Body appendages fine-tune posture and moments in freely manoeuvring fruit flies

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ABSTRACT

The precise control of body posture by turning moments is a key to elevated locomotor performance in flying animals. Although elevated moments for body stabilization are typically produced by wing aerodynamics, animals also steer using drag on body appendages, shifting their centre of body mass, and changing moments of inertia owing to active alterations in body shape. To estimate the instantaneous contribution of each of these components for posture control in an insect, we three-dimensionally reconstructed body posture and movements of body appendages in freely manoeuvring fruit flies *Drosophila melanogaster* by high speed video and experimentally scored drag coefficients of legs and body trunk at low Reynolds number. The results show that the sum of leg- and abdomen-induced yaw moments dominates wing-induced moments during 17% of total flight time but on average is 7.2-times (roll, 3.4-times) smaller during manoeuvring. Our data reject a previous hypothesis on synergistic moment support, indicating that drag on body appendages and mass-shift inhibit rather than support turning moments produced by the wings. Numerical modelling further shows that hind leg extension alters the moments of inertia around the three main body axes of the animal by not more than 6% during manoeuvring, which is significantly less than previously reported for other insects. In sum, yaw, pitch, and roll steering by body appendages likely fine-tunes turning behaviour and body posture, without providing a significant advantage for posture stability and moment support. Motion control of appendages might thus be part of the insect's trimming reflexes that trim out imbalances in moment generation owing to unilateral wing damage and abnormal asymmetries of the flight apparatus.
INTRODUCTION

Locomotion during migration, territory defence, routine commuting, foraging, and escape behaviours is vital to the reproductive effectiveness and survival of many animals (Alexander, 2003). A critical task during locomotion is the control of body posture, which is tightly linked to the production and control of locomotor forces for propulsion and the corresponding moments for turning control (Ellington, 1984a; Ellington, 1984b). While locomotion involving contact with solid ground benefits from static stability, flying animals achieve body stability and thus flight path control with the help of aerodynamic friction of their environment. Active manoeuvring and directed aerial descent such as gliding thus depend on the animal’s ability to fine tune the benefits of three distinct, major physical mechanisms for posture control: aerodynamic lift and drag on wings and body (Pennycuick, 1968; Pennycuick, 1971), active control of the centre of body mass and thus distance to aerodynamic force vectors (Cook and Spottiswoode, 2006; Ellington, 1984a), and modifications of the body’s moments of inertia by active changes in body shape (Libby et al., 2012).

The control of moments of inertia is highly effective even in terrestrial animals, for example, during falling and jumping, in which rats maintain an upright body posture by twisting their entire body (Laouris et al., 1990) and geckos and lizards by beating their heavy tails (Jusufi et al., 2008; Libby et al., 2012). In preparation of targeted jumps, moreover, flightless mantis generate a controlled whole-body spin by adjustment of their center of mass (Burrows et al., 2015). Since active modification in body shape leads to a change in moments of inertia, this mechanism also enables astronauts to control their body orientation without air friction (Kane and Scher, 1970; Kulwicki et al., 1962). By contrast, gliding and actively flying animals typically control moments and posture by alterations in the wings’ lift and drag characteristics (Ellington, 1984a; Ellington, 1984c; Ellington, 1991). Although wing aerodynamics predominantly determines moments for posture control, an increasing number of studies highlights that aerial steering is effectively supported by the aerodynamics of body appendages such as legs and abdomen. Arboreal ants and other wingless, gliding hexapods, for example, effectively control their aerial descent from tree to tree by steering with their hind legs (Yanoviak et al., 2010) and lateral cerci, respectively, (Yanoviak et al., 2009). If the hind legs are cut, the tree trunk landing success is
severely attenuated between 35 and 60%. Leg steering is also of great importance for drag control in birds. Depending on body posture, pigeons and griffon vultures, for example, may increase their total body drag coefficients during forward flight by factors of approximately 2 and 3, respectively, depending on the extension of their feet (Pennycuick, 1968; Pennycuick, 1971). As a consequence, feet adduction in birds during smooth weather conditions leads to an increase in gliding distance, while during manoeuvres the feet appear (Pennycuick, 1960).

The vast majority of previous studies on the significance of body appendages for force and moment support in actively flying animals were conducted in insects such as the small fruit fly (Götz et al., 1979; Zanker, 1988b), the house fly (Zanker, 1991), orchid bees (Combes and Dudley, 2009) and moths (Cheng et al., 2011; Hedrick and Daniel, 2006). Early studies on various freely flying insect species suggested that leg steering and shifting the insect’s centre of body mass support wing-induced moments during manoeuvring (Ellington, 1984d). This hypothesis was further investigated under visual stimulation mimicking yaw turns, during which tethered flying flies bend hind legs and abdomen in the horizontal to the inner side of the intended turn (Götz et al., 1979; Zanker, 1988a; Zanker, 1988b; Zanker, 1991). Visual stimulation mimicking body pitching, by contrast, leads to bending of the abdomen in the vertical, with upward bending during upward motion of the visual pattern (Dyhr et al., 2013; Frye, 2001; Hinterwirth and Daniel, 2010). Mathematical models of the latter behaviour demonstrated that abdominal steering is, at least to some extent, sufficient to maintain body posture in the hawkmoth (Cheng et al., 2011; Dyhr et al., 2013; Hedrick and Daniel, 2006). Besides vision, some insects such as desert locusts also bend their abdomen in response to changing air flow conditions (Arbas, 1986). It has been suggested that this behaviour mimics an aerodynamic rudder that helps the animal to orient into the direction of wind during flight (Camhi, 1970a; Camhi, 1970b).

Here we show the significance of leg and abdominal steering on moments and body posture in freely manoeuvring fruit flies *Drosophila*, estimating instantaneous moments owing to wing motion, hind leg- and abdomen posture around the yaw, pitch, and roll body axes, respectively. For this investigation, we (i) employed high-speed video to three-dimensionally reconstruct the animal’s body posture and extension angles of legs and abdomen during various flight manoeuvres, (ii) measured
drag coefficients of hind legs and the body trunk in a wind tunnel and (iii) derived turning moments from a numerical approach. In contrast to previous hypotheses, our data suggest that body appendages mostly attenuate rather than enhance wing flapping-induced moments. We argue, moreover, that owing to its small contribution to total moments, leg- and abdomen-induced moments should be considered as control systems for fine control rather than systems that significantly enhance the production of moments during extreme flight manoeuvres.

RESULTS

Steering by wings and body appendages

Our recorded flight sequences cover various flight manoeuvres of female fruit flies Drosophila melanogaster including rectilinear horizontal flight, ascending and descending flight, shallow turns and rapid flight saccades, in which animals rotate with angular peak velocity of up to 1074 deg s$^{-1}$ (mean, 504 ± 49.1 deg s$^{-1}$, N = 6 saccades) around the vertical yaw axis (Fig. 1A and B). The mean of all data points within each flight sequence that fell within the top 1% maximum of horizontal (vertical) velocity values was 0.26 ± 0.13 m s$^{-1}$ (0.15 ± 0.11 m s$^{-1}$), while the mean of all data samples amounts to 0.21 ± 0.12 m s$^{-1}$ (0.11 ± 0.11 m s$^{-1}$, N = 81 flight sequences). The free flight analysis highlights that body yaw, pitch, and roll angles continuously change during manoeuvring flight, exhibiting small changes of several degrees during straight flight and pronounced changes in body posture of up to approximately 30 deg roll angle during rapid turns (Fig. 1A and C). The normalized histograms of posture angles demonstrate a mean body pitch of approximately 30.6 ± 9.7 deg and a mean roll angle near zero of −0.6 ± 9.4 deg (N = 24,579 video frames) during flight.

Free flight manoeuvres in Drosophila are accompanied by extensive movements of hind legs and the abdomen. On average, the animals bend their abdomen vertically downward by approximately 10.1 ± 5.3 deg with respect to the longitudinal body axis at a mean horizontal deflection angle of the abdomen close to zero (2.0 ± 3.5 deg). Abdomen steering angles typically vary −15 to 15 deg around its mean value (Fig. 1D). By contrast, leg extension angles (right-minus-left) vary between −35 and 35 deg, with mean vertical and horizontal leg extension angles of 108 ± 15.1 deg and 112
± 13.7 deg, respectively (Fig. 1E and F). For a definition of angles refer to Materials and Methods section.

To evaluate the contribution of moments caused by changes in aerodynamic drag on both body trunk (head, thorax, abdomen, fore- and middle legs) and hind legs to wing flapping-induced moments during flight manoeuvres, we systematically analyzed the magnitude and coherence of the three components for total moment control (Fig. 2B and C). Figure 2 shows the moment components for yaw (Fig. 2E), pitch (Fig. 2F) and roll (Fig. 2G) of the flight manoeuvre in Fig. 2A. The data suggest that aerodynamic drag- and mass shift-induced moments are only small fractions of total moments acting on the fly body (Fig. 2D-G). We derived the total moments from the changes in body posture and a numerical framework (cf. Materials and Methods). The top 1% maximum, absolute total moment of all data around the yaw, pitch, and roll axes was 11.2, 10.2 and 26.8 nN m, respectively (N = 246 samples). On average, the individual contributions of hind leg-induced moments were approximately 41.3- (yaw), 11.2- (roll), and 78.3-times (pitch), and contributions of the body trunk approximately 7.9- (yaw) and 3.8-times (pitch) smaller than total moments produced by wings, hind legs, and trunk (Table 1). Further calculations of moments using static, non-moveable legs and abdomen (\( M_l = 0, \zeta_V = 105 \, \text{deg}, \zeta_H = 143 \, \text{deg}, \psi_V = 0 \, \text{deg}, \psi_H = 0 \, \text{deg} \)) with average posture show that "static" absolute \( M_{D*} \) differs by approximately 3.4 pN m (46%, yaw), 16.7 pN m (47%, pitch), and 3.7 pN m (21%, roll) from \( M_D \) produced by moving legs and abdomen (single animal, Fig. 3). Considering only static legs (abdomen), mean \( M_{D*} \) differs by approximately 10.0 ± 9.5 pN m (6.4 ± 8.7 pN m, yaw), 19.4 ± 18.9 pN m (29.8 ± 21.2 pN m, pitch), and 15.0 ± 14.9 pN m (7.1 ± 8.0 pN m, roll) from \( M_D \) (N = 81 flight sequences).

The magnitude of turning moments depends on the product of moment arm and aerodynamic force, and thus on local air velocities on legs and abdomen. These velocities result from three distinct kinematic components: the body’s translational motion (for-, up-, and sideward), its rotational motion around the three main body axes, and active leg motion relative to the body (Fig. 1A, Table 1). For completeness, we also considered the wing's induced flow (downwash) on legs and body, which is outlined in more detail in a section below. The moments around the fly's main axes (yaw, pitch, roll) owing to translational body motion are shown in Fig. 2H, rotational...
motion is shown in Fig. 2I, active leg motion in Fig. 2J, and moments owing to induced flow from the beating wings in Fig. 2K. The data suggest that body translation predominately determines moment control in fruit flies cruising at mean forward speed of $253 \pm 137 \text{ mm s}^{-1}$, while the contribution of rotational body motion is small owing to small angular speeds and a decreasing velocity gradient from leg tip to base (Table 1). Mean tarsal velocity of the hind legs due to body rotation amounts to only approximately $13.4 \pm 14.7 \text{ mm s}^{-1}$ and the 1% maximum does not exceed $107 \text{ mm s}^{-1}$. The velocity component owing to active leg motion ($7.04 \pm 7.99 \text{ mm s}^{-1}$) is almost negligible and 36- and 2-fold smaller than the velocities induced by body translation and rotation, respectively. We obtained similar results for active translation motion of the abdomen ($3.77 \pm 1.64 \text{ mm s}^{-1}$) that compares to mean body rotation-induced velocity of $6.75 \pm 4.60 \text{ mm s}^{-1}$.

Although our data indicate that drag-based steering by hind legs is likely to be 7.6-fold more effective than drag-based steering by the abdomen, the significance of body appendages for moment control during manoeuvring flight is limited (Fig. 4A and B). An analysis on the relative contribution of drag-, mass shift-, and inertia-induced moments for yaw control shows that the sum of all three moment components exceeds wing flapping-induced moments in only 16.8% (22.9% for roll) of total flight time (Fig. 4C and D). Drag-based moments alone are higher than wing flapping moments in 1.7% (yaw) and 0.9% (roll) of the flight time (Fig. 4E and F). In other words: during half of total flight time, the total moments produced by body appendages for yaw and roll amount to only 2.0% and 3.3% of wing-induced moments, respectively.

**Coherence of steering moment components**

In contrast to previous tethered flight studies on vision-induced yaw steering in *Drosophila*, hind leg and abdomen deflection is more variable in free flight. Our data even suggest that leg and abdomen deflection is broadly independent from total, wing flapping-dominated moment control. We found that only in 51.8% of total flight time, the sign of the instantaneous, relative (left-minus-right), horizontal leg extension angle $\zeta_H$ (cf. Materials and Methods section) equals the sign of the total (sum of wing- and body-induced) yaw moment $M_M$. At these instants, the unsigned difference between left and right horizontal leg extension angle is $11.2 \text{ deg} \pm 8.41 \text{ deg}$ (mean,
N = 81 flight sequences). At times (48.2% flight time) at which relative leg extension angle and total yaw moment had a different sign, the unsigned difference between left and right $\zeta_H$ is 10.1 deg ± 8.17 deg (mean, N = 81 flight sequences). For an additional statistical test, we dichotomized the data with +1 (−1) that represents times at which leg extension and yaw moments had equal (opposite) direction. We found no significant difference between the two means for all flight sequences (0.03 ± 0.35, Wilcoxon test, $p = 0.14$, N = 81). Statistical comparison on the relationship between yaw moments and horizontal abdomen bending yielded a similar result: times with equal sign occurred during 51.2% total time without a statistical difference from zero for the dichotomized data (0.02 ± 0.34, Wilcoxon test, $p = 0.16$, N = 81).

To further investigate the relationship between the various sources of body moments, we conducted moment coherence and correlation analyses on yaw and roll (Figs 5 and 6). The moment coherence analysis suggests that the sign of wing flapping- and body drag-induced yaw moments is opposite during approximately 63% (yaw; Fig. 5A) and 65% (roll) of total flight time. This means that leg-based steering inhibits rather than supports turning moments produced by wing flapping. The result is also consistent with findings from a correlation analysis on the temporal relationship between wing flapping- and body drag-induced moments of each flight sequence. The latter analysis shows significant, negative correlation coefficients of $-0.45 \pm 0.36$ and $-0.54 \pm 0.36$ (Pearson tests, N = 73 and 74 significant correlations with $p < 0.05$) for yaw (Fig. 5D) and roll, respectively. Corresponding coherence and correlation values between wing flapping- and mass shift-induced yaw moments are shown in Fig. 5B and E and data for the relationship between wing flapping- and inertia-induced yaw moments in Fig. 5C and F. For completeness, Fig. 6 shows the remaining dependencies between the four sources of moment production ($M_W$, $M_D$, $M_S$, and $M_I$). For statistical evaluation of the data, we tested the presented mean correlation coefficients against zero. The test yielded no significant differences of coefficients calculated for $M_W$ vs. $M_S$ (coefficient for roll, $-0.01 \pm 0.48$; Wilcoxon-test, $p > 0.99$, N = 64) and $M_W$ vs. $M_I$ (coefficient for roll, $0.12 \pm 0.49$; Wilcoxon-test, $p = 0.09$, N = 58), whereas all other correlation values for yaw and roll moments were significantly different from zero (Wilcoxon-test, $p < 0.01$, Figs 5 and 6).
The significance of induced flow
In the following section, we address the potential significance of the wing's downwash on moment control by body trunk and hind legs. Since wings, legs and abdomen are mechanically linked, and the distance between the wings' stroke plane and hind legs is small, we excluded downwash-induced moments from the analyses in Figs 2 - 6, including table 1. This is reasonable because body lift production by wing flapping should decrease with increasing downwash-induced drag on legs and abdomen. To maintain weight support under these conditions, the animal must moderately increase its total body lift production, which in turn balances the moments produced by downwash-induced drag. However, at least to some degree, the wings' downwash dissipates after its acceleration at the stroke plane, losing kinetic energy and thus altering the efficacy of momentum transfer from the wings to body and hind legs. The downwash-induced moments thus depend on the distance between wings and body appendages (legs, abdomen) that varies during manoeuvring flight. In the following section, we evaluated the potential contribution of downwash to moment balance by estimation of instantaneous downwash velocity derived from body mass, instantaneous vertical body motion, and using actuator disc theory (cf. Materials and Methods section).

We considered downwash at various strength and compared the resulting moments for yaw, pitch, and roll with our previous approach (Figs 2-4). Figure 7A shows a time trace of downwash-induced yaw moments (grey) of the flight sequence in Fig. 2A. We subsequently added fractions of these downwash moments to total drag-induced yaw moments $M_D$, in steps of 10% (coloured, cf. $M_D$ in Fig. 2E). To determine the maximum potential effect of downwash on $M_D$, we calculated means of the unsigned top 1% maximum values of all 81 flight sequences (pooled data set, $N = 24,596$ measurements). These values are approximately 4.7- (yaw), 7.6- (pitch), and 5.3-times (roll) larger than the means in table 1. The results are shown in Fig. 7B for yaw, in Fig. 7C for pitch, and in Fig. 7D for roll moments. Depending on downwash-induced moment, yaw moments change by approximately 21% and have a local minimum at 40% downwash. Pitch moments linearly increase with decreasing downwash by a factor of approximately 2.3, while roll moments appear to be widely independent of downwash-induced moments. Small effects were also obtained for the frequency of moment ratio $M_D$ by $M_W$ (yaw, Fig. 7E). Downwash-induced moments may also
change the outcome of the correlation analysis. In two cases, the correlation coefficients decrease with increasing consideration of downwash-induced moments. This relationship is shown in Fig. 7F for coefficients of drag-induced yaw moments $M_D$ vs. $M_S$ (blue) and $M_D$ vs. $M_W$ (red). By contrast, the correlation coefficient of $M_D$ vs. $M_I$ (yaw, green) is not affected by downwash and remains close to zero. We obtained similar results for roll moments (data not shown).

**The significance of body posture on moments of inertia**

Moment control in insects might also benefit from changes in moments of inertia around the three main body axes owing to the active control of legs and abdomen (see Introduction section). To investigate the contribution of active motions, we numerically modelled the insect body as a solid cylinder with the mass of an average fruit fly and the hind legs as cylinders using typical lengths, diameters and masses of corresponding leg segments (cf. Materials and Methods section, Fig. 8A, Table 2). We first calculated the dependency of yaw, pitch and roll moments of inertia from body pitch angle in a model fly in which hind leg coxae and femurs are in a fixed position relative to the thorax, and without tibiae and tarsi (truncated flies, Fig. 8B). The data suggest that moments of inertia (yaw, roll) in fruit flies may change 9-fold from approximately 0.11 to 9.9 ng m$^2$ depending on body pitch angle. By contrast, the moments of inertia owing to mass motion of the hind leg tibia and tarsi are comparatively small compared to the moments derived from truncated flies, amounting up to an increase in moments of approximately 5% in yaw (Fig. 8C), 0.8% in pitch (Fig. 8D) and 6% in roll (Fig. 8E).

For comparison, we also evaluated the maximum instantaneous increase of moments of inertia that a fly might reach during flight by mass motion of its legs, modelling truncated flies with tibia and tarsi but empirically derived hind leg extension angles that produced maximum moments of inertia. These data are plotted as red lines in Fig. 8C-E and confirm the small benefit of leg steering for the control of moments of inertia in fruit flies. On average, the theoretical prediction differs less than 1% increase in moments of inertia from data based on the kinematic reconstructions of leg angles of tibia and tarsi (black, Fig. 8C-E).
DISCUSSION

Steering by wings and body appendages

Our recorded flight sequences show a broad spectrum of different flight behaviours in freely flying fruit flies, ranging from straight flight, sharp turns, backward and sideward flight to pronounced changes in flight altitude (Figs 1 and 2). The three-dimensionally reconstructed body posture, leg extension angles and abdomen bending highlight active components for body stability and directional control. This is evident from the elevated correlation coefficients between horizontal abdominal bending and leg extension angles (Pearson test, $R = 0.69$), significant correlation coefficients between wing flapping- and drag-induced yaw moments, and the correlation between wing flapping- and inertia-induced yaw moments (Fig. 5A and D). Our findings are also consistent with previous experiments on abdomen control in tethered flying fruit flies (Zanker, 1987). The latter study also demonstrated that abdominal movements may not be caused by flow generated from wing flapping. Moreover, table 1 and Figs 2 and 4 show that the various contributions of hind legs and abdomen to total moments are small and typically restricted to times at which wing flapping-induced moments are small. Our moment ratios analyses suggest that steering by hind legs and abdomen dominates moment control in only approximately 17% of total flight time (Fig. 4) and drag-induced moments are smallest compared to all other moment-generating mechanism in fruit flies (Table 1). Thus, in analogy to ruddering of animals in water and air, the small contribution of drag owing to the legs’ proper motion rejects the idea that fruit flies may produce elevated moments by paddling movements of the hind legs (Ristroph et al., 2011).

As outlined in the Materials and Methods section, the estimation of wing flapping-induced moments is crucial in our analysis on the relative contribution of abdomen- and leg induced moments to total moments. Thus, we here compare our estimated wing flapping-dominated total moments with the moments measured in tethered studies of Drosophila flying under various flight and visual feedback conditions. Table 1 shows that moments around the fly's yaw, pitch, and roll axes peak at approximately 11.2, 10.2, and 26.8 nN m. In tethered fruit flies flying under open-loop visual feedback conditions, for comparison, yaw varies between 3 and 8 nN m (Götz et al., 1979; Heisenberg and Wolf, 1979; Heisenberg and Wolf, 1988; Mayer et
al., 1988) with peak values of 17 nN m (Tammero et al., 2004), roll varies between 3 and 20 nN m (Blondeau and Heisenberg, 1982; Sugiura and Dickinson, 2009) and pitch may reach up to 6 nN m (Blondeau and Heisenberg, 1982). Computational fluid dynamic modeling using free flight kinematics of fruit flies performing a saccadic turn reported a peak yaw moment of 2.0 nN m (mean approximately 1.1 nN m, Ramamurti and Sandberg, 2007) and peak yaw moment derived from a robotic wing mimicking a saccadic turn amounted to approximately 1.9 nN m in the same species (Fry et al, 2003). These values are broadly similar to the values shown in table 1, which gives credence to the method used in the present study for estimation of total moment.

**Coherence of steering**

Previous studies on flight control in tethered flies suggest that hind leg steering during optomotor yaw response reinforces wing flapping-induced moments by strongly increasing (decreasing) the leg extension angle on the inner (outer) side of an intended yaw turn (Zanker, 1988a; Zanker, 1991). The latter studies proposed that this synergy increases the fly's agility and manoeuvrability, which may in turn increase survival rate during aerial predation by dragonflies (Combes et al., 2012a). Our data reject the above hypothesis for unrestrained flying fruit flies. We found no preference for the idea that leg extension and abdomen bending angles coherently support turning direction of the animal. In contrast to leg kinematics, we even found that sequence-averaged yaw moments owing to drag on legs and abdomen significantly inhibit than support wing flapping-induced moments (negative correlation coefficient in Fig. 5D), which might enhance posture stability. The same holds for mass shift-induced moments, suggesting a synergistic function of motor pathways to hind legs and abdomen (Fig. 5E). However, counter moments during yaw turning might also result from an increase in local velocities at the hind leg on the outer side of a flight curve, despite its smaller leg extension angle. Data indeed show that an increase in rotational velocity of the body is positively correlated with an increase in hind leg velocity on the outer side of a turn (Pearson correlation: R = 0.77). While the above mechanism might thus passively restrict angular velocity in turning flight owing to aerodynamic damping, flies actively shift their centre of mass (abdomen bending) to the body side that counteracts moments generated by wing flapping. The latter mechanism is independent from angular turning rate because it solely relies on changes in the length
of the moment arm between the fly's centre of mass and the centre of flight force at mid up-/down stroke (Fig. 2C).

The apparent synergy between drag- and mass shift-induced moments and their attenuation on wing flapping-induced moments is also supported by its positive correlation coefficients during yaw and roll control (Fig. 6A and D, yaw). This result is consistent with previous findings on the coherence of leg and abdominal movements in the tethered housefly (Zanker, 1991). The latter study demonstrated that hind legs and abdomen move in-phase and in the same direction during vision-controlled flight. However, our finding that positive (yaw, 51%; roll, 47%) and negative moment coherence (yaw, 49%; roll, 53% flight time) occur with approximately same frequency suggests a highly flexible system with quite independently acting system components for moment control.

**Significance of induced flow**

This study considered induced flow (wing downwash) in detail because of its unsettled contribution to drag-induced moments. Wings and legs are mechanically connected and thus any increase in downwash-induced force pushing legs and body downward in the vertical attenuates body lift production by wing flapping via the mechanical link. After its initial acceleration, downwash velocity and vorticity are thought to increasingly cease with increasing distance from the wings' stroke plane, owing to the viscous forces of the surrounding air. However, owing to the small distance of less than a millimeter between stroke plane and legs, this effect is assumed to be small. The different lengths of moment arm for wing flapping- and drag-induced moments do not allow simple predictions of moment control by changes in downwash velocity. We tackled this problem by calculation of moments, in which we considered downwash as an intervortex stream with uniform velocity but various strengths. Our results in Fig. 7 suggest that induced flow alters total moments depending on the rotational axis: roll moment is rather independent of induced flow and changes only up to 5%, while yaw moments may potentially change up to 22% and pitch moments up to 56% of total moment. Despite the pronounced percentaged changes, consideration of moments owing to induced flow does not alter the main result of this study, although these changes might matter in times at which wing-induced moments
are relatively small. Collectively, the exact contribution of downwash to body posture and turning control remains somewhat unclear and requires further investigations.

**Significance of body posture on moments of inertia**

An alternative benefit why insects actively control legs and abdomen during manoeuvring flight resides in the associated changes in moments of inertia around the three body axes. Since moments of inertia depend on mass distribution, any changes in vertical and horizontal position of legs and abdomen may potentially modulate this measure. It has previously been shown that orchid bees flying in turbulent air laterally extend their hind legs. This increases drag by approximately 30% but also moments of inertia around the animal's roll axis by up to 53%, which in turn should enhance flight stability (Combes and Dudley, 2009). Owing to the smaller hind leg mass in fruit flies of approximately 9.42 μg or 1.2 ± 0.3% body mass compared to orchid bees (5.9% body mass), the changes in moments of inertia are comparatively small: hind leg motion in *Drosophila* alters moments of inertia of not more than 6% (Fig. 8). Moreover, compared to a model fruit flies without hind leg tibia and tarsi, moments of inertia during yaw, pitch and roll steering may not increase more than 8% of the moments of inertia of the body trunk. The largest benefit of hind leg control in fruit flies is on roll stability, which is consistent with data obtained from the orchid bee. Consequently, leg extension in small insects such as the fruit fly appears to be of little significance for posture stability but, nevertheless, might slightly enhance posture stability of animals flying under turbulent environmental conditions that require elevated steering performance.

**Conclusions**

This study shows how freely flying fruit flies control their flight path by synergistic action of three independently working motor control systems, enhancing the degrees of freedom for heading and posture control. In general, turning moments produced by wing motion dominate both: moments produced by aerodynamic drag on body and hind legs and positional changes of the fly's centre of mass by movements of hind legs and abdomen. Their small contribution suggests that fruit flies broadly employ hind legs and abdomen to fine-tune moments for flight rather than to produce large moments required during flight saccades or optomotor responses. The latter highlights
the potential importance of leg and abdominal steering for aerial manoeuvring during straight flight. Nevertheless, while maximum body drag-induced yaw moments (0.19 nN m) corresponds to a unilateral wing stroke equivalent of only approximately 0.7 deg amplitude, maximum alteration in positional change of centre of body mass (2.6 nN m) converts into pronounced unilateral change in stroke amplitude of 8.8 deg (Hesselberg and Lehmann, 2007). Alternatively, motion control of body appendages might be part of the insect's trimming reflexes to trim out bilateral imbalances in forces and moments during flight. These imbalances may result from unilateral aerodynamic effective changes such wing damage, abnormal asymmetries of the flight apparatus, and an imbalance in muscle mechanical power output and control for wing motion (Bender and Dickinson, 2006; Hesselberg and Lehmann, 2009). In this regard, legs in insects are aerodynamic rudders, similar to those that correct for the counter torque from the propeller in airplanes.

Seen in a larger context, drag-based leg control in flying Drosophila appears similar to the function of middle and hind legs in apterygote hexapods such as wingless gliding ants for aerial manoeuvrability and gliding performance (Yanoviak et al., 2009; Yanoviak et al., 2010). From an evolutionary point of view, fruit flies might thus have inherited leg and abdominal motor control systems from their wingless ancestors. The small benefit of leg control in Drosophila on moments of inertia, however, runs counter to the idea that leg steering has primarily evolved as a mechanism to enhance posture stability. In this respect, the male orchid bee might be an exception because its hind leg tibia is greatly enlarged compared to other insect species in order to collect scents (Combes and Dudley, 2009).

MATERIALS AND METHODS

High-speed video recording inside a free-flight arena

The flies were scored in a free flight arena, allowing automated recordings of body posture, abdominal bending and hind leg motion using three-dimensional high speed video (Shishkin et al., 2012, Fig. 9). To stimulate 0.1 μg fluorescence dye markers on the fly (Fig. 9B and C), we flashed UV-light emitting diodes with 60 μs short voltage pulses. Position accuracy of the video-tracked markers was within ±30 μm and images were recorded inside a volume of 20 mm width × 20 mm length × 25 mm
height at 3500 Hz frame rate (Hedrick, 2008). We scored 81 flight sequences of 14 female, 3–5 day old wild-type *Drosophila melanogaster* (Canton S) with an average body mass of 1.26 ± 0.04 mg. Total flight time of all analysed sequences was 7.03 s, with individual sequences ranging from 15.7 ms to 355 ms, and mean ambient temperature was 23.6 °C.

**Positional reconstruction of leg segments**

We simplified the reconstruction of leg extension angles, performing pre-tests on leg movements in tethered flying flies (N = 7, Fig. 10). A conventional infra-red video camera recorded the animal from lateral (V, vertical angle) and the bottom (H, horizontal angle), while the fly changed wing and leg motion in response to a visual stimulus. We scored the angles between (i) femur and tibia, δ, (ii) tibia and tarsi, ε, (iii) femur and a connection line through the femur-tibia joint and the fifth tarsal segment, ζ, and (iv) femur and longitudinal body axis, κ. From these angles, we calculated mean angles and variances (N = 10 images of each fly and camera view) that yielded: 74.2 ± 36.7 deg (δᵥ), 125 ± 18.3 deg (δ₉ᵥ), 128 ± 25.9 deg (εᵥ), 161 ± 10.5 deg (ε₉ᵥ), 105 ± 27.5 deg (ζᵥ), 143 ± 11.9 deg (ζ₉ᵥ), 58.4 ± 2.4 deg (κᵥ), and 45.9 ± 4.8 deg (κ₉ᵥ).

These measurements and subsequent correlation analyses suggested: (i) the small standard deviations of angle κ indicate that coxa and femur move only little during steering, thus κ was considered to be a constant and the tibia-femur joint position determined from thoracic fluorescent markers; (ii) the high standard deviation of δ indicates that the animal predominately alters this angle during leg steering; (iii) angle δ significantly depends on angle ζ (Pearson test, vertical, p < 0.001, R = 0.98, N = 70; horizontal, p < 0.001, R = 0.66, N = 422); (iv) angle εᵥ linearly depends on δᵥ (Pearson test, p < 0.001, R = 0.82, N = 70); and (v) angle ε₉ᵥ is not linearly correlated with δ₉ᵥ and thus considered to be a constant (Pearson test, p = 0.22, R = 0.06, N = 422). From the leg extension angles ζ in free flight and linear regression analyses on leg angles in tethered animals, we determined remaining angles and leg positions using the equations,

$$δᵥ \text{ deg} = 1.39 \ ζᵥ \text{ deg} - 68.62 \text{ deg},$$

(1)
\[ \delta_H \text{ deg} = 0.87 \zeta_H \text{ deg} + 10.75 \text{ deg}, \quad (2) \]

and

\[ \varepsilon_V \text{ deg} = 0.77 \zeta_V \text{ deg} + 46.90 \text{ deg}. \quad (3) \]

**Estimation of aerodynamic drag on legs and body trunk**

Body appendages and thus the modelled cylinders experience drag by cross flow and lift by flow parallel to the longitudinal cylinder axis. In the latter case, however, the complex zigzag geometry of the leg segments with positive and negative inclination results in a small overall angle of attack (Fig. 2B). In addition, peak lift coefficient of cylinders is only 11-20% of the maximum drag coefficient at Reynolds numbers between 7 and 20 (Babu and Mahesh, 2008; Vakil and Green, 2009). Together, this results in at least 35-times less instantaneous lift than drag for the example in figure 2. Thus, we did not further consider lift-induced moments. We determined aerodynamic drag using a combined approach, in which we estimated the aerodynamic effective, local frontal area with respect to the oncoming flow, the local air flow vector from kinematic reconstruction, an experimentally validated, velocity- and thus Reynolds number-dependent drag coefficient, and equation 7. Drag was estimated separately for each leg and body segment, modelling each segment as a solid, rigid cylinder with appropriate mean length, width and total mass. For cylinders, White (White, 1974) suggested a Reynolds number-based, empirical approximation of drag coefficient, \( C_D \), written as:

\[ C_D = 1 + 10 \cdot \text{Re}^{-2/3}, \quad (4) \]

in which Reynolds number, \( \text{Re} \), is derived from the local velocity of the segment and a characteristic length of twice the cylinder radius. Compared to previous measurements of drag coefficients on cylinders at cross wind, equation 4 yields negligible differences at Reynolds numbers between 1 to 10 (Tritton, 1959). Mean Reynolds number of a single leg is approximately 1.9 (235 mm s\(^{-1}\) body velocity, cylinder radius 60\( \mu \)m, 15 \( \times \) 10\(^{-6} \) m\(^2\) s\(^{-1} \) kinematic viscosity). Besides body motion, local velocity also depends on induced velocity (\( u_{ind} \), downwash) generated by wing flapping, which was calculated by (Ellington, 1984e; Usherwood and Lehmann, 2008):
with $L$, body lift, $\rho$, the density of air, and $A$, the area covered by the beating wings (Fig. 11D). We approximated the latter measure using a mean wing beat amplitude of 162 degrees and wing length of 2.5 mm (Lehmann and Dickinson, 1998). Instantaneous body lift was calculated from translational movements of the fly and a previously derived vertical damping coefficient $C_{\text{vert}}$ of 54.8 mg s$^{-1}$, written as:

$$L(t) = m_b \cdot \ddot{u}_{\text{vert}}(t) + C_{\text{vert}} \cdot \dot{u}_{\text{vert}}(t) + m_b \cdot g,$$

with $m_b$, the body mass, $g$, the gravitational constant, and $t$, the time.

To experimentally validate Reynolds number-dependent drag, we determined drag on body appendages in a 1.05 m s$^{-1}$ laminar flow wind tunnel and using a laser balance (Lehmann and Dickinson, 1998). Reynolds number varied between approximately 2.8 (tarsi) and 8.3 (femur, Table 2). We removed hind legs from female flies, mounted them on a flat surface and dried them over night in a stretched position to avoid changes in leg posture owing to joint flexing. We mounted 7 legs at equal distance of 1.0 mm, orthogonal to a tungsten wire (127 µm diameter), positioned the wire with the legs normal to the air flow, and rotated it to measure the legs’ drag at various angles of attack (Fig. 11). Similar to this procedure, we estimated yaw angle dependent body drag on a fly trunk, removing wings and legs from a dead animal and gluing the trunk with the longitudinal body axis oriented normally to the wire. Drag components owing to the tungsten wire were subtracted from the measures. We subsequently fitted a sinusoidal curve to the data and estimated the drag coefficient, $C_D$, using fitted values and equation:

$$C_D = \frac{2D}{\rho u_{\text{leg}}^2 S},$$
in which $D$ is drag, $u_{leg}$ the velocity at the centre of area of the body segment and $S$ the frontal surface area of the segment facing the flow. At 90 deg angle of attack at which the flow is normal to hind legs and body trunk, drag coefficients were 2.96 and 1.41, respectively. For comparison, drag coefficients for hind leg and body trunk, modelled as a simple cylinder in equation 4 at comparable Reynolds number, are 3.14 and 1.44, respectively, which is only 2-6% higher than the measured coefficients (Fig. 11).

**Estimation of moments**

Moments around the fly’s yaw, pitch, and roll axes rely on at least four, independently acting mechanisms: moments owing to (i) lift (perpendicular) and drag (parallel to relative flow) produced by the flapping wings, (ii) drag on hind legs, thorax, head and abdomen, (iii) changes in moment arm of wing flapping-induced moments by positional alterations of the fly’s centre of mass, and (iv) active mass movements of hind legs and abdomen. In contrast to drag- and mass shift-induced moments, we derived wing-induced moments from (i) instantaneous measures of body motion, (ii) moments of inertia, $I$, with the body and hind leg segments approximated as cylinders (see equations 10–15) and (iii) previously derived damping coefficients of the wings for body rotation in freely flying fruit flies, $C_{rot}$. These coefficients are 176 ng m$^2$ s$^{-1}$ for yaw, 204 ng m$^2$ s$^{-1}$ for pitch, and 352 ng m$^2$ s$^{-1}$ for roll ($N = 170$ flies, Shishkin et al., 2012). Total instantaneous moment, $M_M$, around the centre of body mass thus equals:

$$M_M(t) = I\dot{\omega}(t) + C_{rot}\omega(t),$$

with $\omega$ the rotational, angular velocity of the animal (Hesselberg and Lehmann, 2007). Wing-induced moments, $M_W$, for posture and heading control were then calculated by subtraction of the remaining components, which may be written as:

$$M_W(t) = M_M(t) - M_D(t) - M_S(t) - M_I(t) - M_{DW}(t),$$

with $M_D$ body drag-, $M_S$ body mass shift-, $M_I$ inertia-, and $M_{DW}$ downwash-induced moments. Downwash-induced moments were only considered in the analysis shown in Fig. 7.
We calculated drag-induced moments, $M_D$, from the $x$, $y$, and $z$- components of the cross product between drag on body, abdomen and hind legs using equation 7 and the corresponding moment arm. The local flow vector was derived from the vector sum of body motion, active leg motion, and, in cases in which we considered downwash, from induced velocity and instantaneous body lift in equations 5 and 6, respectively. To derive abdomen-induced mass shift moments, $M_S$, we used a simplified approach: we defined the moment arm as the distance between the aerodynamic centre of force of each wing at 56% wing length and the fly’s centre of body mass (Ramamurti and Sandberg, 2007). Since this distance varies throughout the wing flapping cycle, we used a mean moment arm at mid half stroke, when the wing’s longitudinal axis was in the horizontal and normal to the fly’s longitudinal body axis (Fig. 2C). At mid half stroke and zero vertical body velocity, instantaneous vertical lift of each wing equals to approximately 6.18 μN ($m_b = 1.26$ mg, cf. equation 6), and instantaneous horizontal drag of each wing is approximately 2.25 μN. We calculated the latter value according to (i) the drag characteristics of a robotic fruit fly wing ($Re = 134$, Dickinson et al., 1999), (ii) mean wing velocity at the wing’s centre of force, (iii) mean wing area of one wing of 1.74 mm$^2$ of Drosophila, and (iv) employing equation 7.

**Estimation of moments of inertia**

We estimated the fly’s moments of inertia by modelling the body trunk including fore legs, middle legs and the hind leg coxae and femurs as a single object, composed of solid cylinders (Fig. 8A). By contrast, hind leg tibia and tarsi were modelled separately as moving cylinders with appropriate mass. Total mass of a hind leg was 9.42 ± 2.85 μg ($N = 4$ groups of 10 legs each) and mean mass for hind leg coxa, femur, tibia and tarsi was 2.02, 5.02, 1.72, and 0.66 μg, respectively (Table 2). The yaw, pitch, and roll moments of inertia of the cylinder were derived from the following equation:

$$I = I_a \cos^2(\phi_a) + I_b \cos^2(\phi_b) + I_c \cos^2(\phi_c) + m_{cyl} d^2,$$  \hspace{1cm} (10)

with $I_a$, $I_b$, and $I_c$ the cylinder’s principal moments of inertia, $\phi_a$, $\phi_b$, and $\phi_c$ the angles between the axis of rotation and the cylinder’s principal axes $a$, $b$, and $c$, respectively,
$m_{\text{cyl}}$ the cylinder mass, and $d$ the distance between the centre of mass and the axis of rotation (parallel axis theorem). We may write the principal moments of inertia for the principal axis $a$ thus as:

$$I_a = \frac{m_{\text{cyl}} \cdot r^2}{2},$$  \hspace{1cm} (11)$$

and for the axes $b$ and $c$ as:

$$I_b = I_c = \frac{m_{\text{cyl}} \cdot r^2}{4} + \frac{m_{\text{cyl}} \cdot l^2}{12},$$  \hspace{1cm} (12)$$

with $r$ the cylinder radius and $l$ the cylinder length. The yaw and roll axes of the body trunk cylinder are within the $ac$-plane and the pitch axis is the cylinder $b$-axis. This leads to the following set of equations for moments of inertia of the body trunk about the three axes, i.e. for yaw:

$$I_{\text{yaw}} = \left(1 + \sin^2(\chi)\right) \frac{m_{\text{cyl}} \cdot r^2}{4} + \cos^2(\chi) \frac{m_{\text{cyl}} \cdot l^2}{12},$$ \hspace{1cm} (13)$$

for pitch:

$$I_{\text{pitch}} = \frac{m_{\text{cyl}} \cdot r^2}{4} + \frac{m_{\text{cyl}} \cdot l^2}{12},$$ \hspace{1cm} (14)$$

and for roll:

$$I_{\text{roll}} = \left(1 + \cos^2(\chi)\right) \frac{m_{\text{cyl}} \cdot r^2}{4} + \sin^2(\chi) \frac{m_{\text{cyl}} \cdot l^2}{12},$$ \hspace{1cm} (15)$$

with $\chi$ the pitch angle. Eventually, to achieve total moments of inertia, we calculated the moments of inertia for hind leg tibia and tarsi using equation 10 and added these values to the moments of inertia of the body trunk.
Statistics
If not mentioned otherwise, all data are given as means ± standard deviations throughout the manuscript.
REFERENCES


Table 1. Mean and maximum turning moments in freely manoeuvring fruit flies.

Data are absolute values, ignoring sign and thus direction of moments. Mean performance ± standard deviation was calculated from 81 flight sequences and maximum performance ± standard deviation from means of the 1% largest values of each flight sequence. Value in parentheses is the mean of the 1% largest values of all sequences (N = 24,596 data samples). $M_M$, total moment derived from body motion; $M_D$, sum of moments induced by drag on body trunk and hind legs; $M_S$, moment induced by displacement of the fly’s centre of body mass; $M_I$, moment owing to inertia of hind legs and abdomen; $M_{D, Leg}$, moment induced by drag on hind legs; $M_{D, Abd}$, moment induced by drag on abdomen; $M_{D, Trans}$, drag-induced total moment owing to translational body motion; $M_{D, Rot}$, drag-induced total moment owing to rotational body motion; $M_{D, Act}$, drag-induced moment owing to active movements of abdomen and hind legs relative to fly thorax.

<table>
<thead>
<tr>
<th>Moment</th>
<th>Axis</th>
<th>Mean performance</th>
<th>Maximum performance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_M$ (nN m)</td>
<td>Yaw</td>
<td>1.65 ± 1.00</td>
<td>6.29 ± 3.18 (11.2)</td>
</tr>
<tr>
<td></td>
<td>Pitch</td>
<td>2.23 ± 0.81</td>
<td>7.68 ± 2.73 (10.2)</td>
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<tr>
<td></td>
<td>Roll</td>
<td>3.13 ± 3.41</td>
<td>9.63 ± 8.92 (26.8)</td>
</tr>
<tr>
<td></td>
<td>Yaw</td>
<td>0.03 ± 0.03</td>
<td>0.06 ± 0.05 (0.16)</td>
</tr>
<tr>
<td>$M_D$ (nN m)</td>
<td>Pitch</td>
<td>0.10 ± 0.08</td>
<td>0.16 ± 0.10 (0.36)</td>
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<tr>
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<td>Roll</td>
<td>0.04 ± 0.04</td>
<td>0.07 ± 0.06 (0.22)</td>
</tr>
<tr>
<td>$M_S$ (nN m)</td>
<td>Yaw</td>
<td>0.21 ± 0.39</td>
<td>0.46 ± 0.62 (2.55)</td>
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<tr>
<td></td>
<td>Roll</td>
<td>0.83 ± 0.72</td>
<td>1.52 ± 0.98 (3.81)</td>
</tr>
<tr>
<td></td>
<td>Yaw</td>
<td>0.16 ± 0.05</td>
<td>0.82 ± 0.41 (0.96)</td>
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<tr>
<td>$M_I$ (nN m)</td>
<td>Pitch</td>
<td>0.34 ± 0.10</td>
<td>1.52 ± 0.65 (1.84)</td>
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<td>Roll</td>
<td>0.15 ± 0.08</td>
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<tr>
<td>$M_{D, Leg}$ (pN m)</td>
<td>Yaw</td>
<td>35.2 ± 30.9</td>
<td>63.5 ± 52.1 (171)</td>
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<td></td>
<td>Roll</td>
<td>41.2 ± 39.2</td>
<td>74.0 ± 58.7 (220)</td>
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<tr>
<td>$M_{D, Abd}$ (pN m)</td>
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<td>5.72 ± 5.92</td>
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<tr>
<td></td>
<td>Pitch</td>
<td>13.6 ± 11.2</td>
<td>31.0 ± 19.5 (68.6)</td>
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<td></td>
<td>Roll</td>
<td>4.73 ± 5.56</td>
<td>13.8 ± 14.5 (40.8)</td>
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<tr>
<td>$M_{D, Trans}$ (pN m)</td>
<td>Yaw</td>
<td>19.6 ± 22.8</td>
<td>36.1 ± 40.5 (133)</td>
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<tr>
<td></td>
<td>Pitch</td>
<td>47.0 ± 54.8</td>
<td>78.9 ± 86.9 (324)</td>
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<td></td>
<td>Roll</td>
<td>16.9 ± 22.5</td>
<td>31.2 ± 38.2 (150)</td>
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<td>$M_{D, Rot}$ (pN m)</td>
<td>Yaw</td>
<td>0.39 ± 0.93</td>
<td>1.92 ± 3.58 (9.38)</td>
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<tr>
<td></td>
<td>Pitch</td>
<td>0.39 ± 0.73</td>
<td>1.89 ± 3.34 (8.30)</td>
</tr>
<tr>
<td></td>
<td>Roll</td>
<td>0.55 ± 1.68</td>
<td>2.72 ± 7.14 (16.3)</td>
</tr>
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Table 2. Morphological measures of *Drosophila* hind leg segments. Mass of each leg segment was estimated from its relative volume, determined from 21 blade elements and using total leg mass. The position of centre of mass is given as a fraction of segment length with 0% the proximal segment end. Mean ± standard deviation, N = 11 hind legs from 11 flies.

<table>
<thead>
<tr>
<th></th>
<th>Coxa</th>
<th>Femur-Trochanter</th>
<th>Tibia</th>
<th>Tarsus</th>
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<tbody>
<tr>
<td>Length (µm)</td>
<td>249 ± 30.4</td>
<td>635 ± 24.3</td>
<td>659 ± 23.3</td>
<td>742 ± 25.6</td>
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<tr>
<td>Mean width (µm)</td>
<td>120 ± 9.16</td>
<td>119 ± 5.18</td>
<td>68.3 ± 2.78</td>
<td>39.8 ± 1.88</td>
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<tr>
<td>Area (x10³ µm²)</td>
<td>29.9 ± 5.12</td>
<td>75.4 ± 4.76</td>
<td>45.0 ± 2.91</td>
<td>29.5 ± 1.83</td>
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<tr>
<td>Volume (x10⁶ µm³)</td>
<td>3.02 ± 0.75</td>
<td>7.21 ± 0.74</td>
<td>2.51 ± 0.25</td>
<td>1.01 ± 0.11</td>
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<tr>
<td>Centre of mass (%)</td>
<td>38.5 ± 2.24</td>
<td>44.5 ± 1.32</td>
<td>58.6 ± 1.02</td>
<td>34.8 ± 2.63</td>
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<tr>
<td>Centre of area (%)</td>
<td>43.9 ± 1.29</td>
<td>47.0 ± 0.79</td>
<td>54.8 ± 0.64</td>
<td>42.1 ± 1.42</td>
</tr>
</tbody>
</table>
Figures

**Fig. 1. Body posture, hind leg extension, and abdomen bending in freely manoeuvring fruit flies.** (A) Yaw, pitch and roll angles and corresponding axes. The three-dimensional, instantaneous position of the centre of body mass, $COM_B$, was reconstructed from the centre of abdominal mass, $COM_A$, and the centre of the combined mass of thorax, head, and legs, $COM_T$. $\psi_V$, deflection angle of the abdomen in the vertical; $\chi$, body pitch angle. (B) Top view ($x$-$y$ plane) on a flight path of a single fly cruising freely. Open dots indicate the centre of body mass every 10 ms, i.e. equal to every 35th recorded video frame, and attached lines show the orientation of the animal’s longitudinal body axis. (C) Yaw, pitch, and roll angles plotted for the flight sequence shown in B. Yaw angles are scored with respect to the external coordinate system. Angles around the roll axis to the right (clockwise) and upward pitching are positive. (D–F) Abdominal deflection and leg extension angles in the vertical ($\psi_V$, $\zeta_V$) and horizontal ($\psi_H$, $\zeta_H$) for sequence in B, respectively. Normalized angle histograms of all flight sequences are shown on the right in respective colours. Data were derived from 7.03 s total flight time. N = 81 flight sequences recorded in 14 flies.
Fig. 2. Instantaneous moments of a fruit fly flying freely inside a random dot flight arena. (A) Side view (y-z plane) of a flight path with superimposed body positions (open dot) plotted every 11.4 ms during the 142 ms sequence. Time trace shows the ratio between the sum of body appendage-induced (numerator) and wing flapping-induced moments (denominator). Data are clipped at ±1. (B) Draft illustrating moments induced by aerodynamic forces acting on the fly. (C) Draft illustrating moments owing to body mass shift. (D) Total moment around the fly's centre of mass (COM_B) for sequence shown in A. (E) Yaw, (F) pitch, and (G) roll moments around COM_B. Positive values indicate clockwise moments around yaw, pitch and roll axes (cf. Fig. 1A). Body drag-induced moment (M_D, right axis) results from aerodynamic drag on abdomen and hind legs, while inertia-induced moment (M_I, left axis) is estimated from relative movements of abdomen and hind legs. Mass shift-
induced moment ($M_S$, left axis) is the product of stroke cycle-averaged aerodynamic force of each wing and the moment arm between the wing's centre of force at mid down stroke and $\text{COM}_B$. (H) Fractions of drag-induced moment owing to body translation, $M_{D,\text{Trans}}$, (I) body rotation, $M_{D,\text{Rot}}$, and (J) self-induced moments owing to active movement of abdomen and hind legs ("paddling") relative to thorax, $M_{D,\text{Act}}$. (K) Moment induced by the wings' mean downwash (induced flow), $M_{D,W}$. $M_{D,W}$ is not considered for total $M_D$ in E-G. See text and legend of table 1 for more information.
Fig. 3. Difference of instantaneous drag-induced moments $M_D$ minus $M^*_D$ around $COM_B$. Moments ($M^*_D$) for yaw (black), pitch (red), and roll (blue) were calculated assuming static, non-moveable hind legs and abdomen, for the example shown in figure 2. The difference highlights the contribution of active leg and abdomen movements during manoeuvring flight. See text for more data.
Fig. 4. Frequency of moment ratios during yaw (left column) and roll (right column) steering in fruit flies. (A,B) Ratio between moments produced by body drag ($M_D$), mass shift ($M_S$), inertia ($M_I$), and active wing flapping ($M_W$). (C,D) Moment ratio of the 20 longest flight sequences (blue) with means in red (N = 81 sequences). Unity (dotted) indicates similar contribution of active (wing flapping-induced) and passive (abdomen- and leg-induced) moments to total response. Gray area highlights the relative time at which rotational steering is dominated by leg and abdominal control. (E,F) Mean moment ratio between drag- (red), mass shift- (grey), inertia- (blue), and wing flapping-induced moments, respectively (N = 81 sequences).
Fig. 5. Statistical analysis of coherence between the various components underlying yaw moment control. (A–C) Coherence of moments of the five longest recorded flight sequences (fly 1–5). Instantaneous coherence was scored as the product of moment sign between wing flapping- and body drag-induced moment in A, wing flapping- and mass shift-induced moments in B, and wing flapping- and inertia-induced moments in C. Time-invariant relative frequency of coherence between the two instantaneous moments of all recorded data is shown on the right, respectively, with +/- indicating equal (opposing) sign of moment. (D–F) Histogram of significant correlation coefficients (Pearson test, N = 74 in D, N = 64 in E, N = 68 flight sequences in F) obtained from linear regression analysis between moments shown by the insets in A–C, respectively. A negative correlation coefficient suggests opposing direction of moments. Means ± standard deviation.
Fig. 6. Statistical analysis of coherence between the various components underlying yaw moment. (A–F) Coherence was scored as the product of moment sign between drag- and mass shift-induced moment in A and D, drag- and inertia-induced moments in B and E, and mass shift- and inertia-induced moments in C and F. See legend of Fig. 5 for a more detailed explanation.
Fig. 7. Changes in moments caused by wing flapping-induced flow (downwash).

(A) Various time traces for drag-induced yaw moment ($M_D$) of the flight sequence in Fig. 2A with increasing consideration of downwash-induced moment $M_{DW}$ (colour-coded; 0%, red; 100%, blue, 10% step width). (B-D) Moment means (red) ± standard deviation (red area) and the 1% largest moments of all flight sequences (black, N = 24,596 samples of 81 flight sequences) plotted as a function of $M_{DW}$. Mean yaw is shown in B, mean pitch in C, and mean roll moment in D (N = 81 sequences). (E) Ratio of drag- and wing flapping-induced yaw moments. For colour coding see A. (F) Significance of downwash-induced yaw moments on correlation coefficients calculated in Figs 5 and 6. Coefficients are shown for drag- ($M_D$), mass shift- ($M_S$), inertia- ($M_I$), and wing flapping-induced moments ($M_W$). Asterisk indicates a significant difference from zero (one sample t-test, $p < 0.05$). Mean standard deviations are ±0.4 (red), ±0.6 (blue), and ±0.4 (green, N = 11).
Fig. 8. Alteration in moments of inertia owing to hind leg movements during flight. (A) Moment of inertia of yaw, pitch and roll was determined from a solid model cylinder with appropriate size and mass (cf. Materials and Methods section), rotating around the three body axes (cf. Fig. 1A). (B) Moments of inertia calculated for the model cylinder are plotted as a function of the cylinder’s pitching angle, with zero the horizontal. (C–E) Relative increase in moments of inertia compared to B owing to additional mass motion of tibia and tarsi of two hind legs. Binned moments of inertia within 1.0 deg pitch angle (black) are plotted for yaw in C, pitch in D and roll in E. Gray area indicates the minimum-maximum range within an one-degree-bin and solid lines show a theoretical prediction of maximum increase based on selected hind leg extension angles. See text for more detailed information.
Fig. 9. Video reconstruction of body markers in freely flying fruit flies. (A) Free flight arena (not to scale). HS, high speed camera; IR, infra-red light camera, L; infra-red laser sheet; LED, ultra-violet light emitting diodes; P, starting platform. (B) Fly with fluorescent markers (M1–M6). Note that the image shows an animal with marked wings instead of marked hind legs. (C) Time series of video images recorded by high speed camera HS2. Images show fluorescent markers with tagged positions of the body (M1–5), abdomen (M6) and hind leg tarsi (L1,L2). The white blobs in the lower part of the images result from fluorescent markers on the starting platform. The time interval of 5.7 ms corresponds to 20 recorded frames of the video sequence.
Fig. 10. Abdomen bending and hind leg extension angle during manoeuvring flight. (A,B) Side view of a tethered fruit fly responding to the motion of a visual stimulus. Fruit flies mainly steer by changes in wing motion, abdominal movement, and by moving tibia and tarsi of the hind legs (red). (C,D) Horizontal and vertical leg extension angles, $\zeta_H$ and $\zeta_V$, were reconstructed from the three-dimensional position of the distal tarsal segment and the angular position of the femur, respectively. Abdominal deflection angles, $\psi_H$ and $\psi_V$, were derived from the animal longitudinal axis, the abdomen’s centre of mass, $COM_A$, and the abdominal point of rotation, $P_{TA}$ (cf. Fig. 1A). Mass of abdomen and hind legs, $COM_{L1-4}$, including the combined mass of head and thorax were estimated from weight measurements and using an elementary blade approach. $P_N$, position of the neck connective in the sagittal plane.
Fig. 11. Experimental evaluation of drag coefficients and wake velocity distribution in *Drosophila*. (A, B) The coefficients were estimated from drag measurements of isolated legs, and truncated corpses of fruit flies (without legs and wings) mounted in a low Reynolds number, laminar wind tunnel. Drag \(D\) of a single, stretched out hind leg in A and body trunk in B plotted as the function of angle of attack, \(\alpha\), with respect to the oncoming flow. Blue, sinusoidal fit to data; left, \(D = -0.0043 + 0.292 |\sin(\alpha)|\); right, \(D = 0.709 + 1.585 \sin(\alpha)\). (C) Calculated drag of a single leg during free flight with mean \(\zeta_V = 105\) degrees (\(N = 81\) flight sequences, Fig. 10), and depending on \(\zeta_H\) and the horizontal component of \(u_{leg}\). See figure 2 for leg configuration and Material and Methods section for angles. Grey area indicates the leg's active steering range (see figure 1E and F). Maximum relative change in drag within the grey area is 9.5% for each \(u_{leg}\). (D) Wake velocities measured in the parasagittal plane of a tethered flying fly. The snapshot shows wake and fly from lateral and was recorded by digital particle image velocimetry as described in a previous study (Lehmann, 2012). Note that velocity vectors close to the insect body are reconstructed from surrounding vectors because of laser light reflections at the fly's cuticle. Tethering (pitch) angle was approximately zero and induced flow is thus
directed sideways. For comparison, vertical, lift-supporting, mean induced velocity based on equation 5 was $0.64 \pm 0.13 \text{ m s}^{-1}$ and the 1% maximum in each sequence $0.69 \pm 0.12 \text{ m s}^{-1}$ ($N = 81$ flight sequences). (E) Induced velocity for the flight sequence shown in figure 2. Raw data (black) indicate stroke cycle synchronous alteration in velocity (arrows). Smoothed data are plotted in red.