the control system matrix, and where \( u(t) \) is a vector of control inputs. Because we are only interested in explaining the effects of applied roll, pitch, or yaw moments, which are what we have measured experimentally, we use the control system matrix \( B \) to represent the effect of a unit control input representing a pure moment applied about one specified axis. Moreover, because we only model the effects of single control inputs the vector \( u(t) \) is in fact treated here as a scalar \( u(t) \). We emphasize that we are therefore developing a heuristic model for the purposes of simulating separately the effects of the optomotor responses that we have measured, and do not purport to model the complete control system of the moth.

The only moment that is effective in controlling longitudinal motions is a pitch moment, so for our
purposes the control system matrix for longitudinal motions is simply the vector:

\[
B_{\text{long}} = \begin{bmatrix}
0 \\
0 \\
m_\zeta \\
0
\end{bmatrix}
\]

with:

\[
m_\zeta = \frac{M_\zeta}{I_{yy}}
\]

where \( M_\zeta \) is the pitch moment that is produced when a unit longitudinal control input is applied, and \( I_{yy} \) is the pitch moment of inertia.

Lateral motions can be controlled by the application of a roll moment, a yaw moment, or some combination of the two. Because we are interested in modelling the effects of applying coupled roll and yaw moments in response to either roll or yaw stimuli, the required control system matrix for lateral motions is also a vector, this time of the form:

\[
B_{\text{lat}} = \begin{bmatrix}
0 \\
l_\zeta \\
n_\zeta \\
0
\end{bmatrix}
\]

with,

\[
l_\zeta = \frac{I_{zz}L_\zeta + I_{xz}N_\zeta}{I_{xx}I_{zz} - I_{xz}^2} \quad n_\zeta = \frac{I_{xx}N_\zeta + I_{xz}L_\zeta}{I_{xx}I_{zz} - I_{xz}^2}
\]

where \( L_\zeta \) and \( N_\zeta \), respectively, are the roll and yaw moments produced when a unit lateral control input is applied, where \( I_{xx} \) and \( I_{zz} \) are the roll and yaw moments of inertia, and where \( I_{xz} \) is the product of inertia between roll and yaw. These expressions for \( l_\zeta \) and \( n_\zeta \) are obtained by linearizing Euler’s equations, and are the origin of the inertial coupling between roll and yaw that is discussed in the main text. In order to simulate the effect of applying coupled roll and yaw moments about different axes, we temporarily substitute \( L_\zeta = \cos(\epsilon) \) and \( N_\zeta = \sin(\epsilon) \) for \( L_\zeta \) and \( N_\zeta \) in the expressions for \( l_\zeta \) and \( n_\zeta \), where \( \epsilon \) is a variable that represents the angle of the axis of the applied moment from the roll axis.
In order to identify how a moment about a given axis injects energy into the modes of motion, we first make a similarity transformation to modal coordinates, using the matrix $V$ whose columns are right eigenvectors of the system matrix $A$. The vector $\xi(t) = V^{-1} x(t)$ represents a decomposition of the state vector into its constituent modes, and its entries $\xi = [\xi_1, \xi_2, \xi_3, \xi_4]$ are called modal coordinates because they each measure the state of excitation of the system in the direction of one of its eigenvectors. We may use this similarity transformation to rewrite the equations for the dynamics of the controlled system as:

$$\dot{\xi}(t) = V^{-1} AV \xi(t) + V^{-1} B (\epsilon) u(t)$$

In order to identify the axis of the pure moment that is the most or least effective in transferring energy into a given mode, we set $\xi = 0$ and maximize or minimize the magnitude of the corresponding element of $\dot{\xi}(t)$ as a function of $\epsilon$ for a unit control input $u = 1$. The results of this optimization are shown in Fig. 9, and indicate that a moment applied about an axis angled $3^\circ$ below the roll axis will be most effective in controlling the unstable lateral mode of motion that the flight dynamics model predicts.

**State feedback simulations**

In order to investigate how the unstable flight dynamics can be stabilized through feedback control, we assume state feedback (i.e. we assume that the current values of all of the system states are known). Consequently, we assume that the control input is given by:

$$u(t) = -K x(t)$$

where $K$ is the gain matrix. Substituting this feedback law into the equation for the dynamics of the controlled system, we have:

$$\dot{x}(t) = (A - BK) x(t)$$

where $(A - BK)$ is the closed-loop system matrix.

Because we are only interested in exploring the effects of feeding back pitch angle and pitch rate for longitudinal motions, with gains of $k_\theta$ and $k_q$, respectively, the longitudinal gain matrix has the form:

$$K_{\text{long}} = \begin{bmatrix} 0 & 0 & k_q & k_\theta \end{bmatrix}$$
Similarly, because we are only interested in exploring the effects of feeding back roll angle and roll rate for lateral motions, with gains of $k_\gamma$ and $k_p$, respectively, the lateral gain matrix has the form:

$$K_{\text{lat}} = \begin{bmatrix} 0 & k_p & 0 & k_\gamma \end{bmatrix}$$

In order to identify the effect of feeding back pitch angle and pitch rate to pitch moment, we simply compute the eigenvalues of the longitudinal closed-loop system matrix ($A_{\text{long}} - B_{\text{long}}K_{\text{long}}$) for varying values of the gains $k_q$ and $k_\theta$. The results of these computations are plotted for the unstable longitudinal mode in Fig. 10b of the main text, where the values of the gain coefficients are scaled such that $M_\zeta = 1$.

In the case of the lateral flight dynamics, we simulate the effect of feeding back roll angle and roll rate to a moment applied about the axis that transfers most energy into the unstable lateral mode. In practice, this means that we substitute $L_\zeta = \cos(3^\circ)$ and $N_\zeta = \sin(3^\circ)$ in the expressions for $l_\zeta$ and $n_\zeta$, where $\epsilon = 3^\circ$ is the angle solved for in the previous subsection. In other words, the lateral control system matrix then simulates the effect of a unit control input applied about an axis angled $3^\circ$ below the roll axis. We then compute the eigenvalues of the lateral closed-loop system matrix ($A_{\text{lat}} - B_{\text{lat}}K_{\text{lat}}$) for varying values of the gains $k_p$ and $k_\gamma$. The results of these calculations are plotted in Fig. 10a of the main text, where the values of the gain coefficients are scaled such that $L_\zeta = \cos(3^\circ)$ and $N_\zeta = \sin(3^\circ)$ for the unstable lateral mode. The robustness of these results to the introduction of a time delay was studied numerically by using Simulink (MathWorks, MA, USA) to add a constant time delay to the feedback loop. Time delays of durations ranging from 0.25 wingbeats to 2 wingbeats (in 0.25 wingbeat steps) were tested. If all of the state variables remained within 0.005 SI units of their equilibrium values 50 s after an initial $1^\circ s^{-1}$ perturbation in pitch or roll rate, then the control system was treated as being stable.

References


Tables

Table 1. Morphological and kinematic parameters used to rescale the theoretical flight dynamics model

<table>
<thead>
<tr>
<th>Variable</th>
<th>Symbol</th>
<th>Unit</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Body parameters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mass*</td>
<td>( m )</td>
<td>kg ( \times ) 10^{-3}</td>
<td>0.58</td>
</tr>
<tr>
<td>body length*</td>
<td>( l_b )</td>
<td>m ( \times ) 10^{-3}</td>
<td>33.7</td>
</tr>
<tr>
<td>distance between wing bases†</td>
<td>( l_{wb} )</td>
<td>m ( \times ) 10^{-3}</td>
<td>7.1</td>
</tr>
<tr>
<td>distance from CoM to wing base axis‡</td>
<td>( l_1 )</td>
<td>m ( \times ) 10^{-3}</td>
<td>8.7</td>
</tr>
<tr>
<td>body angle‡</td>
<td>( \chi )</td>
<td>°</td>
<td>40</td>
</tr>
<tr>
<td>free body angle‡</td>
<td>( \chi_0 )</td>
<td>°</td>
<td>79.4</td>
</tr>
<tr>
<td><strong>Wing parameters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>wing mass†</td>
<td>( m_{wg} )</td>
<td>kg ( \times ) 10^{-6}</td>
<td>22.6</td>
</tr>
<tr>
<td>wing length†</td>
<td>( R )</td>
<td>m ( \times ) 10^{-3}</td>
<td>32.0</td>
</tr>
<tr>
<td>mean wing chord†</td>
<td>( c )</td>
<td>m ( \times ) 10^{-3}</td>
<td>10.1</td>
</tr>
<tr>
<td>distance from wing root to wing CoM‡</td>
<td>( r_{1,m} )</td>
<td>m ( \times ) 10^{-3}</td>
<td>9.7</td>
</tr>
<tr>
<td>radius of second moment of wing area‡</td>
<td>( r_2 )</td>
<td>m ( \times ) 10^{-3}</td>
<td>16.6</td>
</tr>
<tr>
<td>total wing area of moth‡</td>
<td>( S_t )</td>
<td>m^2 ( \times ) 10^{-6}</td>
<td>678</td>
</tr>
<tr>
<td>stroke amplitude‡</td>
<td>( \Phi )</td>
<td>°</td>
<td>121</td>
</tr>
<tr>
<td>mean stroke angle§</td>
<td>( \phi )</td>
<td>°</td>
<td>9</td>
</tr>
<tr>
<td>wing beat frequency*</td>
<td>( n )</td>
<td>( s^{-1} )</td>
<td>41.1</td>
</tr>
</tbody>
</table>

Symbols correspond to those used in [2] and [5]. *Mean for all individuals tested. †Measurement from one specimen. ‡Published data for *M. sexta* [6, 7]. §Predicted model equilibrium condition for *M. sexta* [2]. See cited sources for definitions of kinematic parameters.

Table 2. Estimated moments and products of inertia of *H. lineata* used to rescale the theoretical flight dynamics model

<table>
<thead>
<tr>
<th>Variable</th>
<th>Symbol</th>
<th>Unit</th>
<th>Wings</th>
<th>Body</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>roll moment of inertia</td>
<td>( I_{xx} )</td>
<td>kg.m^2 ( \times ) 10^{-9}</td>
<td>9.6</td>
<td>16.4</td>
<td>26.0</td>
</tr>
<tr>
<td>pitch moment of inertia</td>
<td>( I_{xy} )</td>
<td>kg.m^2 ( \times ) 10^{-9}</td>
<td>6.4</td>
<td>30.1</td>
<td>36.5</td>
</tr>
<tr>
<td>yaw moment of inertia</td>
<td>( I_{zz} )</td>
<td>kg.m^2 ( \times ) 10^{-9}</td>
<td>11.9</td>
<td>18.3</td>
<td>30.2</td>
</tr>
<tr>
<td>product of inertia between roll and yaw</td>
<td>( I_{xz} )</td>
<td>kg.m^2 ( \times ) 10^{-9}</td>
<td>-1.3</td>
<td>-13.2</td>
<td>-14.5</td>
</tr>
</tbody>
</table>