



Saccadic body turns in walking *Drosophila*

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Drosophila melanogaster structures its optic flow during flight by interspersing translational movements with abrupt body rotations. Whether these “body saccades” are accompanied by steering movements of the head is a matter of debate. By tracking single flies moving freely in an arena, we now discovered that walking *Drosophila* also perform saccades. Movement analysis revealed that the flies separate rotational from translational movements by quickly turning their bodies by 15 degrees within a tenth of a second. Although walking flies moved their heads by up to 20 degrees about their bodies, their heads moved with the bodies during saccadic turns. This saccadic strategy contrasts with the head saccades reported for e.g., blowflies and honeybees, presumably reflecting optical constraints: modeling revealed that head saccades as described for these latter insects would hardly affect the retinal input in *Drosophila* because of the lower acuity of its compound eye. The absence of head saccades in *Drosophila* was associated with the absence of haltere oscillations, which seem to guide head movements in other flies. In addition to adding new twists to *Drosophila* walking behavior, our analysis shows that *Drosophila* does not turn its head relative to its body when turning during walking.

Keywords: *Drosophila*, saccades, optic flow, visual acuity, halteres, walking, head body coordination

INTRODUCTION

As most insects lack stereoscopic vision (Land, 1999) to gauge the distance of surrounding objects, visual cues created by self-motion must be exploited. Locusts and mantids, for example, perform peering movements with their heads to deduce the distance of objects from the resulting motion parallax (Kral and Poteser, 1997). Motion parallax is also exploited by wasps that perform curved learning flights to remember the sites of their nests (Zeil, 1993, 1996). In more general terms, any movement of the animal's head will create an image shift on the retina—a phenomenon known as optic flow (Gibson et al., 1955). During translations, close objects will travel faster across the retina than distant ones, providing distance information, whereas no such information can be deduced during pure rotations when all objects travel across the retina with equal speeds (Koenderink and Doorn, 1987).

To facilitate distance estimation, insects thus should (i) separate translational movements from rotations and (ii) turn quickly to reduce the rotation time. Both strategies have been reported for flying *Drosophila* (Heisenberg and Wolf, 1979; Tammero and Dickinson, 2002) as well as other insects (Land, 1973; Collett and Land, 1975; Buelthoff et al., 1980; Zeil, 1986; Geurten et al., 2010), which all seem to structure their locomotion into prolonged phases of predominantly translational movement that are interspersed by fast saccadic turns. The active movement of the head during these saccades was analyzed with varying results (Land, 1973; Geiger and Poggio, 1977), but could be clarified by high-speed observations in freely flying insects (Schilstra and van Hateren, 1998): The head rotates relatively to the body, reducing the saccade duration even further. The role of head body coordination in walking insects is gaining new momentum (Ribak

et al., 2009; Kress and Egelhaaf, 2012, 2014a) and questions the information content of the optic flow obtained during walking (Kress and Egelhaaf, 2014b). Nonetheless optic flow has been shown to allow walking *Drosophila* to estimate distances of up to 80 times the length of its body (Schuster et al., 2002). We now tested whether walking *Drosophila* temporally separate rotations from translations and found that this separation is present and that the walking flies perform body saccades.

MATERIALS AND METHODS

WALKING TRAJECTORIES

56 male and 57 female adult Canton S wild-type flies were released one by one into circular arenas (43 mm diameter, 3.5 mm height). The arenas were produced using an Ultimaker 3D printer (Ultimaker LTD, Geldermalsen, Netherlands). The lower 1.5 mm of each arena was filled with 1% agarose containing 1% glucose, leaving the upper 2 mm for the flies to walk around. Each arena was illuminated by three Honeycomb LED lamps (IS, Imaging Solutions GmbH, Eningen, Germany), and the flies were filmed from above with a MotionTraveller 500 camera (IS). Movies were recorded using TroublePix software (NorPix Inc., Montreal, Canada) and trajectories were subsequently traced with ivTools (Jens P. Lindemann and Elke Braun, <https://toolkit.cit-ec.uni-bielefeld.de/components/tools/ivtools>). Only sequences during which the flies did not follow the wall but walked freely through the arena were included in the analysis. The total recording time was about 16 min, yielding half a million frames.

PROTOTYPICAL MOVEMENT PATTERNS

Prototypical movement patterns (PMs) were deduced as described by Braun et al. (2010): Distances between subsequent

fly positions were determined as the squared Euclidian distance, and the respective thrust, slip, and yaw velocities were deduced and z-scored individually. To identify the most common velocity combinations, we used two different clustering algorithms, agglomerative hierarchical clustering, and k-means clustering (MacQueen, 1967; Milligan and Cooper, 1987; Murtagh and Contreras, 2012): agglomerative hierarchical clustering (Ward's criterion) was used to narrow down the number of possible PMs. Because hierarchical clustering is only possible for small data sets, the data was chopped into 200 chunks in a round-robin fashion. Less than 20 possible PMs were identified, which were then tested for the whole data set by k-means clustering. We tested all PMs between number 2 and 20 and every fifth class between 25 and 50. PMs that describe the data set best were then narrowed down using the quality and the stability of the clustering as operational criteria: quality was calculated as the distance between the PMs divided by their individual density. Stability was assessed by omitting 10, 25, and 50% of the data in a round-robin fashion (step size equaling 2% of the data) to test whether the clustering can be reproduced. For more details on clustering movement trajectories see Braun et al. (2010) and Hofmann et al. (2014).

SACCADES

Saccades were defined using a yaw velocity threshold of 200 $\text{deg}^*\text{s}^{-1}$ as the threshold criterion. The peak velocity of each saccade was determined using the “findpeaks” routine of Matlab (R2012b, The Mathworks Inc., Natick, MA, USA). Using these peaks as trigger points, saccades were averaged over a 100 ms time window.

HEAD AND THORAX MOVEMENTS

To simultaneously assess head and body trajectories, flies were filmed while walking through a labyrinth. This labyrinth consisted of two small rectangular boxes (24 x 24 x 3 mm) connected by a 1 cm long 2 x 2 mm tunnel, with a right angle at half its length. Flies were filmed as described above, whereby we used a custom-made planar macroscopic objective to optically resolve thorax and head. Custom-made 3D templates of the fly thorax and head were fitted frame-by-frame to the respective body parts using ivTools (<http://www.ivtools.org/ivtools/index.html>) to deduce their orientation.

RETINAL IMAGES AND IMAGE SHIFTS

Ommatidial maps were adapted from Petrowitz et al. (2000) (blowfly *Calliphora vicina*), Stürzl et al. (2010) and Seidl (1986) (honey bee *Apis mellifera*), and Buchner (1971) and Dickson et al. (2006) (*Drosophila*). A complete data set for the *Drosophila* eye can be found at http://code.astraw.com/Drosophila_eye_map/ (courtesy of Dr. A. Straw). The available map for *Calliphora* is incomplete in that it covers only the frontal part of the eye. Maps were always made for one eye and then mirrored to simulate the opposite eye. Photoreceptor acceptance angles of *Drosophila* were taken from Gonzalez-Bellido et al. (2011), and the corresponding values for *Apis* and *Calliphora* from Laughlin and Horridge (1971) and Smakman et al. (1984), respectively. Acceptance angle data was fitted with a Gaussian. In case of *A. mellifera*, two Gaussians were used for vertical and horizontal acceptance angles (Laughlin

and Horridge, 1971). Retinal inputs for panoramic images were calculated by projecting the Gaussians onto the image along the ommatidial axes. To ensure that the entire input of each ommatidium is covered, we extended the Gaussians to five times the standard deviation σ . We then calculated a weighted mean of the panoramic section defined by the Gaussian with the Gaussian filter strength as weights. To rebuild the optical images, we stitched together the Voronoi cells (Lejeune Dirichlet, 1850; Voronoi, 1908) around the ommatidial axes of the eye. To deduce the retinal image shifts that ensue from yaw rotations, we used fifteen full panoramic images of nature scenes (licensed under creative commons by Janne Voutilainen and Aldo Hoeben). Images are shown in Supplementary Figure 1. Ten images show forest scenes and five show close ups of flowers or trees. We also tested ten random images with 3600 x 1800 pixels each and a $1/f^2$ spatial distribution (Field, 1987; van der Schaaf and van Hateren, 1996; Saremi and Sejnowski, 2013) (see Supplementary Figure 2). We then rotated the images by 360° in steps of 0.1° and calculated the resulting retinal image difference (Zeil, 2012) for each ommatidium. The resulting retinal image differences were averaged across ommatidia. The median image difference over different images was calculated for each rotation and each of the three species. For comparison, we employed the same methods to analyze the raw images, averaging over all pixels instead of ommatidia. The median image difference of the raw image between 170 to 180° and -170 to -180° was used to normalize all image difference functions for a given image.

HALTERE MOVEMENTS

To test for haltere oscillations, we replaced one side of the labyrinth with Perspex glass, allowing us to observe the flies from the side. 10 animals, including 5 males and 5 females were filmed while they walked through the labyrinth. Subsequently, the same animals were tethered on their thorax and filmed during fictive walking and flight. To elicit walking, we allowed the flies to grab a small Styrofoam ball, whose removal initiated flight. By touching the legs of the flying flies with the ball, landing behavior was initiated.

RESULTS

WALKING FLIES SEPARATE TRANSLATIONS AND ROTATIONS

To test whether walking flies might separate translational and rotational movements, we recorded the trajectories of 103 Canton-S wild-type flies walking freely in an arena at 500 frames per second and screened their body trajectories for reoccurring prototypical movement patterns (PMs; Braun et al., 2010). To identify PMs, the respective yaw, slip, and thrust velocities were deduced from the trajectory data, and the most common velocity combinations were extracted using clustering algorithms (see Materials and Methods). Five PMs were identified (Figure 1A), representing translations (PMs 1,2 in Figure 1A), rotations (PMs 3,4), and resting (PM5). Resting (PM5) amounted to 63% of the sampling time, translations (PMs 1,2) for 29%, and only 9% for rotations (PMs 3,4). Consistent with observations on walking *Calliphora*, (Kress and Egelhaaf, 2012, 2014a) walking *Drosophila* showed some residual rotations during translatory phases (Figure 1B), yet the respective rotational velocities

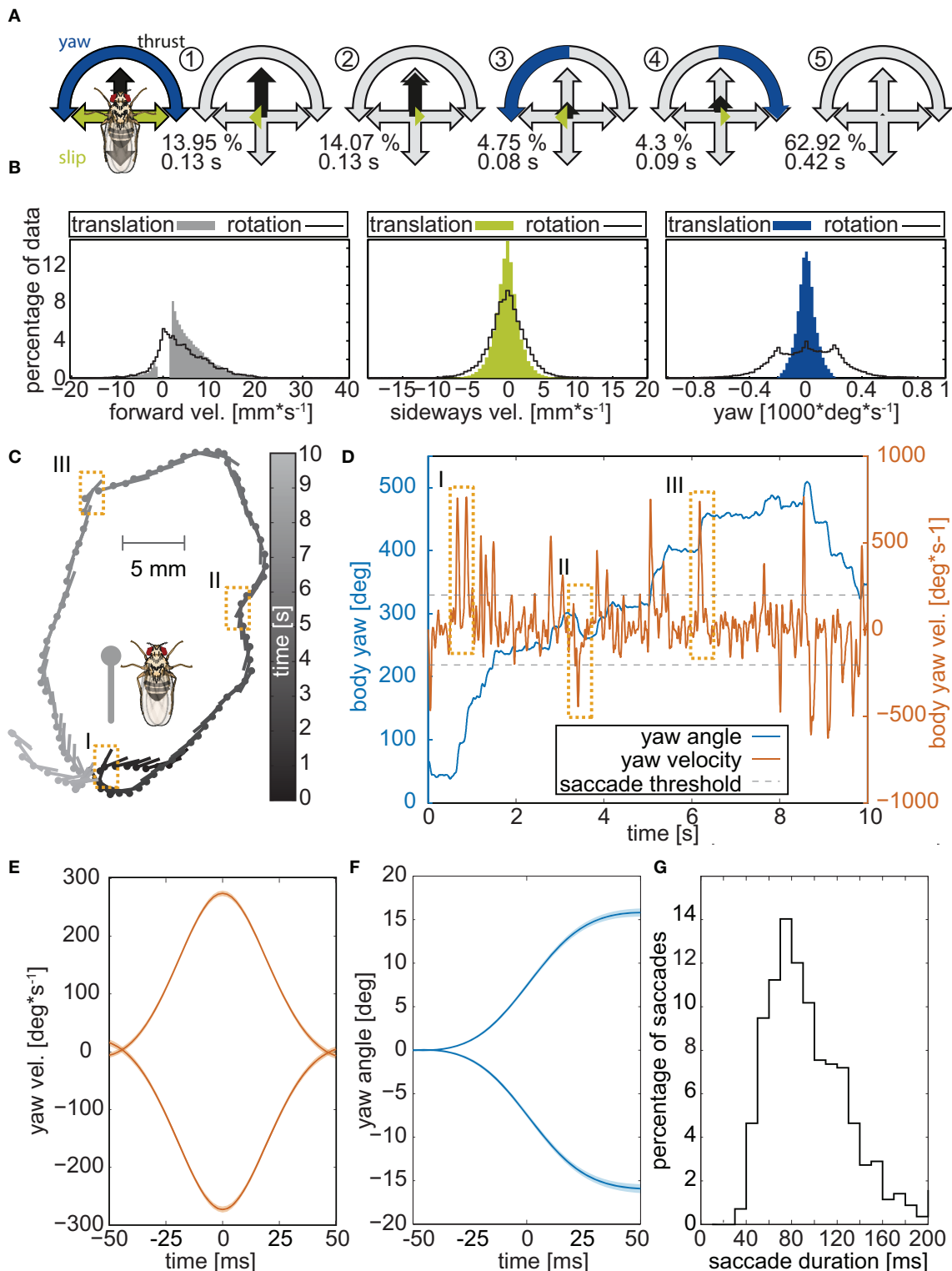


FIGURE 1 | Body trajectories of walking *Drosophila*. (A) Prototypical movement patterns (PMs) of adult *Drosophila* walking freely in a circular arena (56 male 57 female flies, recorded @ 500 fps). Colored arrows highlight the velocity combination that characterizes each PM, and gray arrows indicate the maximum speeds. The color code is given by the legend to the left. For each PM, its respective abundance in the data set is presented in percent,

along with its average duration. (B) Distributions of the three velocities (thrust, slip, yaw) during translational movements and saccadic turns. Yaw velocities cluster around zero during translations but not during rotations. (C) Example of a single trajectory. Circles mark the center of mass of the animal and lines depict the long axis of its body. To facilitate following

(Continued)

FIGURE 1 | Continued

the trajectory, gray scales indicate time. Dashed boxes highlight three saccades. **(D)** Yaw angles and velocities of the trajectory in **(B)** plotted against time. Orange rectangles mark the three saccades that are highlighted in panel **B**. **(E)** Mean velocity of 1885 individual saccades, identified by using a yaw velocity of $200 \text{ deg}^* \text{ s}^{-1}$ as the threshold

criterion and arranged so that their peak velocity is at 0 ms. Leftward and rightward turns were separated prior to the analysis, yielding velocity profiles for each of them that are virtually mirror-symmetric.

(F) Corresponding yaw angles documenting that, within the 100 ms time window, the flies turned by on average 15° . **(G)** Distribution of saccade durations in milliseconds.

were much lower than during phases of turning. Hence, during *Drosophila* walking, (i) translational movements are temporally separated from fast rotations and (ii) translations temporally dominate over rotations.

WALKING DROSOPHILA PERFORM SACCADES

A temporal segregation of translational and rotational movements, as revealed by PM analysis, was also seen within single walking trajectories (**Figure 1C**). Changes in the heading of the flies were associated with rapidly changing yaw angles and sharp yaw velocity peaks (**Figure 1D**). Selecting heading changes with absolute yaw velocities exceeding 200° per second and using the respective velocity maxima as trigger points, we averaged the yaw velocities for 1140 heading changes of the 103 experimental flies (**Figure 1E**). Thereby we discarded 3348 slow rotations, whose velocities were below threshold. Average yaw velocities displayed the bell-shaped form that characterizes saccadic eye movements in mammals (Land, 1992; Stanford et al., 2010) and saccadic body turns in insects (Blaj and van Hateren, 2004; Ribak et al., 2009; Kress and Egelhaaf, 2014a). During a saccadic turn, the flies changed their heading on average by about 15° (**Figure 1F**) within 40 to 120 ms (median 90 ms **Figure 1G**). These angular heading changes are smaller than those reported for tethered flying *Drosophila* (ca. 90° in 100 ms, Tammero and Dickinson, 2002) or even freely flying *Drosophila* which are nearly twice as fast as tethered animals (ca. 90° in 45 ms, Fry et al., 2003), but close to those of walking blowflies (ca. 15° within 50 ms, Blaj and van Hateren, 2004), which also perform saccades while they walk (Blaj and van Hateren, 2004; Kress and Egelhaaf, 2014a,b).

SACCADIC BODY TURNS ARE NOT ASSOCIATED WITH ADDITIONAL HEAD MOVEMENTS

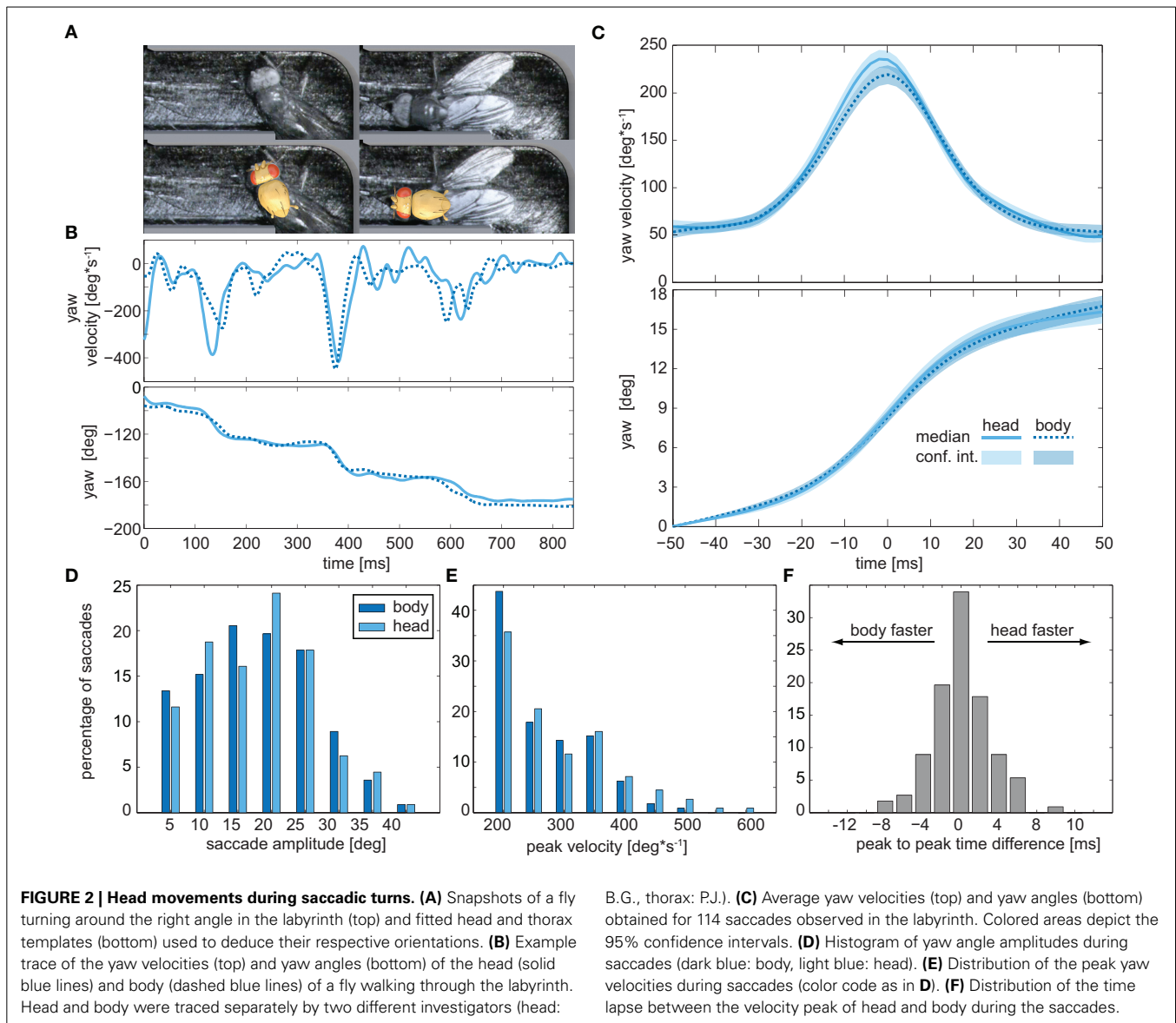
Insects cannot directly move their eyes; in order to change their gaze direction, they have to turn the head about the body or, alternatively, the body together with the head. Because of the small size of *Drosophila*, resolving the relative orientations of the head and the rest of the body requires imaging with a high spatial resolution, which is only possible within a confined space. We spatially confined the flies by letting them pass through an L-shaped labyrinth, which forced them to change their course by an angle of 90° (**Figure 2B**). Seven flies were filmed while each passed the labyrinth three times from either side. Respective head and thorax orientations were subsequently deduced by fitting the head and thorax with 3D templates (**Figure 2A** lower frame). Manual analysis of a total of 16,000 frames revealed that when turning in the labyrinth, the flies also performed saccades (**Figures 2B–D**). Three to six subsequent saccades were observed while the flies passed the 90° corner (**Figure 2B**). Body and head rotations performed in the labyrinth are similar to those seen in the circular arena (compare **Figure 1D** and **Figure 2C**). Moreover, averaged

yaw velocities and yaw angles were virtually identical for thorax and head (**Figures 2C**), as were the respective distributions of the saccade amplitudes and angular velocities (**Figures 2D,E**). The temporal disparity between the peak velocities of head and body (**Figure 2F**) was about 2 ms for approximately 75% of the saccades. Hence, during the saccadic turns, the head does not move faster than the thorax, identifying the saccadic turns of walking *Drosophila* as pure body saccades in which the head moves together with the body. This saccadic behavior differs from the saccades of e.g., flying honeybees and walking blowflies, which rotate the head faster than the body (see **Figure 3A**), reducing the effective duration of the saccades (Blaj and van Hateren, 2004; Boeddeker, 2010): the different rotation speeds of head and body were seen when we extracted their respective yaw angles for blowflies from (Blaj and van Hateren, 2004), where the relative angles between head and body—the φ -angles—reach up to 4° (**Figure 3B**). In *Drosophila*, by contrast, the yaw-angles of the head superimposed with those of the body, yielding φ -angles of maximally 1° (**Figure 3B**).

Judging from the φ -angle distribution obtained for the whole labyrinth passage (**Figure 3C**), *Drosophila* is able to move its head about its body by up to 20° : the φ -angle distribution closely resembled those reported for flying honeybees (Boeddeker, 2010). According to Blaj (2004), the respective distribution for walking *Calliphora* is shifted toward smaller angles (maximum φ -angles around 10°), though recent studies (Kress and Egelhaaf, 2014a) suggest that larger φ -angles occur in this species as well. For *Drosophila*, we cross-correlated the yaw velocities of the head and body during the whole trajectory and found that it peaks at zero phase-lag, whereas the head leads the body by ca. 8 ms in flying honeybees (Boeddeker, 2010) (**Figure 3D**). Hence, unlike bees, walking *Drosophila* does not move its head relative to the body during saccadic body turns.

HEAD MOVEMENTS COULD SPEED UP SACCADES BUT WOULD HARDLY CHANGE THE RETINAL IMAGE

Blowflies and honeybees surpass *Drosophila* in terms of visual acuity: the acceptance angle of *Drosophila* photoreceptors is about 10-fold larger (Laughlin and Horridge, 1971; Smakman et al., 1984; Gonzalez-Bellido et al., 2011), and the bee eye also comprises about 8 times more ommatidia than that of *Drosophila* (Buchner, 1971; Seidl, 1986; Dickson et al., 2008; Stürzl et al., 2010). Using available information about species-specific ommatidium numbers, positions, and orientations (Buchner, 1971; Seidl, 1986; Petrowitz et al., 2000; Dickson et al., 2008; Stürzl et al., 2010), we calculated how different panoramas are mapped onto the retinae of these insects. We modeled the field of view of each ommatidium by fitting Gaussians to published photoreceptor acceptance angles. As expected, Mercator plots of the predicted retinal inputs were more blurred for *Drosophila*



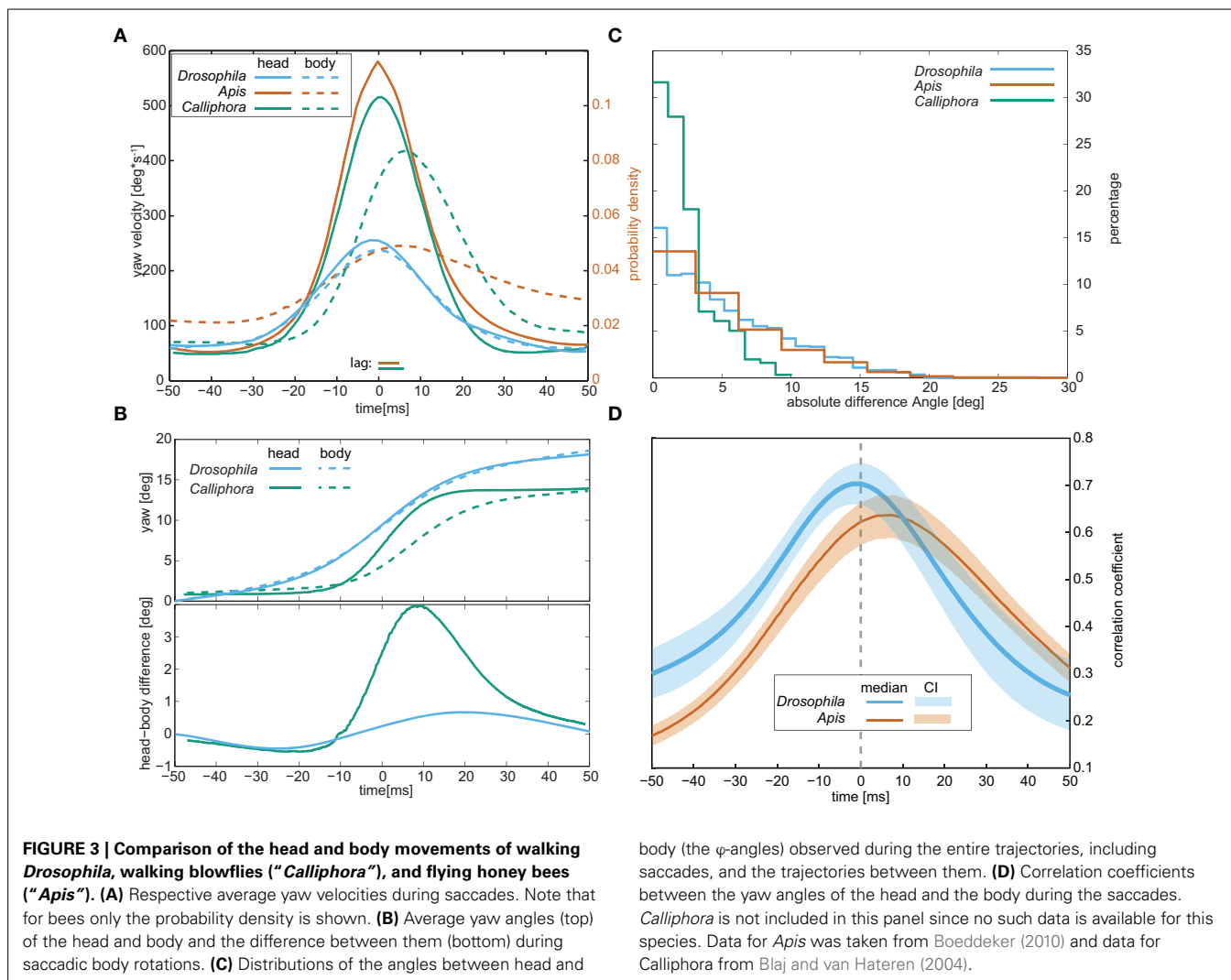
than for blowflies and bees (Figure 4A). Using sinusoidal gratings with different angular frequencies as panoramas, we next determined how the input of each ommatidium changes when the panorama shifts vertically by half a wavelength (Figure 4B). This revealed that blowflies and bees should be able to optically resolve objects with a horizontal angular extension of 1° and *Drosophila* of 7° , consistent with experimental observations (Nordström and O'Carroll, 2006; Fox and Frye, 2014; Fox et al., 2014).

Using panoramic photographs of natural scenes (images courtesy of Janne Voutilainen and Aldo Hoeben) we determined the rotational image difference (Zeil, 2012) to assess how the contrast will change for each ommatidium when the head rotates (Figures 4C,D). For a head rotation of 4° , as observed in blowflies, we obtained relative contrast changes of the retinal image of ca. 48% for blowflies and 33.3% for honeybees. For *Drosophila*, we obtained a contrast change of only 14% for the same rotation (Figure 4D). To achieve a contrast change

of 35%, *Drosophila* would have to turn its head by 15 instead of 4° . We also tested 10 panoramas with a $1/f^2$ frequency distribution (Field, 1987; van der Schaaf and van Hateren, 1996; Saremi and Sejnowski, 2013), which yielded quantitatively equivalent results (see Supplementary Figure 2). Hence, by turning its whole body, *Drosophila* generates the same contrast change that blowflies reach by solely rotating their head. In principle, active head rotations during saccadic body turns of *Drosophila* could reduce the rotation time, as is the case in blowfly and also honeybees (Blaj and van Hateren, 2004; Boeddeker, 2010). Due to the low spatial acuity of the *Drosophila* eye, however, such additional head rotations would result in minor contrast changes that the eye might not be able to detect.

ABSENCE OF HEAD MOVEMENTS ASSOCIATES WITH THE ABSENCE OF HALTERE OSCILLATIONS

Head rotations in flying and walking blowflies are associated with active haltere vibrations (Nalbach and Hengstenberg, 1994; Haag

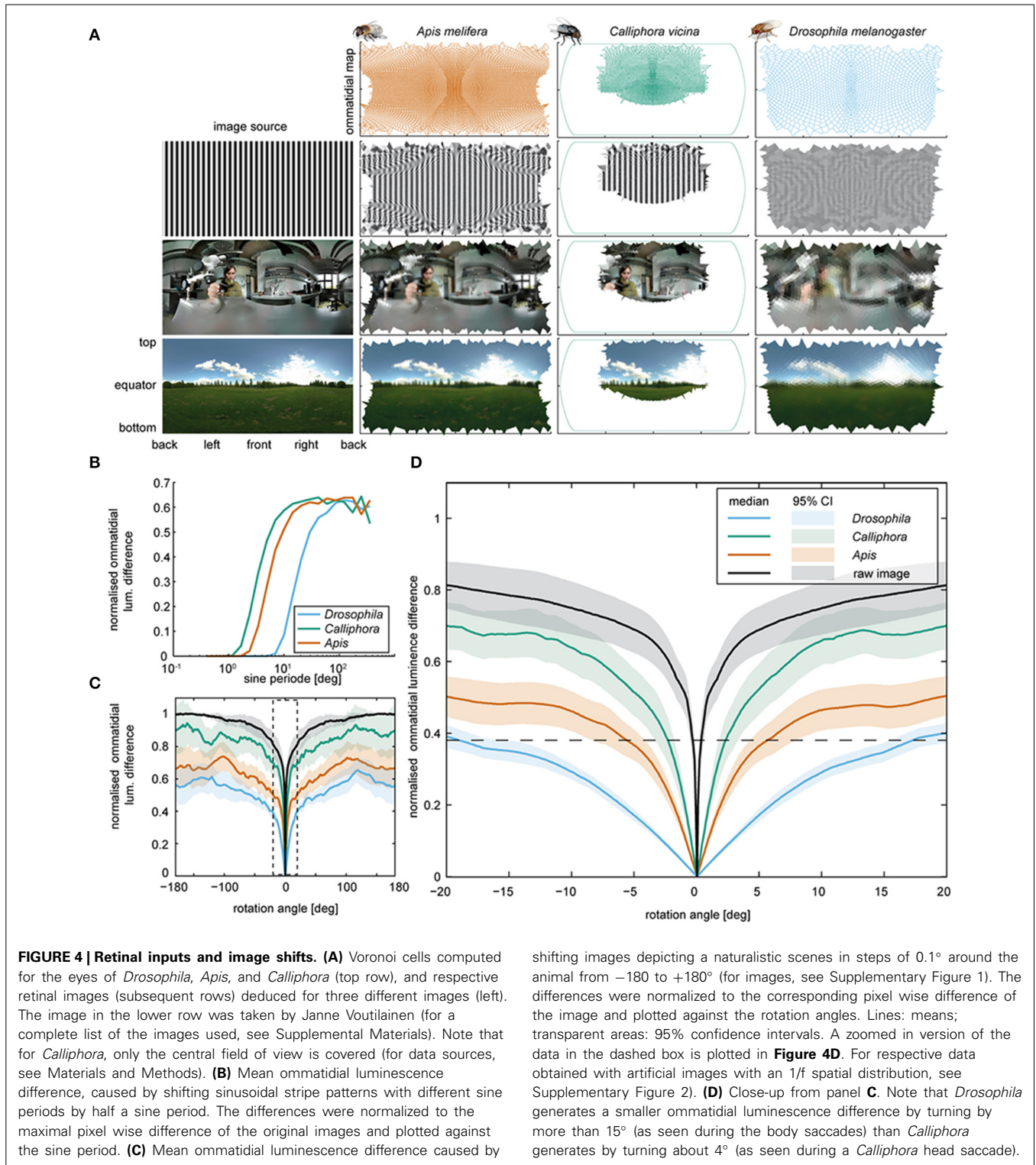


et al., 2010), which continuously oscillate while the flies walk (Sandeman and Markl, 1980). We tested for such haltere oscillations in walking *Drosophila* and found that there are none. Haltere oscillations were observed only upon take-off and during flight, yet they immediately ceased upon landing (see Figure 5). Unlike walking blowflies, *Drosophila* neither performs head saccades nor does it oscillate its halteres while it walks.

DISCUSSION

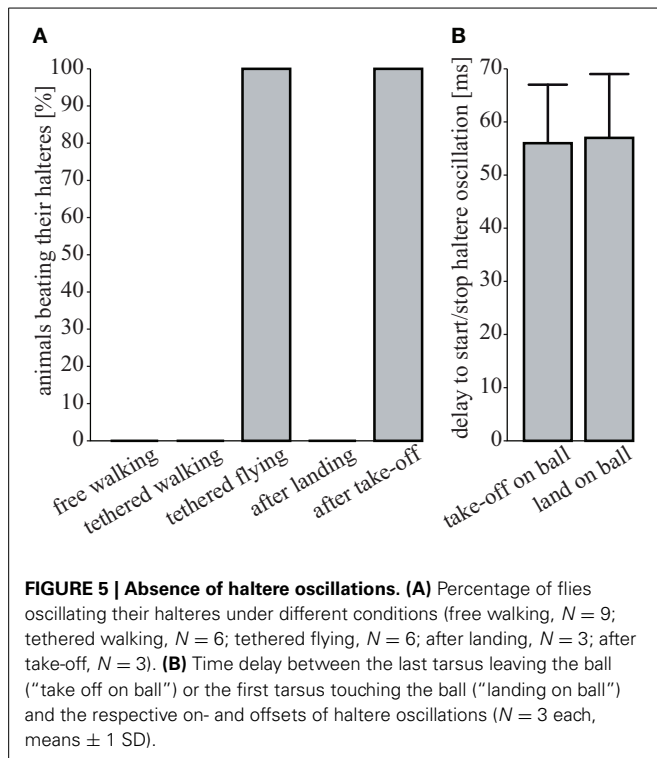
The walking behavior of *Drosophila* imagines has been studied on various levels of complexity, ranging from molecular (Brierley et al., 2012; Baek et al., 2013; Bidaye et al., 2014; Desai et al., 2014) and neuronal mechanisms (Chiappe et al., 2010; Seelig et al., 2010; Ofstad et al., 2011; Ping et al., 2011) to leg movements (Strauß and Heisenberg, 1990; Kain et al., 2013; Wosnitza et al., 2013), walking trajectories (Mendes et al., 2013), and group behavior (Liu et al., 2011; Billeter et al., 2012; Hahn et al., 2013). Walking trajectories and movements have been studied in the context of object fixation, and walking was also shown to facilitate motion detection (Rosner et al., 2009; Chiappe et al., 2010). The need to detect motion is reportedly reflected by the

locomotion behavior of flying *Drosophila* (Heisenberg and Wolf, 1979; Tammero and Dickinson, 2002; Bender and Dickinson, 2006; Censi et al., 2013; Muijres et al., 2014) and other dipteran species. For *Drosophila*, retinal object motion was also shown to serve as a cue for distance estimation (Schuster et al., 2002). Our analysis shows that walking *Drosophila* separate translational movements from rotational ones by performing saccadic turns. These turns are slower than those performed by flying *Drosophila*, with their duration resembling those reported for the saccadic rotations of walking blowflies and bees. We further show that additional, correlated head movements do not accompany the body saccades of walking *Drosophila*, documenting that, while walking, *Drosophila* lacks the head saccades that reduce the effective turning duration in blowflies and bees. This absence of head saccades seems to reflect optical constraints imposed by the eye, whose visual acuity is lower in *Drosophila* than in these other insect species. The absence of head saccades also associates with the absence of haltere oscillations. In blowflies, active haltere oscillations are implicated in the generation of head saccades, indicating that walking *Drosophila* lack both these head saccades and their haltere control.



In addition to facilitating distance estimation, the saccadic movement strategy used by *Drosophila* might reduce motion blur. Motion blur occurs when the speed by which the image changes exceeds the integration time of the photoreceptors and reduces the perceived image contrast. In insects, motion blur

sets in when the stimulus travels faster than one ommatidial acceptance angle ($\Delta\rho$ in deg.) during the integration time of the photoreceptors (Δt in s) (Land, 2003). Photoreceptor integration times Δt are about 20 ms for *Drosophila* (Juusola, 2000; Hardie, 2001; Niven et al., 2004) and 5–10 ms for *Calliphora*



(Tatler et al., 2000). The respective ommatidial acceptance angles $\Delta\rho$ for the two species are 10° (*Drosophila*: Gonzalez-Bellido et al., 2011) and 1° (*Calliphora*: Smakman et al., 1984). These figures translate into motion blur thresholds of $500 \text{ deg}^* \text{ s}^{-1}$ for *Drosophila* and $100\text{--}200 \text{ deg}^* \text{ s}^{-1}$ for *Calliphora*. To avoid motion blur, head stabilization thus seems less critical for *Drosophila* than for *Calliphora*.

According to our analysis, walking *Drosophila*, like flying ones, separate rotations from translations to facilitate motion vision. During walking, however, this separation seems incomplete. During translations, substantial rotations persist, including head rotations with angles of up to 20° relative to the body. Head rotations during translations have also been observed in flying bees (Boeddeker, 2010) and walking blowflies (Blaj and van Hateren, 2004; Kress and Egelhaaf, 2014a), and *Drosophila* during flight (Fox and Frye, 2014). In walking blowflies, these head rotations reportedly arise from the walking apparatus and depend on the substrate the animal is walking on (Kress and Egelhaaf, 2012, 2014a), and in tethered *Drosophila* they were implicated in wide-field image fixation (Fox and Frye, 2014). Judging from our data, about half of the head turning angles of walking *Drosophila* lie below 5° , causing retinal image shifts of less than fifteen percent. Given these rather marginal image shifts, one might speculate that flying *Drosophila* also do not perform head-saccades, although their halteres oscillate.

AUTHOR CONTRIBUTIONS

Bart Geurten and Martin Göpfert designed the study. Kristina Corthals and Bart Geurten conducted the experiments. Philipp Jähde constructed the 3D templates used in manual tracing. Philipp Jähde, Kristina Corthals and Bart Geurten analyzed the

trajectories. Bart Geurten analyzed, modeled and plotted the data. Martin Göpfert and Bart Geurten wrote the manuscript with intellectual contributions from all other authors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://www.frontiersin.org/journal/10.3389/fnbeh.2014.00365/abstract>

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