Saccadic body turns in walking Drosophila

Bart R. H. Geurten *, Philipp Jähde, Kristina Corthals and Martin C. Göpfert

Department of Cellular Neurobiology, Georg-August University of Göttingen, Göttingen, Germany

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 Potser, 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 (Ultimaking 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 deg·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.astroph.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 Vuotilainen and Aldo Hoeber). 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/f² spatial distribution (Field, 1987; van der Schaf 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). Restrering (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)
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 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 when they walk (Blaj and van Hateren, 2004; Kress and Egelhaaf, 2014a,b).

SACCADIC BODY TurnerS NOT ARE 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 HARDDLY 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/f² 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...
FIGURE 3 | Comparison of the head and body movements of walking Drosophila, walking blowflies ("Calliphora"), and flying honey bees ("Apis"). (A) Respective average yaw velocities during saccades. Note that for bees only the probability density is shown. (B) Average yaw angles (top) of the head and body and the difference between them (bottom) during saccadic body rotations. (C) Distributions of the angles between head and body (the φ-angles) observed during the entire trajectories, including saccades, and the trajectories between them. (D) Correlation coefficients between the yaw angles of the head and the body during the saccades. Calliphora is not included in this panel since no such data is available for this species. Data for Apis was taken from Boeddeker (2010) and data for Calliphora from Blaj and van Hateren (2004).

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 (Δρ 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.
and 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). 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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