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Haltere-mediated equilibrium reflexes of the fruit fly, *Drosophila melanogaster*

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Flies display a sophisticated suite of aerial behaviours that require rapid sensory–motor processing. Like all insects, flight control in flies is mediated in part by motion-sensitive visual interneurons that project to steering motor circuitry within the thorax. Flies, however, possess a unique flight control equilibrium sense that is encoded by mechanoreceptors at the base of the halteres, small dumb-bell-shaped organs derived through evolutionary transformation of the hind wings. To study the input of the haltere system onto the flight control system, I constructed a mechanically oscillating flight arena consisting of a cylindrical array of light-emitting diodes that generated the moving image of a 30° vertical stripe. The arena provided closed-loop visual feedback to elicit fixation behaviour, an orientation response in which flies maintain the position of the stripe in the front portion of their visual field by actively adjusting their wing kinematics. While flies orientate towards the stripe, the entire arena was swung back and forth while an optoelectronic device recorded the compensatory changes in wing stroke amplitude and frequency. In order to reduce the background changes in stroke kinematics resulting from the animal's closed-loop visual fixation behaviour, the responses to eight identical mechanical rotations were averaged in each trial. The results indicate that flies possess a robust equilibrium reflex in which angular rotations of the body elicit compensatory changes in both the amplitude and stroke frequency of the wings. The results of uni- and bilateral ablation experiments demonstrate that the halteres are required for these stability reflexes. The results also confirm that halteres encode angular velocity of the body by detecting the Coriolis forces that result from the linear motion of the haltere within the rotating frame of reference of the fly's thorax. By rotating the flight arena at different orientations, it was possible to construct a complete directional tuning map of the haltere-mediated reflexes. The directional tuning of the reflex is quite linear such that the kinematic responses vary as simple trigonometric functions of stimulus orientation. The reflexes function primarily to stabilize pitch and yaw within the horizontal plane.

Keywords: haltere; flight; *Drosophila melanogaster*; vestibular system; aerodynamics; control systems

1. INTRODUCTION

Dipterous insects, the true flies, are among the most manoeuvrable of all flying animals. The elevated performance of flies is partially explained by a number of unique sensory specializations that have evolved in close association with flight behaviour. For example, the eyes of some flies exhibit an elevated temporal resolution that is manifest in a flicker fusion frequency that approaches 300 Hz (Autrum 1958). The visual system is further endowed with a unique neural superposition architecture that achieves high response sensitivity without a concomitant loss in spatial resolution (Braitenberg 1967; Kirschfeld 1967). These characteristics are thought to improve the measurement of optical flow, which flies use to track moving objects, perceive depth, and monitor their own motion through space (Egelhaaf & Borst 1994; Kimmerle *et al*. 1997). Along with these visual specializations, flies possess sensitive mechanosensory structures called halteres that provide an additional means of encoding self-motion during flight. The halteres are minute hindwings that have been modified through evolution into elaborate sensory organs with no direct aerodynamic role (figure 1*a*). Small muscles beat the halteres back and forth during flight in strict antiphase to the motion of the wings (Pringle 1949). When the body of the animal rotates during flight, the halteres are subject to inertial (Coriolis) forces that are linearly proportional to the angular velocity of the body (Nalbach 1993; Pringle 1948). Arrays of mechanoreceptors at the base of the haltere detect the strains produced when the Coriolis forces deflect the end-knob from its beating plane. The sensory afferents are thought to mediate compensatory flight control reflexes through their connections with thoracic motor neurons innervating control muscles of the wings and neck (Fayyazuddin & Dickinson 1996; Hengstenberg 1991).

Although the vast majority of insects can fly quite well without halteres, the tiny structures appear necessary for stable flight in flies. Their importance in flight stability was recognized by Derham (1714), who was the first to examine the free-flight behaviour of flies after surgically removing their halteres. As Derham noted, flies the halteres of which have been ablated rapidly crash to the ground if they attempt to fly. Derham envisioned that flies use their halteres much as tight-rope walkers use their

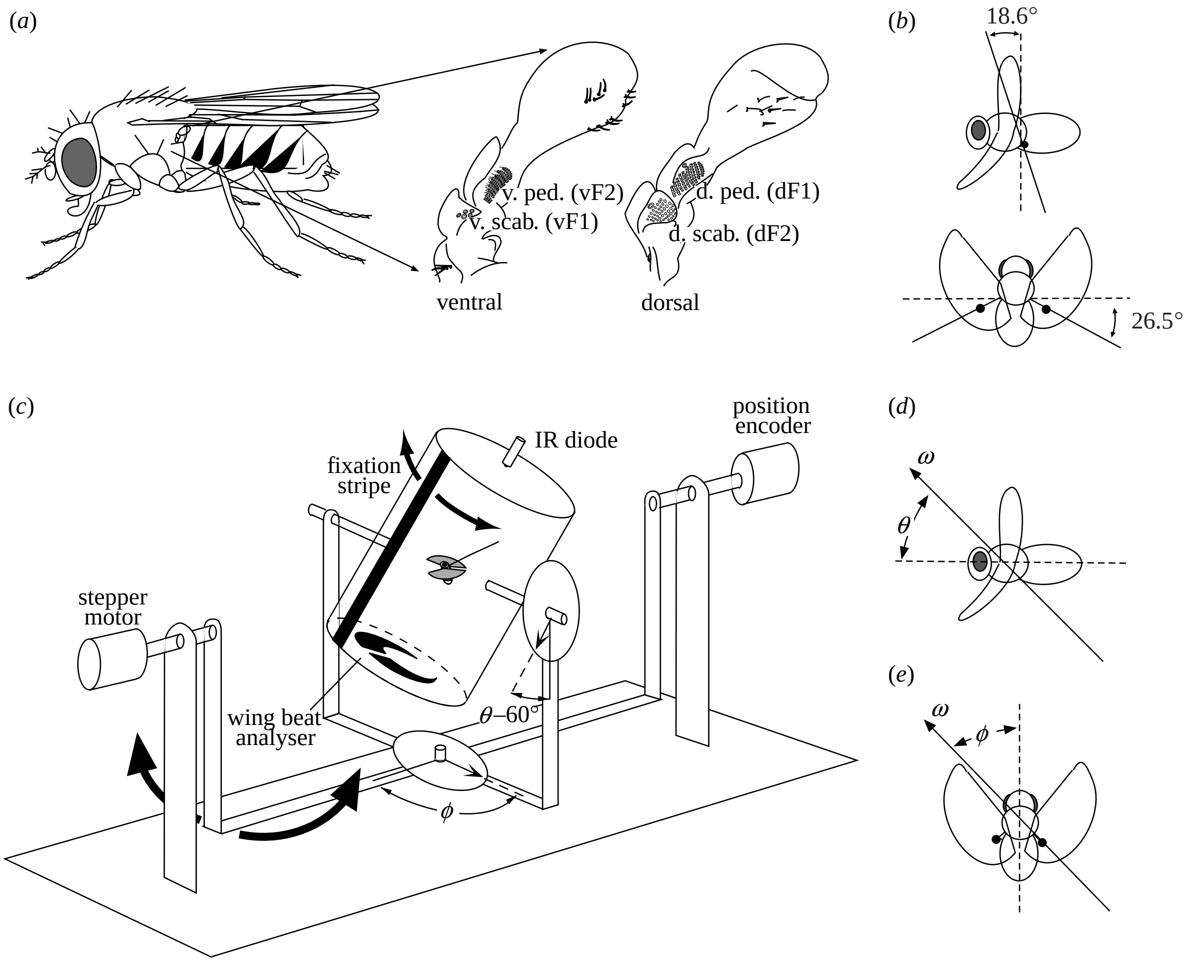

Figure 1. (*a*) Location and external morphology of halteres in the fruit fly, *D. melanogaster*. The images on the right show the position of the four campaniform sensory fields at the base of the haltere: v. scab., ventral scabellum; v. ped., ventral pedicellus; d. scab., dorsal scabellum; d. ped., dorsal pedicellus (haltere drawing modified from Cole & Palka (1982)). (*b*) Angular orientation of the haltere stroke plane. (*c*) Apparatus for testing equilibrium reflexes. A visual closed-loop flight arena equipped with an optical wing-beat analyser is mounted within a motor-controlled gimble. See text for details. By adjusting the alignment of the arena through angles ϕ and θ, it is possible to rotate the animals through any arbitrary axis. Throughout the paper, orientation of the rotation vector in the mid-sagittal (*d*), and horizontal (*e*) planes is defined with respect to the fly's longitudinal body axis.

long balancing poles, giving rise to the original term for halteres ('balancers'). Although many theories for the role of the halteres were advanced in the 19th and 20th centuries (for a review of early studies, see Fraenkel & Pringle (1938)), Pringle (1948) argued convincingly that the halteres must function by detecting Coriolis forces, the inertial forces acting on a moving object in a rotating frame of reference. The magnitude and direction of the Coriolis force is determined by the cross-product of the haltere's linear velocity with the angular velocity of the fly's thorax as well as the mass distribution of the haltere. Evolution appears to have modified both the motion and morphology of the haltere so as to increase the magnitude of the Coriolis force and thus the sensitivity of the haltere system. Each haltere beats through a stroke angle of approximately 180°, the largest sweep possible without striking the thorax at the top and bottom. This extreme angle maximizes the linear velocity of the haltere for a given length and oscillation frequency. In addition, the 'drumstick' morphology, which consists of a narrow stalk and a globular end-knob, distributes most of the mass at the fastest moving portion of the haltere. Nevertheless, the actual deflections of the stroke plane caused by the Coriolis forces are quite small (Nalbach 1993; Pringle 1948) and the oscillatory motion of the haltere lies within a narrow plane whether or not the body is rotating. Because the linear velocity vector of the haltere is constrained to one plane, the Coriolis forces resolve into just two components: a force normal to the stroke plane and a force radial to the long axis of the haltere. Even in the absence of body rotation, however, the back-and-forth oscillation of the haltere generates inertial and centripetal forces with large radial components that haltere sensors could not unambiguously distinguish from radial components of the Coriolis force (Nalbach 1993). For this reason, only the normal component of the Coriolis force (i.e. normal to the haltere stroke plane) provides reliable information on the angular velocity of the body. Because the magnitude and time-course of the normal forces on the two halteres is different depending on the direction of body rotation, it is theoretically possible for the animal to distinguish among yaw, pitch and roll.

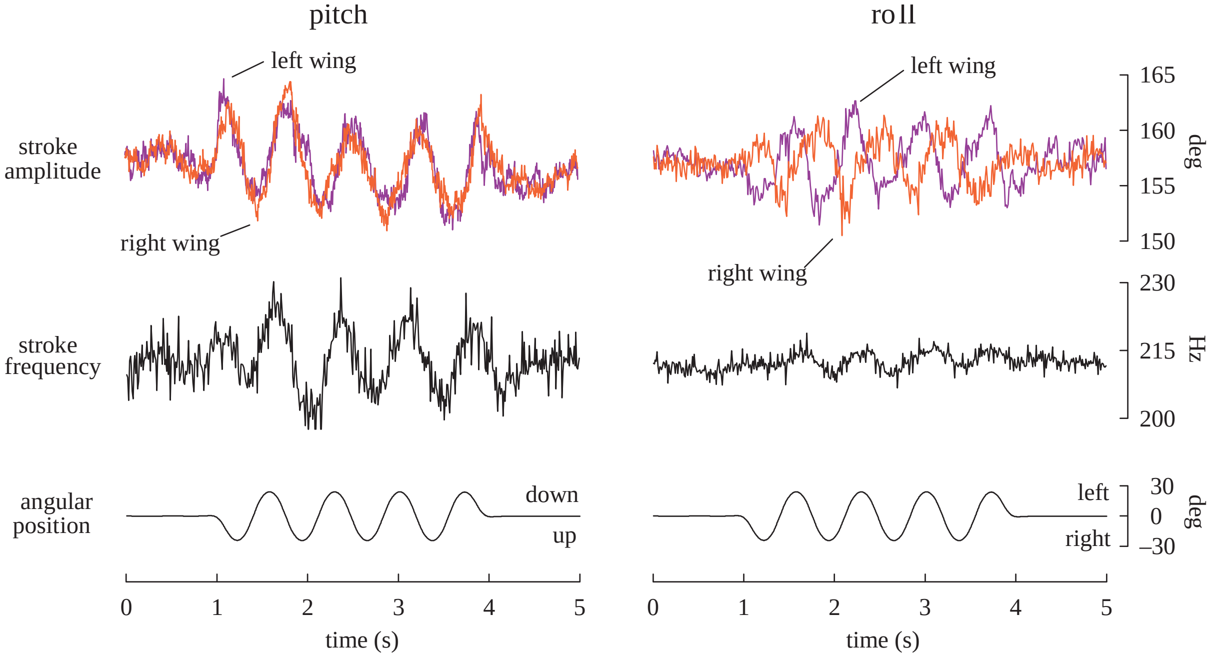

Figure 2. Equilibrium reflexes in response to oscillations about the functional pitch and roll axes. The bottom trace shows the angular position of the arena. Positive angles indicate head down for pitch and left down for roll. Each trace indicates the ensemble average of eight separate stimulus presentations. The middle trace shows the instantaneous wing-beat frequency and the top traces indicate the stroke amplitude of the left and right wings.

One important role of the haltere is to stabilize the position of the head during flight by providing feedback to the neck motor system (Sandeman & Markl 1980). In a series of detailed studies, Nalbach and Hengstenberg demonstrated that the blowfly, *Calliphora eurythrocephala*, discriminates among oscillations about the yaw, pitch and roll axes and uses this information to make appropriate compensatory adjustments in head position (Hengstenberg 1988; Nalbach 1993, 1994; Nalbach & Hengstenberg 1994). Such reflexes probably act to minimize retinal slip during flight, thereby stabilizing the image of the external world and increasing the accuracy with which the visual system encodes motion. Nalbach (1993) also confirmed Pringle's assertion that the halteres function in equilibrium reflexes by detecting forces acting normal to the stroke plane. In most of her experiments, Nalbach stimulated the halteres by linearly oscillating tethered flies back-and-forth so that the amplitude, time-course, and orientation of linear acceleration would simulate the normal components of Coriolis forces generated by rotation. This 'virtual' rotation technique has several experimental advantages, but it assumes an accurate knowledge of haltere kinematics and cannot be used to mimic all directions of body rotation.

Although the role of the haltere in stabilizing gaze may be important, a more essential and immediate role of the haltere is to provide rapid feedback to wing-steering muscles to stabilize aerodynamic force moments. Using high-speed cine film, Faust (1952) showed that blowflies (*C. eurythrocephala*) change the angle of attack and timing of pronation and supination in response to imposed body rotation. The kinematic responses were qualitatively different for yaw, pitch and roll, indicating that the fly could distinguish among rotations around these axes. By quantifying the strength of the airstream behind the two wings of a tethered fly, Schneider (1953) showed that *Calliphora* make compensatory changes in aerodynamic output in response to imposed yaw. Findings in another blowfly, *Lucilia serricata*, suggest that this aerodynamic response to imposed yaw may be mediated in part by changes in the angle of attack of the wings or the timing of wing rotation (Sandeman 1980). In *Calliphora*, pitching motion also elicits a haltere-mediated change in stroke frequency (Nalbach 1994).

While the results summarized above indicate that haltere feedback alters stroke frequency and wing rotation, its effect on stroke amplitude is not well determined. This lapse in knowledge is unfortunate, since studies of the fruit fly, *Drosophila melanogaster*, suggest that modulation of stroke amplitude is the primary means by which flies adjust lift, thrust and yaw torque during flight (Götz *et al*. 1979; Lehmann & Dickinson 1997*a*). The purpose of this paper is to characterize the haltere-mediated changes in stroke amplitude and frequency induced by imposed body rotation in *Drosophila*. Fruit flies are particularly amenable to this analysis because it is possible to track their wing kinematics on a stroke-by-stroke basis using an optical wing-beat analyser (Götz 1987*a*), thereby overcoming the need for labour-intensive high-speed cine or video analysis. Tethered flies are tested in a flight arena under closed-loop conditions in which they actively control the motion of visual targets by changing stroke kinematics (Heisenberg & Wolf 1984). By rotating the visual panorama together with the fly, mechanical rotations of the body are uncoupled from counter rotations of the visual world, thereby isolating the influence of the halteres on the flight control system. The robustness with which *Drosophila* will fly within a closed-loop flight arena make it possible to generate a detailed directional tuning map for haltere-mediated reflexes. The results of this study indicate that the halteres are essential components of a robust equilibrium system in which changes in stroke amplitude reflexively counteract imposed rotations of the body.

2. MATERIALS AND METHODS

(a) *Animals*

All behavioural experiments were performed on 97 two- to four-day-old female fruit flies, *D. melanogaster* Meigen, from a laboratory culture that originated from 50 wild-caught gravid females. The culture is maintained at 22 °C in a 1 m^3 cage containing approximately 10–15 open vials of a cornmeal-based *Drosophila* medium. The culturing regime requires that flies must actively fly and navigate towards new sources of food which are placed in the cage every few days. This technique has been developed to ensure that the animals maintain behavioural and rigor under laboratory conditions. Females were used in the experiments because they are larger and more robust than males and fly for longer periods of time. Preliminary experiments, however, suggest that all the basic results of this study extend to males.

In preparation for each experiment, animals were cooled to 4 °C and tethered at the anterior end of their notum to a tungsten wire using light-activated glue as has been previously described (Lehmann & Dickinson 1997*b*). To standardize the alignment of each fly during the experiments, I took care to tether each animal so that the tungsten wire was fixed at 90° with respect to its longitudinal body axis. After they recovered from the cold, I allowed each animal to rest for at least one hour before placing it within the test arena. To inhibit flight prior to each experiment, the animals were given a small square of tissue paper to which they readily clung with their legs. I initiated flight by removing the tissue-paper platform with forceps or blowing on the fly from above.

Because the primary purpose of this study was to characterize the function of the halteres, in most experiments the head was fixed to the thorax with glue so that the relative motion between the two could not provide a cue for the detection of angular motion. Fixing the head also ensures that the optomotor responses are maximal (Heisenberg & Wolf 1984). However, several preliminary experiments indicated that the equilibrium responses of flies with fixed heads were similar to those of animals the heads of which were left free to rotate.

(b) *Test arena*

The flight arena consisted of an optical wing-beat analyser and a surrounding panorama of close-packed light-emitting diodes (for details, see Dickinson & Lighton (1995) and Lehmann & Dickinson (1997*b*)). The flight arena itself was mounted within a U-shaped gimble that could swing back-and-forth via a stepper motor under computer control (figure 1*c*). The controller that powered the stepper motor (Zeta 601, Parker, Inc., Rohnert Park, CA) employed a micro-stepping algorithm that subdivides 360° of rotation into 24 000 steps to ensure smooth motion. Attaching the motor to the gimble shaft via a timing belt and two pulleys with a 1:4 gear ratio further ensured smooth travel. The flies were aligned within the arena so that their longitudinal body axis was inclined at 60° with respect to the horizontal plane, approximating the orientation of their body during hovering flight (David 1978; Götz & Wandel 1984). Most experiments were performed under visual 'closed-loop' conditions (Götz 1987*a*; Heisenberg & Wolf 1984), such that the flies actively controlled the angular velocity of a dark 30° wide vertical stripe by adjusting the relative stroke amplitude of their wings. Under these conditions, flies robustly attempt to maintain the stripe in the front portion of their visual field. The fly, visual panorama, and wing-beat analyser were rigidly mounted to one another within the oscillating frame of reference to ensure that the mechanical oscillations did not change the orientation of the fly with respect to either the visual display or the wing-beat analyser. The arena was covered with a black opaque cloth, so that the animal could not use optical flow seen through the open top of the arena as a cue to rotation. Using this configuration, it was possible to measure the changes in wing kinematics induced by physical rotation of the body in the absence of visual motion cues. To vary the orientation of the rotation vector, the resting position of the arena could be adjusted within the gimble through two angles (figure 1*d*,*e*). By rotating the base of the arena, it was possible to adjust the orientation of angular rotation in the horizontal plane (ϕ). By changing the resting inclination of the arena within the gimble, it was possible to adjust the orientation of angular rotation in the vertical plane (θ).

At the start of each experiment, a fly was positioned within the arena and the closed-loop gain and offset for visual feedback was adjusted so that the animal could easily stabilize the position of the 30° stripe. I then oscillated the arena back-and-forth under computer control using a series of constant acceleration motions. During the first excursion from rest, the arena moved to an angular displacement of +12° at an acceleration of 1600° s^{-1} and then decelerated to its maximum position of +24° at −1600° s^{-1}. The arena then swung from +24° to −24°, first by accelerating from +24° to 0° at 1600° s^{-2} and than decelerating from 0° to −24° at −1600° s^{-2}. This procedure repeated so that the arena oscillated back-and-forth for three complete cycles before returning to its resting position. Each full excursion from +24° to −24° took 346 ms during which time the velocity changed linearly from −277 to +277° s^{-1}. Because the angular acceleration of the arena followed a square wave trajectory, the angular velocity followed a triangular waveform, and the position of the arena followed a series of normal and inverted parabolas. This complex stimulus waveform was chosen because previous studies suggested that the forces detected by the haltere should vary with the angular velocity of rotation (Nalbach 1993; Pringle 1948). Since the motor was operated in open-loop, the actual trajectories deviated slightly from the programmed motion. However, the true motion of the arena was recorded using an angular displacement transducer (TransTek, Inc., Ellington, CT) mounted to the gimble shaft.

Five channels of data were captured during the experiments at a sampling rate of 200 Hz each: arena position, left-wing amplitude, right-wing amplitude, wing-beat frequency, and the position of the vertical stripe within the visual display. To minimize the variance in stroke kinematics introduced by this close-loop configuration, the responses to eight identical mechanical rotations were averaged for each trial. In experiments designed to map out the directional sensitivity, I adjusted the angular orientation of the arena within the gimble in increments of 15° between trials. The sequential order of angles was chosen randomly to control for monotonic changes in flight performance over time.

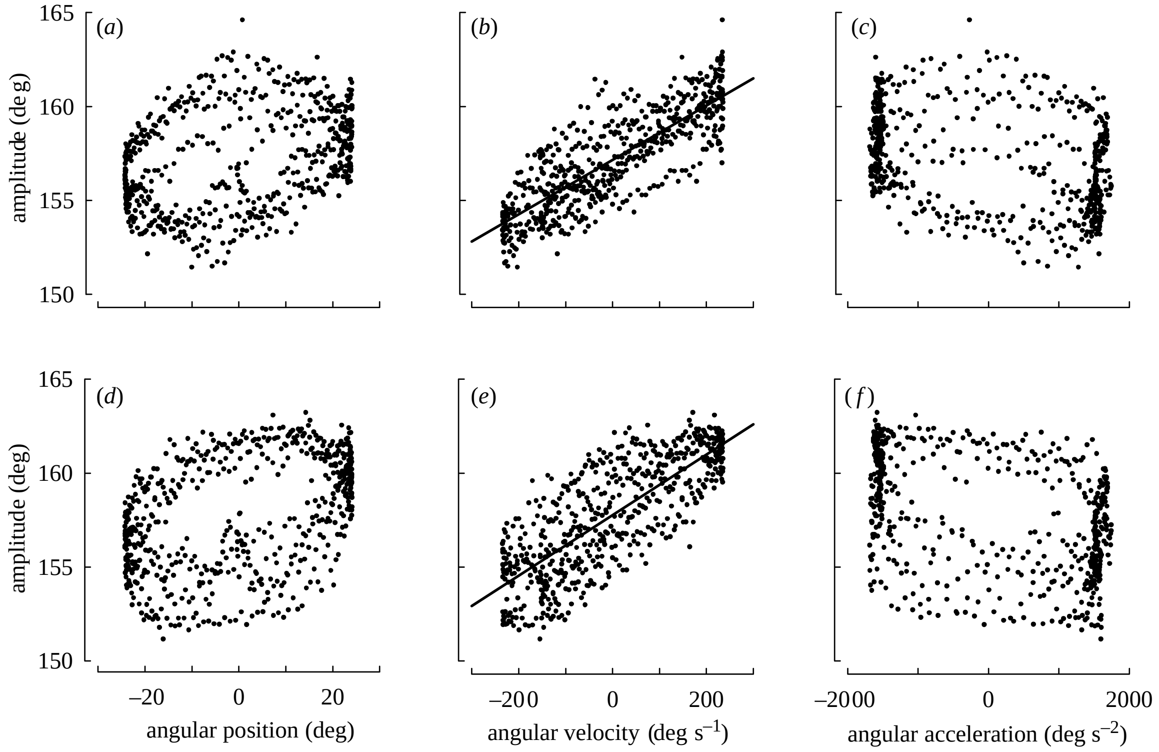

Figure 3. Wing-beat amplitude is correlated with instantaneous angular velocity of the thorax. The amplitude of the left wing is plotted against the instantaneous position (*a*,*d*), velocity (*b*,*e*), and acceleration (*c*,*f*) during the pitch (*a*–*c*) and roll (*d*–*f*) response of one individual. The changes in stroke amplitude are more tightly correlated with the angular velocity of the stimulus than either the position or acceleration. The slope of a linear regression of wing-beat amplitude on angular velocity provides a convenient measure of response sensitivity (gain) and is used throughout the paper (pitch: slope = 0.0145° (deg s^{-1})$^{-1}$, $r^2 = 0.679$; roll: slope = 0.0161° (deg s^{-1})$^{-1}$, $r^2 = 0.621$).

(c) *Anatomical measurements*

The narrow stroke plane within which each haltere beats is inclined with respect to the longitudinal and transverse axes of the fly. Although the directional sensitivity of the haltere system depends critically on these inclination angles, they have never been measured in *D. melanogaster*. To do so, I mounted tethered flies within a calibrated two-axis rotational micromanipulator and illuminated them with a stroboscope under a stereomicroscope. First, the longitudinal and transverse axes of the fly were aligned with the zero positions of the micromanipulator axes. I then adjusted the orientation of the fly until the haltere stroke plane was aligned vertically. The angles of inclination could then be read from the calibrated actuators of the micromanipulator.

(d) *Anatomical and functional definitions of yaw, pitch and roll*

The terms yaw, pitch and roll refer to an orthogonal system of rotation vectors that are usually defined with respect to the morphology of a given object. For animals, yaw, pitch and roll are typically defined as rotations about the dorsoventral, bilateral, and longitudinal axes, respectively. From a functional point of view, the task of an equilibrium system is to stabilize an animal's orientation with respect to its flight trajectory, which for a fly typically lies within a horizontal plane. However, because the longitudinal body axis is inclined with respect to the horizontal during flight, the anatomical yaw and roll axes do not correspond to the functional yaw and roll axes. For this reason, it is necessary to make a distinction between anatomical yaw and roll (defined with respect to the animal's morphological axes), and functional yaw and roll (defined with respect to the flight path). This distinction is especially important because the posture of the animal changes with flight speed. For example, while flying backwards the longitudinal body axis is inclined at an angle of nearly 90°. Under this condition, the anatomical yaw axis would correspond to the functional roll axis and the anatomical roll axis would correspond to the functional yaw axis. At the fastest flight speeds, *Drosophila* hold their body at an angle of 20° with respect to the horizontal (David 1978) and the anatomical and functional yaw axes are in closer alignment. Under no free-flight conditions, however, do the functional and anatomical yaw and roll axes ever precisely correspond. Although it undoubtedly creates some confusion, it is necessary to switch between the anatomical and functional definitions of yaw and roll throughout the paper. No such distinction is necessary for pitch, since the functional and morphological pitch axes are always the same.

3. RESULTS

(a) *Inclination of the haltere stroke plane*

In *Drosophila*, the haltere stroke plane is inclined backwards from the transverse axis by an angle of 26.5 ± 6.78° (mean ± s.d., $n = 12$). This is very close to the value of 30° reported for the blowfly, *Calliphora* (Nalbach 1993). Unlike *Calliphora*, however, the haltere stroke plane in *Drosophila* is also inclined with respect to the vertical by an angle of 18.6 ± 6.78° (mean ± s.d., $n = 12$). Thus, the haltere does not beat precisely up and down with respect to the longitudinal body axis, but rather is closer to the head at its

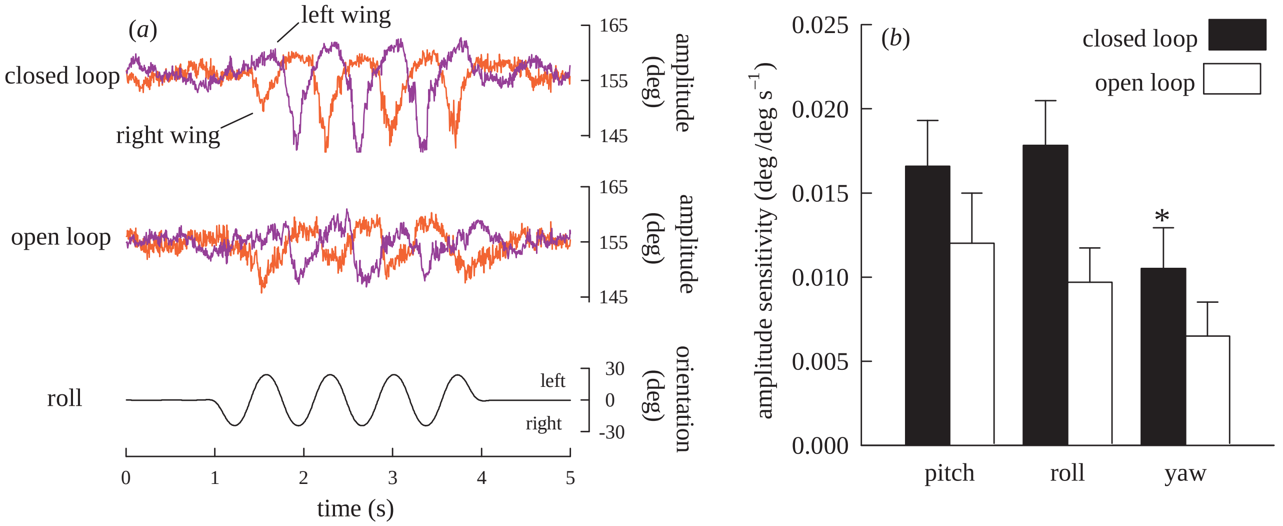

Figure 4. Comparison of equilibrium responses under visual closed- and open-loop conditions. Under closed-loop conditions, the animal actively controlled the angular velocity of a 30° dark stripe by adjusting wing-beat amplitude. When in the open-loop configuration, the stripe was held stationary directly in front of the animal. (*a*) Response to roll stimulus. The compensatory changes in wing-beat amplitude are present under open-loop conditions, although the magnitude of the response is much stronger when the animal is engaged in active optomotor control of its visual world. (*b*) Response sensitivities to pitch, roll, and yaw under closed- and open-loop conditions (mean ± s.e.m., $n = 10$). The equilibrium responses are consistently higher under closed-loop conditions. The asterisk indicates significantly different means in paired comparison of closed- and open-loop conditions ($p < 0.05$, Student's *t*-test).

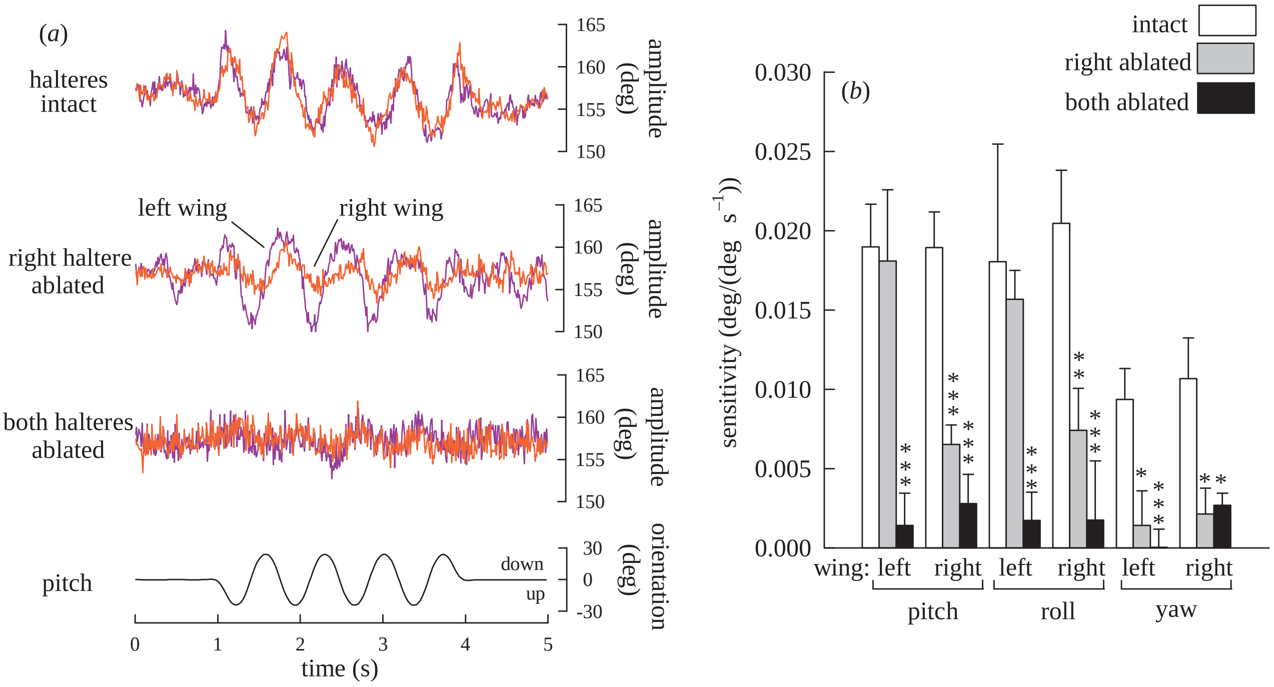

Figure 5. Halteres are required for the stroke amplitude component of equilibrium reflexes. (*a*) Response of an individual fly to pitch stimulus following uni- and bilateral excision of the haltere end-knob. With intact halteres, the pitch oscillation elicits the normal in-phase modulation of left and right stroke amplitude. When the right haltere is ablated the response of the right wing is greatly attenuated, whereas the response of the left wing appears normal. Bilateral excision of the haltere end-knobs almost completely attenuates the equilibrium response. (*b*) Summary of ablation results (mean ± s.e.m., $n = 12$ for unablated control, $n = 6$ for both uni- and bilateral ablation). The effects of haltere ablation are similar for pitch and roll stimuli. In both cases, bilateral ablation attenuates the response of the ipsilateral wing, but not the contralateral wing. Bilateral ablation nearly abolishes the response of both wings. The effect on the yaw response is similar, accept that unilateral ablation attenuates the response of both the ipsi- and contralateral wing. Asterisks indicate levels of significance compared with unablated control using two-tailed *t*-test for independent means (*, ** and *** indicate $p < 0.05$, 0.01 and 0.001, respectively).

extreme dorsal position and closer to the abdomen at its extreme ventral position (figure 1*b*).

(b) *Flies display compensatory equilibrium reflexes*

Flies responded to mechanical rotations with stereotyped changes in wing kinematics (figure 2). When pitched forward (head down), the flies increased both the stroke frequency and stroke amplitude of their two wings. Backward pitching motion elicited a decrease in amplitude and frequency. During functional rolls to the left and right, the flies increased the stroke amplitude of the wing on the side of the body that was rotating downward, and decreased the amplitude of the wing on the side that was rotating upward. In contrast to the pitch response, there was little modulation of stroke frequency during functional roll. Given the force moments expected from these changes in stroke kinematics, these equilibrium reflexes should act to counter the imposed rotation and thus represent compensatory reactions.

(c) *Equilibrium reflexes track angular velocity of stimulus*

The halteres on a rotating fly are subject to several forces that might represent the adequate stimuli for equilibrium reflexes. In addition to Coriolis forces, gravity and angular acceleration could encode the angular position and acceleration of the body (Nalbach 1993; Pringle 1948). Unfortunately, it is not yet possible to directly measure the response of the haltere afferents to different stimulus conditions. However, assuming that the dynamics of the entire reflex are limited by the behaviour of the haltere, then the tuning of the afferents may be inferred from the response of the motor system as a whole. As shown in figure 3, the changes in wing kinematics during equilibrium reflexes are most strongly correlated with instantaneous angular velocity (figure 3*b*,*e*), which is consistent with the halteres acting as Coriolis force detectors (Nalbach 1993; Pringle 1948). The slope of the regression between stroke amplitude and angular velocity provides a convenient means of quantifying the gain of the equilibrium response. Such gain values, and comparable data calculated for stroke frequency, are used throughout the paper to quantify the effects of various experimental treatments.

(d) *Gain of equilibrium reflexes are enhanced by visual closed-loop conditions*

The experiments described so far were performed under visual closed-loop conditions, such that the animals actively controlled the angular velocity of a 30° vertical stripe by adjusting wing stroke kinematics. I chose the closed-loop configuration because previous studies indicate that behavioural and physiological performance of tethered flight in *Drosophila* is enhanced relative to open-loop conditions and better approximates free-flight conditions. One potential artefact, however, is that part or all of the kinematic response to mechanical oscillation is caused by an exaggerated optical flow of the vertical stripe. Such instability might occur if an animal's optomotor performance is compromised during mechanical oscillation. However, as indicated in figure 4, the equilibrium reflexes are not qualitatively altered under open-loop conditions. This result indicates that the equilibrium reflexes are not artefacts of the closed-loop configuration. The stroke amplitude sensitivities to pitch, roll and yaw were, however, reduced under visual open-loop conditions, although the difference was only significant for the roll response ($p < 0.05$, *t*-test). Thus, like several other aspects of flight behaviour under tethered conditions (Heisenberg & Wolf 1988), equilibrium reflexes appear enhanced when the animal is actively engaged in optomotor flight control.

(e) *The halteres are required for equilibrium reflexes*

Although the halteres are the most likely source of mechanosensory feedback for equilibrium responses in flies, they are by no means the only potential source. To test whether the halteres are necessary for the compensatory changes in wing kinematics, I examined the equilibrium reflexes of animals after removing the end-knob of one or both halteres (figure 5*a*). While this ablation procedure should greatly attenuate the magnitude of Coriolis forces, it leaves the fields of campaniform sensilla at the base of the haltere intact. The fact that all individuals tested flew under tethered conditions after both unilateral and bilateral ablation indicates that the severity of the ablation procedure was not so large as to inhibit the basic function of flight circuitry. Bilateral ablation reduced the compensatory changes in stroke amplitude by approximately 90% (pitch, 89%; roll, 91%; yaw, 97%). In contrast, ablation of one haltere only partially inhibited the equilibrium reflexes. While both the pitch and roll responses of the wing ipsilateral to the ablated haltere were diminished by 65%, the response of the contralateral wing was not significantly different from that of unablated controls (figure 5*b*). These results are consistent with the behavioural observation that while a haltere-less fly is completely unstable in free flight, an animal with a single haltere appears to fly almost normally (Fraenkel & Pringle 1938). The results also suggest that the steering muscles controlling compensatory changes in stroke kinematics receive information encoded by both ipsi- and contralateral halteres. The consequences of uni- and bilateral haltere ablation were similar for rotations about the functional pitch, roll and yaw axes, with the exception that unilateral ablation had a more drastic effect on the yaw response. This difference must be interpreted cautiously, however, because the background sensitivity to functional yaw is low even with intact halteres.

The effects of haltere ablation on changes in stroke frequency were subtly different than those on wing-beat amplitude (figure 6*a*,*b*). Because imposed roll and yaw have little effect on stroke frequency, the effects of haltere ablation are presented only for pitch. While unilateral ablation had little or no effect on the modulation in stroke frequency, bilateral ablation nearly abolished the response. Thus, the halteres do provide feedback for the control of stroke frequency during pitch. One curious and unexpected result of haltere ablation was that it significantly increased the background stroke frequency of the fly in the absence of any rotational stimuli (figure 6*c*). Following haltere ablation, flies flew with a wing-beat frequency of 242 ± 9.1 Hz (mean ± s.e., $n = 8$), representing a 24% increase over control levels ($p < 0.001$, *t*-test). This elevated value is significantly higher than maximum stroke frequencies elicited in intact tethered flies by visual stimuli (Lehmann &

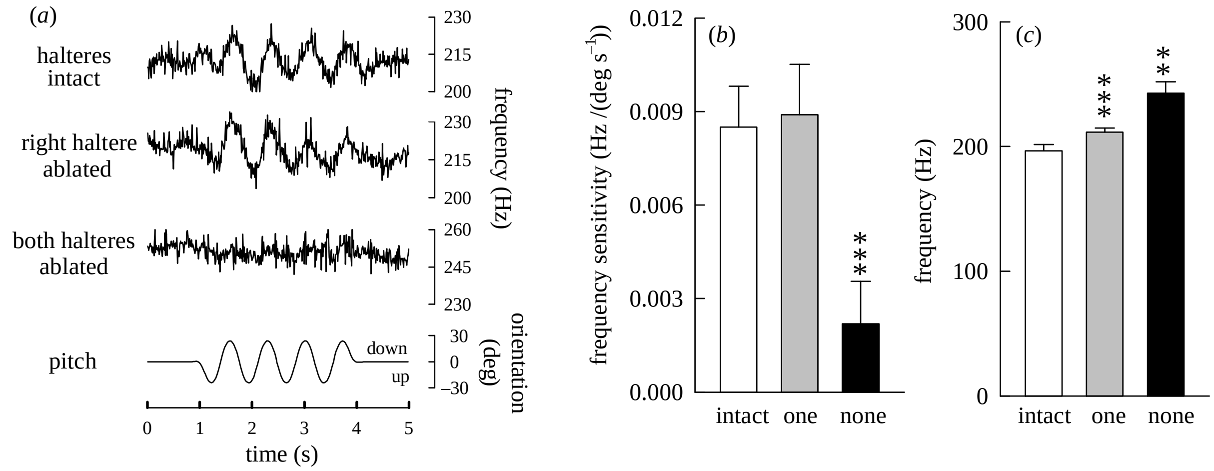

Figure 6. Halteres are required for the stroke frequency component of equilibrium reflexes. (*a*) Response of an individual fly to pitch stimulus following uni- and bilateral excision of the haltere end-knob. The modulation of stroke frequency remains after ablation of a single haltere, but is almost completely abolished by ablation of both halteres. (*b*) Summary of ablation results from the same experimental groups described in figure 5. (*c*) Haltere ablation resulted in an unexpected increase in the background level of wing-beat frequency. All frequency measurements were made prior to rotation of the arena. Even unilateral ablation caused a significant increase in stroke frequency. Asterisks indicate significance as described in figure 5.

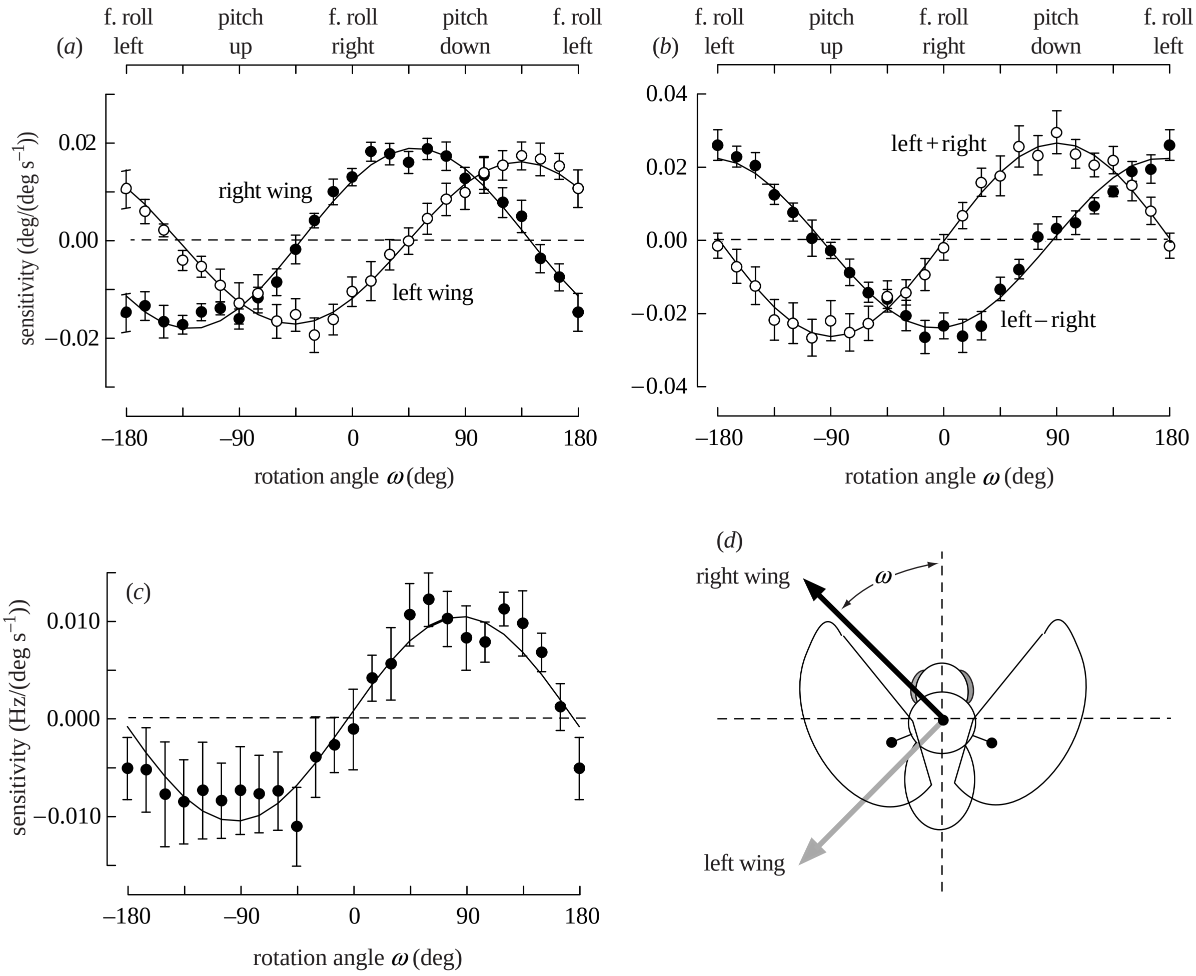

Figure 7. Directional tuning of haltere-mediated equilibrium reflexes in the horizontal plane. These rotations vary from pitch ($\phi = \pm 90°$) to functional roll ($\phi = 0, \pm 180°$), depending on the orientation of the stimulus vector. (*a*) Directional tuning curves of left and right wing ((*a*,*b*), f. roll indicates functional roll). The responses are well fitted by simple harmonic waveforms. The tuning curves of the left and right wings are 90° out of phase (for all panels, data values represent mean ± s.d., $n = 10$). (*b*) Tuning curves of the difference (left – right) and sum (left + right) of stroke amplitude. (*c*) Directional tuning of stroke frequency modulation. (*d*) Vector representation of stroke amplitude tuning. The response vector for each wing points in the direction of the most sensitive stimulus orientation. The length of each vector is proportional to the magnitude of the maximum kinematic response. Direction of rotation is given by the right-hand rule. The responses at other angles are given by the dot product of the response vector with the stimulus vector.

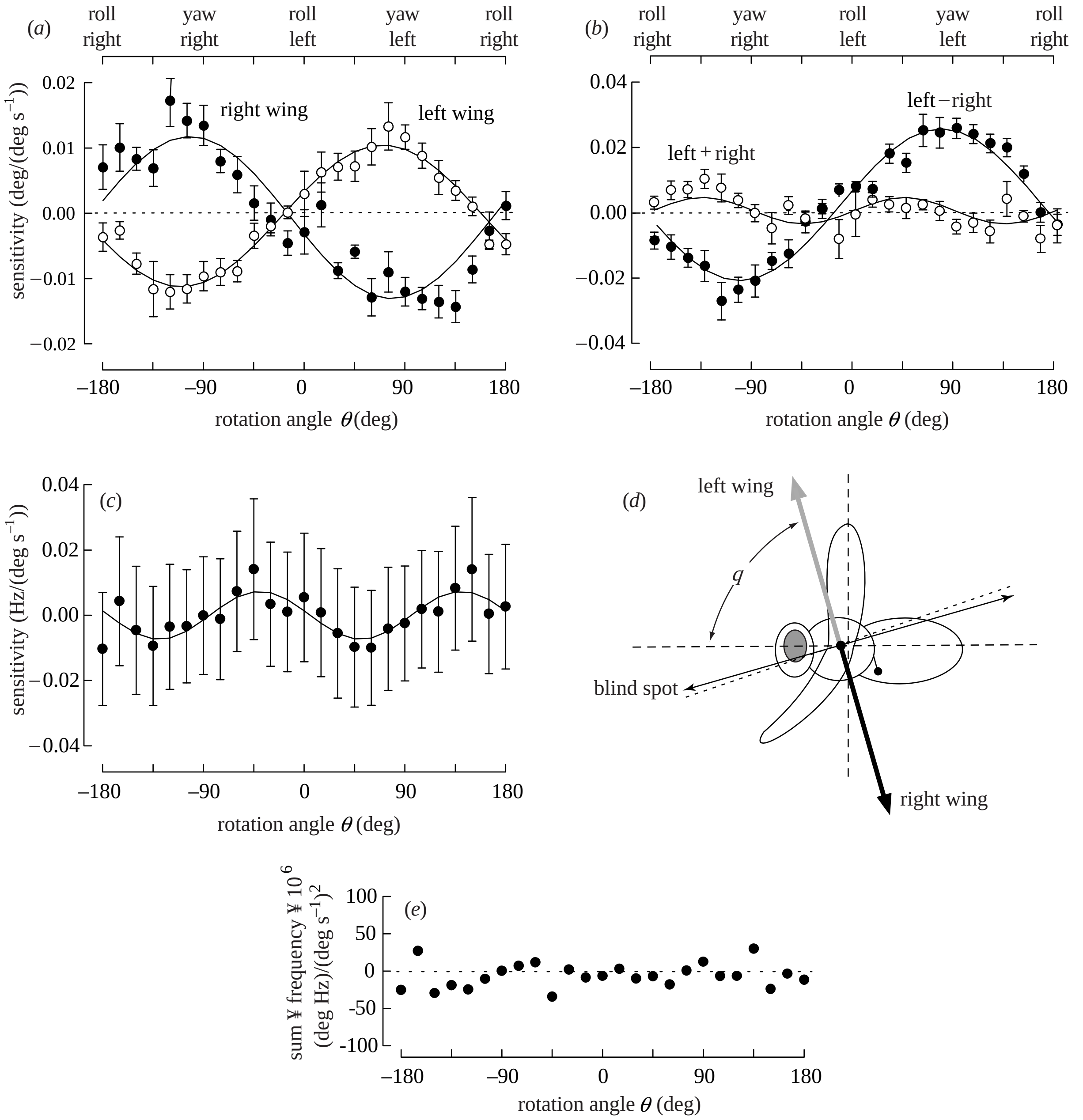

Figure 8. Directional tuning of haltere-mediated equilibrium reflexes to rotations lying in the vertical plane. These rotations vary from anatomical yaw ($\theta = \pm 90°$) to morphological roll ($\theta = 0, \pm 180°$), depending on the orientation of the stimulus vector. (*a*) Directional tuning curves of the left and right wing. The responses are well fitted by two antiphase harmonic waveforms (for all panels, data values represent mean ± s.d., $n = 10$). (*b*) Directional tuning of the difference (left − right) and sum (left + right) of stroke amplitude. (*c*) Directional tuning of stroke frequency modulation. The modulation in stroke frequency is quite small and, as with sum of stroke amplitude, varies as a double harmonic of rotation angle. (*d*) Vector representation of the stroke amplitude tuning. Because the response vectors are 180° out of phase, the flies possess a blind spot (thin arrow) at which there is no kinematic response. The orientation of the blind spot is close to the response minimum predicted from the inclination of the mean haltere stroke plane (dotted line). At this stimulus orientation, the components of the Coriolis force normal to the stroke plane are minimal. Direction of rotation is given by the right-hand rule. (*e*) The product of stroke amplitude sum and stroke frequency as a function of rotation angle. The product is constant suggesting that the animal maintains constant average flight force throughout each stroke during equilibrium reflexes in the vertical plane.

Dickinson 1997*a*,*b*). Unilateral ablation also caused a significant increase in mean stroke frequency ($p < 0.01$).

(f) *Directional sensitivity of the haltere response*

So far, all of the experiments have examined the responses of the flies to rotations about the functional roll and pitch axes. To examine the directional tuning of the equilibrium response in more detail, I varied the angle of the rotation in 15° increments within horizontal and vertical planes (figures 7 and 8). The two planes were mapped in separate experiments using ten flies each. Assuming that the equilibrium system behaves linearly, these two sets of data are sufficient to reconstruct the response of a fly to perturbations about any arbitrary axis. Figure 7 shows the tuning of the equilibrium response to rotation vectors lying in the horizontal plane.

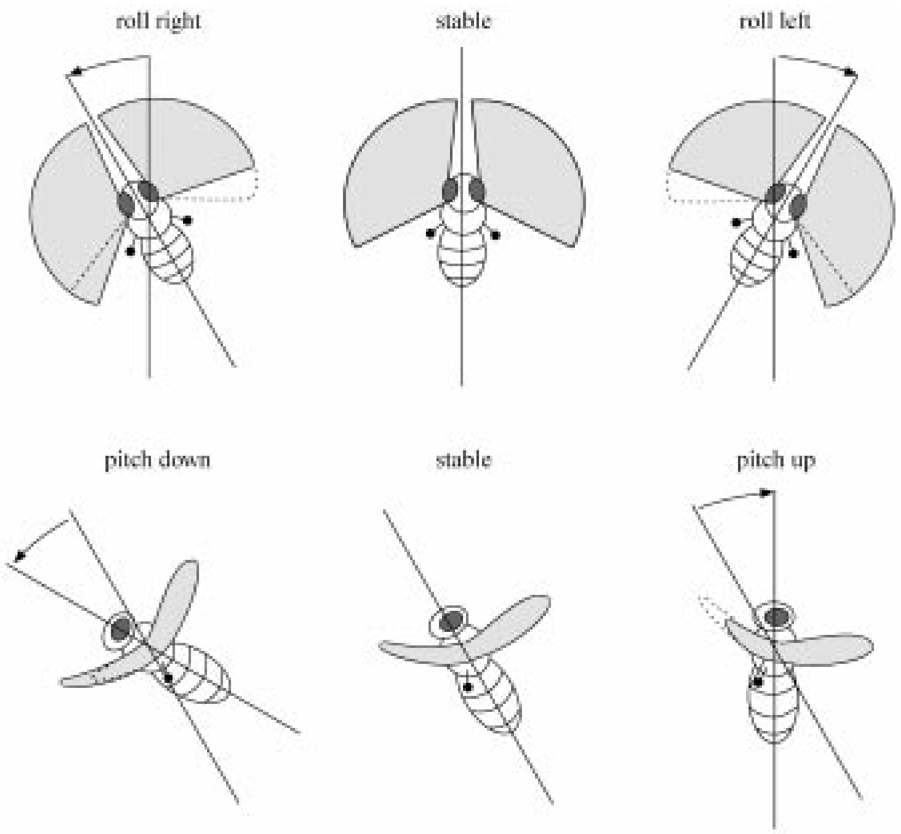

Figure 9. Summary of haltere-mediated equilibrium reflexes. Changes in stroke amplitude elicited by pitch and roll generate restorative moments that maintain a stable flight posture.

As in previous experiments, the longitudinal body axis of the fly was orientated at approximately 60° from the horizontal, the angle typical for hovering flight. As the orientation of the stimulus vector is varied in the horizontal plane, the conditions changed from functional rolls left and right ($\theta = 0$ and ± 180, respectively) to pitches forwards and backwards ($\theta = -90$ and 90, respectively). As expected, the tuning curve was symmetrical about the animal's mid-sagittal plane. Functional rolls elicited the greatest difference in stroke amplitude, while pitches elicited the largest response in the sum of stroke amplitude. At intermediate angles, the difference in stroke amplitude varies as the cosine of the stimulus angle, whereas the sum of stroke amplitude varies as the sine (figure 7*b*). Stroke frequency displays a tuning curve that is nearly identical to the sum of stroke amplitude such that frequency is greatest during forward pitches and lowest during backward pitches (figure 7*c*). The separate tuning responses of the left and right wings are shown in figure 7*a*. To generate the appropriate compensatory responses, the tuning curves of the two wings are 90° out of phase.

The harmonic shape of the tuning curves indicates that the sensory–motor cascade linking haltere mechanoreceptors to changes in stroke amplitude is linear with respect to direction. Thus, the directional tuning of each wing can be characterized by a single response vector with a magnitude equal to the maximum sensitivity and with an orientation equal to the preferred direction of the response (figure 7*d*). The response at any arbitrary angle is given by the dot product of the stimulus with this characteristic response vector. The response vectors were estimated from a least-squares fit of a sinusoid through the directional tuning data of each wing (left wing: 0.018° (deg $\mathrm{s}^{-1})^{-1}$, $-45°$; right wing 0.016° (deg $\mathrm{s}^{-1})^{-1}$, $-135°$). This orientation ensures that the sensitivity to functional roll and pitch will be almost exactly the same.

The directional tuning of the equilibrium reflex to rotations lying within the sagittal plane is shown in figure 8. As with rotations in the horizontal plane, the stroke amplitude responses are well fitted by simple harmonic functions. The greatest difference in stroke amplitude occurs when the rotation vector is close to the anatomical yaw axis. Both the sum of stroke amplitude (figure 8*b*) and stroke frequency (figure 8*c*) are nearly constant at all rotation angles in the sagittal plane. However, in both cases there is a small modulation of the response that appears to vary as the sine of twice the orientation angle. The polarity of the double frequency response is exactly reversed for stroke frequency and the sum of stroke amplitude. In *D. melanogaster*, the product of summed stroke amplitude and frequency is linearly proportional to total flight force (Lehmann & Dickinson 1997*a*,*b*). As shown in figure 8*e*, this product shows little modulation with respect to stimulus angle, suggesting that a reflexive coordination of amplitude and frequency maintains constant total force output during yaw or roll reactions. Such coordination might function to keep the animal from losing or gaining altitude during compensatory reflexes.

The individual tuning responses of the two wings to rotations in the sagittal plane are shown in figure 8*a*. As with the directional tuning in the horizontal plane, the response of each wing is well described by a single response vector (figure 8*d*; left wing: 0.010° (deg $\mathrm{s}^{-1})^{-1}$, 105°; right wing: 0.012° (degs $\mathrm{s}^{-1})^{-1}$, $-75°$). The orientation of these response vectors is such that the flies will be more sensitive to functional yaw during fast forward flight than during hovering. The response exhibits a 'blind spot' about an axis that is inclined at 16° with respect to the longitudinal body axis. That a blind spot exists is not surprising, because the directional tuning curves must cross zero at some angle within the mid-sagittal plane of the fly in order for the compensatory reflexes to be symmetrical for rotations to the left and right.

4. DISCUSSION

The results of these experiments indicate that flies possess a robust equilibrium reflex in which angular rotations of the body elicit compensatory changes in both the amplitude and frequency of the wing-beat (figure 9). Ablation experiments demonstrate that these stability reflexes are elicited by sensory feedback from the halteres. The magnitude of the changes in stroke amplitude and frequency are linearly proportional to the velocity of angular rotation, corroborating previous evidence that the halteres function by detecting Coriolis forces. The robust nature of these reflexes and their absolute dependence on intact halteres explains why flies whose halteres have been ablated cannot remain airborne. Directional tuning experiments indicate that the haltere-mediated equilibrium reflex is quite linear and the kinematics responses vary as simple trigonometric functions of stimulus orientation.

(a) *Are the kinematic changes evoked by the haltere compensatory?*

Several lines of evidence suggest that the haltere-mediated reflexes would function to counter imposed rotations and thus maintain equilibrium during flight. In *Drosophila,* changes in total stroke amplitude are accomplished primarily through changes in the ventral excursion of the wings (Götz 1983; Zanker 1990). Except during very low levels of force production, the wings come to or near their dorsal limit during dorsal stroke reversal. Measurements of instantaneous flight force suggest that the greatest aerodynamic forces are generated during the latter half of the downstroke and early upstroke (Dickinson & Götz 1996). For these reasons, increases in stroke amplitude are likely to elevate instantaneous force production during the ventral portion of the stroke when the wing is anterior to the fly's centre of mass. Although the kinematics of the clap and fling at dorsal stroke reversal also change during steering manoeuvres (Ennos 1989; Götz 1987*a*; Lehmann & Götz 1996), recent calculations suggest that such changes have only a minor influence on rotational moments (Lehmann & Götz 1996). Thus, a bilateral increase in stroke amplitude should generate a moment that would rotate the animal nose up, while a decrease in amplitude would rotate the animal downward. Similarly, an increase in the stroke amplitude of one wing should generate a rotational torque towards the opposite side. These simple models relating stroke amplitude changes to force moments are consistent with experiments that examined the changes in torque (Blondeau & Heisenberg 1982) and stroke kinematics (Götz 1983) elicited by optokinetic stimuli. Thus, although there exist no direct measurements of flight torque during mechanical oscillation, it seems certain that the kinematic changes evoked during haltere-mediated reflexes act to counter the imposed rotation.

Exploring the link between kinematic changes and their aerodynamic consequences raises an important question: how many rotational degrees of freedom can the fly control? The evidence in this paper indicates that *Drosophila* can independently control rotational moments around at least two orthogonal axes. Symmetrical bilateral changes in stroke amplitude permit control around the pitch axis, while adjustments in the difference in stroke amplitude create a combined yaw–roll moment that would allow control around a single axis lying in the mid-sagittal plane. Stroke amplitude changes alone would not, however, enable a fly to control yaw and roll independently. One possibility is that as with many forms of aircraft, three-axis control may not be necessary for a functional stability system. Another possibility is that flies can indeed control yaw and pitch moments independently, but that this control requires more subtle kinematic changes that are not detected by the wing-beat analyser used in this study. For example, by varying the angle of attack, timing of wing rotation, or deviation from the stroke plane, an animal might alter the magnitude and direction of force moments so that it could generate a pure yaw or pure roll moment.

In tethered flight, *Drosophila* produce rapid changes in torque about their anatomical yaw axis called torque spikes, which correspond to the body saccades they produce in free flight (Collett & Land 1975; Heisenberg & Wolf 1979). Superficially, these observations suggest that flies can generate rapid changes in morphological yaw, without producing roll. However, because none of the torque-measuring devices that have been used in flight arena studies can measure rotational moments about more than one axis, the angular composition of torque spikes remains an open question. Further, in experiments using 'torque compensators' (Götz 1964; Heisenberg & Wolf 1979), flies are typically orientated so that the sensor measures torque around the anatomical yaw axis. In free flight, flies are inclined at an angle of about 20–60° with respect to the horizontal plane depending upon flight speed (David 1978). A moment around the anatomical yaw axis, measured in tethered flight, would actually resolve into moments around both the functional roll and yaw axes during free flight. Preliminary high-speed video analysis of animals in free flight confirms that body saccades are accomplished by rotation about both the yaw and roll axes (M. H. Dickinson, personal observation). This is not to say that *Drosophila* cannot independently control yaw and roll, but that they appear to coordinate rotation about these axes during many steering manoeuvres. In summary, from current evidence it is not possible to resolve whether *Drosophila* can control body rotation independently about two axes or three.

(b) *The relationship between haltere reflexes and the visual system*

A fly's ability to produce fine-tuned flight behaviours rests in large part on the rapid integration of motion-sensitive visual circuitry with temporally precise mechanosensory signals from the halteres and wings (Borst & Dickinson 1999). The fly's visual system is divided into at least two main subsystems that serve different functions during flight. Large-field optical flow elicits reflexive changes in wing kinematics that function to minimize the angular velocity of retinal slip (Egelhaaf 1989). These reflexes, termed 'optomotor responses' (Götz 1964), are thought to play an important role in course stabilization and function around all three body axes (Blondeau & Heisenberg 1982; Götz 1983). Because these large-field optomotor reflexes are also compensatory, the system would work in concert with the haltere-mediated responses to counter imposed turns. Thus, if a pocket of turbulence were to spin a fly from its equilibrium position, both the physical rotation of the fly and the large-field motion across the retina in the opposite direction would serve as cues to activate a compensatory change in wing kinematics.

Whereas flies respond to large field objects in order to stabilize angular velocity (Egelhaaf 1989), they respond to small field objects in order to stabilize the position of the object on the retina. Under closed-loop conditions, this response to small field stimuli gives rise to robust fixation behaviour, the active maintenance of a small target in the front portion of the fly's visual world (Götz 1980, 1987*b*). The circuitry that underlies fixation is probably important in the animal's ability to orientate towards targets and landmarks within the visual environment. Unlike the large-field optomotor reflexes, fixation and other object-orientated visual behaviours may be in conflict with haltere-mediated equilibrium reflexes. For example, whereas haltere reflexes function to maintain stability, a fly must actively change direction and body orientation in order to navigate through its world in search of food, mates and oviposition sites. This conflict between flight stability reflexes and goal-orientated manoeuvres is similar to that between vestibular–ocular reflexes and active head rotation in vertebrates. Without some appropriate change in efficacy, haltere-mediated equilibrium reflexes would function to counter goal-orientated motion. To resolve this potential conflict, the nervous system must contain the means of attenuating equilibrium reflexes during the generation of controlled manoeuvres.

There are several mechanisms that might explain how a fly succeeds in changing orientation in the presence of the robust equilibrium reflexes. First, the rapidity of voluntary manoeuvres might allow the fly to change direction before the haltere-mediated reflex impedes rotation. The torque spikes produced by rigidly tethered flies are several times longer than those produced by loosely tethered flies free to rotate about their functional yaw axis (Heisenberg & Wolf 1979). One simple explanation of this result is that haltere reflexes normally act to terminate torque spike commands. In rigidly tethered animals, the haltere feedback is eliminated, resulting in substantially longer torque spikes. Under free-flight conditions, the finite delay between the development of torque following a saccade command and initiation of the haltere-mediated reaction may allow the motor command briefly to 'outrun' the compensatory reflex. Body saccades may represent a means of manoeuvring within the constraints of the equilibrium system. This potential antagonistic interaction between saccade commands and the haltere-mediated reflexes also provides a possible explanation for why the haltere is relatively insensitive to angular rotations around the functional yaw axis. The gain of equilibrium reflexes might be lower about the functional yaw axis so as not to interfere with visually direction manoeuvres.

An alternative mechanism by which the fly might resolve motor conflicts during goal-directed manoeuvres is through active gain control of the haltere-mediated reflexes. Like wings, halteres are equipped with a complex set of steering muscles (Bonhag 1948; Mickoleit 1962). These tiny control muscles might function to change either haltere kinematics or campaniform sensitivity during flight. Recently, the motor neurons of at least two of these muscles in *Calliphora* have been shown to receive directionally sensitive input from descending visual interneurons. This pathway would provide one means by which the visual system could decrease the sensitivity of the haltere during both voluntary and involuntary behaviours. A third possibility is that the descending command neurons actually use the haltere reflexes to generate voluntary manoeuvres (Chan *et al.* 1998). Through their influence on haltere-steering muscles, descending neurons could initiate reflexive responses to 'virtual' flight perturbations. These three mechanisms, passive outrunning, active desensitization and reflex loop activation are not mutually exclusive; all could play a role in allowing the fly to perform active manoeuvres under the constraints of the haltere reflexes.

The influence of the visual system on the sensitivity of the haltere may provide the means of solving a difficult control problem that must emerge when the animal changes speed. As they fly, *Drosophila* maintain the orientation of their body at an angle which ranges from 20° during fast forward flight to 90° when flying backwards. This change in body posture has several implications for proper function of the equilibrium reflexes. First, the set point for proper pitch control may change by as much as 70°. Second, the orientation of the functional yaw and roll axes rotates with respect the haltere's frame of reference. One intriguing possibility is that the descending interneurons from the visual system or antennae might modify the directional sensitivity of the halteres sensilla peripherally, through the influence of the haltere control muscles, or centrally, through their influence on haltere interneurons or target motor neurons.

(c) *The encoding of Coriolis forces by haltere mechanoreceptors*

Because of the potential contamination by large background oscillatory forces acting radially and tangentially, the haltere sensors responsible for encoding Coriolis forces must be directionally sensitive to normal deflections of the haltere from its stroke plane. Based solely on morphology, Pringle (1948) argued that the normal component of the Coriolis forces are encoded by just two groups of sensilla, the basal plate campaniform field (dF2 of Gnatzy (1987) and later authors), and the internal chordotonal organ. Pringle also developed an elegant preparation in which he could mechanically oscillate the haltere while recording from its nerve. Although his extracellular records are difficult to interpret, the experiments did indicate that while many afferents are active during the back-and-forth oscillation of the haltere within its stroke plane, other units were recruited when the fly was rotated about its yaw axis. While subsequent electrophysiological analysis suggested that all the campaniform fields may be partially sensitive to normal deflection (Thurm *et al.* 1975), more recent studies appear to corroborate Pringle's view that the dF2 campaniforms may play a central role in the equilibrium reflexes. In *Calliphora*, the motor neuron of the first basalar muscle (MNB1), an important muscle for the control of stroke amplitude, receives strong monosynaptic input from dF2, but not from any other campaniform fields (Chan & Dickinson 1996; Fayyazuddin & Dickinson 1996). This synapse between dF2 afferents and MNB1 is quite strong and consists of both electrical and chemical components, a result that has been verified by genetic means in *Drosophila* (Trimarchi & Murphey 1997). DF2 is the largest of the campaniform fields, consisting of roughly 110 individual campaniform sensilla in *Calliphora*. I am currently attempting to elucidate further the role of dF2 and the other campaniform fields by examining equilibrium reflexes in flies following selective laser ablation of specific sensilla.

(d) *The directional sensitivity of the haltere-mediated equilibrium reflex*

As indicated in figures 7 and 8, the magnitude of the kinematic changes elicited by angular rotation varies with stimulus direction. This directional tuning represents the net behaviour of a sensory–motor cascade linking haltere afferents, steering muscles, wing kinematics, and the resulting changes in aerodynamic forces. The directional sensitivity of the behaviour as a whole might arise at different levels within this cascade. The most parsimonious explanation is that the directional tuning of the reflexes as a whole reflects the directional sensitivity of a single homogeneous population of primary sensory afferents at the base of the haltere, possibly dF2. In this scheme, the motor neurons and interneurons controlling the steering muscles simply follow the directional sensitivity of the haltere afferents. A second possibility is that the haltere afferents are more broadly tuned, but that the projections are functionally segregated onto different populations of motor neurons and interneurons. In this scheme, the directional response of the kinematics is not a simple echo of sensory cell tuning, but rather results from a complex pattern of sensory–motor mapping. The tuning of the equilibrium reflexes in the vertical plane (figure 8) provides some evidence for the model in which the motor circuitry simply follows the directional sensitivity of the halteres. The normal component of the Coriolis force vanishes at rotations about an axis normal to the haltere stroke plane (Nalbach 1993). The halteres are inclined at an angle of $18.6 \pm 4.7°$ with respect to the vertical, which corresponds almost exactly to the 'blind spot' at 16° below the longitudinal body axis. Thus, the kinematic response vanishes at precisely the stimulus orientation where the haltere response should be minimal. This correlation appears to support the hypothesis that the tuning of the haltere determines the directional sensitivity of the kinematic responses. Other evidence, however, would suggest that the sensory–motor map is more complex. For example, the kinematic response vectors in the horizontal plane are not well aligned with the directional sensitivity of the sensory afferents predicted from haltere orientation (figure 7). While each haltere is inclined at an angle of 26.5° with respect to the transverse axis, the kinematic response of each wing is maximal at 45°. Evidence from the blowfly, *Calliphora*, would also suggest that the equilibrium reflexes function by way of a more complex sensory–motor map. At the anatomical level, the projection patterns of haltere sensory afferents in *Calliphora* vary quite extensively both within and among the five campaniform fields. Hengstenberg (1988) has shown that rotation about the roll axis, which is roughly perpendicular to the haltere stroke plane, does elicit a compensatory roll of the head that is abolished by haltere ablation. Thus, the halteres seem capable, in a blowfly at least, of encoding rotation about an axis roughly normal to their mean stroke plane and conveying that information to appropriate neck muscles. Because flight posture varies quite extensively depending on size and habit, it is not surprising to find species-specific differences in the details and function of the haltere sensory–motor system.

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REFERENCES

Autrum, H. 1958 Electrophysiological analysis of the visual systems in insects. *Expl. Cell Res. Suppl.* **5**, 426–439.

Blondeau, J. & Heisenberg, M. 1982 The three dimensional optomotor torque system of *Drosophila melanogaster*. *J. Comp. Physiol.* A **145**, 321–329.

Bonhag, P. F. 1948 The thoracic mechanism of the adult horsefly (Diptera: Tabanidae). *Mem. Cornell Univ. Agric. Exp. Stat.* **285**, 3–39.

Borst, A. & Dickinson, M. H. 1999 Visual course control in flies. In *The handbook of brain theory and neural networks*, 2nd edn (ed. M. Arbib). Bradford Books and MIT Press.

Braitenberg, V. 1967 Patterns of projections in the visual system of a fly. I. Retina–lamina projections. *Exp. Brain Res.* **3**, 271–298.

Chan, W. P. & Dickinson, M. H. 1996 Position-specific central projections of mechanosensory neurons on the haltere of the blow fly, *Calliphora vicina*. *J. Comp. Neurol.* **369**, 405–418.

Chan, W. P., Prete, F. & Dickinson, M. H. 1998 Visual input to the efferent control system of a fly's 'gyroscope'. *Science* **280**, 289–292.

Cole, E. S. & Palka, J. 1982 The pattern of campaniform sensilla on the wing and haltere of *Drosophila melanogaster* and several of its homeotic mutants. *J. Embryol. Exp. Morph.* **71**, 41–61.

Collett, T. S. & Land, M. F. 1975 Visual control of flight behavior in the hoverfly, *Syritta pipiens* L. *J. Comp. Physiol.* A **99**, 1–66.

David, C. T. 1978 The relationship between body angle and flight speed in free flying *Drosophila*. *Physiol. Entomol.* **3**, 191–195.

Derham, W. 1714 *Physico-theology.* London: W. & J. Innys.

Dickinson, M. H. & Götz, K. G. 1996 The wake dynamics and flight forces of the fruit fly, *Drosophila melanogaster*. *J. Exp. Biol.* **199**, 2085–2104.

Dickinson, M. H. & Lighton, J. R. B. 1995 Muscle efficiency and elastic storage in the flight motor of *Drosophila*. *Science* **128**, 87–89.

Egelhaaf, M. 1989 Dynamic properties of two control systems underlying visually guided turning in house-flies. *J. Comp. Physiol.* A **161**, 777–783.

Egelhaaf, M. & Borst, A. 1994 A look into the cockpit of the fly—visual orientation, algorithms, and identified neurons. *J. Neurosci.* **13**, 4563–4574.

Ennos, A. R. 1989 The kinematics and aerodynamics of the free flight of some Diptera. *J. Exp. Biol.* **142**, 49–85.

Faust, R. 1952 Untersuchungen zum Halterenproblem. *Zool. Jahrb. Allg. Zool. Physiol.* **63**, 325–366.

Fayyazuddin, A. & Dickinson, M. H. 1996 Haltere afferents provide direct, electrotonic input to a steering motor neuron of the blowfly, *Calliphora*. *J. Neurosci.* **16**, 5225–5232.

Fraenkel, G. & Pringle, J. W. S. 1938 Halteres of flies as gyroscopic organs of equilibrium. *Nature* **141**, 919–920.

Gnatzy, W., Grünert, U. & Bender, M. 1987 Campaniform sensilla of *Calliphora vicina* (Insecta: Diptera). I. Topography. *Zoomorphology* **106**, 312–319.

Götz, K. G. 1964 Optomotorische untersuchung des visuellen systems einiger augenmutanten der fruchtfliege *Drosophila*. *Kybernetic* **2**, 77–92.

Götz, K. G. 1980 Visual guidance in *Drosophila*. In *Development and neurobiology of* Drosophila (ed. O. Siddiqi, P. Babu, L. M. Hall & J. C. Hall), pp. 391–407. New York: Plenum.

Götz, K. G. 1983 Bewegungssehen and Flugsteuerung bei der Fliege *Drosophila*. In *BIONA—report 2* (ed. W. Nachtigall), pp. 21–34. Stuttgart: Fischer.

Götz, K. G. 1987*a* Course-control, metabolism and wing interference during ultralong tethered flight in *Drosophila melanogaster*. *J. Exp. Biol.* **128**, 35–46.

Götz, K. G. 1987*b* Relapse to 'preprogrammed' visual flight-control in a muscular subsystem of the *Drosophila* mutant 'small optic lobes'. *J. Neurogenet.* **4**, 133–135.

Götz, K. G. & Wandel, U. 1984 Optomotor control of the force of flight in *Drosophila* and *Musca*. II. Covariance of lift and thrust in still air. *Biol. Cybernet.* **51**, 135–139.

Götz, K. G., Hengstenberg, B. & Biesinger, R. 1979 Optomotor control of wing beat and body posture in *Drosophila*. *Biol. Cybernet.* **35**, 101–112.

Heisenberg, M. & Wolf, R. 1979 On the fine structure of yaw torque in visual flight orientation of *Drosophila melanogaster*. *J. Comp. Physiol.* A **130**, 113–130.

Heisenberg, M. & Wolf, R. 1984 *Vision in* Drosophila. Berlin: Springer.

Heisenberg, M. & Wolf, R. 1988 Reafferent control of optomotor yaw torque in *Drosophila melanogaster*. *J. Comp. Physiol.* A **163**, 373–388.

Hengstenberg, R. 1988 Mechanosensory control of compensatory head roll during flight in the blowfly *Calliphora erythrocephala* Meig. *J. Comp. Physiol.* A **163**, 151–165.

Hengstenberg, R. 1991 Gaze control in the blowfly *Calliphora*: a multisensory, two-stage integration process. *Semin. Neurosci.* **3**, 19–29.

Kimmerle, B., Warzecha, A. & Egelhaaf, M. 1997 Object detection in the fly during simulated translatory flight. *J. Comp. Physiol.* A **181**, 247–255.

Kirschfeld, K. 1967 Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Koplexauge von *Musca*. *Exp. Brain Res.* **3**, 248–270.

Lehmann, F.-O. & Dickinson, M. H. 1997*a* The control of wing kinematics and flight forces in fruit flies (*Drosophila* spp). *J. Exp. Biol.* **201**, 385–401.

Lehmann, F.-O. & Dickinson, M. H. 1997*b* The changes in power requirements and muscle efficiency during elevated force production in the fruit fly, *Drosophila melanogaster*. *J. Exp. Biol.* **200**, 1133–1143.

Lehmann, F.-O. & Götz, K. G. 1996 Activation phase ensures kinematic efficacy in flight-steering muscles of *Drosophila melanogaster*. *J. Comp. Physiol.* A **179**, 311–322.

Mickoleit, G. 1962 Die Thoraxmuskulatur von Tipula vernalis Meigen. Ein Beitrag zur vergleichenden Anatomie des Dipteranthorax. *Zool. Jahrb. Anat. Ontog. Tiere* **80**, 213–244.

Nalbach, G. 1993 The halteres of the blowfly *Calliphora*. I. Kinematics and dynamics. *J. Comp. Physiol.* A **173**, 293–300.

Nalbach, G. 1994 Extremely non-orthogonal axes in a sense organ for rotation: behavioral analysis of the dipteran haltere system. *Neuroscience* **61**, 149–163.

Nalbach, G. & Hengstenberg, R. 1994 The halteres of the blowfly *Calliphora*. II. Three-dimensional organization of compensatory reactions to real and simulated rotations. *J. Comp. Physiol.* A **174**, 695–708.

Pringle, J. W. S. 1948 The gyroscopic mechanism of the halteres of Diptera. *Phil. Trans. R. Soc. Lond.* B **233**, 347–384.

Pringle, J. W. S. 1949 The excitation and contraction of the flight muscles of insects. *J. Physiol.* **108**, 226–232.

Sandeman, D. C. 1980 Angular acceleration, compensatory head movements and the halteres of flies (*Lucilia serricata*). *J. Comp. Physiol.* A **136**, 361–367.

Sandeman, D. C. & Markl, H. 1980 Head movements in flies (*Calliphora*) produced by deflexion of the halteres. *J. Exp. Biol.* **85**, 43–60.

Schneider, G. 1953 Die Halteren der Schmeißfliege (*Calliphora*) als Sinnesorgane und als mechanische Flugstabilisatoren. *Z. Vgl. Physiol.* **35**, 416–458.

Thurm, U., Stedtler, A. & Foelix, R. 1975 Reizwirksame Verformungen der Terminalstrukturen eines Mechanorezeptors. *Verh. Dtsch. Zool. Ges.* **1974**, 37–41.

Trimarchi, J. R. & Murphey, R. K. 1997 The shaking-B^2 mutation disrupts electrical synapses in a flight circuit in adult *Drosophila*. *J. Neurosci.* **17**, 4700–4710.

Zanker, J. M. 1990 The wing beat of *Drosophila melanogaster*. III. Control. *Phil. Trans. R. Soc. Lond.* B **327**, 45–64.