SYMPOSIUM

Dipteran Halteres: Perspectives on Function and Integration for a Unique Sensory Organ

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Synopsis The halteres of dipteran insects (true flies) are essential mechanosensory organs for flight. These are modified hindwings with several arrays of sensory cells at their base, and they are one of the characteristic features of flies. Mechanosensory information from the halteres is sent with low latency to wing-steering and head movement motoneurons, allowing direct control of body position and gaze. Analyses of the structure and dynamics of halteres indicate that they experience very small aerodynamic forces but significant inertial forces, including Coriolis forces associated with body rotations. The sensory cells at the base of the haltere detect these forces and allow the fly to correct for perturbations during flight, but new evidence suggests that this may not be their only role. This review will examine our current understanding of how these organs move, encode forces, and transmit information about these forces to the nervous system to guide behavior.

Introduction

The four largest orders of holometabolous insects are each defined and named by characteristics of their wings: the Coleoptera (beetles, “sheath wing”), Lepidoptera (butterflies and moths, “scale wing”), Hymenoptera (ants, wasps, and bees, “membranous wing”), and Diptera (flies, “two wings”) (Borror et al. 1992). The last of these, the flies, are thus defined not by what they possess, but by what they lack: a second pair of lift-generating wings. In place of these wings is a pair of small dumbbell-shaped appendages known as halteres (from the Greek word for “dumbbell”; Fig. 1). The shape of these organs is such that they do not generate significant lift (unlike the hindwings of other insect orders), but rather experience large inertial forces as they beat with high amplitude during flight (Nalbach 1993). Centuries ago, curious scientists found that if the halteres are removed, flies are unable to fly (Derham 1714). Derham wrote:

For the keeping the Body steady and upright in Flight, it generally holds true, (if I mistake not,) that all bipennated Insects have Poisses joyn’d to the Body, under the hinder Part of their Wings; but such as have four Wings, or Wings with Elytra, none. If one of the Poisses, or one of the lesser auxiliary Wings be cut off, the Insect will fly as if one Side overbalanced the other, until it falleth on the Ground; so if both be cut off, they will fly awkwardly, and unsteadily, manifesting the Defect of some necessary part. These Poisses, or Pointells are, for the most Part little Balls, set at the Top of a slender stalk, which they can move every way at pleasure. In some they stand alone, in others, (as in the whole Flesh-Fly Tribe,) they have little Covers or Shields, under which they lie and move. The Use, no doubt of these Poisses and secondary lesser Wings is to poise the Body, and to obviate all the Vacillations thereof in Flight; serving to the Insect as the long Pole, laden at the Ends with Lead, doth the Ropedancer.

Early ideas about the function of the halteres included this concept of the halteres as “balancers” and a second concept of halteres as “stimulation organs,” in which haltere oscillations would drive...
the flight muscles (v. Buddenbrock 1919), but later data demonstrated that the halteres are organs of control rather than activation (Fraenkel 1939; Pringle 1948). Although the complex high-speed flight behaviors of flies have long fascinated scientists, there are still important unanswered questions on how the fly’s exquisite sensory systems operate to guide their aerial acrobatics. This review will focus on the role of haltere sensory input in fly behavior and examine how this essential organ is used in concert with other senses to guide the fly through its environment.

What are halteres?

The anatomy and development of halteres support the hypothesis that these organs evolved from the hindwings of ancestral insects. They are located on the metathorax and have similar hinges to the forewings, and the muscles of the metathorax that move the halteres are serial homologs of the mesothoracic muscles that move the wings (Chan et al. 1998). These muscles are reduced in both size and number from their mesothoracic counterparts, but have the same functions of oscillating the halteres and providing fine steering motions.

Arrays of the mechanosensory structures known as campaniform sensilla are found on both halteres and wings. On the wings of moths, sensilla are found along the wing veins as well as clustered into small fields at the base (Dombrowski 1991; Dickerson et al. 2014). On the halteres, these sensilla are found exclusively at the base, and their arrangement has been described in two highly-derived fly species: Drosophila (Cole and Palka 1982) and Calliphora (Gnatzy et al. 1987). In these species, the campaniform sensilla are arranged in straight rows and grouped into uniform fields. On both wings and halteres, groups of sensilla at the base are positioned at regions where maximal strain would occur during wing or haltere oscillation and body rotations. Recent data show that the forewings of moths can act as sensors of body rotation (Dickerson et al. 2014), suggesting that the campaniform sensilla on wings and halteres serve similar functions.

In segmented organisms, homeobox (Hox) genes direct the development of serially homologous segments. The Hox gene Ultrabithorax (Ubx) specifies the identity of the third thoracic segment of the insect body (Hersh et al. 2007). Proper hind wing development requires Ubx in a number of taxa, including butterflies, beetles, and flies (Weatherbee et al. 1998; Weatherbee et al. 1999; Tomoyasu et al. 2005). In Drosophila, Ubx controls the formation of the halteres during metamorphosis: if Ubx is deactivated, the haltere develops into a fully-formed wing (Hersh et al. 2007). This single homeotic gene change results in a radical phenotype change, because Ubx activates a cascade of other target genes (Weatherbee et al. 1999; Galant et al. 2002; Hersh and Carroll 2005). Genes expressed in wings and repressed in halteres have also been identified, but whether or not they act as direct targets of Ubx regulation is still unknown (Weatherbee et al. 1998; Crickmore and Mann 2006; Mohit et al. 2006). Although much remains to be explored beyond the level of Ubx activation, this locus provides clues on how the ancestors of flies’ hind wings may have originally evolved into halteres.

What are the dynamics of the halteres as flies perform natural behaviors?

The halteres oscillate when flies are flying, typically at the same frequency and at opposite phase with the wings’ oscillations (Deora et al. 2015; Hall et al.
The tight synchrony of wings and halteres was recently demonstrated to be mechanical, not neural, in origin. When forceps are used to manually move a freshly-killed soldier fly’s (Diptera: Stratiomyidae) wing up and down, not only does the opposite wing move in synchrony, the halteres also beat in antiphase with both wings. This experiment indicates that the coupling of the wings and halteres is driven by mechanical coupling and not neural input (Deora et al. 2015). The source of this coupling between the wings and halteres was found to be two small ridges of cuticle known as the subepimeral ridges (Deora et al. 2015). This mechanical connection ensures that the halteres remain synchronized with the movements of the wings during flight, such that the wings and halteres beat at the same frequency and with a specific phase that does not change between wing strokes. The haltere-wing phase relationship can differ substantially between species, however. Brachyceran (short-antennae) flies, like soldier flies, oscillate their halteres almost exactly opposite their wings (180 degrees out of phase). However, more ancient nematoceran (long-antennae) flies, which include crane flies, midges, and mosquitoes, exhibit wing-haltere phases that remain consistent between wingbeats, but vary substantially between species. These differences in wing-haltere coordination suggest that the activity of the haltere and wing sensors could vary according to a group’s evolutionary relationships (Hall et al. 2015). This in turn affects the mechanisms used to produce adaptive motor responses, which determine the flight behavior of the fly.

In addition to moving the halteres in flight, some calypterate flies also oscillate their halteres while walking, without oscillating their wings (Fraenkel 1939; Miller 1977; Sandeman and Markl 1980). They are able to oscillate them at their typical wingbeat frequency, but without engaging the large indirect flight muscles (Hall et al. 2015), suggesting that the small muscles intrinsic to the haltere (Chan et al. 1998) are responsible for the oscillation. The left and right halteres also show variable phase relationships while walking, in stark contrast to their strict coupling during flight, demonstrating that the thoracic mechanisms that maintain haltere synchrony in flight are not activated while walking (Hall et al. 2015).

What are the forces acting on the haltere?

As the haltere oscillates during walking or flight, several forces act upon it. These forces are largely inertial, with significantly smaller aerodynamic forces (Nalbach 1993). Body rotations in space produce forces acting primarily on the end-knobs of the halteres, as a result of their large and fast-moving mass (Nalbach 1993). These end-knob forces cause torsion or bending of the stalk, which activates fields of mechanosensory structures located at the base of the haltere (Pringle 1948; Eberle et al. 2015). Analysis of these forces demonstrated that halteres are not wind sensors, nor do they detect air currents resulting from the beating of the wings. Halteres are positioned close to the body, in the cleft between the abdomen and thorax, where air currents caused by body rotations have a negligible effect on haltere movements (Nalbach 1993). Furthermore, using high-speed video analysis of tethered flying blowflies, Nalbach calculated the relative contributions of each force during a body rotation and found that the angular velocity dependent force (Coriolis force) had the largest contribution for all three directions of rotation (yaw, pitch, and roll). The halteres only experience Coriolis force while rotating, but always experience a large inertial force when flapping.

Thompson et al. (2009) predicted the end-knob trajectory of the haltere during body rotations of various speeds. When a fly is flying in a straight path, each haltere vibrates in a plane. However, when the fly is rotating, the Coriolis force deflects the halteres laterally in addition to their up- and-down movement, resulting in a figure-of-eight trajectory for the end-knob (Thompson et al. 2009). At different velocities, the phases of the maximum out-of-plane displacement with respect to the haltere oscillation are different. An array of sensilla with precise spike timing and high sensitivity for particular phases of the haltere’s oscillatory movement would be able to detect this change in maximum displacement phase using a population code, and thus encode the fly’s rotational velocity (Fox et al. 2010). Directional selectivity of the campaniform sensilla, as implied by the ovoid shape of some of the sensillar caps (Thurm et al. 1974; Zill and Moran 1981; Gnatzy et al. 1987), could further refine the encoding by increasing sensitivity to forces occurring in specific directions.

Differences in haltere morphology can influence the forces acting on the haltere. More ancient families, such as Tipulidae (crane flies), possess halteres with long stalks (Fig. 1A). The halteres of more derived flies are generally shorter and in some families, such as Calliphoridae (blow flies), specialized flaps of wing tissue called calypters cover the haltere (Fig. 1B). Pringle (1948) hypothesized that the function of calypters was to prevent wind turbulence from affecting haltere movements, allowing more
precise detection of body position, but this idea has not been formally tested. The stalk of the haltere is also not always straight, and in more derived families tends to curve to reflect the shape of the body. This minimizes the amount of air space between the end-knob and the sides of the abdomen and thorax, which, like the calypters, could decrease wind resistance. In all halters, the bulb is asymmetric, with the larger portion of the bulb posterior. The degree of this asymmetry can vary across species but generally increases with evolutionary derivation, from a low asymmetry in crane flies (Fox and Daniel 2008) to extreme asymmetry in hoverflies (Ball and Morris 2015). This asymmetry may lead to increased torsion on the haltere during body rotations, providing a potentially informative force to the campaniform sensilla (Eberle et al. 2015).

What are the sensory structures on the halteres that transduce these forces, and how do they function?

The halteres possess several distinct fields of sensory cells at their base (Fig. 2). These fields, which vary in number and shape depending on species (Gnatzy et al. 1987; Fox and Daniel 2008), are composed of campaniform sensilla. These are dome-shaped protrusions located on the surface of the exoskeleton (cuticle), and are found on all insects in various locations. Attached inside the dome of each campaniform sensillum is a modified cilium extending from the sensory process of a neuron (Fig. 2E). When the cuticle bends and the surface of the dome is deflected, the neurons generate graded receptor potentials mediated by mechanically-activated ionotropic TRPN channels. Upon reaching threshold, these receptor potentials are then encoded as action potentials (Walker et al. 2000; Kernan 2007). These action potentials are sent to the central nervous system to be interpreted (Smith 1969; Thurm 1984; Keil 1997; Chapman et al. 2013). In blowflies (Calliphora), there are more than 400 campaniform sensilla per haltere, which make up the majority of the campaniform sensilla found on the fly’s body (Gnatzy et al. 1987). The sheer number of campaniform sensilla on the haltere suggests that flies may detect forces with high resolution, but the upstream effects of this fine-scale sensitivity are not currently known.

The haltere campaniform sensilla are clustered into groups, the number of which can vary by species. Almost all flies have all the same groups of fields (Fig. 3), though there are some families that do differ. These groups generally comprise cells of a similar orientation, suggesting directional selectivity for particular forces. Anatomical studies show that different fields project their afferents to different specific locations in the thoracic ganglion. In particular, afferents providing input to the first basalar muscle of the wing-steering complex originate from a single field of campaniform sensilla (Chan and Dickinson 1996). The position-specific projections from each field suggest that as different forces impact different sets of campaniform sensilla, the information will be processed in a spatiotopic way by the central nervous system (Barth et al. 1984; Thurm 1984; Dickinson 1990; Chan and Dickinson 1996). A spatiotopic arrangement of force sensitivity could allow higher neural centers to efficiently interpret force information from the halters, but this has not been demonstrated as a mechanism of haltere information processing.

The other major mechanosensory structures involved in sensing haltere movements are chordotonal organs (Pflugstaedt 1912). Chordotonal organs, unlike campaniform sensilla, exist beneath the cuticle and typically respond to stretch or vibration as opposed to distortion or bending (Chapman et al. 2013). Their sensory nerve endings attach between two internal points and when those points move apart, stretching the nerve cell, the difference in length is detected and transformed into action potentials. There are far fewer chordotonal organs at the base of the haltere than campaniform sensilla (two, versus 400 campaniform sensilla), so it is assumed that they are less important for detecting and transmitting rotational information from haltere movements (Pringle 1948). However, their function remains elusive as their axonal projections are localized within the relatively massive bundle of axons from the campaniform sensilla, making them difficult to visualize or access electrophysiologically (Chan and Dickinson 1996).

How do haltere afferent neurons process force information?
The axons of the campaniform sensilla neurons project out of the base of the haltere as a nerve bundle and enter the thoracic ganglion. Extracellular recordings from the haltere nerve showed that when halters are oscillated, bursts of action potentials occur in synchrony with the oscillation frequency (Pringle 1948). When flies are then rotated, these bursts break down into asynchronous spikes. Instead of bursts occurring at particular phases of haltere oscillations, spike times are spread throughout the duration of the haltere movement. Pringle suggested that this
reflects recruitment of different groups of sensilla as the fly rotates.

The oscillation-synchronous action potentials in the haltere nerve can be fired at frequencies well beyond the fly’s natural wingbeat (and, by extension, haltere beat) frequency: crane flies with a natural wingbeat frequency of 40 Hz show haltere-synchronous firing in the primary afferent neurons up to 150 Hz when the haltere is mechanically oscillated (Fox and Daniel 2008). These spikes are highly phase-locked to the haltere’s movement, showing some of the most precise spike-timing measured in any neuron (Fox and Daniel 2008).

This phase-locking activity suggests that small changes in the haltere’s movement might result in large changes in the spike timing activity of the population of haltere afferent neurons. Analysis of the encoding properties of haltere afferent neurons suggests that a population code, in which each haltere afferent fires a spike at a particular phase of movement, may be able to rapidly and accurately encode the out-of-plane haltere movements associated with body rotations (Thompson et al. 2009; Fox et al. 2010).

Where does haltere information go?

Axons within the haltere nerve project to the neuropil in a region-specific manner, in which dye fills of the neurons in specific fields of campaniform sensilla reveal projections to different locations in the central nervous system. However, these projections are numerous and somewhat diffuse for each field, suggesting that haltere information is sent to many postsynaptic targets within the central nervous system. Projections to the metathorax, posterior and midmesothorax, and prothorax are most prominent, and the anterior-most termination is located in the

Fig. 2 (A) Diagram showing the location at the base of the haltere SEMs were taken (B) SEM of halteres of Tipula showing fields of campaniform sensilla (Scale bar: 10 μm). White box indicates location of the following panel. (C) SEM of single campaniform field (dBP; scale bar: 10 μm). White box indicates location of the following panel. (D) SEM showing individual campaniform sensilla (Scale bar: 1 μm). (E) Diagram showing structure of individual campaniform sensillum. Dome-shaped region is composed of flexible cuticle. Downward displacement of this dome is detected by mechanosensory dendritic processes, which relay that information to the haltere nerve. The electrical activity of the campaniform sensilla can be recorded using extracellular electrodes placed in the axon. Adapted from Fox and Daniel (2008) and Keil (1997).
posterior subesophageal ganglion (Chan and Dickinson 1996). The majority of specific synaptic connections between haltere afferents and their targets remain unknown, but one particular synapse between the haltere nerve and a wing steering motor neuron (mnb1, the neuron of the first basalar muscle), has been described (Fayyazuddin and Dickinson 1996). The haltere afferents activating the synapse at mnb1 originate from the campaniform field dF2 (Fayyazuddin and Dickinson 1996). This single known connection suggests that other campaniform fields may also project to wing-steering muscles, but this is certainly not the only possibility. Each sensilla field projects to particular regions within the thoracic ganglion along an ipsilateral tract within the dorsal tectulum, but their post-synaptic targets are currently unknown (Chan and Dickinson 1996).

The synapse between the haltere afferents and mnb1 consists of two components: one fast and electrical, and the other slow and chemical. The electrical synapse is the source of the phase-locked firing pattern of mnb1 with the halteres during flight. With each haltere beat, information from haltere campaniform sensilla is sent almost instantaneously to the wing steering muscles (Fayyazuddin and Dickinson 1996). This fast electrical synapse allows changes in body position detected by the halteres to be sent directly to the wing steering muscles with a very short delay (≤5 ms).

In addition to the electrotonic input from the haltere, mnb1 receives mechanosensory input from the wings. To determine how haltere and wing afferents influence the firing of mnb1, Fayyazuddin and Dickinson electrically stimulated the wing and the haltere nerves, varying the phase of stimulation. They found that mnb1 was entrained by the wing afferent stimulation over a wider range of phase differences than by haltere afferent stimulation. The activity at the haltere afferent-mnb1 synapse indicates that the phase of firing in mnb1 is constrained by the wing afferents during straight flight, but that phase-shifted spikes from the haltere can change mnb1’s spike timing and thus, adjust the tension on the wing-steering basalar muscle to turn the fly (Fayyazuddin and Dickinson 1999). Rotational perturbations cause the haltere to be laterally deflected (Thompson et al. 2009) and the dF2 campaniform field is oriented such that it could detect this deflection for certain types of rotation (Pringle 1948; Gnatzy et al. 1987; Chan and Dickinson 1996). The haltere afferents activating the synapse at mnb1 originate from dF2 (Fayyazuddin and Dickinson 1996), and thus dF2 may be essential for detecting Coriolis forces caused by rotations in a particular direction, while other directions of rotation may activate other campaniform fields. These careful electrophysiological experiments thus provided a mechanism by which flies can use haltere sensory information to sense rotations and rapidly adjust their motor output.

How is haltere information integrated with vision to guide wing-steering behavior?

Because flies lacking halteres are unable to maintain stable free flight (Derham 1714), finer analyses of the behavioral effects of haltere input have been limited. By tethering flies and observing their attempted body rotations through torque sensors or wingbeat amplitude measurements, however, we can determine how the loss of haltere input influences behavior and draw inferences about how the fly’s brain uses haltere information. Flies adjust the tension in direct wing-steering muscles to control the amplitude and attack angles of their wings (Heide 1983; Dickinson and Tu 1997), and thus haltere inputs to motoneurons controlling these muscles have been of particular interest.

An experiment in which flies were rotated in various directions while fixating a closed-loop visual target provided evidence that halteres detect body rotations in each of the major rotational axes. Intact flies were able to adjust their wingbeat amplitudes to maintain a stable flight path (correcting for imposed body rotations) when rotated in any direction, but when one haltere was ablated, the flies’ ability to correct their flight path was unilaterally diminished for motions toward the ablated side (Dickinson 1999). In flies with both halteres removed, the flight path correction was nearly
eliminated. The fly’s wing-steering adjustments were correlated with the body’s rotational velocity, and not its position or acceleration, indicating that halteres detect the velocity of the fly’s body rotations and act as gyroscopes to stabilize the fly against imposed rotations.

How do the halteres contribute to behavior when the flies are allowed to turn themselves, rather than experiencing imposed turns? During free flight, flies exhibit periods of smooth linear motion interspersed with rapid turns called saccades. Bender and Dickinson (2006) found that when flies were fixed to a magnetic tether, such that they were able to perform free turns in the yaw direction, the amplitudes of their body saccades (rapid turns) did not depend on visual feedback. Instead, saccade amplitude was only affected when the halteres were weighted or ablated, increasing or decreasing the Coriolis forces acting on the haltere, respectively. When the mass was increased, saccade amplitude decreased, and when mass was decreased, saccade amplitude increased (Bender and Dickinson 2006). These results indicate that when flies perform voluntary, high-speed rotations, feedback from the halteres is essential to properly execute the behavior. Furthermore, body saccades are under sensory feedback control, and are not ballistic maneuvers: despite their rapidity, they can be modulated throughout their execution.

If haltere feedback controls the amplitude and duration of saccades, which are often stimulated by visual input, how might visual information integrate with haltere information to control flight behavior? It is clear that flies employ both vision and halteres to maintain stable flight. The halteres and eyes are tuned to complementary speeds of rotations for correcting the body position of the fly. When flies steer their wings in response to a moving visual stimulus, peak responses occur at lower speeds, whereas peak responses to physical rotations of the fly’s body occur at higher speeds (Sherman and Dickinson 2003). The compensatory head roll response shows a similar pattern of range fractionation (Hengstenberg 1988; Schwyn et al. 2011). The faster haltere system provides rapid feedforward information, whereas the slower visual system permits more accurate feedback (Sherman and Dickinson 2003; Schwyn et al. 2011). Because the halteres and eyes detect different ranges of angular velocities, the integration of these two separately tuned senses increases the fly’s ability to correct its body position over a wide range of angular velocities.

Can halteres influence flight behavior when the fly’s body is not rotating? In quiescent preparations of Calliphora, the intrinsic muscles of the halteres, but not the wing-steering muscles, are stimulated by moving wide-field visual stimuli (Chan et al. 1998). This curious result suggests that visually guided, self-generated turns could be driven by an active movement of the halteres, triggering a corrective reflex to steer the fly’s wings. This manipulation of the fly’s control loop would take advantage of the fly’s haltere-driven reflexes to escape from a reflex loop that would otherwise trap them in straight flight (Chan et al. 1998).

This interesting hypothesis would imply that flies might rely on their halteres to perform visually-stimulated turns. When halteres are removed from tethered flying flies, however, they are still able to steer their wings toward moving figures, but they struggle to stabilize moving wide-field visual stimuli (Mureli and Fox 2015). Halteres are thus not necessary for visually guided wing-steering movements, and visual information can reach wing-steering muscles through some haltere-independent connection. However, halteres do contribute to wing-steering maneuvers in a context-dependent manner, even when the behavior is separated from body rotations.

**How is haltere information integrated with vision for gaze control?**

Primary afferent neurons from the haltere synapse on neck motoneurons (NMNs) that control the position of the fly’s head (Strausfeld and Seyan 1985; Milde et al. 1987; Strausfeld et al. 1987). This input allows the head to counter-rotate against the body’s rotation, keeping the head stable even as the body rotates behind it. Because the fly’s eyes cannot move independently of its head, stabilization of the head via visual and haltere input keeps the visual scene fixed on the retina, and prevents self-generated optic flow from entering the visual information stream (Hengstenberg 1991; Lappe et al. 1999).

Hengstenberg tested flies’ ability to stabilize their heads when rotated over a large range of angular velocities and found that in the roll direction of rotation, flies were able to maintain their head position in response to angular motion only at speeds above 50°/s. He found that flies were most adept at detecting angular rotations at ~1500°/s (Hengstenberg 1988). Nalbach and Hengstenberg (1986) showed velocity dependencies for yaw and pitch rotations as well, but specific ranges similar to those published for roll were not defined. When haltere inputs were removed entirely, the fly’s ability to perceive roll movements at high angular velocities (above 1000 degrees per second) disappeared. These results
indicate that the fastest stabilization responses are supported entirely by the relatively faster mechanosensory pathway from the halteres.

Flies are still able to perform compensatory head movements without the use of their halteres at slower angular velocities (Hengstenberg 1991; Schwyn et al. 2011). However, differences between this visually-guided response and that of a purely mechanosensory compensation do exist. Head stabilization outputs due to visual inputs alone are slower and longer-lasting than haltere-driven reflexes (Hengstenberg 1991). Thus, the visual and mechanosensory systems work together to stabilize the visual field of the animal: first, by quickly responding to fast changes, and second, by maintaining that response until it is fully corrected (Hengstenberg 1991).

A possible mechanism for the integration of visual and haltere inputs to head steering has recently been described (Huston and Krapp 2009). A sub-population of NMNs exhibit what are described as “gating-like” properties of multi-sensory integration. When these NMNs were recorded extracellularly and the fly was given visual stimuli alone, these neurons did not fire action potentials. However, when the halteres were concurrently activated by oscillating them with a small motor while the visual stimulus was presented, the NMNs fired action potentials. Intracellular recordings showed that NMNs receive subthreshold inputs from both visual motion and haltere movements. The subthreshold inputs from the halteres were larger than the visual motion inputs, and were also phase locked with the haltere oscillations. These results indicate that the “gating-like” behavior of the NMNs is a result of the convergence of these two subthreshold inputs.

Are halteres useful for behaviors other than flight?

The necessity of halteres in flight has been well documented, but little is known about their use in other behaviors. Flies in the clade Calyptratae (a large group including some of the most speciose families like Calliphoridae and Muscidae) have been documented to oscillate their wings while walking in addition to during flight (Fraenkel 1939; Miller 1977; Sandeman and Markl 1980; Hall et al. 2015). The oscillation of the halteres is similar in amplitude and frequency during walking and flight for these flies, and the halteres always oscillate when walking or when flying. Similar haltere oscillations have been observed during walking in Micropezidae (Hall et al. 2015), which are outside the Calyptratae but which use walking as a primary means of locomotion. Indeed, some species of Micropezidae are wingless (McAlpine 1990), indicating that their haltere movements are used exclusively for walking. All other families of Diptera do not generally oscillate their halteres while walking, but always do so while flying.

Are these movements important to the fly’s behavior, or are they simply an epiphenomenon of walking? When a species of fly that oscillates its halteres during walking (Sarcophaga bullata) is challenged to walk on a vertical surface, removal of the halteres impairs its ability to climb, as well as its ability to resist falling when perturbed. Haltere removal had no effect on the climbing or falling behavior of Drosophila, which does not move its halteres during walking. This indicates that haltere inputs are behaviorally relevant to those species which oscillate them while walking, and that they aid in walking behavior when the task is challenging (Hall et al. 2015).

How do other insects sense forces for flight control?

Our current understanding of haltere function suggests that any oscillating mass may act as an inertial sensor during flight, opening the possibility that non-dipteran insects may detect body rotations using other body parts. A haltere-like function for an oscillating appendage has been demonstrated in two other orders, the Strepsiptera and the Lepidoptera. In the Strepsiptera, which are more closely related to beetles than to flies, the front pair of wings is modified into a haltere-like organ (Wigglesworth 1946; McKenna and Farrell 2010; Wiegmann et al. 2011). Although Strepsipterans are not only rare, but tiny, difficult to collect, and short-lived, Pix et al. (1993) were able to demonstrate through behavior and morphology that the specialized forewings of male strepsipterans perform the same function as the dipteran halteres. Rotational movements of the body combined with the oscillating forewings produce forces that can be detected by fields of campaniform sensilla located at the base of the forewings. Pix et al. showed that the forewing sensors transmit body rotation information to the head and abdomen to produce compensatory movements (Pix et al. 1993).

In the Lepidoptera, the antennae have been demonstrated to play a haltere-like role in flight control. Antennae of the hawkmoth Manduca sexta exhibit small amplitude oscillations of their antenna at constant angles during flight (Sane et al. 2007). By separating the long part of the antenna (the flagella) from the mechanosensory cells at the antennal base
role in their flight behavior. Thus, the antennae of moths may play a haltere-like role in experiencing Coriolis forces during body rotations. The passive oscillations of the antennae, combined with their mass, allow them to experience Coriolis forces during body rotations. Thus, the antennae of moths may play a haltere-like role in their flight behavior.

We noted above that the halteres are serial homologs of the wings, which themselves contain fields of campaniform sensilla. These sensilla permit the wings to act as both actuators of movement, and as sensors of that movement (Dickinson 1990; Dickerson et al. 2014). Recent work indicates that the forewings of Manduca can act as pitch rotation sensors, driving a corrective abdominal movement when stimulated (Dickerson et al. 2014). These data suggest that the wings of insects acted as sensors of body rotation before their specialization into halteres. Further questions remain about the trade-offs between a lift-generating role and a sensing role for the halteres: whereas moths perform both sensing and actuation with both pairs of wings, flies have separated the lift and sensing functions such that halteres provide no lift and act as sensors only. What were the evolutionary forces driving this trade-off? This remains an open question, but one that is applicable to one of the largest and most successful groups of animals on the planet.

**Open questions on haltere function for fly behavior**

Through careful anatomical, electrophysiological, and behavioral studies, significant progress has been made toward understanding the function of these curious but essential sensory organs. Several questions remain, and current research on these topics will lead us toward a more global understanding of sensory information processing for fly flight.

**Do the broad encoding properties of haltere primary afferent neurons suggest a broad role in behavior?**

The electrophysiological responses of haltere primary afferent neurons to motion stimuli show that they provide rapid, precise input to the central nervous system over a broad range of stimulus frequencies (Pringle 1948; Fox and Daniel 2008; Fox et al. 2010). These results demonstrate that haltere sensory neurons are able to play their canonical role as body rotation sensors, but also that they are able to transmit force information well beyond the narrow range of frequencies in which the Coriolis and oscillation-related inertial forces might occur. Rather, recordings from haltere neurons suggest that any in-plane vibration of the haltere above a certain amplitude threshold should result in spike activity in the primary afferent neurons. There are two important implications of this finding: first, the halteres may play a role in sensing other forces beyond those associated with body rotations, and second, the movements of the haltere during natural behavior are the primary determinant of the neural response, with neural tuning playing only a very minor role in structuring the information sent to the nervous system.

**How is sensory information from the haltere decoded into behavioral commands?**

Because there is little filtering of information at the neural level, spikes resulting from different types of haltere movements will reach the central nervous system. What are the resulting responses in higher-order neurons, and how are these interpreted into behavioral commands at the motor level? Presently, the integration of haltere input has been studied in only two groups of peripheral motoneurons: the wing-steering motoneurons (Fayyazuddin and Dickinson 1996, 1999) and the head-steering NMNs (Huston and Krapp 2009). However, the haltere afferents project to many locations in the thoracic ganglion, as observed by dye-filling anatomical descriptions (Chan and Dickinson 1996), and their post-synaptic targets are unknown. Similarly, the responses of these post-synaptic targets to haltere input, as well as their responses to inputs from other sensory systems, motor feedback, or state-dependent modulation, are unknown. Haltere input has been demonstrated to provide behaviorally relevant information during multiple behaviors (Dickinson 1999; Hall et al. 2015), but it is not known how the input is decoded during these behaviors.

**Is haltere information represented in the brain, and if so, how?**

Our current understanding of haltere inputs is limited to synapses at the periphery, in the wing, and NMNs. Is haltere information represented in neurons in the brain? It is possible that haltere information remains peripheral only, and is used exclusively for the fast reflexes necessary for high-speed flight (Land and Collett 1974; Wagner 1986). However, it is also possible that haltere information may ascend to the
brain and be integrated with other sensory information, like vision, to modulate slower or more complex responses to stimuli or experiences. Current research suggests that in the central complex, a brain region known to integrate feedback from multiple sensory systems as well as motor information, the firing of specific cells indicates the fly’s position and orientation in space (Seelig and Jayaraman 2015). Might halteres have a place in this encoding scheme? This question is somewhat difficult to answer in Drosophila, because haltere movement occurs only during flight, confounding haltere input with similar-frequency input from the campaniform sensilla on the flapping wing. However, in those flies showing a diversity of haltere movements and behaviors, haltere input to higher-level centers may provide a means of sensory flexibility and control, allowing the fly to transition from one behavior to another at high speed and precision.

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