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Body rate decoupling using haltere mid-stroke measurements for inertial flight stabilization in Diptera

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Abstract Halteres, the modified rear wings of Diptera, have long been recognized as sensory organs necessary for basic flight stability. These organs, which act as vibrating structure gyroscopes, are known to sense strains proportional to Coriolis accelerations. While compensatory responses have been demonstrated that indicate the ability of insects to distinguish all components of the body rate vector, the specific mechanism by which the halteres are able to decouple the body rates has not been clearly understood. The research documented in this report describes a potential mechanism, using averaged strain and strain rate at the center of the haltere stroke, to decouple the inertial rate components. Through dynamic simulation of a nonlinear model of the haltere 3-dimensional trajectory, this straightforward method was demonstrated to provide an accurate means of generating signals that are proportional to three orthogonal body rate components. Errors associated with residual nonlinearity and rate-coupling were quantified for a bilaterally reconstructed body rate vector over a full range of pitch and yaw rates and two roll rate conditions. Models that are compatible with insect physiology are proposed for performing necessary signal averaging and bilateral processing.

Keywords Diptera · Haltere · Flight stability · Strain rate · Campaniform sensilla

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Abbreviations

dF1	Dorsal 'hicks papillae'			
dF2	Dorsal basal plate			
dF3	Dorsal scapal plate			
vF1	Ventral 'hicks papillae'			
vF2	Ventral scapal plate			
MEMS	Micro electro mechanical sensor			
mnb1	First basalar motor neuron			
γ	Haltere stroke angle			
θ_{μ}	Out of plane deflection angle			
$a \tilde{\omega}^{\nu}$	Angular rate vector of reference frame "b"			
L	with respect to frame "a"			
$a \overline{\alpha}^{D}$	Angular acceleration of reference frame "b"			
	with respect to frame "a"			
\overline{P}_{12}	Position vector from point 1 to point 2			
Ω_i	Angular rate component in the haltere reference			
	frame			
W_{i_i}	Angular rate component in the body frame			
e_a^{-1}	Acceleration vector of point 1 with respect to			
1	frame "e"			
$e_{\mathcal{V}}^{-1}$	Velocity vector of point 1 with respect to frame			
	"e"			
ζ	Critical damping ratio for out-of-plane motion			
ω_n	Haltere out-of-plane natural frequency			
$\hat{b_1}, \hat{b_2}, \hat{b_3}$	Unit vectors defining the " b " reference frame			
r	Haltere radius of gyration			

Introduction

The halteres of Diptera (Fig. 1) are well established as organs necessary for flight stabilization. The mechanism by which the stabilization occurs was debated between the 18th and the first half of the twentieth century, with some



Fig. 1 Characteristic locations of the halteres and their strain sensors. Fields of campaniform (# of sensilla): dF1: dorsal 'Hicks papillae' (17), dF2: dorsal basal plate (100), dF3: dorsal scapal plate (110),

vF1: ventral 'Hicks papillae' (10), vF2: ventral scapal plate (100). Not shown are the large and small chordotonal organs

1993) and elaborated on the potential benefits of non-

arguing that the haltere was a "stimulant" for flight motor function, others claiming the haltere functioned as an inertial balancing system, and still others claiming the halteres were a gyroscopic sensory mechanism (Fraenkel and Pringle 1938; Fraenkel 1939). However, the work of Pringle (1948) provided a firm basis for viewing the haltere as a gyroscopic sensor, optimized for sensitivity to Coriolis forces. The Coriolis force occurs when an object with mass and a finite velocity is constrained to move in a fixed path within a reference frame that is rotating. The Coriolis force is proportional to the reference frame rotation rate, so if through an appropriate strain sensor the force is measured, then a signal is available for rate damping in a stabilizing control loop. Pringle initially did not recognize the ability of the mechanical configuration of the halteres to distinguish between pitch (transverse axis) and roll (longitudinal axis) rotations and therefore assumed the use of the halteres was limited to yaw (vertical axis) rotations. This position was later recanted (Pringle 1957) based on the findings of Faust (1952) that demonstrated stabilizing wing reflexes associated with pitch, yaw and roll in *Calliphora*. It was not until much later that Nalbach reviewed in detail the significance of all forces acting on the halteres (Nalbach

orthogonality of the haltere pair (Nalbach 1994). A number of authors have demonstrated the compensatory reactions of the head and wings to independent components of the body rate vector, thereby demonstrating the role of halteres in both image stabilization and attitude control (Faust 1952; Sandeman and Markl 1980; Hengstenberg et al. 1986; Dickinson 1999; Bender and Dickinson 2006). Heide (1983) performed extensive research associated with the haltere phase tuning of the first basalar motor neuron (mnb1) in control of wing kinematics. This was followed by a number of related studies of flight motor control, e.g.,

Pringle (1948) and Nalbach (1993) recognized that each haltere, due to its large amplitude motion, is sensitive to two orthogonal rate components in its plane of motion, and, further, describe the distinct impacts of the vertical and horizontal rate components on the haltere. The vertical rate component, Ω_x in Fig. 2, generates a force with twice the frequency content of the horizontal component. This knowledge has been the basis for the acceptance, with incomplete understanding, of the apparent ability of flies to distinguish between body rate components. Given the

Fig. 2 As the haltere beats back and forth the velocity component perpendicular to Ω_x changes sign at twice the frequency as the component perpendicular to Ω_y . This results in a Coriolis force with two distinct frequency components



Tu and Dickinson (1994, 1996).

haltere specific rate components, variations of bilateral summing and differencing allow construction of signals proportional to components of the body rate vector in any body-fixed direction. Studies have demonstrated the location and activation of both ipsilateral and contralateral neural pathways between the halteres and the muscles of the wing and neck (Sandeman and Markl 1980; Fayyazuddin and Dickinson 1996, 1999). Further studies have demonstrated visual pathways to the halteres allowing speculation of a feedforward process that introduces virtual rate "errors" into the control loop through the manipulation of a complex of muscles at the base of the haltere (Chan et al. 1998).

The objective of the current research is to use the techniques of engineering mechanics to analyze the haltere and thereby establish the fundamental quantities required for and mathematical limitations associated with reconstruction of body rate components. The only viable mechanism documented so far for decoupling of the two haltere rate components has been frequency demodulation (Wu and Wood 2006). In contrast to frequency demodulation, the methods of this paper demonstrate the potential to use strain and strain rate encoded by the mechanoreceptors at the base of the haltere to measure the same two rate components. This measurement is possible due to the natural decoupling of the rate components at the center of the haltere stroke and the approximately linear nature of the governing equation of motion. An error analysis is also provided that illustrates how relative errors inherent in the measurement of all three body rate components can be inferred due to the nonlinearities in the "true" equations of motion. These results have implications to interpretation of past experimental results and understanding of sensory structures associated with the halteres.

Methods

Previous work on haltere mediated reflexes (Dickinson 1999) describes the physical geometry of the fruit fly, Drosophila melanogaster. This description of the geometry (Fig. 3) is used as a starting point for the haltere analysis in this paper. The predominant characteristics of the biological system used in the current development are the amplitude of the haltere stroke and the configuration of the halteres with respect to the mid-sagittal and transverse planes of the fly body. The halteres on Drosophila oscillate in a plane that is tilted back roughly thirty degrees toward the mid-sagittal plane. The line that defines the intersection of the haltere stroke plane with the sagittal plane is rotated toward the head by approximately twenty degrees so that at the top of its stroke the tip of the haltere is in a more anterior position than at the bottom of the stroke as shown in Fig. 3. However, since the line of intersection of the haltere planes is, for convenience, used to define the body yaw axis, \hat{x}_3 , the value of this angle is arbitrary. For the purpose of this study the intersection of the haltere planes is assumed to be fixed relative to the body. The wing beat frequency, which was nominally 215 Hz in the data reported by Dickinson (1999) for Drosophila, varies significantly both within and between species. For the sake of analytical convenience, a haltere frequency of 200 Hz was used in simulations where general effects of out-of-plane stiffness and damping impact on the trajectory were simulated.

The equations of motion developed in this study are nondimensional and describe the system in terms of its natural frequency and damping coefficient. The component of the haltere motion in the primary plane of oscillation is assumed to be deterministic and purely harmonic as observed in the

Fig. 3 Reference frame definitions for the halteres, *b* and *c*, and frame *x*, which defines the roll (x_1) , pitch (x_2) and yaw (x_3) axis. The angle beta is arbitrary with this definition of reference frames





body reference frame, oscillating through a range of $\pm 90^{\circ}$. Damping of out-of-plane motion is assumed to be proportional to the angular rate of the out-of-plane motion and the stiffness proportional to out-of-plane displacement. The source of stiffness is not specified, whether it is due to the resiliency of the haltere stalk or the joint and its associated musculature. The haltere model for out-of-plane motion can be considered as an equivalent mass at the radius of gyration of the haltere on a rigid massless structure with a torsional spring and damper at the base. The actual dynamics and control of the haltere may be much more complex and is an area of ongoing research. Chan et al. (1998) describes eight direct control muscles at the base of the haltere similar to the muscles at the base of the wing. These muscles could possibly fine tune the kinematics of the haltere.

The equations of motion are generated without any small angle assumptions for the purpose of simulating the haltere trajectory under the influence of constant inertial body rates. Transients are not considered in this phase of the research and only the haltere response under the ideal conditions of constant angular rate were examined to draw preliminary conclusions about the fundamental limitations of the haltere or haltere pair. This steady-state assumption is equivalent to assuming that the body rates have a significantly longer period than the period of haltere oscillation and any associated transients.

Finally, the component of angular rotation of the haltere in its primary plane is assumed to be sinusoidal. That is, the angular position γ of the haltere in its primary plane of motion is assumed to be

$$\gamma = \frac{\pi}{2}\sin(\omega t),$$

where ω is the constant beat frequency of the haltere. The actual profile has been observed to be closer to a saw-tooth pattern (Nalbach 1993) having a flatter angular velocity profile for the majority of the stroke and a quicker turn around at the ends. The sinusoidal model provides an analytically simpler form that can be used to develop valid conclusions due to the similar symmetry of motion with respect to the center of the stroke.

Results

Kinematic assessment

Insight regarding the forces acting in the out-of-plane direction can be examined by first assuming no out-of-plane haltere deflection. The right half of Fig. 3 shows the right haltere and reference frame directions associated with the haltere and inertial space. In the following sections, hatted variables represent unit vectors that describe orthogonal directions for the required reference frames. Left

superscripts describe which reference frame the vector quantity is observed within. Right superscripts identify the point or reference frame the quantity characterizes. The body angular rate vector relative to the inertial frame, ${}^{e}\vec{\omega}^{b} = {}^{e}\vec{\omega}^{x}$, is represented in the right haltere reference frame as

$$\vec{\omega}^{o} = \Omega_1 \hat{b}_1 + \Omega_2 \hat{b}_2 + \Omega_3 \hat{b}_3.$$
⁽¹⁾

In this expression, Ω_i are the angular velocity components and \hat{b}_i are the body fixed unit vectors as shown in Fig. 3. The position, velocity and acceleration of a point mass at the radius of gyration of the haltere are found through successive differentiation to be

$$\vec{P}_{02} = \vec{P}_{01} + \vec{P}_{12} \tag{2}$$

$$e\bar{v}^{2} = e\bar{v}^{1} + b\bar{v}^{2} + e\bar{\omega}^{b} \times \bar{P}_{12}$$
 (3)

$$e\overline{a}^{2} = e\overline{a}^{1} + b\overline{a}^{2} + 2(e\overline{\omega}^{b} \times b\overline{v}^{2}) + e\overline{\omega}^{b} \times (e\overline{\omega}^{b} \times \overline{P}_{12}) + e\overline{\alpha}^{b} \times \overline{P}_{12}.$$

$$(4)$$

In these expressions, 0, 1, and 2 refer to an arbitrary point fixed in inertial space, a point at the base of the haltere, and a point at the radius of gyration of the haltere, respectively. The first acceleration term, $e\vec{a}^{1}$, which is the acceleration of the base of the haltere with respect to the inertial frame is assumed to be small. The second term, $ba^{-2}a$ which represents acceleration of the haltere mass as observed from the body, is entirely in the plane of the haltere. Nalbach (1993) showed that these primary accelerations in the plane-of-motion are much higher than contributions associated with the body angular rates, and therefore, useful information pertaining to the body rates is unlikely to be ascertained from in-plane force measurements. The last term, $e_{\alpha}^{\vec{D}} \times \vec{P}_{12}$, which involves the angular acceleration of the body, was also shown by Nalbach to be a factor of 5 or more less than the third (Coriolis) term for sinusoidal body oscillations under 50 Hz. The remaining two terms after taking the appropriate vector products are

$$2({}^{e}\bar{\omega}^{b} \times {}^{b}\bar{v}^{2}) = 2r\dot{\gamma}[-\Omega_{2}\sin(\gamma)\hat{b}_{1} + (\Omega_{1}\sin(\gamma) + \Omega_{3}\cos(\gamma))\hat{b}_{2} - \Omega_{2}\cos(\gamma)\hat{b}_{3}]$$
(5)

$${}^{e}\bar{\omega}^{b} \times ({}^{e}\bar{\omega}^{b} \times \bar{P}_{12}) = r[(-\Omega_{2}^{2}\sin(\gamma) - \Omega_{3}^{2}\sin(\gamma) + \Omega_{1}\Omega_{2}\cos(\gamma))\hat{b}_{1} + (\Omega_{1}\Omega_{2}\sin(\gamma) + \Omega_{2}\Omega_{3}\cos(\gamma))\hat{b}_{2} + (\Omega_{1}\Omega_{3}\sin(\gamma) - \Omega_{1}^{2}\cos(\gamma) - \Omega_{2}^{2}\cos(\gamma))\hat{b}_{3}].$$
(6)

The expression in Eq. 5 is the Coriolis term which generates out-of-plane (\hat{b}_2) force components associated with the in-plane body rates. These components are

proportional to $2\dot{\gamma}\Omega_1$ and $2\dot{\gamma}\Omega_3$. The other components represent an in-plane acceleration directed along the stalk of the haltere proportional to Ω_2 . The expression in Eq. 6 describing the centripetal accelerations, also generates outof-plane forces on the haltere proportional to $\Omega_1\Omega_2$ and $\Omega_2\Omega_3$. The relative magnitudes of $\dot{\gamma}$ and Ω_2 will determine the significance of these centripetal terms. Errors introduced by these terms are quantified subsequently. If the centripetal terms are small, the out-of-plane force on the haltere should be predominantly due to the Coriolis term and therefore will be associated with the body rate components that are in the primary plane of the haltere motion. Equations 5 and 6 are based on the assumption that the haltere is infinitely rigid and does not deflect out-of-plane. This assumption is the basis for the previous kinematic analysis of the haltere by Pringle and Nalbach and is useful for developing intuition regarding the predominant forces that impact the problem. In the following section, this assumption is eliminated to simulate the out-of-plane motion, or equivalently the strains resulting from that motion.

If the halteres are assumed to measure forces associated with the Coriolis accelerations, the measured signals should be proportional to the in-plane body rate components, Ω_1 and Ω_3 , as shown in Eq. 5. If two halteres that are initially in a common plane are rotated out of the plane by an angle α as shown in Fig. 3, then all three components of the body inertial rate vector can be reconstructed. The body rate vector represented in the body-fixed roll, pitch, yaw frame is

$${}^{e}\bar{\omega}^{\nu} = W_1 \hat{x}_1 + W_2 \hat{x}_2 + W_3 \hat{x}_3, \tag{7}$$

where (W_1, W_2, W_3) are the body roll, pitch, and yaw rates, respectively.

The relationships between the components of the body rate vector represented in the body roll, pitch, yaw frame and the components represented in the right haltere frame \hat{b} and the left haltere frame \hat{c} are

$${}^{e}\bar{\omega}^{b} = W_{1}\hat{x}_{1} + W_{2}\hat{x}_{2} + W_{3}\hat{x}_{3}, \tag{7}$$

$$W_1 = -\frac{\Omega_{b3} + \Omega_{c3}}{2\sin(\alpha)} \tag{9}$$

$$W_2 = \frac{\Omega_{b3} - \Omega_{c3}}{2cos(\alpha)} \tag{10}$$

$$W_3 = -\frac{\Omega_{b1} + \Omega_{c1}}{2} = -\Omega_{b1} = -\Omega_{c1}.$$
 (11)

The importance of these transformations is that they allow a direct calculation of rate components along the body roll, pitch, and yaw axes, W_1 , W_2 , and W_3 , given the two rate components that are measurable in each of the haltere reference frames. The research on halteres by Pringle (1948) did not recognize the ability of the insect to combine the output of two halteres and thereby distinguish between pitch and roll components of the body rate vector. Pringle initially assumed that the halteres represented a redundant means of measuring yaw rate. Later experimental results by Faust (1952) demonstrated the ability of flies to react independently to each of the body rates. Nalbach (1994) also published an article that experimentally demonstrated the bilateral combination of haltere measurements in Calliphora. Therefore, within the neural architecture of dipteran insects there may be a basic representation of Eqs. 9-11, although this does not rule out fusion of measurements from other sensors that support inertial stabilization.

Dynamics equation allowing for out-of-plane motion

For the purpose of simulating the dynamics of the haltere, out-of-plane motion is considered. With the out-of-plane deflection angle defined as θ , summing moments associated with damping, stiffness, and inertial forces around the base of the haltere results in the following expression:

$$\ddot{\theta} + 2\zeta\omega_n\dot{\theta} + \omega_n^2\theta = \dot{\Omega}_3\sin(\gamma) - \dot{\Omega}_1\cos(\gamma) - \dot{\gamma}^2\cos(\theta)\sin(\theta) + 2\dot{\gamma}[(\Omega_3\cos(\gamma) + \Omega_1\sin(\gamma))\cos^2(\theta) - \Omega_2\cos(\theta)\sin(\theta)] + (\Omega_3^2\cos^2(\gamma) + \Omega_1^2\sin^2(\gamma) - \Omega_2^2)\cos(\theta)\sin(\theta) + (\Omega_2\Omega_3\cos(\gamma) + \Omega_1\Omega_2\sin(\gamma))\cos(2\theta) + 2\Omega_1\Omega_3\cos(\theta)\sin(\theta)\cos(\gamma)\sin(\gamma).$$
(12)

In Eq. 12, ζ is the damping ratio, and ω_n is the natural frequency that characterizes the out-of-plane stiffness and mass characteristics of the haltere. In this form, the haltere can be simulated by varying the out-of-plane natural frequency relative to the haltere beat frequency as well as varying the haltere damping characteristics. Again, the haltere stroke angle is assumed to vary with a simple characteristic motion $\gamma = \frac{\pi}{2} \sin(\omega_h t)$, with the angular frequency of the haltere, $\omega_h = 200$ Hz. The derivation of Eq. 12 is described in the "Appendix". The relationship describing the single axis sensitivity of a micro-electromechanical (MEMS) vibrating structure gyroscope can be found through simplification of this expression (e.g., Apostolyuk 2006).¹

¹ For the case where both θ and γ are much less than 1, damping is small, $\omega_n^2 \gg A^2 \omega_h^2$, and $\omega_n^2 \gg \omega_h^2$, Eq. 12 reduces to $\ddot{\theta} + \omega_n^2 \theta = 2\Omega_3 \dot{\gamma} = 2\Omega_3 A \omega_h \cos(\omega_h t)$. The forced solution to this equation, $\theta = 2\Omega_3 A \omega_h \cos(\omega_h t) / \omega_n^2$, is the solution for the out-of-plane displacement of the MEMS gyro mechanism.

Haltere trajectory simulations

Simulations of the developed equation of motion were executed for a variety of cases with variations in the damping ratio and out-of-plane stiffness. The intent was to determine the characteristics of the displacement trajectories and the impact of nonlinear coupling of out-of-plane rate components into the in-plane component measurements. All simulations were executed with constant body rates. For the purpose of generating the plots, the haltere motion was initiated with no out-of-plane displacement and the haltere was allowed to transiently respond to the forces resulting from input body rates. The simulation was executed for 40 oscillations, with the last 20 used for making the plots. Because the haltere reaches a steady state trajectory, the 20 oscillations overlap, appearing as one closed loop. The only cases in which the haltere did not reach steady state were when the out-of-plane natural frequency was significantly less than the haltere oscillation frequency, or for low damping. These plots are not shown since they represent very large out-of-plane motion for the assumed model, which would not be representative of the biological system.

Out-of-plane stiffness variations

Figures 4 and 5 show the trajectories associated with a haltere out-of-plane natural frequency equal to and

double the beat frequency of 200 Hz, respectively. The plots show out-of-plane displacement in radians as the ordinate, plotted against the stroke angle of the haltere as the abscissa. A haltere stroke angle of 0 has the haltere at the center of the stroke. The Ω_1 input generates the expected frequency doubled signal as the haltere sweeps through a semi-circular arc causing the velocity component perpendicular to Ω_1 to change sign twice, therefore the Coriolis force changes sign twice. The haltere velocity perpendicular to Ω_3 only changes sign once, giving no frequency doubling effect. The angular displacements peak at approximately half a degree for the conditions shown. When the natural frequency is significantly below 200 Hz, the out-of-plane motion is driven to very large angles and never reaches a steady state pattern.

Damping variations

Examples of damping variations are shown in Fig. 6 for the case of $\omega_n = 200$ Hz and input body rates of $\Omega_1 = \Omega_3 = 10$ rad/s. These plots demonstrate the significant impact that damping variations, whether passively or actively induced, can have on the haltere trajectory. At low damping levels, $\zeta \approx 0.01$, the trajectory never reached steady state within the forty oscillation (0.2 s) simulation time (data not shown).









The haltere displacement averaged with respect to haltere stroke angle is also shown in Fig. 6. However, when the average displacement is plotted separately for the two rate components as in Fig. 7, an interesting characteristic emerges that may provide insight into a possible mechanism by which the body rates are decoupled by the insect.

Figure 7 demonstrates a natural decoupling of the body rate components at the center of the haltere stroke. At $\gamma = 0$, the averaged magnitude of the response driven by Ω_3 is zero and the averaged slope of the response driven by Ω_1 is zero. If the governing differential equation (i.e., Eq. 12) that describes the motion of the haltere is approximately linear, then the final trajectory of the haltere would simply be the superposition of the response of the two plots shown. Also, each of these plots would scale in proportion to the magnitude of the associated body rate since the Coriolis forces driving the motion are proportional to the respective body rates. Therefore, by measuring the slope and the magnitude of the response near the peak of the haltere trajectory, and having tuned in the appropriate proportionality constants, the body rate components in the plane of the haltere motion could be directly obtained. These observations suggest the following hypotheses:



- 1. An organism with halteres measures a signal proportional to the magnitude of the averaged strain at the peak of the haltere stroke and takes advantage of the approximate linearity of the haltere dynamics to estimate Ω_1 (i.e., Ω_1 is proportional to the averaged magnitude of the strain at the middle of the stroke).
- 2. An organism with halteres measures a signal proportional to the magnitude of the averaged strain rate² at the peak of the haltere stroke and takes advantage of the approximate linearity of the haltere dynamics to estimate Ω_3 (i.e., Ω_3 is proportional to the averaged magnitude of the strain rate at the middle of the stroke).

Measurements by Pringle (1948) gave indication that the nerve afferents at the end of the stroke may be overwhelmed by signals associated with haltere motion reversal. This would support the supposition that the response of Coriolis-sensitive sensilla during the middle of the haltere stroke is of primary use by insects. The

² Note that the term strain rate can refer to two quantities that are proportionally related at the center of the haltere stroke. Because the angular acceleration of the stroke is approximately zero at the middle of the stroke, the strain rate is proportional to the spatial derivative of strain (ε) with respect haltere position (γ). That is $\frac{dc}{dt} = \frac{d\varepsilon}{dt}\frac{d\gamma}{dt} = \text{Const} \cdot \text{sgn}(\frac{d\gamma}{dt}) \cdot \frac{d\varepsilon}{d\tau}$.

proposed method of determining the body rates is more direct than that patented by Wu and Wood (2006). In their patent, the fundamental frequency doubling is taken advantage of through a demodulation scheme to separate the two signals and determine the driving forces. The method proposed here may be directly realizable using discrete measurements, although it remains to be proven that the fields of strain mechanoreceptors (campaniform sensilla) existing at the base of the haltere encode quantities proportional to both strain and strain rate.

The described mechanism for measuring the body rates requires three characteristics of Eq. 12.

- 1. Linearity
- 2. Minimal dependence on the out-of-plane body rate Ω_2
- 3. Two independent forcing functions proportional to the in-plane body rate components Ω_1 and Ω_3

If these characteristics are met, the response to the two in-plane body rate components is uncoupled and the two independent responses are linearly proportional to the magnitudes of the respective body rates. By making various approximations associated with small displacement angles and the magnitudes of the various coupling terms, Eq. 12 can be reduced to a form that expresses the desired characteristics.

$$\ddot{\theta} + 2\zeta\omega_n\dot{\theta} + (\omega_n^2 + \dot{\gamma}^2)\theta = 2\dot{\gamma}\Omega_3\cos(\gamma) + 2\dot{\gamma}\Omega_1\sin(\gamma).$$
(13)

If $\dot{\gamma}^2$ is further assumed to be small compared to ω_n^2 then a second form that satisfies the desired characteristics can be found.

$$\ddot{\theta} + 2\zeta\omega_n\dot{\theta} + \omega_n^2\theta = 2\dot{\gamma}\Omega_3\cos(\gamma) + 2\dot{\gamma}\Omega_1\sin(\gamma).$$
(14)

The second form, shown in Eq. 14, is intuitive since it is a simple spring-mass-damper driven by Coriolis forces.

An open question is whether either Eq. 13 or Eq. 14 are a valid approximation of the full non-linear equation. Comparative simulations were performed between Eqs. 12 and 14. The closeness of the two darker curves in Fig. 8 demonstrate that the first form of the linear approximations

-2

-1

Haltere Position (rad)

in Eq. 13 is an accurate representation of the haltere response, unlike the results from Eq. 14 which are plotted in the lighter color. Since Eq. 13 is a good approximation, the natural decoupling of the trajectories is assumed to be a generally valid assumption.

Analysis of errors due to non-linearity

An error analysis was performed to demonstrate the limitations the non-linear and out-of-plane cross-coupling terms imposed on the linear approximation of Eq. 13. Simulations were executed over a full range of pitch and yaw body rates (i.e., $-20 \le W_1 \le 20$ and $-20 \le W_2 \le 20$ rad/s). Although Schilstra and van Hateren (1999) described a maximum angular rate of 2,000 deg/s (34 rad/s) for Calliphora vicina, measurements included intentional saccadic maneuvers. The lower rate used in these simulations (20 rad/s) is considered a sufficient maximum for rate errors incurred during typical stabilized flight. These rates were transformed into the reference frames for each of the halteres and then the dynamics for the haltere were simulated using the full nonlinear model in Eq. 12. Using best estimates of the strain rate and strain magnitude proportionality constants (i.e., constants found to give near zero error for an idealized linear model) the body rates in the haltere frames were estimated. The estimates from the two halteres were then combined using Eqs. 9-11 to reconstruct an estimate for the roll, pitch and yaw rates in the body frame. Each plot represents errors associated with 1681 combinations of yaw and pitch rate for a fixed roll rate. The error is the difference between the exact input body rates and the estimated body rates as demonstrated in Fig. 9.

Figure 10 depicts the absolute errors for the pitch, yaw, and roll components of the body rates for the case of critical damping ($\zeta = 1$) and 400 Hz out-of-plane natural frequency. Figure 11 shows the errors for the case where the body roll rate is 5 rad/s.

The change in characteristics shown in Fig. 11 can be explained by examining the governing equation of motion (Eq. 12). The terms involving Ω_2 , which is the out-of-plane



2



Fig. 8 Comparison of the linear simplifications represented by Eq. 13 (red) and Eq. 14 (green) with the non-linear Eq. 12 (blue). Results are shown for W_3 = (10, 10, 10) on the *left* and W = (10, 10, 0) on the right



Fig. 9 The error analysis compared the true rate components along the roll, pitch, and yaw body axis with those reconstructed using the proportional assumptions described in the text. Results are reported as absolute error in rad/s



Fig. 10 Error in estimates of rate components along the body yaw, pitch, and roll axes for case roll rate = 0. Conditions vary over a range of -20 to 20 rad/s for the true yaw and pitch rates. The *color* indicates the level of *error* as indicated on the *color bar* to the right of each plot

rate component and the component most closely aligned with the body roll axis, are summarized below after assuming a small out-of-plane displacement angle, θ

$$-2\dot{\gamma}\Omega_2\theta + \Omega_2^2\theta + \Omega_2\Omega_3\cos(\gamma) + \Omega_1\Omega_2\sin(\gamma). \tag{15}$$

Since θ is small, the last two terms in Eq. 15 will dominate. Note that $\cos(\gamma)$ will always be positive for all stroke angles, γ , and will be symmetric around $\gamma = 0$. Therefore, the term involving $\cos(\gamma)$ will influence the magnitude of the out-of-plane displacement at $\gamma = 0$ (i.e., the term will influence the yaw error). The term is also proportional to Ω_3 , which is closely aligned with the body pitch axis. Therefore, roll coupling will introduce error in the yaw rate estimate that is proportional to the pitch rate. This linear relationship between yaw rate estimation error and pitch rate is exactly what is depicted in the left hand plot in Fig. 11. Similar arguments, accounting for the influence of the $\sin(\gamma)$ function on the slope of the haltere out-of-plane motion at $\gamma = 0$ and the proportionality of pitch rate estimation error to the body yaw rate Ω_2 , can be made to explain the second plot in Fig. 11. The similarity of the third plots in Figs. 10 and 11 indicate that the errors from the two halteres cancel, leaving the roll estimate error unaffected by roll rate.



Fig. 11 Error in estimates of rate components along the body yaw, pitch, and roll axes for case roll rate = 5 rad/s. Conditions vary over a range of -20 to 20 rad/s for the true yaw and pitch rates

Discussion

The intent of this research was to complement previous studies of halteres by performing a more rigorous analysis of mechanical response, establishing the potential mechanisms and inherent limitations for reconstruction of a complete body inertial rate vector (e.g., pitch, yaw and roll rate). In summary, a derivation of the kinematic and dynamic relationships is provided, allowing for simulation of out-of-plane displacement trajectories of the haltere. In reviewing these trajectories, a natural decoupling of the two in-plane inertial rate components is apparent. This is the most significant result of the current research. The vertical and lateral components of rate were, respectively, found to be proportional to the time averaged amplitude and time averaged slope of the trajectory at the center of the haltere stroke. When the dynamics were simplified, an approximate linear form was found, thereby allowing the observation of decoupling of the rate components to be held as a general conclusion. Through coordinate transformation, the mathematical relations allowing for bilateral combination of the haltere-measured rates to construct signals proportional to the conventional body pitch, yaw, and roll rate components were summarized.

Simulations were constructed based on the assumed ability to measure averaged trajectory amplitude and slope, or equivalently strain and strain rate, at the center of the haltere stroke. These simulations quantify the error associated with the assumed linearity and associated rate decoupling. Simulations were executed over a wide range of pitch and yaw rate (-20 to 20 rad/s) and were presented for two roll rate cases (0 and 5 rad/s).

Mechanoreceptive encoding

The question remains as to whether the haltere mechanoreceptors provide rate component information to the insect motor control functions in a way that is compatible with the mathematical constructs described. Ideally, the insect could discretely sample strain and strain rate signals at the center of the haltere stroke, average these values over time, and thereby perfectly decouple the two inertial rate components in the plane of the haltere motion. The subsequent discussion will suggest ways in which the proposed decoupling mechanism may be consistent with the insect sensory and neuronal anatomy.

The haltere sensor structure is composed of a finite number of campaniform sensilla distributed in fields at the base of the haltere and an internal chordotonal organ (Pringle 1938, 1948; Gnatzy et al. 1987). The homologs to the haltere sensilla on the forewings are thought to individually be poor magnitude detectors due to their rapid saturation and high frequency functionality (Dickinson 1990). Unlike campaniform sensilla on locust wings that operate at lower beat frequencies and provide a burst of action potentials whose strength may correlate well with strain magnitude (Elson 1987), the campaniform sensilla on *Calliphora* wings are thought to fire phasically, perhaps once per stroke cycle (Dickinson 1990) at saturation.

Favyazuddin and Dickinson (1996, 1999) documented research that characterized the afferents of the basal plate sensilla (dF2) and attempted to rule out the other campaniform fields in ipsilateral control of the basalar wing muscles. Their conclusion was that dF2 was primarily responsible for steering motor control associated with mnb1 and that the connection consisted of both a fast monosynaptic electrical component and a slow chemical component. These studies did not report any attempt to distinguish between strain and strain rate as parameters for which there may be distinct proportional sensitivity. Additional studies are required to measure bilateral signal combination and the potential role of the sensilla of the chordotonal organ in the haltere which Pringle (1948) estimated were oriented preferentially to measure bending shear.

The basal field (dF2) is composed of one hundred spatially distributed campaniform sensilla in *Calliphora vicina* (Gnatzy et al. 1987). Assuming dF2 is primarily responsible for Coriolis sensing, the proposed hypothesis requires, either through direct sensing or through appropriate processing, measurement of distinct signals proportional to both averaged strain rate and averaged strain magnitude using only the sensilla in dF2. For example, as has been proposed for the insect wing (Dickinson 1990), if the magnitude of strain is encoded through enlistment of increased numbers of sensilla within dF2, the compound extracellular potential and the related synaptic drive would increase with strain magnitude. Similarly, the asymmetry of the haltere trajectory represented by strain rate at the center of the stroke might be encoded through differencing of upstroke and downstroke response of dF2. The phasing of the dF2 response might be related to the sign of the rate being measured. Pringle (1948) reported a correlation of the temporal phasing of the spikes, believed to be coming from the basal field and large chordotonal organs, to the magnitude of yaw rate. Fayyazuddin and Dickinson (1999) also demonstrated the impact of phasing of the signal from the haltere on wing muscle response, causing both adduction/abduction and amplitude variation in wing kinematics. The monosynaptic connection between the halteres and mnb1 is sufficiently fast to synchronously transmit phasing information (Fayyazuddin and Dickinson 1999).

As described in Fig. 1, there are a number of fields of strain sensors that are not indicated in the encoding of Coriolis forces. These fields, along with the chordotonal organ, may facilitate other aspects of haltere motion, e.g., the motion reversal at the ends of the stroke or articulation of the haltere during abdominal cleaning or tactile retraction (Sandeman and Markl 1980). The work of Heide (1983) also suggests the possibility that these other fields may provide synchronous timing signals that influence the firing phase of the many steering muscles involved in wing

control. In this way, they may play a role similar to the proximal campaniform sensilla of the wing which Fayyazuddin and Dickinson (1996) indicated could control firing phase of the first basalar muscle during non-rotating flight.

Mechanoreceptive averaging modality

The mechanism proposed for rate decoupling requires averaging of strain parameters on the upstroke and downstroke of the haltere. Averaging, as well as the bilateral combinations described by Eqs. 9-11, can be accomplished through a number of mechanisms. In addition to direct signal summation, low pass filtering resulting from tonic response may also provide a signal proportional to the average. A third possibility is to obtain the end effect of a difference or summation of drive signals through application of opposing force generation. For example, commanding increased wing stroke amplitude on one side and independently commanding a decrease on the other side effectively provides the bilateral summation of the two commands in the form of a roll moment.

For pitch rate as defined in this paper, the downstroke and the upstroke response is simultaneously expressed by the opposing halteres due to the bilateral symmetry of the sensor fields and the anti-symmetry of the Coriolis forces (see Figs. 12, 13). Therefore, the strain magnitude from the upstroke of the two halteres could be simultaneously encoded and combined to generate a stabilizing torque proportional to pitch rate. Alternatively, if averaged strain rate were encoded by each haltere, the signals could be ipsilaterally expressed by the wings so that the net result is proportional to the pitch rate. Bilateral processing is not required in the case of the yaw rate component due to the bilateral symmetry of the halteres (Fig. 13). Either haltere



Fig. 12 The Coriolis force induced by pitch rate has bilateral symmetry, but yaw and roll have asymmetric forces. As a result, summing *left* and *right* haltere response allows direct determination of pitch rate without pre-averaging

	Left Haltere	Right Haltere	Sum/2	Dif/2
Upstroke	$(m_r+m_p-m_y)^*\gamma+(-b_r-b_p-b_y)$	$(-m_r+m_p+m_y)^* \gamma + (b_r-b_p+b_y)$	m _p * γ -b _p	$(m_r-m_y)^* \gamma + (-b_r-b_y)$
Downstroke	$(m_r+m_p+m_y)^* \gamma + (b_r+b_p-b_y)$	$(-m_r+m_p-m_y)^* \gamma + (-b_r+b_p+b_y)$	$m_p^* \gamma + b_p$	(m _r +m _y)* γ +(b _r -b _y)
Average	(m _r +m _p)* γ -b _y	(-m _r +m _p)* γ +b _y	$m_p^* \gamma$	m _r * γ -b _y

Fig. 13 Linear approximations of the strain at the center of the haltere stroke (m_r, m_p, m_y) represent the magnitudes of the roll, pitch and yaw rate of change of strain with respect to stroke angle. (b_r, b_p, b_y) represent the magnitudes of the roll, pitch and yaw strain with

respect to stroke angle. The unilateral and bilateral processing required to decouple the components is clearly seen by summing and differencing the right and left haltere responses

can provide a signal proportional to yaw rate by averaging the upstroke and downstroke strain magnitude of that haltere. Fayyazuddin and Dickinson (1996) showed both a phasic and a tonic component between the halteres and mnb1. The tonic response was sufficiently slow to effectively average the upstroke and downstroke signals at the wing beat frequency. Unambiguously responding to roll rate errors would require bilateral summation of the averaged strain rate response from both halteres. Assuming some means of encoding strain rate, roll correction could be accomplished by ipsilaterally transmitting the upstroke and downstroke signals through a signal path or muscle associated with wing stroke amplitude that is sufficiently tonic to average the signal. The combined effect of the two wings would then bilaterally combine to create the correcting roll torque.

Preliminary simulation results (data not shown) indicate that the rate decoupling mechanism described is fairly insensitive to the details of the encoding scheme. For example, when continuous, modeled strain and strain rate signals are passed through a weak low pass filter and then bilaterally combined according to Eqs. 9-11, the mean signals track the true rate components well. This indicates that encoding precisely at the center of the haltere stroke is not critical. Other preliminary results have demonstrated the feasibility of encoding and reconstructing the full body rate vector using only discreet compressive strain magnitude measurements to describe the symmetric and asymmetric aspects of the haltere trajectory. These results indicate that while direct encoding of strain rate would represent a useful submodality of the dF2 field, it is not necessary. Future research will develop and document a more detailed model of the mechanoreceptor physiology and the torque motor steering control mechanisms in order to further establish the proposed model as a biologically plausible mechanosensory mechanism.

The reported simulation results assume a constant angular rate and therefore isolate the impact of Coriolis forces from body angular acceleration. For the case of low angular acceleration, the results imply the potential to distinguish the components of the body rate vector. Some authors have entertained the possibility that halteres are primarily angular acceleration sensors (Sandeman and Markl 1980; Sandeman 1980) used for stabilization after extreme saccadic maneuvers. In contradiction, Hengstenberg et al. (1986) later demonstrated a direct correlation between angular rate magnitude and compensatory response. The mechanics dictate that both yaw rate and yaw acceleration will cause the halteres to respond with a strain magnitude at the center of the stroke. These two effects will be indistinguishable and a stabilizing response to one will also be a stabilizing response to the other. Similarly, roll and pitch accelerations will increase the average strain rate in a way that provides negative feedback consistent with the Coriolis forces. The role of the halteres during saccades needs to be further investigated given the ability of flies to generate large angular maneuvers in the span of a few wingbeats (Schilstra and van Hateren 1999). Assuming similar amplitudes, as the period of a maneuver approaches the period of haltere motion, the impact of angular acceleration and Coriolis force will approach the same order of magnitude. While the model generated in this report (Eq. 12) includes the body acceleration terms, it was outside the scope of the current effort to fully evaluate the impact of all possible kinematic scenarios on flight stability.

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Appendix: Derivation of the haltere dynamics equation

The expression in Eq. 12 can be determined by defining two reference frames in addition to the body fixed frame. These frames are related by the stroke angle γ and the outof-plane displacement angle θ , as shown in Fig. 14. When these angles are zero, the three frames are co-aligned. The associated angular velocities are

$${}^{e}\bar{\omega}^{\nu} = \Omega_1 \hat{b}_1 + \Omega_2 \hat{b}_2 + \Omega_3 \hat{b}_3 \tag{16}$$

$${}^{b}\bar{\omega}^{h} = \dot{\gamma}\,\hat{b}_{2} \tag{17}$$

$${}^{h}\bar{\omega}^{f} = \dot{\theta}\,\hat{h}_{1}\,. \tag{18}$$

The position and velocities, as observed in the various reference frames, of the mass at the end of the haltere (Point 2) are

$$\vec{P}_{12} = r\hat{f}_3 \tag{19}$$

$${}^{h}\overline{v}^{2} = {}^{h}\overline{\omega}^{f} \times \overline{P}_{12} \tag{20}$$

$${}^{b}\bar{v}^{2} = {}^{b}\bar{v}^{2} + {}^{b}\bar{\omega}^{h} \times \bar{P}_{12}$$
(21)

$${}^{e}\overline{v}^{2} = {}^{b}\overline{v}^{2} + {}^{e}\overline{\omega}^{h} \times \overline{P}_{12}$$

$$\tag{22}$$

The expressions leading to the acceleration of the haltere relative to the inertial frame are

$${}^{h\vec{a}^{2}} = {}^{h\vec{\alpha}^{f}} \times \vec{P}_{12} + {}^{h}\vec{\omega}^{f} \times {}^{h}\vec{\omega}^{f} \times \vec{P}_{12}$$
(23)

$${}^{b}\overline{a}^{2} = {}^{h}\overline{a}^{2} + 2({}^{b}\overline{\omega}^{h} \times {}^{h}\overline{v}^{2}) + {}^{b}\overline{\alpha}^{h} \times \overline{P}_{12} + {}^{b}\overline{\omega}^{h} \times {}^{b}\overline{\omega}^{h} \times \overline{P}_{12}$$
(24)

$${}^{e}\overline{a}^{2} = {}^{b}\overline{a}^{2} + 2({}^{e}\overline{\omega}^{b} \times {}^{b}\overline{v}^{2}) + {}^{e}\overline{\alpha}^{b} \times \overline{P}_{12} + {}^{e}\overline{\omega}^{b} \times {}^{e}\overline{\omega}^{b} \times \overline{P}_{12} \,.$$

$$(25)$$

The expression in Eq. 25 assumes that the acceleration of the body (Point 1) is small relative to the relevant haltere acceleration terms. This results in the acceleration of point



Fig. 14 The relative orientation of the reference frames associated with the equation of motion derivation are shown above. The "h" frame is rotated by angle γ with respect the "b" frame. The "f" frame is rotated by angle θ with respect to the "h" frame

2 with respect to the earth (inertial) frame in the \hat{f}_2 direction as

$$\hat{f}_{2} \cdot {}^{e} \vec{a}^{2} = r [\dot{\Omega}_{3} \sin(\gamma) - \dot{\Omega}_{1} \cos(\gamma) - \dot{\gamma}^{2} \cos(\theta) \sin(\theta) + 2\dot{\gamma} [(\Omega_{3} \cos(\gamma) + \Omega_{1} \sin(\gamma)) \cos^{2}(\theta) - \Omega_{2} \cos(\theta) \sin(\theta)] + (\Omega_{3}^{2} \cos^{2}(\gamma) + \Omega_{1}^{2} \sin^{2}(\gamma) - \Omega_{2}^{2}) \cos(\theta) \sin(\theta) + (\Omega_{2} \Omega_{3} \cos(\gamma) + \Omega_{1} \Omega_{2} \sin(\gamma)) \cos(2\theta) + 2\Omega_{1} \Omega_{3} \cos(\theta) \sin(\theta) \cos(\gamma) \sin(\gamma) - \ddot{\theta}].$$
(26)

The final expression in Eq. 12 is obtained by taking the dot product of the inertial force, $(-m^e \bar{a}^2)$, in the direction of the out-of-plane deflection (\hat{f}_2) and then adding the forces associated with stiffness and damping to create a zero sum as

$$\hat{f}_2 \cdot (\vec{F}_{\text{intual}} + \vec{F}_{\text{damping}} + \vec{F}_{\text{stiffness}}) = 0.$$
(27)

Since $r\theta$ increases in the negative \hat{f}_2 direction, the stiffness and damping forces were defined as

$$\hat{f}_2 \cdot \vec{F}_{\text{damping}} = rm2\zeta\omega_n \dot{\theta} \tag{28}$$

$$\hat{f}_2 \cdot \vec{F}_{\text{stiffness}} = rm\omega_n^2 \theta.$$
 (29)

The resulting expression was divided by the product of the radius of gyration and mass to put it in the final nondimensional form as

$$\frac{-\hat{f}_2 \cdot e_a^{-2}}{r} + 2\zeta \omega_n \dot{\theta} + \omega_n^2 \theta = 0$$
(30)

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