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Takeoff diversity in Diptera

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The order Diptera (true flies) are named for their two wings because their hindwings have evolved into specialized mechanosensory organs called halteres. Flies use halteres to detect body rotations and maintain stability during flight and other behaviours. The most recently diverged dipteran monophyletic subsection, the Calyptratae, is highly successful, accounting for approximately 12% of dipteran diversity, and includes common families like house flies. These flies move their halteres independently from their wings and oscillate their halteres during walking. Here, we demonstrate that this subsection of flies uses their halteres to stabilize their bodies during takeoff, whereas non-Calyptratae flies do not. We find that flies of the Calyptratae are able to take off more rapidly than non-Calyptratae flies without sacrificing stability. Haltere removal decreased both velocity and stability in the takeoffs of Calyptratae, but not other flies. The loss of takeoff velocity following haltere removal in Calyptratae (but not other flies) is a direct result of a decrease in leg extension speed. A closely related non-Calyptratae species (*D. melanogaster*) also has a rapid takeoff, but takeoff duration and stability are unaffected by haltere removal. Haltere use thus allows for greater speed and stability during fast escapes, but only in the Calyptratae clade.

1. Introduction

For flying animals and flying machines, the initiation of flight is a central challenge. The flier must generate significant lift in a short time to gain altitude, and stabilizing the process requires rapid responses to perturbations. The trade-off between speed and stability leads flies to use multiple strategies for takeoffs, using rapid but unstable escapes when threatened and slower, steadier takeoffs when searching for food or otherwise voluntarily initiating flight [1]. Organizing the motions of the legs and wings to generate power and lift probably requires neural input from the fly's various sensory organs. Once aloft, flies stabilize their flight using specialized organs called halteres. These are modified hindwings that act as gyroscopes, sensing body rotations [2–5] and as metronomes, sending timing information to the wings [6,7]. The contribution of wing and leg muscles in determining takeoff strategy is well established [8–14], but the role of halteres during takeoff has not been examined. The halteres may be providing critically timed neural input that is needed to coordinate the wings and legs to generate the directed power necessary for takeoff, which results from a combination of leg and wing movements that can vary by species [13–15] or context [16,17]. Flies with ablated halteres will fly on tethers [3,18], indicating that the neural circuits that initiate flight do not require haltere input. However, free takeoffs will necessarily be less stable than tethered flight, and the mechanosensory input provided by halteres could be used to direct the initial wingbeats of flight.

Vision is known to direct much of the escape behaviour in fruit flies and other insects [1,16,17,19–21]. Jump responses to looming visual stimuli can be initiated by a single spike in the giant fibre, and multiple characteristics of the visual stimulus can be encoded in the timing of this spike [19,21]. Once the jump is initiated, however, the wings must begin to flap in order to execute a stable response. Input to steer the wings can come from the descending visual neurons [22] and from the halteres [23].

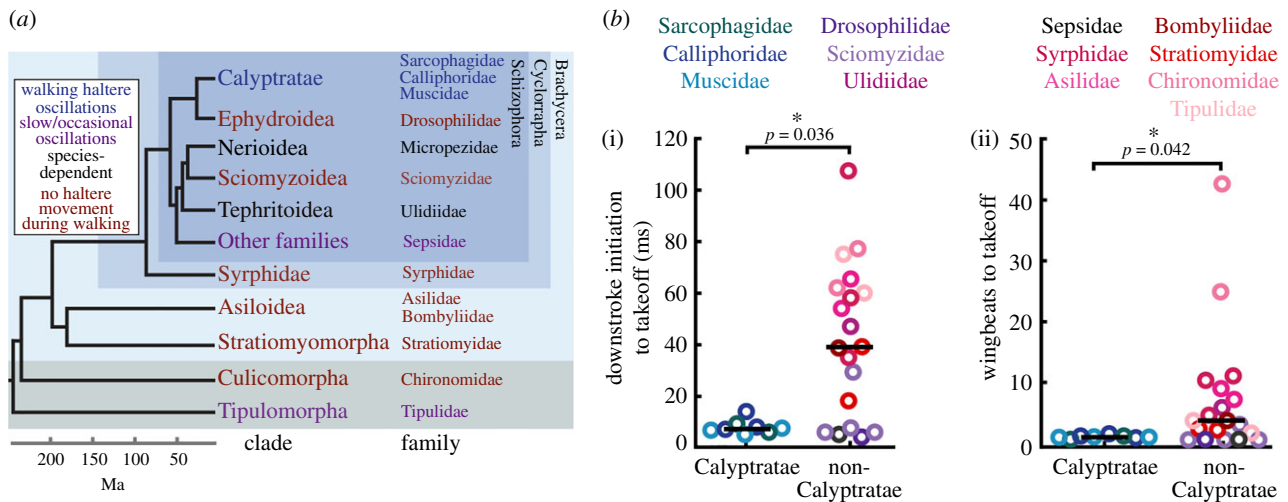


Figure 1. Locomotor behaviours across fly families. (a) Diptera phylogeny of relevant families adapted from Wiegmann *et al.* [33]. Calypttratae flies shown in blue. Non-Calypttratae flies shown in red, black and purple. (b) Time from downstroke initiation (i) and number of wingbeats (ii) before feet lose contact with ground during spontaneous takeoffs in representative fly families. Each data point represents an individual species within its colour-coded family (averages of 1–15 individuals per species; 1–3 takeoffs per animal. For all data see electronic supplementary material, table S1). (Online version in colour.)

The halteres of some flies oscillate during walking (electronic supplementary material, movie S1), flapping independently from the wings [24,25]. If haltere input is available to non-flying flies, it may be used to stabilize takeoff. We hypothesized that flies that oscillate their halteres in walking may use them to inform the nervous system about movement (body rotations and/or wing flaps) during takeoff. By ablating halteres of representative fly species, we demonstrate that those flies that rapidly oscillate their halteres in non-flight behaviour also use them to increase the speed and stability of their takeoffs.

2. Results

(a) Spontaneous takeoffs in Calypttratae flies are faster than in non-Calypttratae flies

All flying dipterans use the reduced hindwings known as halteres to stabilize their flight [2,24,26–28]. Additionally, a subsection of flies (Calypttratae) has been shown to oscillate their halteres during walking behaviour [25,29,30], but the utility of this behaviour, if any, is unknown. All Calypttratae flies (e.g. the blow fly *Calliphora vomitoria*, electronic supplementary material, figure S1A and movie S1) oscillate their halteres when they are walking, whereas non-Calypttratae flies (e.g. the soldier fly *Hermetia illucens*, electronic supplementary material, figure S1A) only move their halteres when the wings are also flapping. Two notable exceptions are the family Micropezidae, which oscillate their halteres during walking but are relatively rare flies and rarely fly, and some members of the Tephritoidea (including Tephritidae, Ulidiidae and Sepsidae), which show slow movements of the halteres during walking or standing [24]. Although the Calypttratae subsection exhibits extensive genetic and ecological diversity [31–33], they display similar locomotor behaviours, and walking speed is not affected by haltere removal (electronic supplementary material, figure S1B). There is one notable difference between the haltere movements during walking and takeoff in Calypttratae flies, and that is that the left and right halteres are only synchronized

when the wings begin to move (electronic supplementary material, figure S1A). Although Calypttratae blow flies move their halteres differently than non-Calypttratae soldier flies during walking, the mechanisms that synchronize the halteres in flight—physical linkages in the thorax, including the subepimeral ridge and the scutellum [34]—exist in both flies (electronic supplementary material, figure S1C). Thus, the observed differences in haltere movements are probably not a result of the biomechanics of the wings, halteres or thorax.

Although similar biomechanics exist for both Calypttratae and non-Calypttratae representative species (blow flies and soldier flies), which allows for haltere synchronization during takeoff, we found that takeoff execution differs substantially between clades. We recorded several species during spontaneous takeoffs (flight bouts not elicited by any obvious external sensory stimulus). We measured the time between downstroke initiation (the first frame when the wings moved downward) and takeoff completion (the first frame when no feet were on the platform). The wings were always synchronized at the initial downstroke, which in all cases was unambiguous. We found that both takeoff duration and number of wingbeats in the takeoff differed significantly between Calypttratae and non-Calypttratae (rank sum $p = 0.036$, $p = 0.042$ respectively). Calypttratae were roughly five times faster, with takeoffs lasting an average of 7.34 ± 2.24 ms and 1.37 ± 0.225 wingbeats, compared to non-Calypttratae with takeoffs lasting 39.1 ± 52.5 ms and 4.0 ± 7.34 wingbeats (figure 1b). Some of the slowest non-Calypttratae flapped their wings multiple times before beginning to extend their legs for takeoff (electronic supplementary material, movie S2). We might expect less variability in the Calypttratae because it necessarily contains fewer families of flies than non-Calypttratae. Though we do find non-Calypttratae with rapid takeoffs, none of the Calypttratae had a takeoff duration longer than 14 ms.

(b) Fast leg extensions and stout bodies increase takeoff speeds

Could the fast takeoffs of Calypttratae be explained by body morphology or kinematic strategy? Of the observed

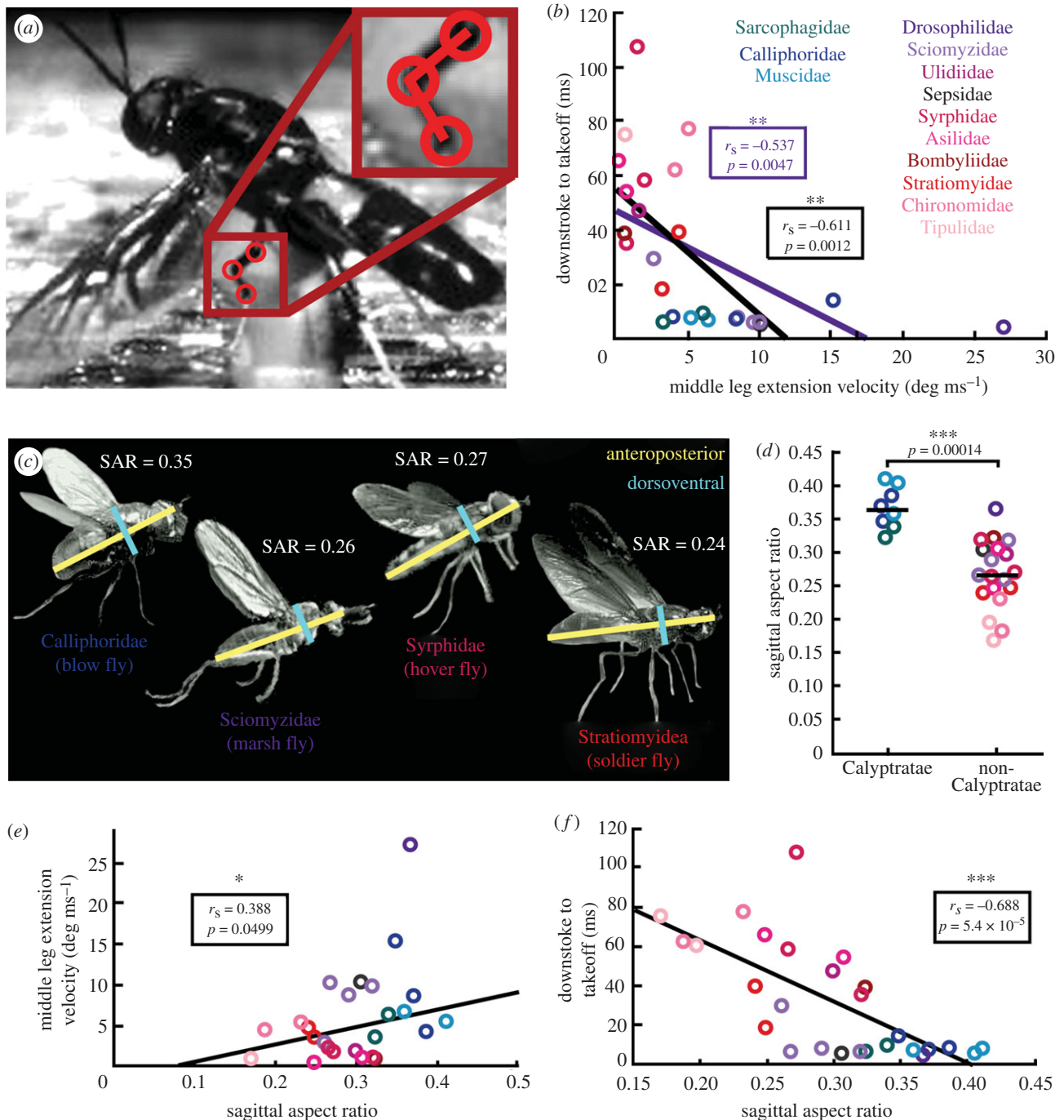


Figure 2. Increased leg extension velocity and larger sagittal aspect ratios allow flies to take off faster. (a) Schematic demonstrating digitized middle leg femorotibial angle. (b) Correlation between leg extension velocity and time from wing downstroke initiation to takeoff for intact spontaneous takeoffs in all representative families (purple) and in all families excluding Drosophilidae (black). (c) Schematic demonstrating sagittal aspect ratio (SAR; dorsoventral axis length divided by anteroposterior axis length). (d) SAR of all representative fly families. Each data point represents an individual species within its colour-coded family ($n = 1\text{--}15$ individual animals per species; see electronic supplementary material, table S1 for all data). Black bar represents median. (e) Correlation between SAR and leg extension velocity for intact spontaneous takeoffs in all representative families. (f) Correlation between SAR and time from wing downstroke initiation to takeoff for intact spontaneous takeoffs in all representative families. See electronic supplementary material, table S2 for all data statistics. (Online version in colour.)

Calypttratae, all used both jumping legs and flapping wings to take off. Calypttratae flies in general required fewer wingbeats to take off than non-Calypttratae (figure 1b), indicating that Calypttratae may rely more on jumping legs than flapping wings to initiate flight. To estimate the speed of these jumps, we measured the extension velocity of the femorotibial joint of the mesothoracic leg (figure 2a) during spontaneous takeoffs in each of the representative families. Takeoff duration was negatively correlated with leg extension velocity (figure 2b). In general, flies with faster jumps (as measured by leg extension speeds) were able to complete

takeoffs in less time. Notably, the non-Calypttratae fruit fly *Drosophila* has the fastest jump by far, more than double the speed of any other fly. Leg extension time did not differ between the Calypttratae and non-Calypttratae clades ($p = 0.123$), in large part because many non-Calypttratae also showed fast leg extensions.

There are obvious differences in overall body morphology between the stout Calypttratae and many of the non-Calypttratae, which are often elongate (e.g. soldier flies, midges and others). Indeed, the fastest takeoff measured was that of the fruit fly *Drosophila melanogaster*, a very stout-bodied

non-Calyptratae. Does body morphology further explain some of the variation in takeoff speeds? We estimated each fly's 'stoutness' by measuring its sagittal aspect ratio (SAR), the ratio of the dorsoventral and anteroposterior axes. In doing so, we quantified a difference in body shape (figure 2c). Flies with higher SARs are stouter, and those with lower SARs are more elongate.

Calyptratae flies had significantly higher SARs than non-Calyptratae flies (figure 2c,d; rank sum $p = 0.00014$). SAR was negatively correlated with total takeoff time and with number of wingbeats to takeoff (figure 2f; electronic supplementary material, figure S2A; Spearman's rank correlation $p < 0.0001$, $p = 0.0066$ respectively). This was expected because increasing surface area increases drag [35]. SAR was not correlated with wingbeat frequency, suggesting that a stouter body is not an indicator of overall faster flight dynamics (electronic supplementary material, figure S2B; Spearman's rank correlation $p = 0.820$).

The non-Calyptratae superfamily most closely related to the Calyptratae subsection is Ephydroidea, which contains the family Drosophilidae [33]. The common fruit fly *Drosophila melanogaster* has a SAR and takeoff speed similar to the Calyptratae flies. Like other non-Calyptratae flies, fruit flies do not use their halteres when walking, but they share a similar body shape to the Calyptratae clade (high SAR). This suggests that the increased speed of takeoff exhibited by the Calyptratae flies is partially a result of body morphology.

(c) Haltere removal decreases leg extension velocity and takeoff speed in Calyptratae

Given the dramatic difference in takeoff duration between the Calyptratae and non-Calyptratae flies (with the exception of *Drosophila*; see below), we hypothesized that the haltere oscillations performed by Calyptratae are essential to their rapid takeoffs. We compared takeoff behaviour of intact flies to the same flies with their halteres ablated (electronic supplementary material, movie S3). In insects, escapes tend to be faster and less stable than spontaneous takeoffs [1,8,16,17]. We predicted that differences between Calyptratae and non-Calyptratae will be more obvious during escapes than spontaneous takeoffs. We chose representative laboratory-reared species of similar body size (the blow fly *Calliphora vomitoria*, weight = 48.6 ± 10.2 mg, and the soldier fly *Hermetia illucens*, weight = 48.9 ± 13.4 mg). We analysed their flight dynamics during takeoffs in which we gently heated the substrate to an aversive temperature. This stimulus caused flies to escape but did not encourage them to escape in a specific direction [36]. We did not examine spontaneous takeoffs in haltere-ablated animals because they rarely occurred.

Because we chose laboratory-reared animals here, we were able to collect a higher number of takeoffs and performed more detailed analyses than on the multi-species survey above. To quantify the contribution of jumping legs in blow fly and soldier fly takeoffs, we again measured the middle leg femorotibial angle (figure 2a) from takeoff initiation (initial elevation of the centre of mass; COM) to liftoff (time when feet lost contact with ground; figure 3a–c). We found that blow flies have faster middle leg extension velocities during escapes than soldier flies (figure 3a–c; rank sum $p = 0.0023$; blow fly intact escape median $\pm$ IQR = 4.97 ± 0.99 deg ms⁻¹, soldier fly intact escape median = 3.75 ± 1.24 deg ms⁻¹). Haltere removal

decreases blow fly middle leg extension velocity (figure 3a–c; rank sum $p = 0.0006$; blow fly haltereless escape median = 1.42 ± 2.07 deg ms⁻¹), but has no significant effect on leg extension velocity in soldier flies (figure 3a–c; rank sum $p = 0.397$; soldier fly haltereless escape median = 5.53 ± 4.65 deg ms⁻¹).

Due in part to their faster leg extensions, blow fly (Calyptratae) spontaneous takeoffs were shorter in duration than soldier fly (non-Calyptratae) takeoffs (figure 3d; rank sum $p < 0.0001$; blow fly median = 12.5 ± 6.63 ms, soldier fly median = 38.0 ± 29.1 ms), consistent with multi-family comparisons above (figure 1b). Blow fly escapes were also shorter than soldier fly escapes (figure 3d; rank sum $p = 0.0007$; blow fly median = 9.00 ± 6.33 ms, soldier fly median = 18.3 ± 18.5 ms).

Removing the halteres significantly increased blow fly escape duration (rank sum $p = 0.0007$; blow fly haltereless median = 16.2 ± 19.25 ms), slowing them to the same duration as soldier fly escapes (figure 3d; rank sum $p = 0.845$). Removing soldier fly halteres had no effect on escape duration (rank sum, $p = 0.729$; soldier fly haltereless escape median = 18.7 ± 14.8 ms). Haltere removal thus lengthens escape duration in a representative Calyptratae fly, but not in the non-Calyptratae soldier fly.

(d) Haltere ablation makes Calyptratae takeoffs less stable

To estimate stability during takeoff, we measured change in pitch and translation (distance travelled at the centre of mass) over the course of the first three wingbeats of each takeoff (figure 4a), because blow fly and soldier fly spontaneous takeoffs were completed within 2–3 wingbeats (figure 1b). We define a metric of pitch stability as total pitch change (°) divided by body translation (mm). Using this definition, a fly that maintained a consistent orientation over its takeoff, even if the orientation was steep, would be more stable than a fly whose orientation changed during the takeoff. We found that blow flies are less stable than soldier flies during escapes with or without halteres removed, but they are equally stable during spontaneous takeoffs (figure 4b,c; rank sum $p < 0.0001$, $p = 0.0001$, $p = 0.315$ respectively; blow fly median spontaneous = 1.61 ± 2.90 deg mm⁻¹, escape intact = 6.58 ± 3.63 deg mm⁻¹, escape haltereless = 11.5 ± 18.2 deg mm⁻¹; soldier fly median spontaneous = 1.19 ± 1.51 deg mm⁻¹, escape intact = 1.47 ± 1.15 , escape haltereless = 2.34 ± 3.15). Soldier fly escape and spontaneous takeoff pitch stability were not different ($p = 0.604$) and removing the halteres did not change their pitch stability ($p = 0.141$). Many haltereless soldier flies were even able to escape the filming enclosure without crashing. In blow flies, however, escapes were less stable than spontaneous takeoffs ($p = 0.0001$), and removing the halteres made their escapes even less stable ($p = 0.0001$; figure 4b,c). Haltereless blow flies' escapes always resulted in a crash landing.

(e) A closely related non-Calyptratae fly can escape rapidly without haltere input

We noted above that the fruit fly has a much faster leg extension than any of the other flies measured and has a fast takeoff similar in duration to that of the Calyptratae. Fruit flies are similar in body shape and leg extension velocity to the Calyptratae, but they do not use their halteres in the

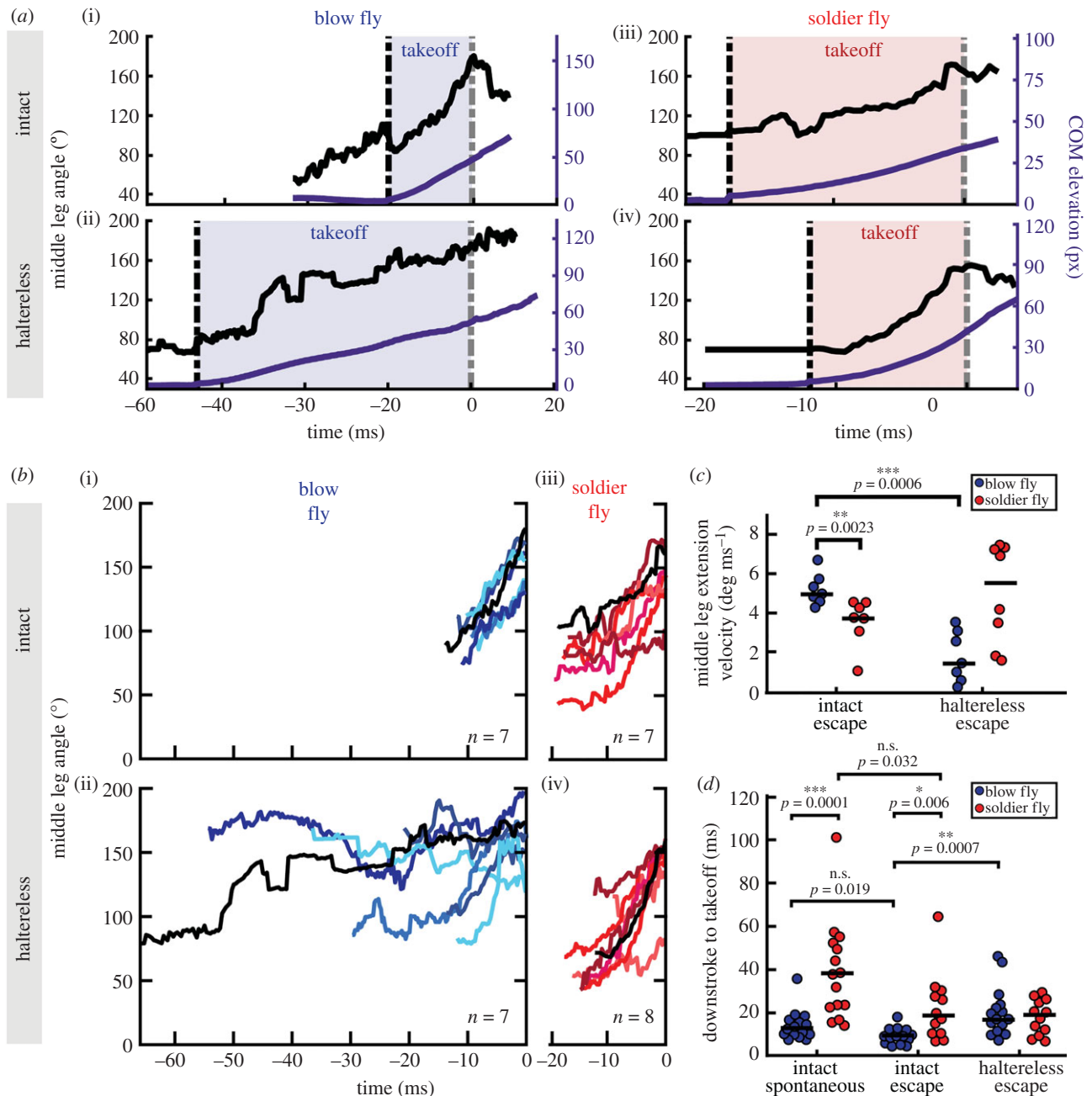


Figure 3. Calypttratae flies without halteres decrease leg extension velocity during escapes. (a) Raw example traces of middle leg femur-tibia angle (black) and COM elevation (purple) in blow flies (i, ii) and soldier flies (iii, iv). Takeoffs indicated by shaded region. Black dotted line indicates takeoff initiation and grey dotted line indicates liftoff. Top traces (i, iii) show intact escapes. Bottom traces (ii, iv) show haltereless escapes. Note difference in x-axis scale. (b) Raw traces of middle leg femur-tibia in blow flies (i, ii) and soldier flies (iii, iv). Top traces (i, iii) show intact escapes. Bottom traces (ii, iv) show haltereless escapes. Example traces represented in A are shown in black. Each trace represents the leg angle only during the takeoff period (c) Middle leg extension velocity in blow flies (blue) and soldier flies (red) during takeoff (start of COM elevation to liftoff) for intact escape (left) and haltereless escape (right) takeoffs ($n = 7$ – 8 takeoffs per condition, Bonferroni correction threshold = 0.0125). Black bar represents median. (d) Time from wing downstroke initiation to takeoff in blow flies (blue) and soldier flies (red) for intact spontaneous (left), intact escape (middle) and haltereless escape (right) takeoffs ($n = 12$ – 15 takeoffs per condition, Bonferroni correction threshold = 0.007). Black bar represents median. (Online version in colour.)

same ways. We predicted that fruit flies, unlike blow flies, will still be able to perform fast takeoffs with halteres removed, because they have not been shown to rely on haltere input for non-flying behaviours [37].

Fruit fly takeoffs were conservatively defined as the first two wingbeats (based on spontaneous takeoff results; figure 1b). We found fruit flies have short takeoffs (figures 1b; 5a), and escape durations in intact fruit flies were not significantly different from blow fly takeoffs (rank sum, $p = 0.334$; fruit fly intact escape median = 8.00 ± 2.25 ms). Fruit fly escapes, like blow fly escapes, are less stable than

spontaneous takeoffs [1]. Unlike blow fly escapes, however, fruit fly escape duration and pitch stability were not affected by haltere removal (figure 5; fruit fly haltereless escape median = 8.00 ± 1.00 ms). Haltere removal did not affect escape duration or pitch stability (fruit fly intact escape stability median = 1.15 ± 1.85 , haltereless = 1.07 ± 0.77), and thus fruit flies, like soldier flies, do not require haltere input to perform escapes.

Most groups of flies outside the Calypttratae, like the fruit flies, keep their halteres motionless unless in flight (the one exception, in the family Micropezidae, is not cultured in

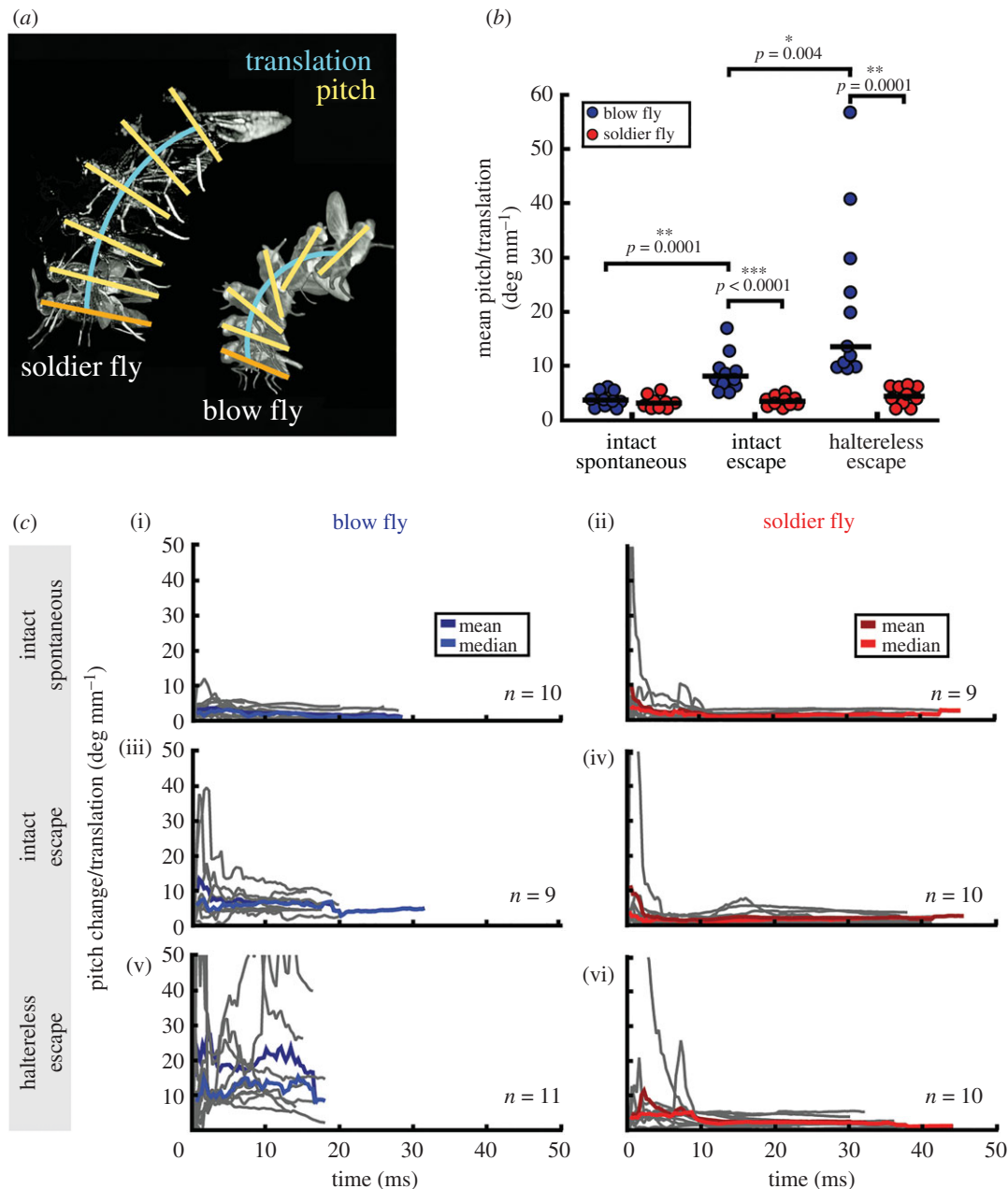


Figure 4. (a) Schematic demonstrating digitized body angle (yellow) and translation (cyan) over time during an escape in a haltereless soldier fly (left) and a haltereless blow fly (right). (b) Mean pitch change divided by mean translation in blow flies (blue) and soldier flies (red) during the first three wingbeats of intact spontaneous (left), intact escape (middle) and haltereless escape (right) takeoffs ($n = 9$ – 11 takeoffs per condition, Bonferroni correction threshold = 0.007). Black bar represents median. (c) Raw traces (grey), mean (dark red or dark blue) and median (red or blue) of pitch change divided by mean translation in blow flies (blue) and soldier flies (red) during the first three wingbeats of intact spontaneous (i, ii), intact escape (iii, iv) and haltereless escape (v, vi) takeoffs. Some raw traces extend beyond the axis limits; see electronic supplementary material, figure S3 for expanded trace. (Online version in colour.)

laboratories and was not captured in this study). However, there are some families that move their halteres in slow, irregular motions when they are not flying. These include some families of the Tephritoidea (Tephritidae and Ulidiidae) [24] and the closely related family Sepsidae. Do these flies use their halteres to stabilize takeoff, even though their kinematics are quite different from Calyptratae? A representative species, *Sepsis puncta*, was collected and filmed in intact and haltereless escapes. Though its body was too small to accurately measure pitch stability in our setup, we found that intact *Sepsis puncta* has rapid takeoffs like the Calyptratae, but haltere removal has no effect on its takeoff speed (figure 5d). Our results suggest that rapid oscillations of the halteres are necessary to make their input useful for stabilizing fast takeoffs.

3. Discussion

Fruit flies have been shown to generate most or all (depending on takeoff type) of their lift through jumping legs [1,16,17,38], whereas other non-Calyptratae flies like mosquitoes and hover flies generate lift primarily from wings [13,14]. Here, we surveyed a larger range of the dipteran phylogeny and found a notable difference in one of the most successful clades. Our analysis of takeoff dynamics across the fly phylogeny suggests that body morphology (stouter flies) and takeoff strategy (jumping over flapping) result in shorter takeoff durations. For flies in the Calyptratae, taking advantage of sensory halteres during the transition from standing to flight provides a measure of control during these high-speed manoeuvres.

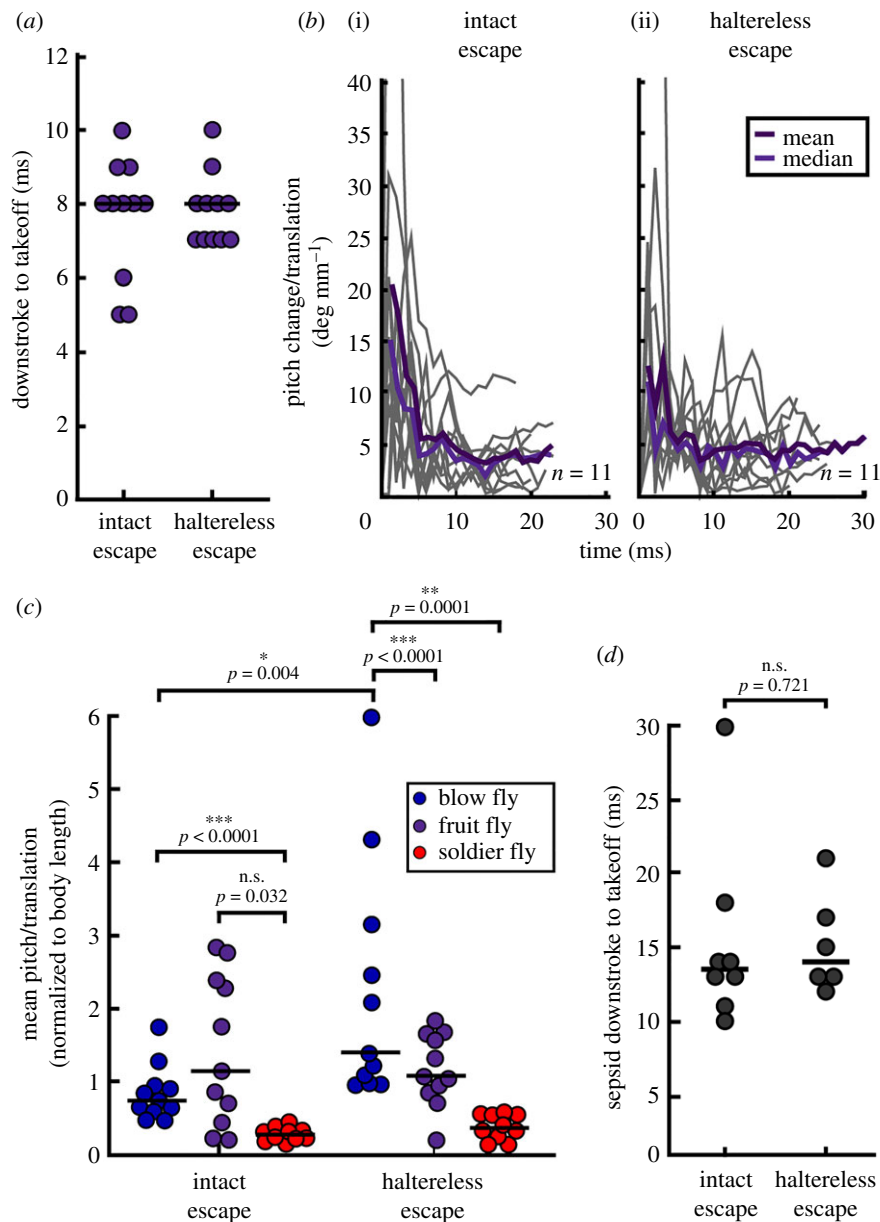


Figure 5. Fruit fly escapes are fast, but are not affected by haltere removal. (a) Time from wing downstroke initiation to takeoff in fruit flies for intact escape (left) and haltereless escape (right) takeoffs ($n = 11$ animals). Black bar represents median. (b) Raw traces (grey), mean (dark burgundy) and median (burgundy) of pitch change divided by mean translation in fruit flies during the first two wingbeats of intact escape (i) and haltereless escape (ii) takeoffs. (c) Mean pitch change divided by mean translation normalized to body length in blow flies (blue), fruit flies (burgundy) and soldier flies (red) during intact escape (left) and haltereless escape (right); rank sum intact escape blow fly versus fruit fly $p < 0.0001$, haltereless escape blow fly versus fruit fly $p = 0.0001$, Bonferroni correction threshold = 0.0056). Black bar represents median. (d) Time from wing downstroke initiation to takeoff in *Sepsis puncta* for intact escape (left), and haltereless escape (right) takeoffs ($n = 8$ and 6 animals). Black bar represents median. (Online version in colour.)

Recordings of haltere afferent neurons from two dipteran species that diverged more than 100 Ma reveals remarkable similarity [28,39], and the similarity extends to the neural activity in the forewing of a lepidopteran [40]. All of these recordings suggest that any large movement of the halteres or wings, like the oscillations seen in walking Calypttratae, results in spiking activity in the associated nerve [39,41]. This information is passed directly to wing-steering motoneurons [6], allowing the fly to receive potentially useful information anytime the haltere moves. The neural mechanism by which the halteres would contribute to takeoff strategy is still unclear. Direct connections between the haltere nerve and the legs have not been identified, but haltere information is represented in the brain [42] and indirect connections through the frontal nerve and thoracic ganglion have

been shown to exist [43]. One possibility is that haltere activation could contribute to a CNS 'warm-up' prior to the initiation of flight. This general activation of the CNS would be analogous to the slow depolarization in neurons seen previously in the initiation of walking in other insects [44,45]. Haltere primary afferents fire phase-locked spikes when the haltere is moving, and thus the fly could oscillate its haltere before taking off to provide excitatory input to its CNS. It is possible that this input could reach leg motoneurons and thus influence leg extension velocity.

Behavioural state has a profound impact on neural activity, which increases sensorimotor flexibility [46–49]. A state change in flies may be induced by haltere input to the CNS. Alternatively, distinct mechanisms for gating specific actions or pathways may exist (e.g. in visually mediated

escape responses in *Drosophila* [49–51]). Here, we might predict that mechanosensory input from the halteres can be transmitted to the legs to induce fast escapes. A fly with ablated halteres would be forced to use a different pathway to take off, resulting in the slower takeoffs observed here. The loss of one pathway may also explain why flies are less likely to perform spontaneous takeoffs when the halteres are removed. Though its specific mechanism is unknown, information from an oscillating haltere can be used beyond its canonical role in free-flight to help these highly successful flies take to the air.

4. Methods

(a) Recording ethological data

A high-speed camera (Fastec Imaging, San Diego, CA, USA) captured tethered and freely behaving flies at 1000–3000 frames per second. Positions of wings, halteres, head, abdomen and centre of mass were digitized using DLT DataViewer [52]. One limitation of this study is a lack of three-dimensional video data. Future studies that extract all rotation directions (yaw, pitch and roll) will give a fuller picture of the specific aspects of stability the halteres contribute most. In trials where wings were cut with scissors or halteres were ablated by plucking with forceps (under a dissection microscope to ensure total removal), flies were anaesthetized at 0°C for 2–3 min before surgery. Experiments were performed on adult female black soldier flies (*Hermetia illucens*; Symton, College Station, TX), blue bottle flies (*Calliphora vomitoria*; Josh's Frogs, Owosso, MI, USA) and flesh flies (*Sarcophaga bullata*; Carolina Biological, Burlington, NC, USA) taken from laboratory colonies. Animals were given food and water ad libitum, and kept on a 12 L:12 D cycle at 25°C. All additional flies used were collected in northeastern Ohio with insect nets (Bioquip, Rancho Dominguez, CA) and identified to family level with a dichotomous key, and to genus or species level with various resources [53]. Wild-caught flies were either used immediately or stored at 4°C for no longer than 5 days before use.

(b) Takeoffs

Flies were anaesthetized and placed inside plastic tubes (8 mm diameter opening) with an electrical breadboard at the top.

After waking up, the flies climbed to the top of the platform, from which they could take off. The platform's surface was metal and connected to a power supply and a resistor, and could be triggered to heat up, eliciting an escape. The same platform was used at room temperature to observe spontaneous takeoffs, in which no external stimuli were provided. Due to their small size, fruit fly takeoffs were filmed using a smaller platform (a plastic pipette tip) and escapes were elicited by gently touching the abdomen with a paintbrush bristle. Paired comparisons for intact and haltereless trials were used for the majority of laboratory-reared animals.

Pitch change was measured by digitizing the body angle (head to abdomen; figure 2e) for each frame of the takeoff relative to the initial position of the body (to account for the possibility of steeper/shallower initial angles between species). Videos where the animals were not oriented perpendicular to the camera were discarded.

For leg extension experiments, the initial COM elevation was estimated by digitizing the scutellum and plotting its elevation over time (figure 2a). For each takeoff, there was a visually evident frame at which elevation began.

(c) Statistics

All data were non-normally distributed. Comparisons between groups were made using the Wilcoxon rank sum test with Bonferroni correction. Correlations between two variables were made using Spearman's rank correlation (electronic supplementary material, table S2).

Data accessibility. Data and code are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.zw3r22873> [54].

Authors' contributions. A.M.Y. designed the study, collected data, analysed data and drafted the manuscript. K.A.J. and A.J.S. collected and analysed data. J.L.F. obtained funding, designed the study, coordinated the study and revised the manuscript.

Competing interests. The authors declare no competing interests.

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References

- Card G, Dickinson M. 2008 Performance trade-offs in the flight initiation of *Drosophila*. *J. Exp. Biol.* **211**, 341–353. (doi:10.1242/jeb.012682)
- 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)
- 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)
- 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)
- Sherman A, Dickinson MH, Nasir N, Schützner P. 2004 Summation of visual and mechanosensory feedback in *Drosophila* flight control. *J. Exp. Biol.* **207**, 133–142. (doi:10.1242/jeb.00731)
- 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)
- 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)
- Burrows M. 2007 Kinematics of jumping in leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae). *J. Exp. Biol.* **210**, 3579–3589. (doi:10.1242/jeb.009092)
- Siwanowicz I, Burrows M. 2017 Three dimensional reconstruction of energy stores for jumping in planthoppers and froghoppers from confocal laser scanning microscopy. *Elife* **6**, e23824. (doi:10.7554/eLife.23824)
- Burrows M. 2009 Jumping performance of planthoppers (Hemiptera, Issidae). *J. Exp. Biol.* **212**, 2844–2855. (doi:10.1242/jeb.032326)
- Burrows M, Ghosh A, Yeshwanth HM, Dorosenko M, Sane SP. 2019 Effectiveness and efficiency of two distinct mechanisms for take-off in a derbid planthopper insect. *J. Exp. Biol.* **222**, jeb191494. (doi:10.1242/jeb.191494)
- Burrows M, Dorosenko M. 2014 Jumping mechanisms in lacewings (Neuroptera, Chrysopidae

- and Hemerobiidae). *J. Exp. Biol.* **217**, 4252–4261. (doi:10.1242/jeb.110841)
13. Muijres FT, Chang SW, van Veen WG, Spitzen J, Biemans BT, Koehl MAR, Dudley R. 2017 Escaping blood-fed malaria mosquitoes minimize tactile detection without compromising on take-off speed. *J. Exp. Biol.* **220**, 3751–3762. (doi:10.1242/jeb.163402)
14. Chen MW, Zhang YL, Sun M. 2013 Wing and body motion and aerodynamic and leg forces during take-off in droneflies. *J. R. Soc. Interface* **10**, 20130808. (doi:10.1098/rsif.2013.0808)
15. Sun MCM. 2014 Wing/body kinematics measurement and force and moment analyses of the takeoff flight of fruit flies. *Acta Mech. Sin.* **30**, 495–506. (doi:10.1007/s10409-014-0059-0)
16. Trimarchi JR, Schneiderman AM. 1995 Initiation of flight in the unrestrained fly, *Drosophila melanogaster*. *J. Zool.* **235**, 211–222. (doi:10.1111/j.1469-7998.1995.tb05138.x)
17. Trimarchi JR, Schneiderman AM. 1995 Flight initiations in *Drosophila melanogaster* are mediated by several distinct motor patterns. *J. Comp. Physiol. A* **176**, 355–364. (doi:10.1007/BF00219061)
18. 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)
19. Ache JM, Polsky J, Alghailani S, Parekh R, Breads P, Peek MY, Bock DD, von Reyn CR, Card GM. 2019 Neural basis for looming size and velocity encoding in the *Drosophila* giant fiber escape pathway. *Curr. Biol.* **29**, 1073–1081.e4. (doi:10.1016/j.cub.2019.01.079)
20. Judge S, Rind F. 1997 The locust DCMD, a movement-detecting neurone tightly tuned to collision trajectories. *J. Exp. Biol.* **200**, 2209–2216.
21. Fotowat H, Harrison RR, Gabbiani F. 2011 Multiplexing of motor information in the discharge of a collision detecting neuron during escape behaviors. *Neuron* **69**, 147–158. (doi:10.1016/j.neuron.2010.12.007)
22. Suver MP, Mamiya A, Dickinson MH. 2012 Octopamine neurons mediate flight-induced modulation of visual processing in *Drosophila*. *Curr. Biol.* **22**, 2294–2302. (doi:10.1016/j.cub.2012.10.034)
23. 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)
24. Hall JM, McLoughlin DP, Kathman ND, Yarger AM, Mureli S, Fox JL. 2015 Kinematic diversity suggests expanded roles for fly halteres. *Biol. Lett.* **11**, 20150845. (doi:10.1098/rsbl.2015.0845)
25. Sandeman DC, Markl H. 1980 Head movements in flies (*Calliphora*) produced by deflexion of the halteres. *J. Exp. Biol.* **85**, 43–60.
26. Derham W. 1714 *Physico-theology: or, a demonstration of the being and attributes of God, from His works of creation. Being the substance of XVI sermons preached in St Mary Le Bow-church, London, at the honble Mr Boyle's lectures, in the years 1711 and 1712*. London, UK: W Innys.
27. Fraenkel G, Pringle JWS. 1938 Biological sciences: halteres of flies as gyroscopic organs of equilibrium. *Nature* **141**, 919–920. (doi:10.1038/141919a0)
28. 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)
29. Miller PL. 1977 Haltere activity in a flightless hippoboscids fly, *Crataerina pallida*. *J. Insect Physiol.* **23**, 855–860. (doi:10.1016/0022-1910(77)90010-5)
30. Fraenkel G. 1939 The function of the halteres of flies (Diptera). *Proc. Zool. Soc. Lond.* **109**, 69–78.
31. Kutty SN *et al.* 2019 Phylogenomic analysis of Calypttratae: resolving the phylogenetic relationships within a major radiation of Diptera. *Cladistics* **35**, 605–622. (doi:10.1111/cla.12375)
32. Stireman JO, O'Hara JE, Wood DM. 2006 Tachinidae: evolution, behavior, and ecology. *Annu. Rev. Entomol.* **51**, 525–555. (doi:10.1146/annurev.ento.51.110104.151133)
33. Wiegmann BM *et al.* 2011 Episodic radiations in the fly tree of life. *Proc. Natl Acad. Sci. USA* **108**, 5690–5695. (doi:10.1073/pnas.1012675108)
34. Deora T, Sin\gh AK, Sane SP. 2015 Biomechanical basis of wing and haltere coordination in flies. *Proc. Natl Acad. Sci. USA* **112**, 1481–1486. (doi:10.1073/pnas.1412279112)
35. Alexander D, David E. 2004 *Nature's flyers: birds, insects, and the biomechanics of flight*. Baltimore, MD: Johns Hopkins University Press.
36. Card G, Dickinson MH. 2008 Visually mediated motor planning in the escape response of *Drosophila*. *Curr. Biol.* **18**, 1300–1307. (doi:10.1016/j.cub.2008.07.094)
37. Daltorio KA, Fox JL. 2018 Haltere removal alters responses to gravity in standing flies. *J. Exp. Biol.* **221**, jeb181719. (doi:10.1242/jeb.181719)
38. Fontaine EI, Zabala F, Dickinson MH, Burdick JW. 2009 Wing and body motion during flight initiation in *Drosophila* revealed by automated visual tracking. *J. Exp. Biol.* **212**, 1307–1323. (doi:10.1242/jeb.025379)
39. 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)
40. Pratt B, Deora T, Mohren T, Daniel T. 2017 Neural evidence supports a dual sensory-motor role for insect wings. *Proc. R. Soc. B* **284**, 20170969. (doi:10.1098/rspb.2017.0969)
41. 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)
42. Kathman ND, Fox JL. 2019 Representation of haltere oscillations and integration with visual inputs in the fly central complex. *J. Neurosci.* **39**, 4100–4112. (doi:10.1523/JNEUROSCI.1707-18.2019)
43. 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)
44. Rosenbaum P, Schmitz J, Schmidt J, Büschges A. 2015 Task-dependent modification of leg motor neuron synaptic input underlying changes in walking direction and walking speed. *J. Neurophysiol.* **114**, 1090–1101. (doi:10.1152/jn.00006.2015)
45. Ludwar BC, Westmark S, Büschges A, Schmidt J. 2005 Modulation of membrane potential in mesothoracic moto- and interneurons during stick insect front-leg walking. *J. Neurophysiol.* **94**, 2772–2784. (doi:10.1152/jn.00493.2005)
46. Maimon G, Straw AD, Dickinson MH. 2010 Active flight increases the gain of visual motion processing in *Drosophila*. *Nat. Neurosci.* **13**, 393–399. (doi:10.1038/nn.2492)
47. Longden KD, Krapp HG. 2009 State-dependent performance of optic-flow processing interneurons. *J. Neurophysiol.* **102**, 3606–3618. (doi:10.1152/jn.00395.2009)
48. Longden KD, Muzzu T, Cook DJ, Schultz SR, Krapp HG. 2014 Nutritional state modulates the neural processing of visual motion. *Curr. Biol.* **24**, 890–895. (doi:10.1016/j.cub.2014.03.005)
49. Ache JM, Namiki S, Lee A, Branson K, Card GM. 2019 State-dependent decoupling of sensory and motor circuits underlies behavioral flexibility in *Drosophila*. *Nat. Neurosci.* **22**, 1132–1139. (doi:10.1038/s41593-019-0413-4)
50. Von Reyn CR, Nern A, Williamson WR, Breads P, Wu M, Namiki S, Card GM. 2017 Feature integration drives probabilistic behavior in the *Drosophila* escape response. *Neuron* **94**, 1190–1204; e6. (doi:10.1016/j.neuron.2017.05.036)
51. Cheong H, Siwanowicz I, Card GM. 2020 Multi-regional circuits underlying visually guided decision-making in *Drosophila*. *Curr. Opin. Neurobiol.* **65**, 77–87. (doi:10.1016/j.conb.2020.10.010)
52. Hedrick TL. 2008 Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001. (doi:10.1088/1748-3182/3/3/034001)
53. Borror DJ, Triplehorn CA, Johnson NF. 1992 *An introduction to the study of insects*. Fort Worth, TX: Saunders College.
54. Yarger AM, Jordan KA, Smith AJ, Fox JL. 2021 Data from: Takeoff diversity in Diptera. Dryad Digital Repository. (<http://dx.doi.org/10.5061/dryad.zw3r22873>)