PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Timing precision in fly flight control: integrating mechanosensory input with muscle physiology

Bradley H. Dickerson

Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA

BHD, 0000-0002-1185-3223

Review

Cite this article: Dickerson BH. 2020 Timing precision in fly flight control: integrating mechanosensory input with muscle physiology. *Proc. R. Soc. B* **287**: 20201774. https://doi.org/10.1098/rspb.2020.1774

Received: 27 July 2020
Accepted: 25 November 2020

Subject Category:
Morphology and biomechanics

Subject Areas:
biomechanics, neuroscience, physiology

Keywords:
insect flight, *Drosophila*, haltere, timing, muscle physiology

Author for correspondence:
Bradley H. Dickerson
e-mail: bdicker@email.unc.edu

Special Feature paper: Stability and manoeuvrability in animal movement: lessons from biology, modelling, and robotics. Guest edited by Andrew Biewener, Richard Bomphrey, Monica Daley and Auke Ijspeert.

Downloaded from https://royalsocietypublishing.org/ on 03 June 2021

Animals rapidly collect and act on incoming information to navigate complex environments, making the precise timing of sensory feedback critical in the context of neural circuit function. Moreover, the timing of sensory input determines the biomechanical properties of muscles that undergo cyclic length changes, as during locomotion. Both of these issues come to a head in the case of flying insects, as these animals execute steering manoeuvres at timescales approaching the upper limits of performance for neuromechanical systems. Among insects, flies stand out as especially adept given their ability to execute manoeuvres that require sub-millisecond control of steering muscles. Although vision is critical, here I review the role of rapid, wing-beat-synchronous mechanosensory feedback from the wings and structures unique to flies, the halteres. The visual system and descending interneurons of the brain employ a spike rate coding scheme to relay commands to the wing steering system. By contrast, mechanosensory feedback operates at faster timescales and in the language of motor neurons, i.e. spike timing, allowing wing and haltere input to dynamically structure the output of the wing steering system. Although the halteres have been long known to provide essential input to the wing steering system as gyroscopic sensors, recent evidence suggests that the feedback from these vestigial hindwings is under active control. Thus, flies may accomplish manoeuvres through a conserved hindwing circuit, regulating the firing phase—and thus, the mechanical power output—of the wing steering muscles.

1. Introduction

Timing plays a critical role in the nervous system, where the ability to rapidly detect and process subtle disturbances in the environment determines whether an animal can attain its next meal or successfully navigate complex, unpredictable terrain. Previous work on a number of animals has made tremendous strides toward uncovering the specialized biomechanical mechanisms and neural circuits used to resolve timing differences with nano- to microsecond resolution [1]. Although much of this work has focused on the detection of timing differences in *sensory* systems, the importance of sub-millisecond precision in structuring *motor* output is becoming increasingly appreciated [2]. Indeed, long-standing evidence shows that the timing of neural input determines how a muscle functions in the context of locomotion [3]. These issues converge in the context of insect flight, as these organisms perform behaviours at rapid timescales, suggesting that they operate near the performance limits of neuromechanical mechanisms for control.

Members of Diptera, the true flies, are among nature's most agile flying creatures [4,5]. This exquisite manoeuvrability is due in part to the rapid integration of multimodal sensory input from the visual system and wingbeat-synchronous mechanosensory feedback [6,7]. Furthermore, flies are unique in that they possess specialized mechanosensory organs known as the halteres, which until recently were primarily renowned for being the only true biological 'gyroscopes,' but may serve a broader role in flight control [8,9]. In the light of this new evidence,

THE ROYAL SOCIETY PUBLISHING

© 2020 The Author(s) Published by the Royal Society. All rights reserved.

Downloaded from https://royalsocietypublishing.org/ on 03 June 2021

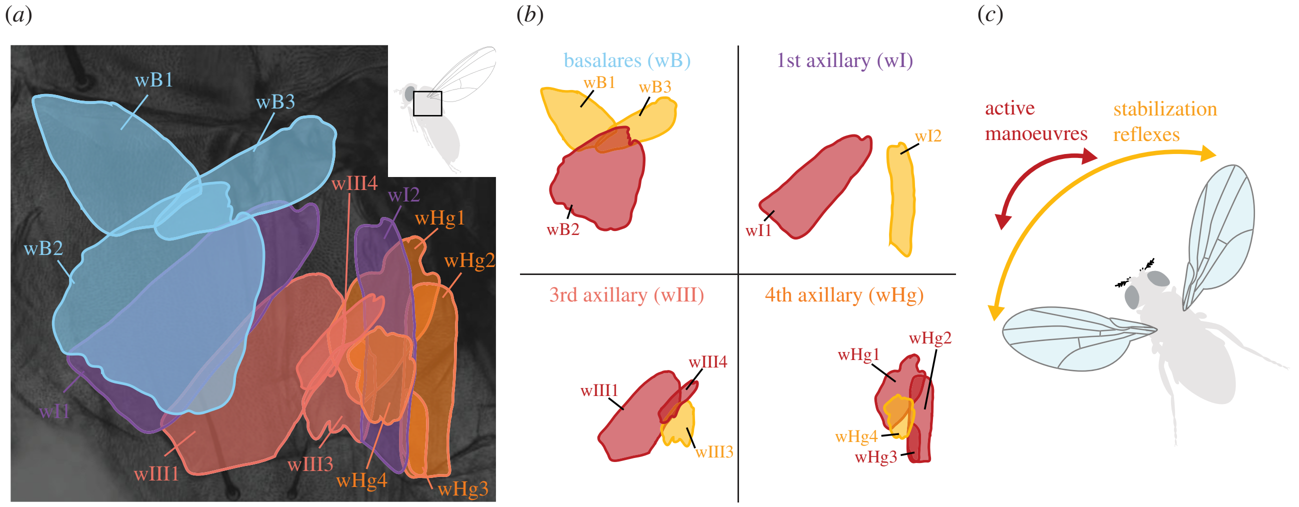

Figure 1. Anatomy and function of the dipteran wing steering system. (*a*) Steering manoeuvres in *Drosophila* and other flies are controlled by a set of steering muscles that attach to sclerites, which control the conformation of the wing hinge. Redrawn from Lindsay *et al.* [17]. (*b*) The muscles associated with each sclerite can be divided into two functional classes: muscles that are tonically active (yellow) or phasically recruited (red) during flight. (*c*) The tonic muscles allow fine-scale control of manoeuvres, whereas phasic muscles are engaged for large, rapid manoeuvres. Both types of steering muscles receive descending visual commands and are activated at precise phases of the wingstroke. Arrows do not indicate the size of manoeuvres controlled by each muscle type. (Online version in colour.)

and the wings' established role in maintaining the flight rhythm [6,10], it seems appropriate to re-evaluate our knowledge of how mechanosensory input regulates the muscles that control flight manoeuvres. Here, I outline the role of timing in determining wing steering muscle physiology. I then address the sources of this timing information and detail multiple hypotheses of how flies modulate mechanosensory feedback to execute their aerial manoeuvres. Finally, I place flies' flight control architecture in an evolutionary context, suggesting a parsimonious scenario that led to the evolution of the haltere. I focus my attention on the blowfly *Calliphora vicina* in which much of the original physiological work was conducted, and the fruit fly, *Drosophila melanogaster*, an organism in which modern genetic tools have deepened our insight into Dipteran flight control circuitry. Examining fly flight through this comparative lens allows for an understanding of how flies evolved their remarkable aerial manoeuvrability and provides powerful examples of how the timing of motor output is structured by precise sensory input.

2. Motor control of flight manoeuvres

Unlike other extant flying taxa such as birds and bats, all the musculature for power and control in flying insects resides in the thorax [11–16]. The majority of the thoracic volume is occupied by the power muscles, which are responsible for the back-and-forth motion of the wings and provide all the mechanical power for flight. There are two groups of power muscles: the dorsoventral muscles, which contract during the upstroke, and their antagonists, the dorsolongitudinal muscles, which contract during the downstroke [11,12]. The power muscles do not attach to the wing directly; instead, they insert onto the thorax, with their reciprocal contraction resulting in its deformation, which is transmitted to the wings via the complex wing hinge. As flying insects radiated, they became much smaller, and consequently, the required wingbeat frequency needed to support their weight increased. For example, whereas the large damselfly *Megaloprepus coerulatus* flaps its wings at only 5.5 Hz, the tiny midge *Forcipomyia* has a reported wingbeat frequency of 1046 Hz [11]. The typical so-called *synchronous* muscle which contracts in a one-to-one fashion with neural excitation would not be able to cycle calcium fast enough each wing stroke to produce the necessary forces to generate lift. In flies and many other orders, contraction of the power muscles is decoupled from their neural excitation; a single muscle action potential leads to multiple contraction cycles. As a result, they are termed *asynchronous* flight muscle. Asynchronous muscle has evolved independently at least seven times in flying insects and reflects one solution regarding the relative importance of power versus precision in muscle function.

The other side of this trade-off are the small synchronous steering muscles that regulate flight manoeuvres. These muscles insert directly on the wing hinge onto invaginated cuticular elements known as sclerites. The motion of the sclerites changes the conformation of the wing hinge, leading to subtle changes in wing motion and large changes in aerodynamic force production [4,12,13]. The wing hinge is made of four sclerites, known as the first to fourth axillaries. For historical reasons, the fourth axillary is known as the Hg. Additionally, the basalar sclerite, which is not part of the wing hinge, connects to the hinge via a ligamentous connection and influences wing motion. Each sclerite except for the second axillary is associated with a subset of steering muscles that insert onto it.

The flight steering system of *Drosophila* is composed of only 12 muscles divided among the four sclerites, compared with 13 in *Calliphora* (figure 1*a*), and each steering muscle is innervated by a single motor neuron. Previous electrophysiological recordings in *Calliphora* along with recent calcium imaging experiments in *Drosophila* revealed that the wing steering system can be further divided into two broad classes: the tonic and phasic muscles ([17–20]; figure 1*b*). Tonic muscles regulate stabilization reflexes and are active throughout flight, firing once per wingstroke at a precise time, or phase, in the stroke cycle (figure 1*c*). The only mechanism available to flies for controlling tonic muscle activity is regulating the phase of activation [6,18–22]; flies are largely unable to regulate the spike rate of tonic muscle firing, with some

Downloaded from https://royalsocietypublishing.org/ on 03 June 2021

exceptions [22]. Phasic muscles control active manoeuvres and are typically quiescent, firing in bursts where each action potential is phase-locked to the stroke cycle [18–20,23]. The classification of the wing steering muscles into tonic and phasic can be further subdivided by anatomical location (figure 1*b*). At least one muscle of each physiological class inserts onto each sclerite, and each sclerite is hypothesized to control a specific mode of wing motion [17].

A preparation known as the work-loop technique has demonstrated the importance of the activation phase for determining muscle function [3]. By contrast to experiments where muscle function is examined under isometric (constant length) or isotonic (constant force) conditions, the work-loop method is most suitable for muscles that undergo cyclic changes in length, as during locomotion. Imposing cyclic length changes while stimulating the muscle at a specific phase of oscillation and measuring force output allows calculation of the muscle's work per cycle, or mechanical power output. This technique has been used in animals across a range of taxa to demonstrate that depending on the locomotor context, muscle can act as an actuator, brake or strut [3,21,24–29]. Such biomechanical analyses on the tonic first basalar muscle (wB1) demonstrated that this muscle exhibits *negative* power output at wingbeat frequency; it effectively operates as a variable stiffness spring to absorb energy during flight [21]. The mechanical power output of wB1 has important consequences for wing motion and the production of flight forces. Phase advances of wB1 are associated with increased wingbeat amplitude, and thus greater aerodynamic forces [18,19,30]. Experiments directly stimulating the phasic second basalar wing steering muscle, wB2, at different points in the stroke cycle showed that wB2's effect on wingbeat amplitude is highly sensitive to the activation phase [23]. Thus, through the action of a limited set of muscle and motor neuron pairs, flies can finely control wing motion and aerodynamic forces at rapid timescales.

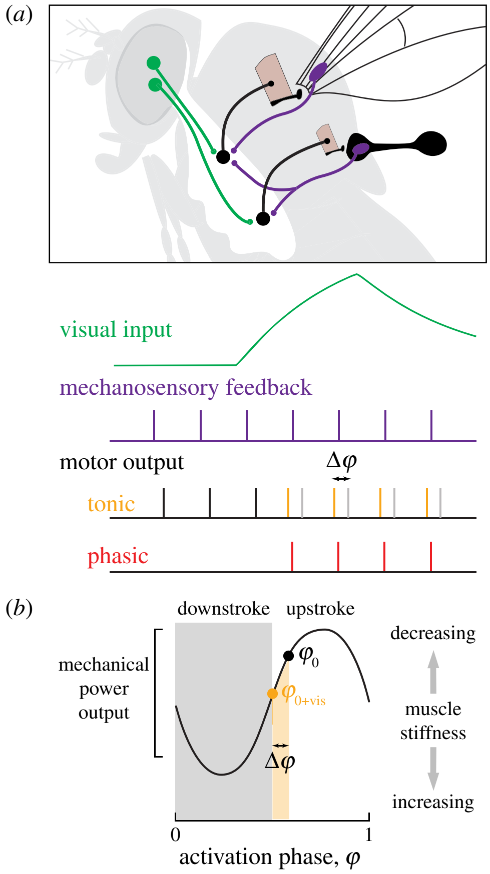

Figure 2. Flies integrate visual and mechanosensory input to regulate wing steering muscle phase or activation. (*a*) Hypothesis of how flies structure the firing of wing steering muscle motor neurons, redrawn from Heide [6]. Relatively slow, graded visual commands (green) are combined with wingbeat-synchronous mechanosensory input (purple) from embedded sensors from the wings and halteres, either adjusting firing phase ($\Delta\varphi$, black and yellow) or gating (red) of tonic or phasic wing steering muscle motor neurons, respectively. (*b*) The effects of changing the activation phase of the tonic wing steering muscle wB1. This wing steering muscle has a preferred phase of activation, φ_0, near the downstroke–upstroke transition. Descending commands shift the firing phase to an earlier or later portion of the stroke cycle, $\varphi_{0+\mathrm{vis}}$, which changes the mechanical power output of the muscle. These biomechanical changes either increase or decrease muscle stiffness each wingstroke, resulting in subtle kinematic changes and large modulations in aerodynamic force production. (Online version in colour.)

3. How do flies regulate wing steering muscle activity?

Flies' reliance on the timing of motor signals to control wing motion necessitates the question of the source of this precise phase control. Unlike the power muscles, the wing steering muscles are not supplied by any central pattern generator [12,31,32]. Descending commands from the brain are one potential source for controlling the steering muscles. Indeed, anatomical work across dipterans shows that a number of multimodal descending interneurons project from the brain to the wing neuropil of the ventral nerve cord (VNC; [33–35]). However, there is not yet any electrophysiological evidence that the brain sends commands to the wing steering muscles in a phase-locked manner [36]. Instead, descending commands are sent via slow, graded potentials that are consistent with a spike rate coding mechanism, not timing.

Previous researchers hypothesized that flies use wingbeat-synchronous mechanosensory feedback to regulate the steering muscle activation phase ([6,32]; figure 2). At the wing base and along its blade, flies are equipped with dozens of mechanosensory structures known as *campaniform sensilla*. These dome-shaped sensors possess a single neuron that is directly underneath a cap embedded in spongy tissue [37]. Cuticular strain due to bending or twisting results in the cap rising or falling, pulling on the neuron's dendrite and eliciting an action potential that is phase-locked to the stimulus cycle ([38]; figure 2*a*). Campaniform sensilla are found across insects, particularly in places that experience significant bending or twisting, such as the wings or legs [37,39–44]. Experiments systematically ablating each wing showed that flies only need mechanosensory feedback from one wing to entrain the firing phase of wB1 [6,32]. Thus, the previous working hypothesis of how flies regulate wing steering muscle motor neuron phase was that slow descending visual input converges with rapid mechanosensory feedback at the level of the motor neuron (figure 2*b*; [6]). Depending on the direction of visual motion, this multimodal feedback will shift the firing phase of the motor neuron, changing the biomechanical properties of the muscle (figure 2*b*). These sub-millisecond timing shifts will very slightly change the fly's stroke kinematics, but have large consequences on the resulting aerodynamic forces and moments.

Downloaded from https://royalsocietypublishing.org/ on 03 June 2021

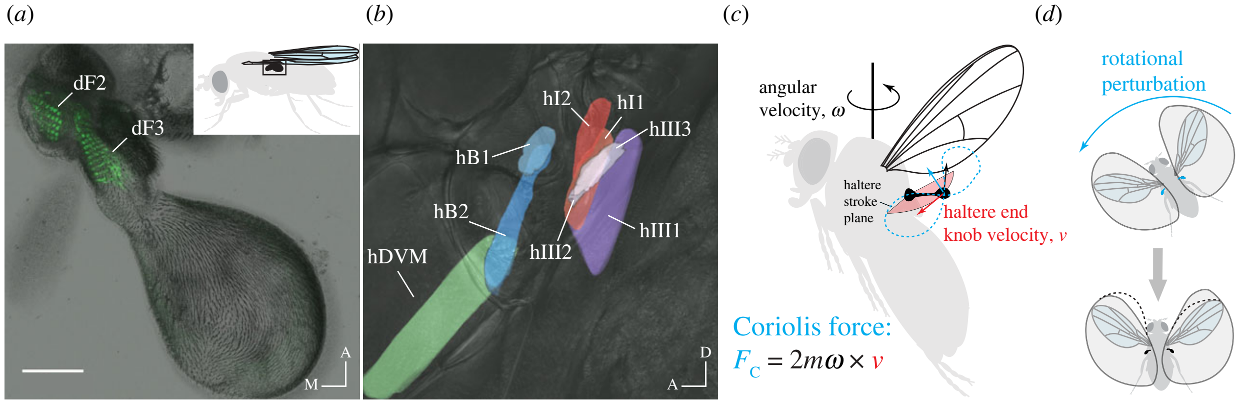

Figure 3. Halteres help flies maintain aerial stability. (*a*) Confocal micrograph of the dorsal surface of the right haltere of *Drosophila*. Each haltere possesses hundreds of strain-sensitive campaniform sensilla that are found on the base and stalk of the haltere's dorsal and ventral aspects. dF2: dorsal field 2; dF3: dorsal field 3. Scale bar: 50 µm. (*b*) In addition, the haltere has a power muscle, hDVM, that is responsible for driving its oscillations during flight and seven tiny steering muscles: the basalares (hB1, hB2) and the axillaries (hI1, hI2, hIII1–3), all of which receive visual input. Reproduced from Dickerson *et al.* [9]. (*c*) During flight, the haltere beats antiphase to the wings with an amplitude of nearly 180° (red). During rotational perturbations (black), the haltere experiences the Coriolis force, changing its tip path (blue) and altering the pattern of strain at the organ's base and stalk. These new strain patterns recruit additional campaniform sensilla each stroke. Field dF2 may be particularly sensitive to these out-of-plane motions, and may thus confer the haltere its gyroscopic capabilities. Haltere tip path changes due to Coriolis forces are exaggerated for clarity. (*d*) Haltere-mediated detection of the Coriolis force triggers equilibrium reflexes of the wings and neck, rapidly stabilizing flight posture and gaze. (Online version in colour.)

Recent computational studies and behavioural experiments support this form of multimodal integration [45–47]. Simple models can recapitulate the behaviour of the wB1 or wB2 motor neurons just by layering visual feedback on top of wingbeat-synchronous mechanosensory feedback [46]. Moreover, flies can perform visually mediated steering manoeuvres when the wings are the sole source of wingbeat-synchronous feedback following experimental ablation [45,47]. Yet, these responses are greatly diminished compared with intact flies, underscoring the importance of the full suite of mechanosensory feedback available to flies in flight. Moreover, wing motion—and the resulting mechanosensory feedback from wing campaniforms—are the direct result of the wing steering muscles. Wing campaniforms can only provide information about the current status of the wing, not the animal's future intentions. In addition, wing mechanosensory feedback entrains *both* the ipsilateral and contralateral wB1 [6], making manoeuvres that require asymmetric changes in wingstroke amplitude difficult. Thus, the wings and visual system may provide input to *set* the firing phase of the wing steering muscles. But the question of how flies *adjust* activation phase independently of the wingstroke to control manoeuvres remains.

4. The haltere, flies' metronome/gyroscope

Although the wings provide crucial mechanosensory input on a stroke-by-stroke basis, flies also rely on feedback from the halteres to structure the output of the wing steering system. These tiny, club-shaped structures beat during flight and serve no direct aerodynamic function. Nevertheless, halteres retain several features that are consistent with their evolutionary history as hindwings. For example, whereas the wings contain dozens of campaniform sensilla, these sensory structures have hypertrophied on the haltere such that *Drosophila* have 140 haltere campaniforms compared with the wing's 48 while *Calliphora* have 340 haltere campaniforms compared with 150 on the wing ([8,9,40,41,48–52], figure 3*a*). Halteres vary broadly regarding their relative size and shape; however, across species, haltere campaniforms are arranged in highly stereotyped groups [8,9,50]. Further, haltere and wing campaniforms are serially homologous [53]. Indeed, mutations of the *Drosophila* Hox gene *Ultrabithorax* transform the halteres into a second pair of wings [39]. Additionally, haltere motion is controlled by a power muscle—the first identified asynchronous muscle [54]—and a small set of steering muscles (figure 3*b*) [9,54–58].

The proliferation of the haltere's sensory apparatus is such that this tiny organ can entrain the timing of the ipsilateral wB1 [6]. Based on the number of campaniform sensilla the haltere possesses, von Buddenbrock argued that halteres served as 'stimulation organs' for the flight circuit, providing the necessary input for the normal production of flight muscle forces [59]. More recent electrophysiological experiments have demonstrated that wing and haltere feedback structures wB1 firing on a wingstroke-to-wingstroke basis [10]. Thus, one major role for the haltere is to act as a metronome for the wing steering system by providing rhythmic mechanosensory feedback during normal flight.

In addition to their role as metronomes for the flight circuit, halteres are commonly known as the only true biological gyroscopes. Derham first noted that flies crash catastrophically once their halteres are removed and named them 'haltere' for their role in maintaining a fly's balance through the air [60]. Although this simple experiment elegantly demonstrated that halteres are necessary for flight, how these unique organs helped flies stay aloft remained elusive for centuries. In an extensive analysis that remains at the forefront of our understanding of haltere function after more than 70 years, Pringle analysed the dynamics of a moving haltere and the anatomy of its campaniforms [8]. He postulated that during rotations, the haltere experiences an inertial force that is orthogonal to its original plane of oscillation, also known as the Coriolis force:

$$F_C = 2m\omega \times v, \tag{4.1}$$

where m is the mass of the haltere end knob, ω is the angular velocity of the body and v is the haltere tangential (tip) velocity. Coriolis forces would change the haltere tip path from a straight

Downloaded from https://royalsocietypublishing.org/ on 03 June 2021

line to a figure-eight or oval, depending on the direction of rotation (figure 3*c*). Furthermore, Coriolis forces only occur in a rotating frame of reference, and later analyses showed that only Coriolis forces acting on the haltere can inform flies of the direction and magnitude in which they are rotating [61,62]. Thus, the haltere could help flies monitor their self-motion, similar to the vertebrate vestibular system [63–66].

A great deal of behavioural and electrophysiological work supports a gyroscopic function for the haltere. For example, flies that are subjected to mechanical rotational stimuli exhibit compensatory reflexes of the head and wings, which are abolished upon haltere removal [67–70]. Furthermore, the campaniform sensilla at the haltere's base, known as dorsal field 2 (dF2; figure 3*a*), provide direct, excitatory input to the ipsilateral wB1 motor neuron via a mixed electrotonic and chemical synapse [52,71,72]. Feedback from dF2 has the ability to induce a phase advance in wB1's firing pattern at specific stimulus intervals relative to wing mechanosensory feedback [10]. The sensilla of this field are arranged in a way that suggests they are most sensitive to the shear strains that occur when the haltere tip path is deflected as a result of Coriolis forces [8,73], and along with a similarly arranged chordotonal organ, may endow the haltere with its gyroscopic capacity. Also, haltere feedback is nonlinearly integrated with visual input to control the firing of neck muscle motor neurons, pointing to a role in gaze stabilization for extracting visual motion cues [74,75].

One expectation that follows from equation (4.1) is that gyroscopic sensing should exhibit the characteristics of a high-pass filter, with haltere-mediated reflexes being more sensitive to faster rotations. Behavioural experiments indicate that this is indeed the case, whereas visually mediated reflexes are more sensitive to slower rotations [67,70,76]. More recently, a number of papers have used a control-theoretic framework to model the haltere's role in flight control [77–82]. Flies subjected to an applied torque from a magnetic field with a metal pin that is dorsally tethered recover from this perturbation within five wingbeats [77]. Fitting the body dynamics to a linear control model suggests that in the context of rotational perturbations, haltere feedback acts as a proportional-integral controller on the body's angular velocity [77,79–81]. Such a control architecture may allow flies to correct for the current angular velocity error signal due to Coriolis forces via the proportional term while also adjusting for estimates of the past error via the integral term. Based on experiments using a dynamically scaled model of a flapping fly, a separate hypothesis instead suggests that the haltere provides active feedback during flight—particularly about the yaw axis—which can be modelled using a proportional controller alone [78,82]. This may allow the visual system to operate with higher sensitivity, or gain, without making the fly unstable. At this time, further experiments are needed to distinguish between these models. Regardless, flies combine haltere gyroscopic sensing with visual feedback to broaden their sensitivity to external perturbations during flight, making them remarkably stable.

Altogether, the working model of the haltere until recently was that it serves as a mostly passive sensor. Campaniform sensilla on the stalk fire single, phase-locked action potentials during normal beating [83–85], providing wingbeat-synchronous feedback to the wB1 muscle. This ensures that wB1 fires at the proper phase of the stroke cycle. Then, during sudden instabilities due to wind gusts, differential wing loading or wing damage, the haltere experiences Coriolis forces resulting from the fly's body rotation. The Coriolis forces alter the haltere's tip path trajectory, changing the pattern of strain at its base. This new strain pattern recruits additional campaniform sensilla, which fire at different phases of the stimulus cycle [85–87]. Through the campaniforms' connection to the wing steering system, this increased activity elicits a phase advance in wB1. As a result, wingbeat amplitude increases, resulting in increased aerodynamic force production, allowing the fly to correct for instabilities in its flight path (figure 3*d*).

5. The control-loop hypothesis: converting graded visual input into a phase code

The reflexes mediated by the halteres are extremely rapid. For example, stimulation of haltere campaniforms results in depolarizations of the wB1 motor neuron in approximately 4 ms [71,72]. The existence of such fast reflex loops connecting sensing to motor output via the haltere poses a serious problem to understanding how flies execute voluntary flight manoeuvres [88]. Recent work on a number of insect flight behaviours suggests a role for efference copy in suppressing visually mediated reflexes during voluntary manoeuvres [89–91]. In the case of silencing the haltere's reflexes during active turns, alternative strategies that take into account its evolutionary history as a hindwing exist. Previous electrophysiological studies on *Calliphora* demonstrated that the haltere steering muscles receive descending visual input [58]. This result suggests that flies may actively tune the strength of haltere mechanosensory feedback to achieve flight turns, rather than use the haltere for passively detecting gyroscopic forces. In what is known as the *control-loop hypothesis*, descending visual commands activate the haltere muscles, resulting in changes to the structure's motion or mechanics. The resulting changes alter the strain experienced by haltere campaniform sensilla, recruiting additional mechanosensors to fire each stroke cycle at different phases of haltere oscillation. Then, owing to the haltere's direct connection to the wB1 muscle, wingbeat amplitude, and thus aerodynamic forces increase, allowing the fly to change its heading. This way, the visual system could indirectly initiate voluntary changes in the flight path through its connection to the haltere steering muscles.

New evidence using the neurogenetic tools uniquely available in *Drosophila* has confirmed the control-loop hypothesis as a plausible mechanism for regulating the timing and activation of the wing steering system via three lines of evidence [9]. First, the haltere steering muscles are tuned to rotations about the body's cardinal axes, matching an identified descending interneuron (DNHS1) that projects to the haltere neuropil of the VNC [36]. This result suggests that the visual system controls the haltere muscles, implying the modulation of mechanosensory input via visual input [9]. Second, the haltere primary afferent projections in the brain are also responsive to global visual rotations during tethered flight, indicating that haltere motion is controlled in a similar manner to the wings. Finally, activation of the haltere steering muscle motor neurons either alters the activation phase of wB1 or recruits wB2. Taken together, these data are the first direct observations that flies can use changes in haltere steering muscle activity to co-opt mechanosensory reflexes, thereby enabling the execution of voluntary manoeuvres.

Downloaded from https://royalsocietypublishing.org/ on 03 June 2021

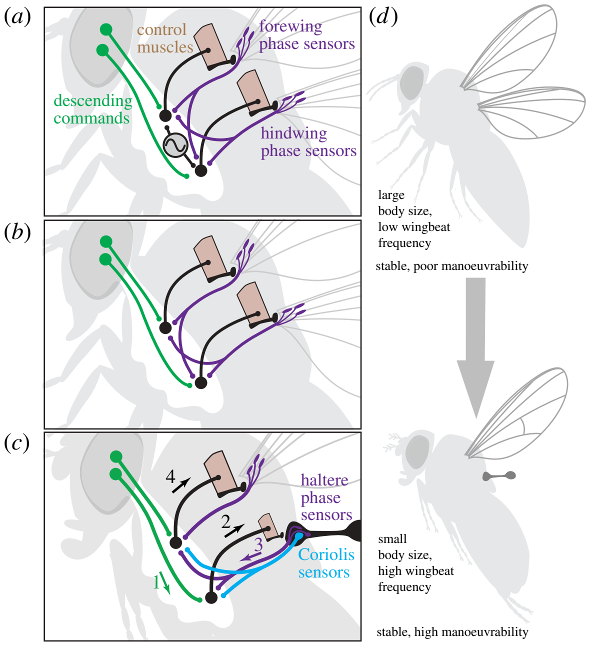

Figure 4. Proposed scenario leading to the evolution of halteres. (*a*) Flies' evolutionary ancestor was a four-winged flyer that used a central pattern generator along with sensory feedback. (*b*) The radiation of flying insects led to a decrease in body size along with necessary increase in wingbeat frequency, leading to the evolution of asynchronous flight muscle. In many small fliers, the timing of the control muscles may depend on mechanosensory feedback from the hindwing. (*c*) In flies, the control-loop pathway allows the regulation of wing steering muscle timing or activation separate from the detection of aerodynamic forces via the haltere. Visual commands (1) to the haltere muscles (2) leads to the recruitment of additional campaniform sensilla at each stroke (3); changing the firing phase of tonic wing steering muscles activates phasic muscles (4). The haltere's gyroscopic sensing may be an elaboration of its timing function. Reproduced from Dickerson *et al.* [9]. (*d*) Flies' evolutionary ancestor had a relatively large body size and low wingbeat frequency, making it passively stable in flight but with poor manoeuvrability. The evolution of Diptera—and the haltere's dual role as an adjustable timing mechanism and gyroscope—allow these insects to both reject instabilities and rapidly initiate changes in their flight trajectories. (Online version in colour.)

Although the control-loop hypothesis is a mechanism unique to flies, it is based on the haltere's evolutionary history. Indeed, past work in locusts demonstrates that mechanosensory feedback from the hindwing is strongly coupled to the motor neurons of the forewing control muscles [42,92,93]. In addition, ablating hindwing mechanosensory feedback in the hawkmoth *Manduca sexta* alters forewing kinematics and resultant lift force production [94]. Taken together, the picture that emerges is one where the regulation of wing steering muscle activation phase was the principal selective pressure that led to the evolution of the haltere (figure 4; [59,60]). In this scenario, flies' evolutionary ancestor was a large, four-winged flyer that used a central pattern generator to generate the flight rhythm, layering wingbeat-synchronous mechanosensory feedback and descending visual commands for steering commands (figure 4*a*). Owing to the tight neuromechanical coupling between the fore- and hindwings, this insect could maintain flight stability but had poor manoeuvrability. As flying insects radiated and decreased in body size, the evolution of asynchronous flight muscle marked a transition from a neural oscillator to a biomechanical oscillator for powering flight. While this mechanism enabled small fliers to achieve the necessary high wingbeat frequencies to stay aloft, the steering muscles still required precise timing input for executing manoeuvres. Thus, wingbeat-synchronous mechanosensory feedback became an essential modality for controlling wing motion (figure 4*b*). These flies may have been more manoeuvrable compared with their ancestor because of their reduced body size. However, the activation phase of the steering muscles in these animals would still depend on sensory feedback due to bending of the fore and hindwings.

Relying on both wings for producing aerodynamic forces and controlling the timing of the wing steering system would require complex information processing to disambiguate wing bending due to normal flapping from perturbations or voluntary steering commands. Although recent modelling efforts suggest that such processing could be accomplished by the wings [95], the evolution of the haltere and the control-loop pathway represents a clean division of labour between the production of aerodynamic forces and regulating the precision of motor output. The wings produce flight forces and their embedded campaniforms set the rhythm of the wing steering system. Meanwhile, the halteres convert visual commands into a phase code for the wing steering muscles via the haltere motor system, dynamically controlling the steering muscle activation phase or recruitment on a stroke-by-stroke basis, independently of the wings (figure 4*c*). The detection of rotational perturbations via the Coriolis force is, therefore, a likely elaboration of this conserved circuit. Thus, although commonly described as flies' 'gyroscope,' a more accurate description of the haltere is that it is a multifunctional sensory organ; the haltere enables flies to maintain stability in the face of external perturbations without sacrificing manoeuvrability at rapid timescales (figure 4*d*). Furthermore, the haltere's direct connection to the neck motor system and its crucial role in gaze stabilization suggest that the visual system regulates the level of haltere feedback and *vice versa*.

6. Future directions

The potential for understanding how precise mechanosensory feedback structures the timing of motor output is greater than ever before, especially with the advent of new genetic tools for labelling and manipulating specific cell types in *Drosophila*. Moreover, all flying insects possess four wings or wing-like structures, making the control-loop hypothesis a useful starting point for studying the role of timing across insects, although the role of local VNC circuits or descending commands cannot be excluded. Thus, as genome editing approaches become more tractable in traditional model systems of insect flight that are not *genetic* models, we will gain comparative insight into this problem at a mechanistic level. The use of these modern methods will highlight the tremendous importance of timing in neural systems as well as the selective pressures that led to the diversification of nature's most successful organisms.

Data accessibility. This article has no additional data.

Competing interests. I declare I have no competing interests.

Funding. This work was supported by startup funds from UNC Chapel Hill and NSF award IOS-2006284.

Acknowledgements. Alysha de Souza provided helpful comments on early drafts.

Downloaded from https://royalsocietypublishing.org/ on 03 June 2021

References

1. Carr CE. 1993 Processing of temporal information in the brain. *Annu. Rev. Neurosci.* **16**, 223–243. (doi:10.1146/annurev.ne.16.030193.001255)
2. Sober SJ, Sponberg S, Nemenman I, Ting LH. 2018 Millisecond spike timing codes for motor control. *Trends Neurosci.* **41**, 644–648. (doi:10.1016/j.tins.2018.08.010)
3. Josephson RK. 1985 Mechanical power output from striated muscle during cyclic contraction. *J. Exp. Biol.* **114**, 493–512.
4. Fry SN, Sayaman R, Dickinson MH. 2003 The aerodynamics of free-flight maneuvers in *Drosophila*. *Science* **300**, 495–498. (doi:10.1126/science.1081944)
5. Muijres FT, Elzinga MJ, Melis JM, Dickinson MH. 2014 Flies evade looming targets by executing rapid visually directed banked turns. *Science* **344**, 172–177. (doi:10.1126/science.1248955)
6. Heide G. 1983 Neural mechanisms of flight control in Diptera. *BIONA Rep.* **2**, 35–52.
7. Lehmann F-O, Bartussek J. 2017 Neural control and precision of flight muscle activation in *Drosophila*. *J. Comp. Physiol. A* **203**, 1–14. (doi:10.1007/s00359-016-1133-9)
8. Pringle JWS. 1948 The gyroscopic mechanism of the halteres of Diptera. *Phil. Trans. R. Soc. Lond. B* **233**, 347–384. (doi:10.1098/rstb.1948.0007)
9. Dickerson BH, de Souza AM, Huda A, Dickinson MH. 2019 Flies regulate wing motion via active control of a dual-function gyroscope. *Curr. Biol.* **29**, 3517–3524.e3. (doi:10.1016/j.cub.2019.08.065)
10. Fayyazuddin A, Dickinson MH. 1999 Convergent mechanosensory input structures the firing phase of a steering motor neuron in the blowfly, *Calliphora*. *J. Neurophysiol.* **82**, 1916–1926. (doi:10.1152/jn.1999.82.4.1916)
11. Dudley R. 2002 *The biomechanics of insect flight: form, function, evolution*. Princeton, NJ: Princeton University Press.
12. Dickinson MH, Tu MS. 1997 The function of dipteran flight muscle. *Comp. Biochem. Physiol. A* **116**, 223–238. (doi:10.1016/S0300-9629(96)00162-4)
13. Walker SM, Schwyn DA, Mokso R, Wicklein M, Müller T, Doube M, Stampanoni M, Krapp HG, Taylor GK. 2014 *In vivo* time-resolved microtomography reveals the mechanics of the blowfly flight motor. *PLoS Biol.* **12**, e1001823. (doi:10.1371/journal.pbio.1001823)
14. Dickinson M. 2006 Insect flight. *Curr. Biol.* **16**, R309–R314. (doi:10.1016/j.cub.2006.03.087)
15. Nachtigall W, Wilson DM. 1967 Neuro-muscular control of dipteran flight. *J. Exp. Biol.* **47**, 77–97.
16. Nachtigall W, Oldroyd H, Biederman-Thorson MA, Abbot RH. 1974 *Insects in flight: a glimpse behind the scenes in biophysical research*. New York, NY: McGraw-Hill.
17. Lindsay T, Sustar A, Dickinson M. 2017 The function and organization of the motor system controlling flight maneuvers in flies. *Curr. Biol.* **27**, 345–358. (doi:10.1016/j.cub.2016.12.018)
18. Heide G, Götz KG. 1996 Optomotor control of course and altitude in *Drosophila melanogaster* is correlated with distinct activities of at least three pairs of flight steering muscles. *J. Exp. Biol.* **199**, 1711–1726.
19. Tu MS, Dickinson MH. 1996 The control of wing kinematics by two steering muscles of the blowfly (*Calliphora vicina*). *J. Comp. Physiol. A* **178**, 813–830.
20. Balint CN, Dickinson MH. 2001 The correlation between wing kinematics and steering muscle activity in the blowfly *Calliphora vicina*. *J. Exp. Biol.* **204**, 4213–4226.
21. Tu MS, Dickinson MH. 1994 Modulation of negative work output from a steering muscle of the blowfly *Calliphora vicina*. *J. Exp. Biol.* **192**, 207–224.
22. Egelhaaf M. 1989 Visual afferences to flight steering muscles controlling optomotor responses of the fly. *J. Comp. Physiol. A* **165**, 719–730. (doi:10.1007/BF00610871)
23. Lehmann F-O, Götz KG. 1996 Activation phase ensures kinematic efficacy in flight-steering muscles of *Drosophila melanogaster*. *J. Comp. Physiol. A* **179**, 311–322. (doi:10.1007/BF00194985)
24. Ahn AN, Full RJ. 2002 A motor and a brake: two leg extensor muscles acting at the same joint manage energy differently in a running insect. *J. Exp. Biol.* **205**, 379–389.
25. Girgenrath M, Marsh RL. 1999 Power output of sound-producing muscles in the tree frogs *Hyla versicolor* and *Hyla chrysoscelis*. *J. Exp. Biol.* **202**, 3225–3237.
26. Marsh RL, Olson JM. 1994 Power output of scallop adductor muscle during contractions replicating the *in vivo* mechanical cycle. *J. Exp. Biol.* **193**, 139–156.
27. Tu MS, Daniel TL. 2004 Submaximal power output from the dorsolongitudinal flight muscles of the hawkmoth *Manduca sexta*. *J. Exp. Biol.* **207**, 4651–4662. (doi:10.1242/jeb.01321)
28. Dickinson MH, Farley CT, Full RJ, Koehl MAR, Kram R, Lehman S. 2000 How animals move: an integrative view. *Science* **288**, 100–106. (doi:10.1126/science.288.5463.100)
29. Roberts TJ, Marsh RL, Weyand PG, Taylor CR. 1997 Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113–1115. (doi:10.1126/science.275.5303.1113)
30. Balint CN, Dickinson MH. 2004 Neuromuscular control of aerodynamic forces and moments in the blowfly, *Calliphora vicina*. *J. Exp. Biol.* **207**, 3813–3838. (doi:10.1242/jeb.01229)
31. Josephson RK, Malamud JG, Stokes DR. 2000 Asynchronous muscle: a primer. *J. Exp. Biol.* **203**, 2713–2722.
32. Heide G. 1979 Proprioceptive feedback dominates the central oscillator in the patterning of the flight motoneuron output in *Tipula* (Diptera). *J. Comp. Physiol. A* **134**, 177–189. (doi:10.1007/BF00610477)
33. Gronenberg W, Strausfeld NJ. 1990 Descending neurons supplying the neck and flight motor of Diptera: physiological and anatomical characteristics. *J. Comp. Neurol.* **302**, 973–991. (doi:10.1002/cne.903020420)
34. Strausfeld NJ, Gronenberg W. 1990 Descending neurons supplying the neck and flight motor of Diptera: organization and neuroanatomical relationships with visual pathways. *J. Comp. Neurol.* **302**, 954–972. (doi:10.1002/cne.903020419)
35. Namiki S, Dickinson MH, Wong AM, Korff W, Card GM. 2018 The functional organization of descending sensory-motor pathways in *Drosophila*. *eLife* **7**, e34272. (doi:10.7554/eLife.34272)
36. Suver MP, Huda A, Iwasaki N, Safarik S, Dickinson MH. 2016 An array of descending visual interneurons encoding self-motion in *Drosophila*. *J. Neurosci.* **36**, 11 768–11 780. (doi:10.1523/JNEUROSCI.2277-16.2016)
37. Keil TA. 1997 Functional morphology of insect mechanoreceptors. *Microsc. Res. Techniq.* **39**, 506–531. (doi:10.1002/(SICI)1097-0029(19971215)39:6<506::AID-JEMT5>3.0.CO;2-B)
38. Chapman KM, Smith RS. 1963 A linear transfer function underlying impulse frequency modulation in a cockroach mechanoreceptor. *Nature* **197**, 699–700. (doi:10.1038/197699a0)
39. Cole ES, Palka J. 1982 The pattern of campaniform sensilla on the wing and haltere of *Drosophila melanogaster* and several of its homeotic mutants. *Development* **71**, 41–61.
40. Gnatzy W, Grünert U, Bender M. 1987 Campaniform sensilla of *Calliphora vicina* (Insecta, Diptera). I. Topography. *Zoomorphology* **106**, 312–319. (doi:10.1007/BF00312005)
41. Grünert U, Gnatzy W. 1987 Campaniform sensilla of *Calliphora vicina* (Insecta, Diptera). II. Typology. *Zoomorphology* **106**, 320–328. (doi:10.1007/BF00312006)
42. Gettrup E. 1965 Sensory mechanisms in locomotion: the campaniform sensilla of the insect wing and their function during flight. *Cold Spring Harb. Symp. Quant. Biol.* **30**, 615–622. (doi:10.1101/SQB.1965.030.01.059)
43. Zill SN, Moran DT. 1981 The exoskeleton and insect proprioception. I. Responses of tibial campaniform sensilla to external and muscle-generated forces in the American cockroach, *Periplaneta americana*. *J. Exp. Biol.* **91**, 1–24.
44. Tuthill JC, Wilson RI. 2016 Mechanosensation and adaptive motor control in insects. *Curr. Biol.* **26**, R1022–R1038. (doi:10.1016/j.cub.2016.06.070)
45. Bartussek J, Lehmann F-O. 2016 Proprioceptive feedback determines visuomotor gain in *Drosophila*. *R. Soc. Open Sci.* **3**, 150562. (doi:10.1098/rsos.150562)
46. Bartussek J, Lehmann F-O. 2018 Sensory processing by motoneurons: a numerical model for low-level flight control in flies. *J. R. Soc. Interface* **15**, 20180408. (doi:10.1098/rsif.2018.0408)
47. Mureli S, Fox JL. 2015 Haltere mechanosensory influence on tethered flight behavior in *Drosophila*. *J. Exp. Biol.* **218**, 2528–2537. (doi:10.1242/jeb.121863)
48. Chevalier RL. 1969 The fine structure of campaniform sensilla on the halteres of *Drosophila melanogaster*. *J. Morphol.* **128**, 443–463. (doi:10.1002/jmor.1051280405)
49. Smith DS. 1969 The fine structure of haltere sensilla in the blowfly *Calliphora erythrocephala* (Meig.),

Downloaded from https://royalsocietypublishing.org/ on 03 June 2021

with scanning electron microscopic observations on the haltere surface. *Tissue Cell* **1**, 443–484. (doi:10.1016/S0040-8166(69)80016-9)

50. Agrawal S, Grimaldi D, Fox JL. 2017 Haltere morphology and campaniform sensilla arrangement across Diptera. *Arthropod Struct. Dev.* **46**, 215–229. (doi:10.1016/j.asd.2017.01.005)
51. Toh Y. 1985 Structure of campaniform sensilla on the haltere of *Drosophila* prepared by cryofixation. *J. Ultrastruct. Res.* **93**, 92–100. (doi:10.1016/0889-1605(85)90089-8)
52. Chan WP, Dickinson MH. 1996 Position-specific central projections of mechanosensory neurons on the haltere of the blow fly, *Calliphora vicina*. *J. Comp. Neurol.* **369**, 405–418. (doi:10.1002/(SICI)1096-9861(19960603)369:3<405::AID-CNE6>3.0.CO;2-9)
53. Weatherbee SD, Halder G, Kim J, Hudson A, Carroll S. 1998 Ultrabithorax regulates genes at several levels of the wing-patterning hierarchy to shape the development of the *Drosophila* haltere. *Genes Dev.* **12**, 1474–1482. (doi:10.1101/gad.12.10.1474)
54. Pringle JWS. 1949 The excitation and contraction of the flight muscles of insects. *J. Physiol.* **108**, 226–232. (doi:10.1113/jphysiol.1949.sp004326)
55. Bonhag PF. 1949 Thoracic mechanism of the adult horsefly: Diptera, Tabanidae. *Cornell Univ. Agric. Exp. Stat.* **285**, 3–39.
56. Mickoleit G. 1962 Die Thoraxmuskulatur von *Tipula vernalis* Meigen. Ein Beitrag zur vergleichenden Anatomie des Dipterenthorax [The thoracic muscles of *Tipula vernalis* Meigen. A contribution to the comparative anatomy of the dipteran thorax]. *Zool. Jb. Anat. Bd.* **80**, 213–244. [In German.]
57. Ulrich H. 1984 Skelett und Muskulatur des Thorax von *Microphor holosericeus* (Meigen) (Diptera, Empidoidea) [Skeleton and muscles of the thorax of *Microphor holosericeus* (Meigen) (Diptera, Empidoidea)]. *Bonn Zool. Beitr.* **35**, 351–398. [In German.]
58. Chan WP, Prete F, Dickinson MH. 1998 Visual input to the efferent control system of a fly's 'gyroscope'. *Science* **280**, 289–292. (doi:10.1126/science.280.5361.289)
59. v. Buddenbrock W. 1919 Die vermutliche Lösung der Halterenfrage [The presumed solution of the haltere question]. *Pflügers Arch.* **175**, 125–164. [In German.] (doi:10.1007/BF01722145)
60. Derham W. 1714 *Physico-theology*. London, UK: W. & J. Innys.
61. Nalbach G. 1993 The halteres of the blowfly *Calliphora*. I. Kinematics and dynamics. *J. Comp. Physiol. A* **173**, 293–300. (doi:10.1007/BF00212693)
62. Thompson R, Rummelt N, Dixon W. 2012 Angular rate encoding in haltere feedback for flight stabilization of dipteran insects. In Proc. *AIAA Guidance, Navigation, and Control Conference, 10–13 August 2009, Chicago, Illinois,* pp. 1–14. (doi:10.2514/6.2009-5657)
63. Cullen KE. 2004 Sensory signals during active versus passive movement. *Curr. Opin. Neurobiol.* **14**, 698–706. (doi:10.1016/j.conb.2004.10.002)
64. Angelaki DE, Cullen KE. 2008 Vestibular system: the many facets of a multimodal sense. *Annu. Rev. Neurosci.* **31**, 125–150. (doi:10.1146/annurev.neuro.31.060407.125555)
65. Cullen KE. 2012 The vestibular system: multimodal integration and encoding of self-motion for motor control. *Trends Neurosci.* **35**, 185–196. (doi:10.1016/j.tins.2011.12.001)
66. Hardcastle BJ, Krapp HG. 2016 Evolution of biological image stabilization. *Curr. Biol.* **26**, R1010–R1021. (doi:10.1016/j.cub.2016.08.059)
67. Hengstenberg R. 1988 Mechanosensory control of compensatory head roll during flight in the blowfly *Calliphora erythrocephala* Meig. *J. Comp. Physiol. A* **163**, 151–165. (doi:10.1007/BF00612425)
68. 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* **175**, 695–708. (doi:10.1007/BF00191842)
69. Dickinson MH. 1999 Haltere-mediated equilibrium reflexes of the fruit fly, *Drosophila melanogaster*. *Phil. Trans. R. Soc. Lond. B* **354**, 903–916. (doi:10.1098/rstb.1999.0442)
70. Sherman A, Dickinson MH. 2003 A comparison of visual and haltere-mediated equilibrium reflexes in the fruit fly *Drosophila melanogaster*. *J. Exp. Biol.* **206**, 295–302. (doi:10.1242/jeb.00075)
71. Fayyazuddin A, Dickinson MH. 1996 Haltere afferents provide direct, electrotonic input to a steering motor neuron in the blowfly, *Calliphora*. *J. Neurosci.* **16**, 5225–5232. (doi:10.1523/JNEUROSCI.16-16-05225.1996)
72. Trimarchi JR, Murphey RK. 1997 The *shaking-B*^{2} mutation disrupts electrical synapses in a flight circuit in adult *Drosophila*. *J. Neurosci.* **17**, 4700–4710. (doi:10.1523/JNEUROSCI.17-12-04700.1997)
73. Fraenkel G, Pringle JWS. 1938 Halteres of flies as gyroscopic organs of equilibrium. *Nature* **141**, 919. (doi:10.1038/141919a0)
74. Strausfeld NJ, Seyan HS. 1985 Convergence of visual, haltere, and prosternal inputs at neck motor neurons of *Calliphora erythrocephala*. *Cell Tissue Res.* **240**, 601–615. (doi:10.1007/BF00216350)
75. Huston SJ, Krapp HG. 2009 Nonlinear integration of visual and haltere inputs in fly neck motor neurons. *J. Neurosci.* **29**, 13 097–13 105. (doi:10.1523/JNEUROSCI.2915-09.2009)
76. Sherman A, Dickinson MH. 2004 Summation of visual and mechanosensory feedback in *Drosophila* flight control. *J. Exp. Biol.* **207**, 133–142. (doi:10.1242/jeb.00731)
77. Ristroph L, Bergou AJ, Ristroph G, Coumes K, Berman GJ, Guckenheimer J, Wang ZJ, Cohen I. 2010 Discovering the flight autostabilizer of fruit flies by inducing aerial stumbles. *Proc. Natl Acad. Sci. USA* **107**, 4820–4824. (doi:10.1073/pnas.1000615107)
78. Elzinga MJ, Dickson WB, Dickinson MH. 2012 The influence of sensory delay on the yaw dynamics of a flapping insect. *J. R. Soc. Interface* **9**, 1685–1696. (doi:10.1098/rsif.2011.0699)
79. Ristroph L, Ristroph G, Morozova S, Bergou AJ, Chang S, Guckenheimer J, Wang ZJ, Cohen I. 2013 Active and passive stabilization of body pitch in insect flight. *J. R. Soc. Interface* **10**, 20130237. (doi:10.1098/rsif.2013.0237)
80. Beatus T, Guckenheimer JM, Cohen I. 2015 Controlling roll perturbations in fruit flies. *J. R. Soc. Interface* **12**, 20150075. (doi:10.1098/rsif.2015.0075)
81. Whitehead SC, Beatus T, Canale L, Cohen I. 2015 Pitch perfect: how fruit flies control their body pitch angle. *J. Exp. Biol.* **218**, 3508–3519. (doi:10.1242/jeb.122622)
82. Dickinson MH, Muijres FT. 2016 The aerodynamics and control of free flight manoeuvres in *Drosophila*. *Phil. Trans. R. Soc. B* **371**, 20150388. (doi:10.1098/rstb.2015.0388)
83. Fox JL, Daniel TL. 2008 A neural basis for gyroscopic force measurement in the halteres of *Holorusia*. *J. Comp. Physiol. A* **194**, 887–897. (doi:10.1007/s00359-008-0361-z)
84. Dickinson MH. 1990 Comparison of encoding properties of campaniform sensilla on the fly wing. *J. Exp. Biol.* **151**, 245–261.
85. Mohren TL, Daniel TL, Eberle AL, Reinhall PG, Fox JL. 2019 Coriolis and centrifugal forces drive haltere deformations and influence spike timing. *J. R. Soc. Interface* **16**, 20190035. (doi:10.1098/rsif.2019.0035)
86. Yarger AM, Fox JL. 2018 Single mechanosensory neurons encode lateral displacements using precise spike timing and thresholds. *Proc. R. Soc. B* **285**, 20181759. (doi:10.1098/rspb.2018.1759)
87. Fox JL, Fairhall AL, Daniel TL. 2010 Encoding properties of haltere neurons enable motion feature detection in a biological gyroscope. *Proc. Natl Acad. Sci. USA* **107**, 3840–3845. (doi:10.1073/pnas.0912548107)
88. Dickinson MH. 2005 The initiation and control of rapid flight maneuvers in fruit flies. *Integr. Comp. Biol.* **45**, 274–281. (doi:10.1093/icb/45.2.274)
89. Mischiati M, Lin H-T, Herold P, Imler E, Olberg R, Leonardo A. 2015 Internal models direct dragonfly interception steering. *Nature* **517**, 333–338. (doi:10.1038/nature14045)
90. Kim AJ, Fitzgerald JK, Maimon G. 2015 Cellular evidence for efference copy in *Drosophila* visuomotor processing. *Nat. Neurosci.* **18**, 1247–1255. (doi:10.1038/nn.4083)
91. Kim AJ, Fenk LM, Lyu C, Maimon G. 2017 Quantitative predictions orchestrate visual signaling in *Drosophila*. *Cell* **168**, 280–294.e12. (doi:10.1016/j.cell.2016.12.005)
92. Gettrup E. 1966 Sensory regulation of wing twisting in locusts. *J. Exp. Biol.* **44**, 1–16.
93. Wolf H. 1993 The locust tegula: significance for flight rhythm generation, wing movement control and aerodynamic force production. *J. Exp. Biol.* **182**, 229–253.
94. Frye MA. 2001 Effects of stretch receptor ablation on the optomotor control of lift in the hawkmoth *Manduca sexta*. *J. Exp. Biol.* **204**, 3683–3691.
95. Eberle AL, Dickerson BH, Reinhall PG, Daniel TL. 2015 A new twist on gyroscopic sensing: body rotations lead to torsion in flapping, flexing insect wings. *J. R. Soc. Interface* **12**, 20141088. (doi:10.1098/rsif.2014.1088)