Stabilization of Insect Flight via Sensors of Coriolis Force

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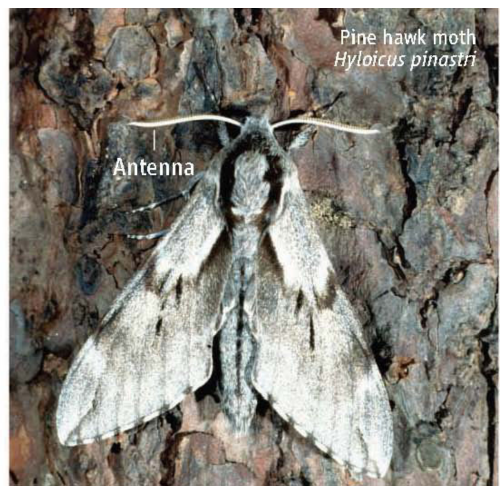
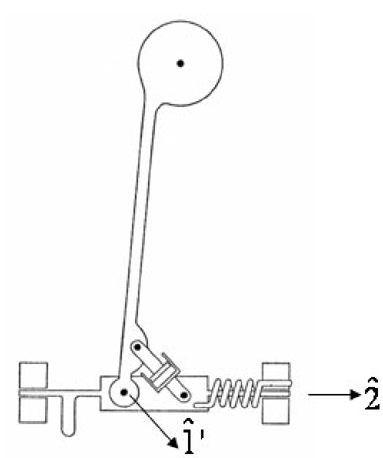
(February 17, 2007)

1 Problem

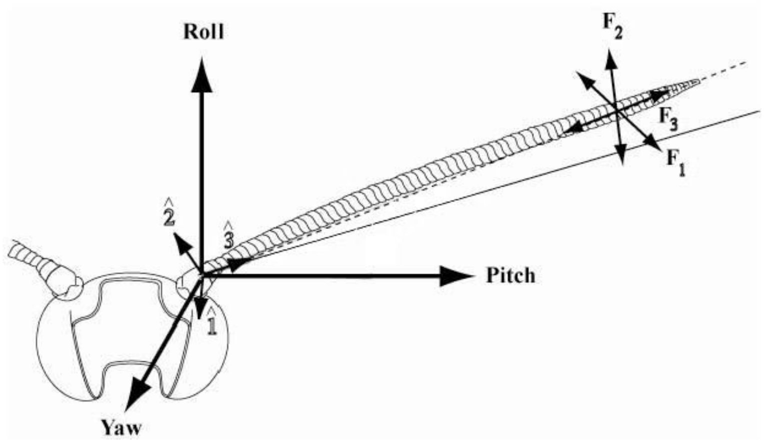
The dynamics of insect flight is remarkably complex (see, for example, [1, 2]). Consider here the possibly simpler problem of the stabilization of the hovering and steady flight of some insects, which appears to be based on detection of an undesirable angular velocity $\mathbf{\Omega}$ via the associated Coriolis force on vibrating antennae [3] or on vestigial wings called halteres [4]. See also [5, 6].



The antennae or halteres vibrate at the same angular frequency ω as do the insect's wings. The articulation of the antennae and halteres appears to involve rotations about two orthogonal axes that we label $\hat{\mathbf{1}}'$ and $\hat{\mathbf{2}}$, for which an equivalent mechanical linkage is sketched below [4]. The insects have sensors that report the time dependence of the force/torque at the joints of the antennae or halteres.



The flight of the insect should be stable against roll, pitch and yaw with respect to a coordinate system $(\hat{\mathbf{R}}, \hat{\mathbf{P}}, \hat{\mathbf{Y}})$ defined by the body of the insect, as sketched below for an insect with antenna-based stabilization (from [3]). The insect's sensors report force components $\mathbf{F}_1$, $\mathbf{F}_2$ and $\mathbf{F}_3$ on the antenna or haltere with respect to the body axes $(\hat{\mathbf{1}}, \hat{\mathbf{2}}, \hat{\mathbf{3}})$ defined by the quiescent orientation of the antenna or halter and its joints.



The body axes $(\hat{\mathbf{R}}, \hat{\mathbf{P}}, \hat{\mathbf{Y}})$ and $(\hat{\mathbf{1}}, \hat{\mathbf{2}}, \hat{\mathbf{3}})$ rotate with angular velocity $\mathbf{\Omega}$ with respect to the inertial lab frame. In the latter frame the antenna or haltere experiences a force $\mathbf{F}_0$ due to gravity, air resistance, and the muscles that cause the vibration. For hovering or flight with a steady velocity, the force $\mathbf{F}$ on the antenna or haltere, whose mass is m, in the rotating body frame can be written as,

$$\mathbf{F} = \mathbf{F}_0 + m\,\mathbf{r} \times \dot{\mathbf{\Omega}} + m\,\mathbf{\Omega} \times (\mathbf{r} \times \mathbf{\Omega}) + 2m\,\mathbf{v} \times \mathbf{\Omega}, \tag{1}$$

where $\mathbf{r}$ is the position of the center of mass of the antenna or haltere and $\mathbf{v}$ is its velocity (with respect to the rotating frame).

For nearly stabilized flight the rate of change $\dot{\mathbf{\Omega}}$ of angular velocity is small, and the coordinate force $m\,\mathbf{r} \times \dot{\mathbf{\Omega}}$ can be neglected.

Then, the centrifugal force term $m\,\mathbf{\Omega} \times (\mathbf{r} \times \mathbf{\Omega})$ is nearly constant, and is not prominent compared to the low-frequency components of the force $\mathbf{F}_0$. Hence, the centrifugal force provides no useful measure of the destabilizing rotation $\mathbf{\Omega}$.

Nature is left with the challenge of utilizing the Coriolis force term $2m\,\mathbf{v} \times \mathbf{\Omega}$ to provide a measure of the undesirable rotation $\mathbf{\Omega}$.

By vibrating its antennae or halteres at the wing frequency $\omega \gg \Omega$, the insect renders the Coriolis force distinct from the low-frequency components of $\mathbf{F}_0$. However, for a velocity of the form $v = v_0 \cos \omega t$, the acceleration has magnitude $a = \omega v_0$ and the force F_0 must include a component with frequency ω whose magnitude is at least $m v_0 \omega \gg m v_0 \Omega$. That is, the component of the Coriolis force $2m\,\mathbf{v} \times \mathbf{\Omega}$ at frequency ω is small compared to the component of the drive force at the same frequency. Hence, it is not obvious that the Coriolis force can provide a suitable signal for the insect to stabilize its flight against the rotation $\mathbf{\Omega}$.

Show that the model for the articulation of the antennae and halteres given on p. 1 implies that the Coriolis force includes small components at integer multiples of the wing frequency ω, which permits separate determination of the components $(\Omega_1, \Omega_2, \Omega_3)$ of the destabilizing angular velocity $\mathbf{\Omega}$.

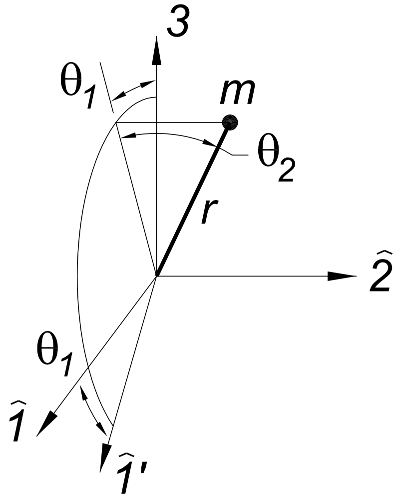
Details of the use of this information to control the flight is beyond the scope of this problem. Some discussion of this issue is given in [5].

2 Solution

Technical details of a solution are presented in secs. 2.1-2.6, and a summary is given in sec. 2.7.

2.1 Fourier Series Description of the Angles of the Antenna/Haltere

We consider the antenna or haltere to be a massless rod of length r with mass m concentrated at its free end, and with its pivoted end at the origin of the $(\hat{\mathbf{1}}, \hat{\mathbf{2}}, \hat{\mathbf{3}})$ body frame, as shown in the figure below.



The pivot of the rod is double jointed so that the rod can rotate about both the $\hat{\mathbf{1}}'$ and the $\hat{\mathbf{2}}$ axes. The $\hat{\mathbf{1}}'$ axis makes angle θ_1 with respect to the $\hat{\mathbf{1}}$ axis in the $\hat{\mathbf{1}}$-$\hat{\mathbf{3}}$ plane as it rotates about the $\hat{\mathbf{2}}$ axis, and the rod makes angle θ_2 with respect to the $\hat{\mathbf{1}}$-$\hat{\mathbf{3}}$ plane as it rotates about the $\hat{\mathbf{1}}'$ axis.

The position of mass m is therefore,

$$\mathbf{r} = r \sin\theta_1 \cos\theta_2\, \hat{\mathbf{1}} + r \sin\theta_2\, \hat{\mathbf{2}} + r \cos\theta_1 \cos\theta_2\, \hat{\mathbf{3}}. \tag{2}$$

The muscles of the insect drive the rod at the wing frequency ω so that the time dependence of angles θ_1 and θ_2 can be represented by Fourier series as,

$$\theta_1 = \sum_{m=1}^{\infty} \theta_{1m} \sin(m\omega t + \phi_{1m}), \qquad \theta_2 = \sum_{n=1}^{\infty} \theta_{2n} \sin(n\omega t + \phi_{2n}), \tag{3}$$

since by definition the average values of θ_1 and θ_2 are zero. All of the Fourier coefficients θ_{ij} are small, and all except θ_{11} and θ_{21} are very small. A difference between the phase factors ϕ_{11} and ϕ_{21} corresponds to an elliptical orbit of mass m.

2.2 A Possible Condition on the Fourier Series

Since muscles only pull, and with a roughly constant force, it may be that the driving force on the antenna or haltere is better approximated by a square wave than by a sine wave. In this case, the Fourier expansion of the driving force would have the form,

$$F = \frac{4F_0}{\pi}\left(\sin\omega t + \frac{1}{3}\sin 3\omega t + \frac{1}{5}\sin 5\omega t + ...\right). \tag{4}$$

If drag forces are small, we can integrate eq. (4) twice to infer that the time-dependence of the angles θ_1 and θ_2 would be of the form,

$$\theta_i = \frac{4\theta_{i0}}{\pi}\left(\sin\omega t + \frac{1}{27}\sin 3\omega t + \frac{1}{125}\sin 5\omega t + ...\right). \tag{5}$$

It will prove desirable that the Fourier series for the angles θ_i have only odd frequency components. A general condition that this be so is that the waveforms $\theta_i(t)$ in their second half period are the negative of those for the first half period,

$$\theta_i(t + T/2) = -\theta_i(t), \tag{6}$$

where $T = 2\pi/\omega$.

This condition appears to be met for the wing velocities in the model of insect flight of [1].

2.3 Fourier Series for the Velocity

Returning to the general forms of eq. (3), the time derivatives of angles θ_1 and θ_2 are,

$$\dot\theta_1 = \omega\sum_{m=1}^{\infty} m\theta_{1m}\cos(m\omega t + \phi_{1m}), \qquad \dot\theta_2 = \omega\sum_{n=1}^{\infty} n\theta_{2n}\cos(n\omega t + \phi_{2n}). \tag{7}$$

The velocity of mass m respect to the body frame is the time derivative of eq. (2),

$$\begin{aligned}
\mathbf{v} &= \dot{\mathbf{r}} \\
&= r(\dot\theta_1\cos\theta_1\cos\theta_2 - \dot\theta_2\sin\theta_1\sin\theta_2)\,\hat{\mathbf{1}} + r\dot\theta_2\cos\theta_2\,\hat{\mathbf{2}} - r(\dot\theta_1\sin\theta_1\cos\theta_2 + \dot\theta_2\cos\theta_1\sin\theta_2)\,\hat{\mathbf{3}} \\
&= \omega r\left[\sum_{k=1}^{\infty} k\theta_{1k}\cos(k\omega t + \phi_{1k})\cos\left(\sum_{m=1}^{\infty}\theta_{1m}\sin(m\omega t + \phi_{1m})\right)\cos\left(\sum_{n=1}^{\infty}\theta_{2n}\sin(n\omega t + \phi_{2n})\right)\right. \\
&\quad \left. -\sum_{k=1}^{\infty} k\theta_{2k}\cos(k\omega t + \phi_{2k})\sin\left(\sum_{m=1}^{\infty}\theta_{1m}\sin(m\omega t + \phi_{1m})\right)\sin\left(\sum_{n=1}^{\infty}\theta_{2n}\sin(n\omega t + \phi_{2n})\right)\right]\hat{\mathbf{1}} \\
&\quad +\omega r\sum_{k=1}^{\infty} k\theta_{2k}\cos(k\omega t + \phi_{2k})\cos\left(\sum_{m=1}^{\infty}\theta_{2m}\sin(m\omega t + \phi_{2m})\right)\hat{\mathbf{2}} \qquad (8) \\
&\quad -\omega r\left[\sum_{k=1}^{\infty} k\theta_{1k}\cos(k\omega t + \phi_{1k})\sin\left(\sum_{m=1}^{\infty}\theta_{1m}\sin(m\omega t + \phi_{1m})\right)\cos\left(\sum_{n=1}^{\infty}\theta_{2n}\sin(n\omega t + \phi_{2n})\right)\right. \\
&\quad \left. +\sum_{k=1}^{\infty} k\theta_{2k}\cos(k\omega t + \phi_{2k})\cos\left(\sum_{m=1}^{\infty}\theta_{1m}\sin(m\omega t + \phi_{1m})\right)\sin\left(\sum_{n=1}^{\infty}\theta_{2n}\sin(n\omega t + \phi_{2n})\right)\right]\hat{\mathbf{3}}.
\end{aligned}$$

We now recast eq. (8) as a single Fourier series,

$$\mathbf{v} = \sum_{n=1}^{\infty} \mathbf{v}_{n\omega}, \tag{9}$$

where $\mathbf{v}_{n\omega}$ contains only terms of frequency $n\omega$. We keep terms only to third order of smallness, *i.e.*, terms with coefficients such as θ_{11}^3, $\theta_{11}\theta_{12}$ or θ_{31}. The terms in frequency ω are, to third order,

$$\begin{aligned}
\mathbf{v}_\omega &= \omega r \left\{ \theta_{11} \cos(\omega t + \phi_{11}) - \frac{\theta_{11}\theta_{21}^2}{8} [\cos(\omega t - \phi_{11} + 2\phi_{21}) - 2\cos(\omega t + \phi_{11})] - \frac{\theta_{11}^3}{8} \cos(\omega t + \phi_{11}) \right\} \hat{\mathbf{1}} \\
&\quad + \omega r \left(\theta_{21} + \frac{\theta_{21}^3}{8} \right) \cos(\omega t + \phi_{21})\, \hat{\mathbf{2}} \\
&\quad - \frac{\omega r}{2} [\theta_{11}\theta_{12} \cos(\omega t + \phi_{11} - \phi_{12}) + \theta_{21}\theta_{22} \cos(\omega t + \phi_{21} - \phi_{22})]\, \hat{\mathbf{3}}.
\end{aligned} \tag{10}$$

The first-order terms in frequency ω are,

$$\mathbf{v}_\omega = \omega r \theta_{11} \cos(\omega t + \phi_{11})\, \hat{\mathbf{1}} + \omega r \theta_{21} \cos(\omega t + \phi_{21})\, \hat{\mathbf{2}}. \tag{11}$$

The terms in frequency 2ω are of second (or higher than third) order,

$$\begin{aligned}
\mathbf{v}_{2\omega} &= 2\omega r \theta_{12} \cos(2\omega t + \phi_{12})\, \hat{\mathbf{1}} + 2\omega r \theta_{22} \cos(2\omega t + \phi_{22})\, \hat{\mathbf{2}} \\
&\quad - \frac{\omega r}{2} [\theta_{11}^2 \sin(2\omega t + 2\phi_{11}) + \theta_{21}^2 \sin(2\omega t + 2\phi_{21})]\, \hat{\mathbf{3}}.
\end{aligned} \tag{12}$$

The terms in frequency 3ω are of third (or higher) order,

$$\begin{aligned}
\mathbf{v}_{3\omega} &= \omega r \left[3\theta_{13} \cos(3\omega t + \phi_{13}) + \frac{3\theta_{11}\theta_{21}^2}{8} \cos(3\omega t + \phi_{11} + 2\phi_{21}) + \frac{\theta_{11}^3}{8} \cos(3\omega t + 3\phi_{11}) \right] \hat{\mathbf{1}} \\
&\quad + \omega r \left[3\theta_{23} \cos(3\omega t + \phi_{23}) + \frac{\theta_{21}^3}{8} \cos(3\omega t + 3\phi_{21}) \right] \hat{\mathbf{2}} \\
&\quad - \frac{5\omega r}{2} [\theta_{11}\theta_{12} \sin(3\omega t + \phi_{11} + \phi_{12}) + \theta_{21}\theta_{22} \sin(3\omega t + \phi_{21} + \phi_{22})]\, \hat{\mathbf{3}}.
\end{aligned} \tag{13}$$

2.4 The Forces at Frequency ω

The Coriolis force $\mathbf{F}_C$ on the antenna or haltere with respect to the $(\hat{\mathbf{1}}, \hat{\mathbf{2}}, \hat{\mathbf{3}})$ axes is,

$$\begin{aligned}
\mathbf{F}_C &= 2m\mathbf{v} \times \mathbf{\Omega} \\
&= 2m(v_2\Omega_3 - v_3\Omega_2)\, \hat{\mathbf{1}} + 2m(v_3\Omega_1 - v_1\Omega_3)\, \hat{\mathbf{2}} + 2m(v_1\Omega_2 - v_2\Omega_1)\, \hat{\mathbf{3}}.
\end{aligned} \tag{14}$$

Using eqs. (11) we obtain the components of the Coriolis force at frequency ω,

$$\begin{aligned}
\mathbf{F}_{C,\omega} &= 2mr\omega\Omega_3\theta_{21} \cos(\omega t + \phi_{21})\, \hat{\mathbf{1}} - 2mr\omega\Omega_3\theta_{11} \cos(\omega t + \phi_{11})\, \hat{\mathbf{2}} \\
&\quad + 2mr\omega[\Omega_2\theta_{11} \cos(\omega t + \phi_{11}) - \Omega_1\theta_{21} \cos(\omega t + \phi_{21})]\, \hat{\mathbf{3}}.
\end{aligned} \tag{15}$$

Can this force be distinguished from the much larger drive force?

If, as considered above, any drag forces are also small compared to the drive force $\mathbf{F}_D$, then the latter is given to a good approximation by,

$$
\begin{aligned}
\mathbf{F}_D &= m\ddot{\mathbf{r}} = m\dot{\mathbf{v}} \\
&= \quad mr[\ddot{\theta}_1 \cos\theta_1 \cos\theta_2 - \ddot{\theta}_2 \sin\theta_1 \sin\theta_2 - (\dot{\theta}_1^2 + \dot{\theta}_2^2) \sin\theta_1 \cos\theta_2 - \dot{\theta}_1\dot{\theta}_2 \cos\theta_1 \sin\theta_2]\,\hat{\mathbf{1}} \\
&\quad + mr[\ddot{\theta}_2 \cos\theta_1 - \dot{\theta}_2^2 \cos\theta_2 \sin\theta_2]\,\hat{\mathbf{2}} \qquad (16) \\
&\quad - mr[\ddot{\theta}_1 \sin\theta_1 \cos\theta_2 + \ddot{\theta}_2 \cos\theta_1 \sin\theta_2 + (\dot{\theta}_1^2 + \dot{\theta}_2^2) \cos\theta_1 \cos\theta_2 - \dot{\theta}_1\dot{\theta}_2 \sin\theta_1 \sin\theta_2]\,\hat{\mathbf{3}},
\end{aligned}
$$

recalling eq. (10). The component of the drive force at frequency ω is (to lowest order),

$$\mathbf{F}_{D,\omega} = -mr\omega^2\theta_{11} \sin(\omega t + \phi_{11})\,\hat{\mathbf{1}} - mr\omega^2\theta_{21} \sin(\omega t + \phi_{21})\,\hat{\mathbf{2}}. \qquad (17)$$

If $\phi_{11} = \phi_{21}$ the $\hat{\mathbf{1}}$ and $\hat{\mathbf{2}}$ components of the Coriolis force (15) are 90° out of phase with the corresponding components of the drive force (17), and phase-sensitive force sensors could make useful measurements of the Coriolis force on the antenna or haltere as frequency ω.

We infer that in fact the phases in the series (3) are all identical, and we set them to zero henceforth. Then, the component of the drive force at frequency ω is,

$$\mathbf{F}_{D,\omega} = -mr\omega^2(\theta_{11}\,\hat{\mathbf{1}} + \theta_{21}\,\hat{\mathbf{2}}) \sin\omega t, \qquad (18)$$

and the component of the Coriolis force at frequency ω is,

$$\mathbf{F}_{C,\omega} = 2mr\omega[\Omega_3(\theta_{21}\,\hat{\mathbf{1}} - \theta_{11}\,\hat{\mathbf{2}}) + (\Omega_2\theta_{11} - \Omega_1\theta_{21})\,\hat{\mathbf{3}}] \cos\omega t. \qquad (19)$$

The ratio of the Coriolis force to the drive force at frequency ω is roughly $2\Omega_3/\omega$.

Phase-sensitive force sensors responsive to the Coriolis force at frequency ω along either the $\hat{\mathbf{1}}$ or $\hat{\mathbf{2}}$ axes would suffice to detect a nonzero rotation component Ω_3. Sensors responsive to forces along the $\hat{\mathbf{3}}$ axis at frequency ω could detect a particular combination of components Ω_1 and Ω_2, but they could not resolve these components separately.[1]

2.5 The Forces at Frequency 2ω

Additional information as to the components of the destabilizing angular velocity $\mathbf{\Omega}$ are obtained from consideration of the Coriolis force at frequency 2ω (henceforth assuming that all phases $\phi_{ij} = 0$). Combining eqs. (12) and (14), we find,

$$
\begin{aligned}
\mathbf{F}_{C,2\omega} &= \quad 2mr\omega \left[2\Omega_3\theta_{22} \cos 2\omega t - \frac{\Omega_2}{2}(\theta_{11}^2 + \theta_{21}^2) \sin 2\omega t\right] \hat{\mathbf{1}} \\
&\quad - 2mr\omega \left[2\Omega_3\theta_{12} \cos 2\omega t - \frac{\Omega_1}{2}(\theta_{11}^2 + \theta_{21}^2) \sin 2\omega t\right] \hat{\mathbf{2}} \\
&\quad + 4mr\omega\,[\theta_{12}\Omega_2 - \theta_{22}\Omega_1] \cos 2\omega t\,\hat{\mathbf{3}}, \qquad (20)
\end{aligned}
$$

[1]Sensors along, say, only axes $\hat{\mathbf{1}}$ and $\hat{\mathbf{3}}$ together with drive motion only along axis $\hat{\mathbf{2}}$ would suffice to determine components Ω_1 and Ω_3.

If the angular waveforms $\theta_i(t)$ obey the condition (6), then $\theta_{12} = \theta_{22} = 0$, and the Coriolis force at frequency 2ω takes on the desirable form,

$$\mathbf{F}_{C,2\omega} = 2mr\omega(\theta_{11}^2 + \theta_{21}^2)(-\Omega_2\,\hat{\mathbf{1}} + \Omega_1\,\hat{\mathbf{2}})\sin 2\omega t. \tag{21}$$

In this case, force sensors along only the $\hat{\mathbf{1}}$ and $\hat{\mathbf{2}}$ axes that are responsive to frequencies ω and 2ω can separately determine components Ω_1, Ω_2 and Ω_3 of the destabilizing rotation $\boldsymbol{\Omega}$. For this, only one of the two vibrations $\theta_1(t)$ or $\theta_2(t)$ need be nonzero.

The component of the drive force (16) at frequency 2ω is, supposing that condition (6) holds,

$$\mathbf{F}_{D,2\omega} = -\frac{mr\omega^2}{2}(\theta_{11}^2 + \theta_{21}^2)\cos 2\omega t\,\hat{\mathbf{3}}, \tag{22}$$

which has no component along either the $\hat{\mathbf{1}}$ or $\hat{\mathbf{2}}$ axes. Hence, it is very favorable that the force sensors are responsive to frequency 2ω.

2.6 The Forces at Frequency 3ω

While it appears sufficient to determine the destabilizing angular velocity $\boldsymbol{\Omega}$ via sensors operating at frequencies ω and 2ω, we explore the merits of operation of the sensors at frequency 3ω as well. We restrict the discussion to the case that all phases ϕ_{ij} are zero, and the only odd harmonics of frequency ω are present in the Fourier expansions of angles $\theta_1(t)$ and $\theta_2(t)$ according to condition (6).

Combining eqs. (13) and (14), we find,

$$\begin{aligned}
\mathbf{F}_{C,3\omega} \;=\;& 2mr\omega\Omega_3\left[3\theta_{23} + \frac{\theta_{21}^3}{8}\right]\cos 3\omega t\,\hat{\mathbf{1}} \\
&-2mr\omega\Omega_3\left[3\theta_{13} + \frac{3\theta_{11}^1\theta_{21}}{8} + \frac{\theta_{11}^3}{8}\right]\cos 3\omega t\,\hat{\mathbf{2}} \\
&+2mr\omega\left\{\Omega_2\left[3\theta_{13} + \frac{3\theta_{11}^1\theta_{21}}{8} + \frac{\theta_{11}^3}{8}\right] - \Omega_1\left[3\theta_{23} + \frac{\theta_{21}^3}{8}\right]\right\}\cos 3\omega t\,\hat{\mathbf{3}}.
\end{aligned} \tag{23}$$

This form is very similar to that of the forces (15) at frequency ω.

The components of the drive force (16) at frequency 3ω are,

$$\mathbf{F}_{D,3\omega} = -\frac{mr\omega^2}{8}(3\theta_{11}^3 + 5\theta_{11}\theta_{21}^2)\sin 3\omega t\,\hat{\mathbf{1}} - \frac{3mr\omega^2}{8}\theta_{21}^3\sin 3\omega t\,\hat{\mathbf{2}}, \tag{24}$$

such that the drive force is 90° out of phase with the Coriolis force (23) at this frequency.

The angular velocity component Ω_3 could be determined by phase-sensitive sensors along either or both of body axes $\hat{\mathbf{1}}$ and $\hat{\mathbf{2}}$ at either or both frequencies ω and 3ω. It may be that the signal-to-noise ratio is better at frequency 3ω than ω.

Sane et al. [3] report that $\theta_{11} \approx \theta_{21} \approx 0.02$ *rad for the antennae of the hawk moth Manduca sexta. In the approximation of eq. (5),* $\theta_{i3} = \theta_{i1}/27$. *Then, the ratio of the Coriolis force to the drive force along axis* $\hat{\mathbf{2}}$ *at frequency* 3ω *would be roughly* $1500\Omega_3/\omega$, *which is far superior to that at frequency* ω.

If the Coriolis signal is large compared to the drive force at frequency 3ω, then the force sensors need not be phase sensitive.

Sane et al. also report that the force sensors of the antennae of the hawk moth operate primarily at frequencies 2ω and 3ω, as seems well justified by the present analysis.

2.7 Summary

- All three components $(\Omega_1, \Omega_2, \Omega_3)$ of the destabilizing angular velocity $\mathbf{\Omega}$ can be determined by sensors of transverse forces at the bases of the antennae or halteres. No detection of the longitudinal force (along axis $\hat{\mathbf{3}}$) is needed.

- Only one antennae or haltere suffices for this determination. The usual conformation with pairs of antennae or halteres provides redundancy, rather than an essential aspect of the measurement.

- It is very advantageous if the vibrational waveforms of the antennae or halteres satisfy condition (6), so that only odd harmonics appear in the Fourier expansions of these waveforms. *The force waveform nonetheless contains all integer harmonics.*

- Components Ω_1 and Ω_2 (in the body frame defined by the antenna or haltere) are determined by the forces detected at frequency 2ω.

- The component Ω_3 could be determined from the forces detected at either frequency ω or 3ω, but the signal to noise is much superior at frequency 3ω in which case the force sensors may not need to be phase sensitive.

- It suffices that the antenna or haltere vibrate only in a single transverse plane. That is, the antennae or haltere need not possess the double articulation sketched on p. 1.

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