

SHORT COMMUNICATION

Haltere removal alters responses to gravity in standing flies

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ABSTRACT

Animals detect the force of gravity with multiple sensory organs, from subcutaneous receptors at body joints to specialized sensors like the vertebrate inner ear. The halteres of flies, specialized mechanoreceptive organs derived from hindwings, are known to detect body rotations during flight, and some groups of flies also oscillate their halteres while walking. The dynamics of halteres are such that they could act as gravity detectors for flies standing on substrates, but their utility during non-flight behaviors is not known. We observed the behaviors of intact and haltere-ablated flies during walking and during perturbations in which the acceleration due to gravity suddenly changed. We found that intact halteres are necessary for flies to maintain normal walking speeds on vertical surfaces and to respond to sudden changes in gravity. Our results suggest that halteres can serve multiple sensory purposes during different behaviors, expanding their role beyond their canonical use in flight.

KEY WORDS: Fly, Mechanoreception, Free fall

INTRODUCTION

Flies, some of the most agile animal fliers, use specialized sensors called halteres to sense accelerations. Halteres are dumbbell-shaped organs derived from hindwings (Pringle, 1948). During flight, halteres oscillate at wingbeat frequency, allowing them to experience Coriolis forces that are sensed with campaniform sensilla (Agrawal et al., 2017; Gnatzy et al., 1987; Smith, 1969) to measure body rotations (Nalbach, 1993; Pringle, 1948; Thompson et al., 2009). If the halteres are removed, flies cannot fly (Derham, 1714).

Though many species do not move their halteres except in flight, many of the Calyptratae (a large clade including houseflies and blowflies) oscillate their halteres at their normal wingbeat frequency (~200 Hz) while walking (Hall et al., 2015; Sandeman and Markl, 1980). These flies walk normally after haltere ablation, which is unsurprising given the array of alternative sensors: a walking fly experiences equal force on each of its six sensor-equipped legs (Gnatzy et al., 1987; Horn and Lang, 1978), and could also use antennae (Horn and Kessler, 1975; Kamikouchi et al., 2009; Yorozu et al., 2009) or prosternal organs (Horn and Lang, 1978) to detect forces. In other insects, the head itself acts as a statolith (Mittelstaedt, 1950), and specialized cercal sensilla can be used for graviperception (Walthall and Hartman, 1981). Like these other organs, the halteres possess a distal mass and are putative gravity-detecting organs (Bender and Frye, 2009). Haltere-ablated flies are less likely to continue walking in a straight line against gravity if their path is

disrupted, but the effects are slight (Sandeman and Markl, 1980). But what happens if the fly experiences a sudden change in gravity? A common perturbation for both flight and walking is a free fall. Flies use vision to guide landing when dropped from a 40 cm height (Goulard et al., 2016), but in a shorter fall, vision may not be sufficiently fast.

A sudden acceleration could be detected in several ways. When resting on a surface, the force of gravity is equal and opposite to ground reaction forces at the legs. Should the legs detach, the will body accelerate at a rate determined by $F=ma$, where the force is mg , and thus the acceleration will be equal to the gravitational constant g . The fly could detect the fall by sensing (1) changing leg loads (Zill et al., 1992), (2) increasing visual flow (Goulard et al., 2016, 2018) or (3) inertial body forces. Inertial body forces (fictitious or d'Alembert forces) act on accelerating masses; for example, causing a person to feel a sideways pull on a spinning fairground ride. Because gravity and inertial forces act on masses directly, they can be sensed with the same organs. Here, we present behavioral and kinematic evidence that a gravity free fall can be detected with halteres. Taken together, our results suggest that halteres are useful beyond their canonical role in flight.

MATERIALS AND METHODS

Behavioral effects of haltere ablation

We used high-speed video cameras (Fastec Imaging, San Diego, CA, USA) to film freely behaving *Sarcophaga bullata* (Parker 1916) (Carolina Biological, Burlington, NC, USA; males and females 2–3 weeks after eclosion) as they walked on clear plastic surfaces oriented horizontally and vertically. In each experiment, we filmed intact flies and then gently and completely removed both halteres using fine forceps (Fine Science Tools, Foster City, CA, USA). Flies were allowed to recover from surgery for 30 min before the experiment was repeated. Each fly was thus tested in both intact and haltereless conditions, controlling for individual differences in behavior.

To measure walking behavior on a horizontal surface, flies were allowed to walk freely in a plastic Petri dish, 87 mm in diameter ($n=16$ flies, one intact and one haltereless trial for each fly). The dish was placed on a piece of graph paper for scale. Flies were filmed at 200 frames s^{-1} and films were digitized (Hedrick, 2008). We captured uninterrupted trials ranging in length from 700 ms to 10.2 s. To find the average walking speed for each trial, we excluded frames in which the fly was standing still, which we defined as a body speed of less than 1 mm s^{-1} . After this exclusion, trial lengths included 0.56–2.94 s of active walking time. Overall walking speeds were similar to those measured in freely walking blowflies (Blaj and van Hateren, 2004; Kress and Egelhaaf, 2012).

To measure walking behavior on a vertical surface and responses to gravitational perturbations, flies were placed in clear plastic containers (Shenzhen Lifbetter Technology Co., Ltd, Shenzhen, China). These containers were rectangular prisms measuring 98.5×56.8×24.0 mm. To make the impact with the ground as consistent and stable as possible, a piece of corrugated cardboard

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was attached to the bottom to mitigate bouncing and prevent toppling. A steel ball bearing was attached with hot glue to the top of the container and the container was suspended 2 cm above the table surface using a powered electromagnet. The electromagnet was fabricated by wrapping a bolt with conductive wire. When the power to this magnet was turned off, the container and fly fell to the table surface (Movie 1). In each trial, the fly was stationary and standing on the vertical surface of the container before the power to the electromagnetic was turned off. The nearest visual stimulus to provide a reference outside the box was the camera; the stand was blocked with white paper.

To measure the free, spontaneous walking behavior of these flies, we excluded frames in which the speed was less than 1 mm s^{-1} (as above) and also excluded frames that occurred 0.5 s before or after the start of a falling event (a conservative means of excluding any frames in which the fly was perturbed; the duration of the falling event was always $<0.1 \text{ s}$). After this exclusion, trial lengths included 0.35–3.06 s of active walking time ($n=3$ flies, 8 intact trials and 6 haltereless trials).

Modeling accelerations at the haltere tip

To determine the role of halteres in detecting gravity falls, we considered the physics of flapping halteres, as might occur in a walking fly, and of the stationary halteres of standing flies. In a drop test, the fly experiences a nearly instantaneous increase in acceleration (from 0 to 9.8 m s^{-2}). Here, the fly does not rotate. Our experimental data suggest that this acceleration can be sensed by the haltere campaniform sensilla. In other types of falls, however, the fly might also be rotating. The possibility of differentiating between swinging falls and straight falls may explain why halteres flap during walking.

We considered the dynamics of falls with four different haltere orientations that provide an orthogonal basis for flies on inclines and at head orientations relative to gravity (Table S1). On a horizontal surface, the halteres start in a horizontal position and move up and down. In orientation 1, the haltere flapping axis is parallel to the swinging fall axis. In orientation 2, the haltere flapping axis and the swing axis are perpendicular. Because a fly has two halteres, oriented $\sim 60^\circ$ apart, any given fall axis will have some parallel and some perpendicular components to the halteres. In other words, a real fly would be partially aligned with each of these directions, so although the magnitudes of each force might be slightly less, the same force information would be available. Thus, a fly on a horizontal surface is able to sense in orientations 1 and 2 using both halteres. Orientations 3 and 4 are for flies on vertical surfaces, where for orientation 3, the haltere is moving in a plane perpendicular to the fall direction and in orientation 4, the fall direction is parallel to the haltere motion plane.

Next, we aligned a coordinate system with the resting direction of the halteres. The \hat{r} direction is along the length of the haltere. The \hat{s} direction is tangent to the active motion of the haltere (down relative to the fly). The lateral direction, \hat{l} , is orthogonal to both. If the body is stationary and the haltere is flapping, there will be accelerations sensed in the \hat{r} and \hat{s} directions but not in the \hat{l} direction. These accelerations were calculated in detail as described below. Note that we assume the haltere bases are co-located because the measured distance between them is small ($1.69 \pm 0.27 \text{ mm}$, $n=11$ flies) compared with the overall length scale of the body. Thus, the body acceleration is the same at the two points but the direction relative to the flapping axis is different, which changes the resulting Coriolis forces.

Stationary fly, stationary halteres

If the fly is stationary and the halteres are stationary, there is no acceleration.

Stationary fly, moving halteres

If the fly is stationary and the halteres are moving, the position of the haltere can be described with angle α and haltere length h . The end of the haltere has centripetal acceleration due to the angular velocity, $\dot{\alpha}$. Furthermore, the angular velocity is not constant because the haltere must stop and reverse direction to return to its original position. Thus, the relative position of the haltere tip is:

$$\vec{h}(t) = h(\cos(\alpha(t))\hat{r} + \sin(\alpha(t))\hat{s}). \quad (1)$$

Note that the length of the haltere does not change, only the direction, so the relative velocity of the halteres to the body is:

$$\vec{v}_{\text{rel}}(t) = \dot{\alpha}(t)\hat{l} \times \vec{h}(t) \quad (2)$$

and the relative acceleration of the haltere to the body of the fly is:

$$\vec{a}_{\text{rel}}(t) = \ddot{\alpha}(t)\hat{l} \times \vec{h}(t) + \dot{\alpha}(t)\hat{l} \times (\dot{\alpha}(t)\hat{l} \times \vec{h}(t)). \quad (3)$$

Nalbach (1993) previously measured the haltere angle over time, which provides $\alpha(t)$, and is differentiated to find the haltere angular velocity $\dot{\alpha}(t)$ and angular acceleration $\ddot{\alpha}(t)$. When the halteres are moving, the $\vec{a}_{\text{rel}}(t)$ term is large (two orders of magnitude greater than gravity); however, it is always in the $\hat{r}\hat{s}$ plane because it is perpendicular to the lateral direction, as indicated by the cross-product. Thus, the fly is stationary, there is no acceleration in the lateral direction even if the halteres are moving.

Falling fly, moving halteres

During a straight, non-rotating fall, the acceleration of the body due to gravity is added to the relative acceleration of the haltere:

$$\vec{a}_{\text{total}}(t) = \vec{a}_{\text{body}}(t) + \vec{a}_{\text{rel}}(t). \quad (4)$$

In the example of a fly on a vertical wall with a horizontal initial position of the haltere, gravity is in the \hat{l} direction, and thus:

$$\vec{a}_{\text{body}}(t) = g\hat{l}, \quad (5)$$

where $g=9.81 \text{ m s}^{-2}$, the standard acceleration due to gravity.

Swinging fly, moving halteres

During a swing, in which the body rotates about a fixed point due to gravity, the fly coordinate system unit vectors (\hat{r} , \hat{s} , \hat{l}) are rotating, which adds other terms to the acceleration equation. If the body rotation is described by angle θ about the axis in some $\hat{\theta}$ direction, and the vector between a fixed point (an attached leg perhaps) and the base of the haltere is \vec{L} , then the total acceleration of the haltere tip is:

$$\vec{a}_{\text{total}}(t) = \ddot{\theta}(t)\hat{\theta} \times \vec{L}(t) + \dot{\theta}(t)\hat{\theta} \times (\dot{\theta}(t)\hat{\theta} \times \vec{L}(t)) + 2\dot{\theta}(t)\hat{\theta} \times \vec{v}_{\text{rel}}(t) + \vec{a}_{\text{rel}}(t), \quad (6)$$

where, in the example in Fig. 3A, $\hat{\theta}=\hat{r}$ and $\vec{L}(t)=L(\cos(\theta(t))\hat{s}+\sin(\theta(t))\hat{l})$ and in the plot in Fig. 3B, the original \hat{s} direction is horizontal, the original \hat{l} direction is vertical and the original \hat{r} direction is out of the paper.

Finally, all that remains is to calculate $\theta(t)$, which can be determined via the standard pendulum equation of motion:

$$\ddot{\theta}(t) = -gL \cos(\theta(t)). \quad (7)$$

To plot these values in Matlab, the pendulum equation was solved with ode45, and four different orientations were considered (Table S1). The length of the haltere h was approximated as 1 mm and the pendulum swing length L was considered as 10 times that at 1 cm.

RESULTS AND DISCUSSION

Haltere removal has no effect on horizontal walking but results in slower vertical walking

We measured free, spontaneous walking behavior in intact and haltereless flies on horizontal and vertical surfaces (Fig. 1A,B). Average speed of intact flies was not different between horizontal and vertical walks (median average speed for intact flies on horizontal surface: 45.4 mm s^{-1} ; on vertical surface, 42.4 mm s^{-1} ; Wilcoxon rank-sum test, $P=0.56$). However, average speed of haltereless flies was significantly lower on vertical surfaces than on horizontal surfaces (median average speed for haltereless flies on horizontal surface: 40.6 mm s^{-1} ; on vertical surface, 20.3 mm s^{-1} ; Wilcoxon rank-sum test, $P=0.001$). Similarly, average speed of haltereless flies on vertical surfaces was also lower than average speed of intact flies on vertical surfaces (Wilcoxon rank-sum test, $P=0.005$), but there were no differences between intact and haltereless flies on horizontal surfaces (Wilcoxon rank-sum test, $P=0.27$). Thus, haltere removal caused a significant slowing of walking, but only on vertical surfaces.

Intact flies react to sudden vertical acceleration but haltereless flies do not

We tested flies' responses to vertical perturbations by placing them in a clear plastic container, waiting for them to come to a stationary posture on the side of the container, and dropping the container (Fig. 2A). Each trial was filmed and select trials were digitized for further analysis ($n=10$ flies, 1–5 trials per fly in both intact and haltereless conditions). Immediately following acceleration, some intact flies used their leg joints to adjust their center of mass (COM), lifted their feet to adjust one or more legs (Bartling and Schmitz, 2000; Zill et al., 1992) or flew off the wall before impact (Fig. 2B).

Repeated trials did not change the probabilities of these responses. Haltereless flies, in contrast, very rarely made such adjustments (22 of 66 trials for intact flies; 4 of 72 trials for haltereless flies; Fisher's exact test, $P<<0.001$; Fig. 2C). Haltereless flies were more likely to cling to the wall after impact (Fig. 2C): intact flies clung in 41 of 119 trials, whereas haltereless flies did so in 78 of 124 trials (Fisher's exact test, $P<<0.001$). Thus, intact flies' postural adjustments did not necessarily aid in resisting falls. One explanation is that postural changes provide information about which legs are still attached. Haltereless flies appear to choose a stance that provides a stronger hold, perhaps because they sense that they are 'gravity blind' or because the loss of halteres makes their standing posture less stable. They may also sense that they are less able to fly off the wall as a result of their missing halteres.

Haltereless flies are slower to flap their wings following a fall

All flies that lost surface contact attempted to fly. We measured the latency between the beginning of the fall and wing opening for both intact ($n=15$ trials in six flies) and haltereless flies ($n=10$ trials in the same six flies) and found no differences (median latency for intact flies, 72 ms; for haltereless flies, 85 ms; Wilcoxon rank-sum test, $P=0.08$; Fig. 2D). We also measured the latency between wing opening and flapping initiation. Haltereless flies were significantly delayed (median latency for intact flies, 8 ms; for haltereless flies, 36 ms; Wilcoxon rank-sum test, $P=0.03$). Rapid responses of haltere afferent neurons (Fox and Daniel, 2008), combined with a fast synapse onto a wing motoneuron (Fayyazuddin and Dickinson, 1996), allow flies to respond to flight perturbations with a latency as low as a few milliseconds. Without halteres, flies may rely on vision, with a higher latency of ~ 30 ms (Hardie and Raghu, 2001; Land and Collett, 1974), to sense that their bodies are falling.

Reactions to free fall occur rapidly and in all directions

We measured the direction of movement for each intact fly that adjusted its body in reaction to the fall. These adjustments could stabilize body position against the fall in different ways: passively,

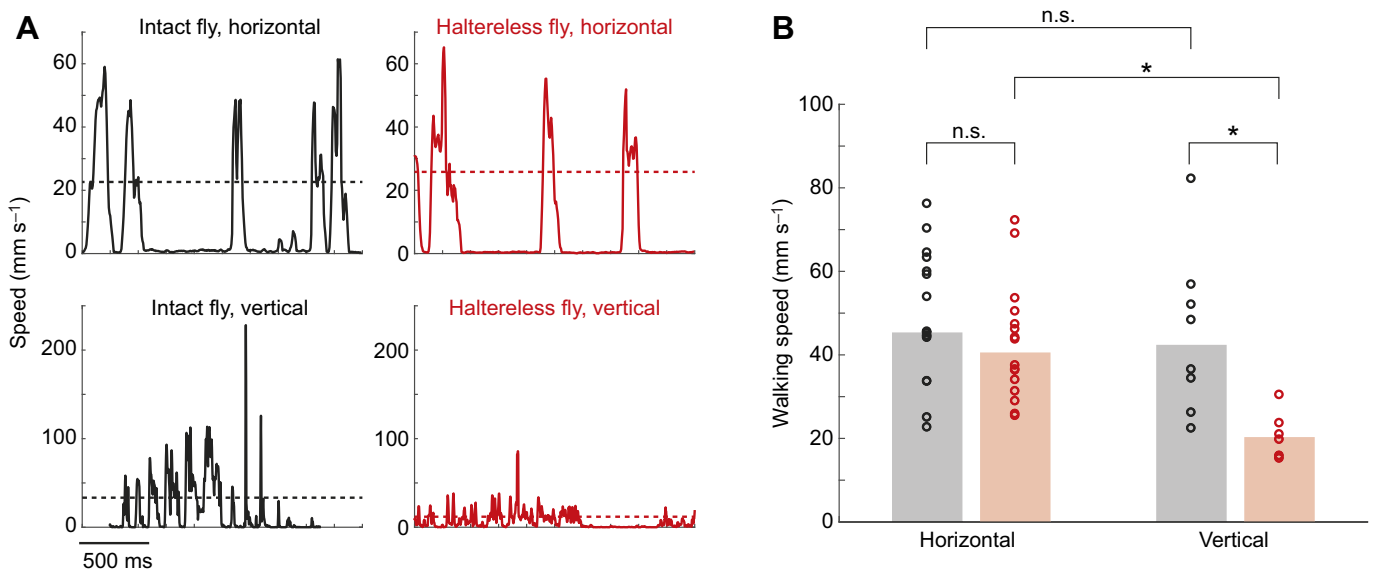


Fig. 1. Haltere removal decreases speed of vertical, but not horizontal, walking. (A) Raw traces of walking speed over time in individual horizontally and vertically oriented flies. Dashed line shows average speed over the trial. Top left: an intact fly walking on a horizontal surface. Top right: same fly on the same surface with halteres removed. Bottom left: an intact fly walking on a vertical surface. Bottom right: same fly on the same surface with halteres removed. (B) Mean walking speed in each trial for intact and haltereless flies on horizontal and vertical surfaces. $P<0.005$.

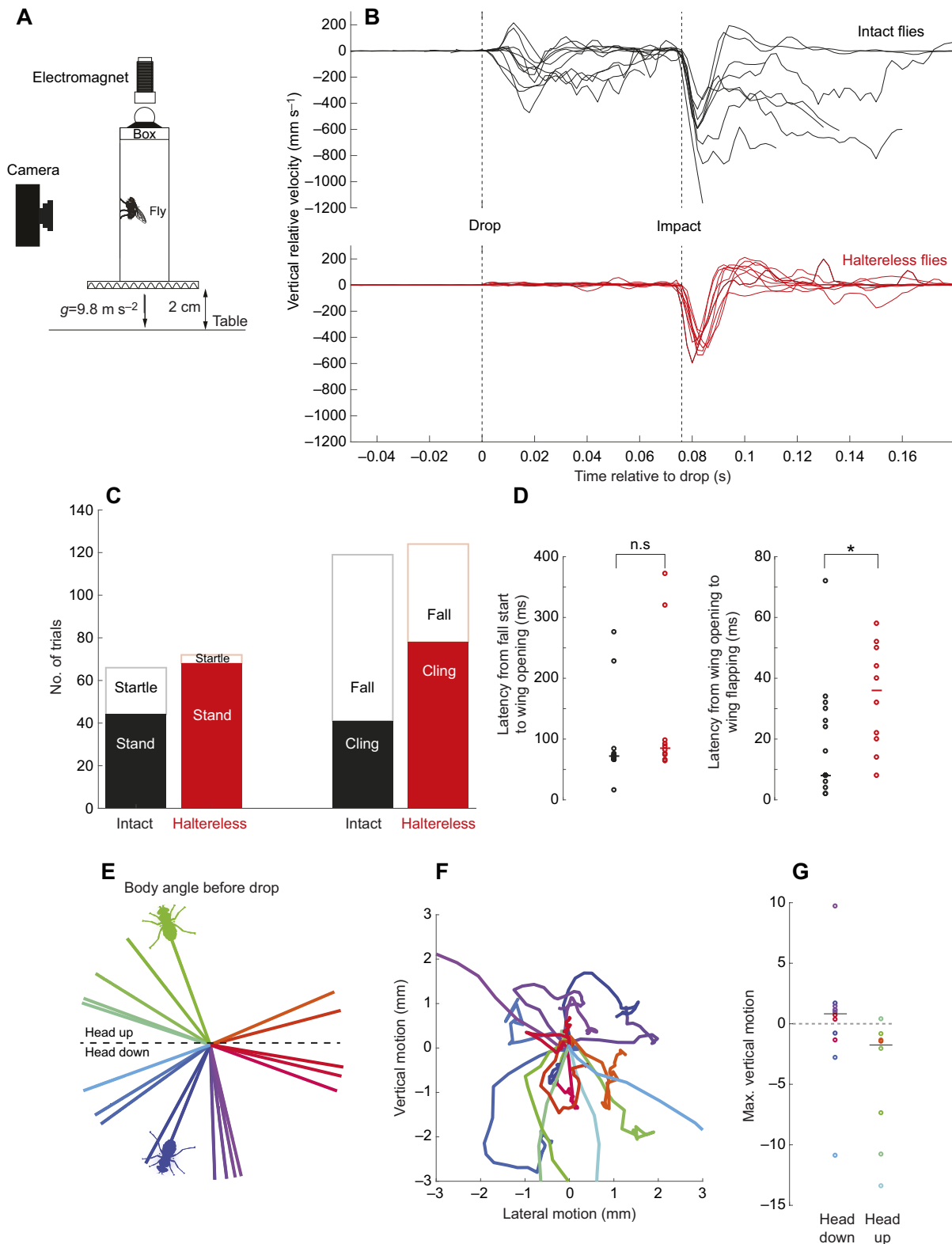


Fig. 2. Haltere removal alters responses to gravity falls. (A) Experimental scheme. Flies fell when the electromagnet was powered off. (B) Intact and haltere-ablated flies respond differently to sudden changes in gravity. Intact flies startle at drop initiation; haltereless flies do not. (C) The proportion of flies that startle and attempt to take off is significantly greater in intact flies than in haltereless flies. (D) Intact (black) and haltereless (red) flies have equal latencies to wing opening (left), but haltereless flies take significantly longer to begin wing flapping (right). (E) Flies that adjusted their posture were oriented in different directions before the drop. Colors here correspond to data in F and G. (F) Center of mass (COM) path (relative COM motion) between the drop until 10 ms before impact (mean duration $58.4 \pm 9.8 \text{ ms}$) is shown for each of the adjustments. (G) Greatest distance from starting position for all flies shown in E. Dashed line separates trials in which the fly moved upward from those in which it moved downward.

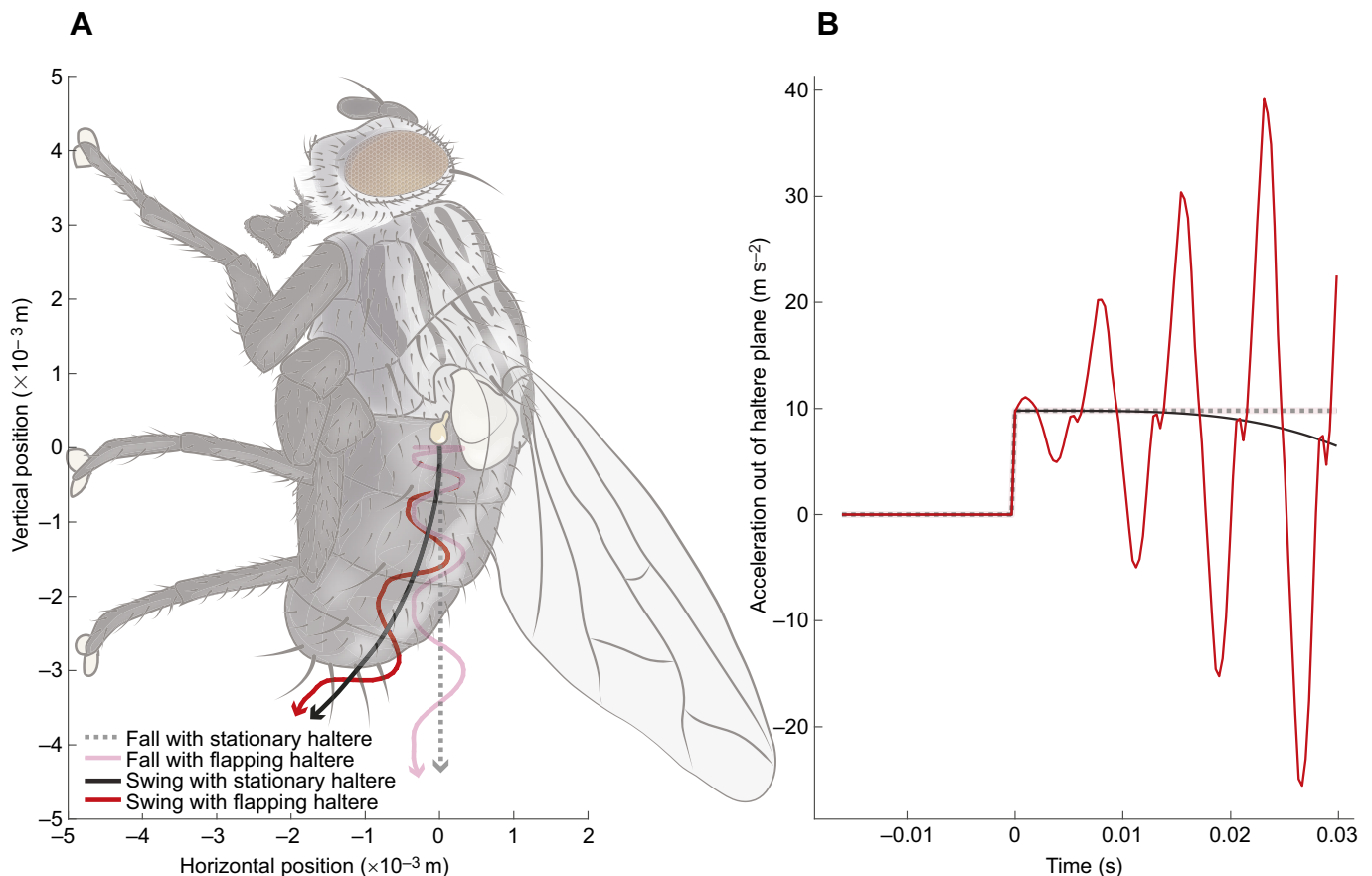


Fig. 3. Haltere dynamics modeled for a straight vertical drop (all legs detached) and a swing (some legs detached) with both stationary and oscillating halteres. (A) Relative haltere tip position and (B) acceleration at the haltere base (sensed acceleration) during each type of fall. Acceleration increases immediately at the onset of a vertical fall and is identical for stationary and oscillating halteres. In a swinging fall, the oscillating haltere experiences a faster and larger increase in acceleration than the stationary haltere.

with greater leg compliance, or actively, by leg pushing. An active response would likely move the body in a single direction against gravity. However, fall adjustments occur in every radial direction (Fig. 3B), with no specific orientation relative to the fall. Adjustments begin within a few milliseconds of the drop, with peak amplitudes often occurring less than 20 ms after the fall begins. The haltere (and, likely, other mechanosensors) can provide signals to motoneurons that initiate reflexes within a very short time frame, around 5 ms (Fayyazuddin and Dickinson, 1999); a planned turn can take 30 ms or more (Card and Dickinson, 2008; Land and Collett, 1974). Rapid position adjustment during free fall suggests that this is a reflex and not a planned motor response to gravity direction.

Next, we determined whether the adjustment is influenced by body orientation before the fall. Flies stood facing various directions (Fig. 2E). Intact flies stood head down in 53% of trials ($n=39$ of 73 trials), but haltereless flies were more likely to face head up (71%, $n=53$ of 75 trials; Fisher's exact test, $P=0.01$). In intact flies that made COM adjustments, head-down animals (blue and red) tended to move up relative to the ground, and head-up animals (orange and green) tended to move down, with variation in lateral motion as well (Fig. 2F). The total extrema of vertical motion (Fig. 2G) for head-up and head-down flies are significantly different (head-up flies' median extreme position = -1.8 mm; head-down flies' median extreme position = 0.8 mm; $P=0.02$, Wilcoxon rank-sum test). Unlike escape responses (Card and Dickinson, 2008), COM adjustment

responses to free fall do not correspond to relative stimulus direction, but rather seem to be backward regardless of orientation.

Taken together, our data suggest that leg movement responses are startles, not stabilizations, with direction determined by relative leg position. As the back legs are larger and stronger, equal activation of all legs will move the body backward, as observed (Fig. 2G). This distributed inward pulling has been theorized to be essential for increasing gripping forces on vertical surfaces (Wile et al., 2008) and also provides proprioceptive information on which legs are attached to the ground, as attached legs would not move under large inward forces. Furthermore, this movement might also cause the fly to initiate haltere oscillations, allowing the fly to determine whether the body was in a straight free fall or whether it was rotating (which would indicate that there were still some support forces). Below, we describe the haltere movements that permit this discrimination.

Haltere dynamics for gravity sensing

Consider a straight downward fall in which the fly does not rotate. This is the case in the drop experiment, and would also be the case if all feet detached simultaneously, perhaps as a result of surface wetting or a wind gust moving the substrate. Without support, the fly experiences a sudden acceleration of magnitude g . In a straight free fall, a stationary haltere would be better able to sense this sudden acceleration than an oscillating haltere, because the oscillating haltere also experiences centripetal and

tangential accelerations two orders of magnitude higher than the gravitational acceleration. For some fly orientations, these accelerations would occur in the same direction as gravity, making them impossible to distinguish. However, we show that flapping the haltere would help distinguish between a straight fall and a swinging fall, in which only some feet detach and the body swings like a pendulum.

For horizontal flies, both a straight fall and a swing cause an instantaneous increase in acceleration in the \hat{s} direction for both halteres. To distinguish between the two, if the halteres are stationary, the fly could detect body rotation by the change in the direction of acceleration from the \hat{s} direction to the \hat{r} and \hat{l} directions. However, this change is gradual: for example, acceleration in \hat{l} reaches half g in 0.033 s. In contrast, if halteres are moving during a swing, lateral acceleration reaches half g in 0.0038 s, an order of magnitude faster than for stationary halteres (Fig. 3B). However, there is a trade-off: a straight fall would be undetectable when the halteres are moving, as gravity forces are small compared with flapping forces, and in the same direction (\hat{r} and \hat{s} as the haltere moves). Thus, for a horizontal fly, a possible strategy is to begin flapping after initial acceleration is detected, and use the dynamics of resulting forces on the haltere base to determine whether that acceleration indicates a fall or swing.

For vertical flies, the dynamics are similar, except that at least one haltere should be flapping with horizontal components perpendicular to gravity, which enables detection of a vertical fall with flapping halteres. In our experiments, flies were standing still and presumably not moving their halteres when they fell. These calculations show that flies can use their halteres to detect vertical accelerations whether they are moving or stationary.

A function for halteres beyond flight

In summary, haltere physics indicate that forces present during falls could be used to inform the nervous system of the body's accelerations due to gravity. Taken together, our data and modeling show that flies can use their halteres to detect the direction and magnitude of the force of gravity. The information about gravity that can be obtained from the halteres is supplemental to information obtained from the antennae, leg campaniform sensilla, and other gravity-sensitive mechanoreceptors. Thus, although halteres are not essential for gravity sensing, we show that they may be useful for distinguishing between different types of body movements and perturbations. This analysis provides a possible explanation for the haltere oscillations of the flies of Calyptratae during walking.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: K.A.D., J.L.F.; Methodology: K.A.D., J.L.F.; Software: K.A.D., J.L.F.; Formal analysis: K.A.D., J.L.F.; Investigation: K.A.D.; Resources: J.L.F.; Writing - original draft: J.L.F.; Writing - review & editing: K.A.D., J.L.F.; Visualization: J.L.F.; Project administration: J.L.F.; Funding acquisition: J.L.F.

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Data availability

Data are available from the Dryad Digital Repository (Daltorio and Fox, 2018): <https://doi.org/10.5061/dryad.kg52rj5>.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.181719.supplemental>

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