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SHORT COMMUNICATION

Head orientation of walking blowflies is controlled by visual and mechanical cues

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ABSTRACT

During locomotion, animals employ visual and mechanical cues in order to establish the orientation of their head, which reflects the orientation of the visual coordinate system. However, in certain situations, contradictory cues may suggest different orientations relative to the environment. We recorded blowflies walking on a horizontal or tilted surface surrounded by visual cues suggesting a variety of orientations. We found that the different orientations relative to gravity of visual cues and walking surface were integrated, with the orientation of the surface being the major contributor to head orientation, while visual cues and gravity also play an important role. In contrast, visual cues did not affect body orientation much. Cue integration was modeled as the weighted sum of orientations suggested by the different cues. Our model suggests that in the case of lacking visual cues, more weight is given to gravity.

KEY WORDS: *Lucilia cuprina*, Multisensory integration, Insect vision, Head–body coordination

INTRODUCTION

During locomotion, many animals aim to keep their visual systems aligned with an external frame of reference. Insects, having immobile eyes in their head capsule, achieve this by choosing and maintaining an appropriate head orientation. The frame of reference can be defined by a variety of sensory cues. The gravity vector, pointing downwards, offers a clear and constant reference, but visual structures in natural surroundings can also be used to align the visual system, as they contain a preponderance of horizontal and vertical edges (Baddeley and Hancock, 1991; Coppola et al., 1998; Hancock et al., 1992; Keil and Cristóbal, 2000; Schwegmann et al., 2014; Switkes et al., 1978), even if the horizon is not visible (Hansen and Essock, 2004). Moreover, the overall asymmetry in brightness between the upper and the lower parts of the environment can be used for alignment of the visual system, given that the sky is usually brighter than the ground. This manifests itself in a behavior known as dorsal light response (Hengstenberg, 1993; Meyer and Bullock, 1977), which results in the animal keeping its dorsal towards the light source. In walking animals the orientation of the walking surface, perceived through proprioception, can also act as a reference. Consequently, a variety of cues can be used to establish the frame of reference for an animal and, thus, the orientation of its visual system.

Humans have been shown to use visual, gravitational and proprioceptive input to control and maintain body posture (Chiba et al., 2016; Day et al., 1993; Massion, 1994; Previc et al., 1993; Straube et al., 1994; Winter, 1995) and compensate for body rotations (Guitton et al., 1986). Fish reach a compromise between gravitational and light position to determine the orientation of their body (von Holst, 1935; Kasumyan, 2004; Watanabe et al., 1989). Insects employ visual cues (Goulard et al., 2015; Horn and Knapp, 1984; Srinivasan, 1977; Viollet and Zeil, 2013) as well as the position of the light source (Hengstenberg, 1993; Mittelstaedt, 1950, 1997; Tomioka and Yamaguchi, 1980) to control body orientation. Gravity is also used, though this has only been shown in crickets (Horn and Bischof, 1983) and walking dipterans (Horn and Lang, 1978; Horn, 1982). How these cues may interact to determine the final head and gaze orientation largely remains an open question.

To the best of our knowledge, all work published until now has considered the visual system to be consistently providing a single cue. In reality, an animal may encounter conditions in which different visual cues may suggest different frames of reference for the visual system. For example, an animal walking on a tilted surface is expected to see a horizon defined by the surface it is standing on. But it may also see plants which, growing in alignment with gravity, generate vertical features that may not be perpendicular to the visual horizon. As a result, two visual frames of reference oppose each other. This is particularly relevant for blowflies, which often land on irregular, tilted or outright vertical surfaces without a clear axis of reference.

In this study, we aim to understand how visual and mechanical cues are integrated to determine the frame of reference for the alignment of the visual system in freely walking blowflies. This is achieved by letting blowflies walk on a tilted surface, while presenting multiple visual cues potentially contradicting both each other and the mechanical cues, i.e. orientation of the gravity vector and of the walking surface. We analyzed the contribution of the different cues to the resulting orientation of the head orientation and, thus, of the visual coordinate system. Furthermore, we addressed how changes in body orientation contribute to head alignment, an issue that has not been addressed in walking blowflies.

MATERIALS AND METHODS

Animals and animal preparation

Female blowflies [*Lucilia cuprina* (Wiedemann 1830)] bred in our laboratory were prepared 1–3 days after hatching. The animals were briefly anesthetized with CO_2, and a drop of beeswax was placed on the wing joints to prevent flight.

We placed markers on the head and thorax that could be tracked semi-automatically (see Video analysis) to allow the reconstruction of head and body orientation. The markers consisted of dots of white acrylic paint (Revell 36301, REVELL GmbH, Bünde, Germany): two on the head between the ocelli and the antennae, and two on the thorax, approximately at the level of the wing joints. Reflections on the wings and the cuticle that could interfere with the automatic tracking of the markers were prevented by painting the thorax, the wings and the head area surrounding the proboscis and located

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directly below the antennae with matt black acrylic paint (Revell 36108) prior to placing the markers. To allow individual identification without disturbing the tracking process, a number was painted with matt bronze green acrylic paint (Revell 36165) on the animal. No noticeable changes in the animals' behavior were observed by these manipulations. The animals were kept in a cage with free access to water and sugar.

Experimental setup

Blowflies were released into a cylindrical PVC arena (diameter of 60 cm) through an entry hole (diameter of 2.5 cm) in the center of the ground (Fig. 1). The ground of the arena was covered with black paper to allow easy tracking of the markers (see Video analysis). The walls were covered with white paper and could additionally be outfitted with three red stripes (4 cm wide, located 8 cm from the ground and at the same distance from one another) placed either horizontally or in a tilted position at an angle of 30 deg. A vertical bar made of red cardboard (6.5×58 cm) and of the same height as the arena walls was attached to the wall as a target for the blowflies, as walking flies have previously been shown to be attracted by dark vertical bars (Bülthoff et al., 1982; Kress and Egelhaaf, 2014). Both the stripes and the bar provide high-contrast cues, as blowfly photoreceptors are insensitive in the long-wavelength range (Bernard and Stavenga, 1979).

The animals were recorded by two synchronized cameras (Basler ac A2040–90 µm, Basler AG, Ahrensburg, Germany) controlled by

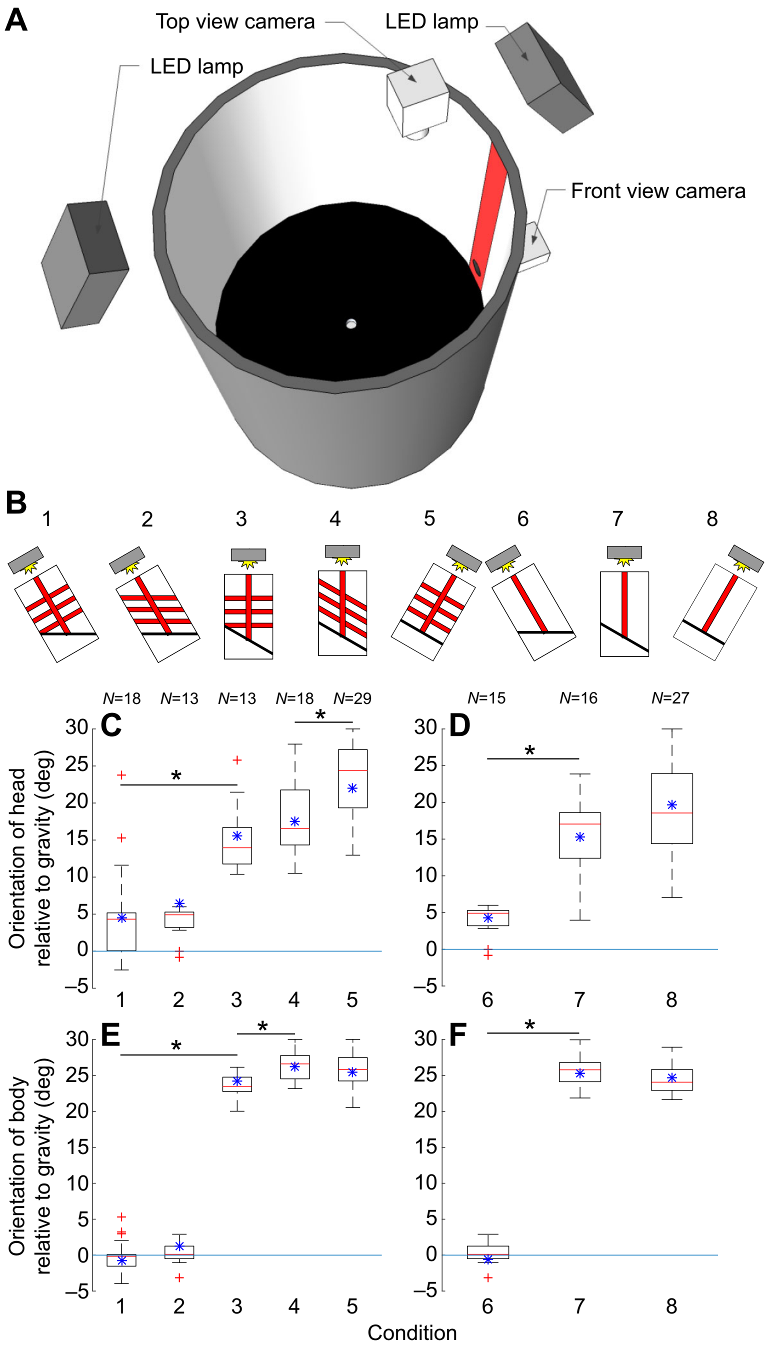

Fig. 1. Head and body orientation as a result of the integration of multiple cues. (A) The experimental setup. (B) Sketch of the experimental arena cut at the entrance hole. The black thick line indicates orientation of the ground surface, the rectangle indicates the drum orientation. Diagrams 1 to 8 show the different experimental conditions as encountered by an animal in the different experimental situations when the fly walks towards the target. (C–F) Orientation of head (C,D) and body (E,F) relative to the horizontal determined by gravity with various cues indicating different frames of reference and orientation predicted by the weighted sum of the suggested orientations. Box and whisker plots indicate median (red line) and first and third quartiles with outliers (red plus). Asterisks indicate significant differences (Wilcoxon rank sum test, $P<0.05$). Blue asterisk indicates the value predicted by the weighted sum of the cues.

a custom program based on the Pylon 4 software suite (Basler AG). One camera was placed for a top-view of the arena and equipped with a Kowa TV Zoom Lens (12.5–75 mm f/1.8, Kowa Company Ltd, Nagoya, Aichi, Japan); the other recorded a frontal view of the fly approaching the bar through a hole (diameter of 5 cm) in the arena wall. The latter was equipped with a Pentax TV Lens (C20616TH 6.5 mm f/1.8, C. R. Kennedy & Co., Port Melbourne, Australia). Recordings were made at 90 frames s^{-1} and 4 megapixel resolution. The arena was illuminated with white light by two lamps (GSVITEC Marathon MultiLED, GS Vitec GmbH, Gelnhausen, Germany), one pointing to the target bar and the other illuminating the opposite side of the arena. The lamps were fixed to the walls of the arena and tilted with it (see below).

The ground of the arena and the cylindrical walls could be tilted independently by up to 30 deg along the axis connecting the entrance hole and the base of the red bar. By tilting the ground, we manipulated the mechanosensory input to the legs, and by tilting the walls of the arena along the path to the bar, we manipulated the orientation of the visual input, which could be further modified by additional bars on the walls. As the animals approach the target along the rotation axis of the ground and of the visual cues, this setup allowed us to estimate the alignment of the roll angle of the body and head, respectively, according to different possible frames of reference.

Experimental procedure

The recording process started when a fly was released into the arena. Once the walking fly had reached the red bar, recorded data were stored for analysis. If the animal did not approach the bar, the recording was rejected and the run restarted. For each animal, five approaches of the bar were recorded.

To calibrate marker positions, every animal was recorded in the arena with both the ground and the walls in the horizontal position (reference condition). Then the animals were recorded while approaching the target bar under different arena settings (experimental conditions).

Animals were allowed to rest overnight between tests under the reference and the eight different experimental conditions (Fig. 1B): the floor was either horizontal with respect to gravity (conditions 1, 2 and 6) or tilted by 30 deg (conditions 3, 4, 5, 7 and 8). It should be noted that the floor provides mechanical cues as well as a visual horizon line. This was combined with different visual conditions: the orientation of the walls, which was always aligned with light direction and target orientation, was either parallel to gravity (conditions 3, 4 and 7) or tilted by 30 deg (conditions 1, 2, 5, 6 and 8). Horizontal stripes on the wall, if present (conditions 1–5), were either parallel to the floor (conditions 2, 4 and 5) or perpendicular to the target orientation (conditions 1 and 3).

Video analysis

The video recordings were analyzed frame by frame using the open-source software ivTrace (https://opensource.cit-ec.de/projects/ivtools). With this software it was possible to automatically track the markers on head and body using a simple binarization of the brighter spots in the image, in this case the markers. Using custom-written MATLAB scripts and Jean-Yves Bouguet's MATLAB Camera Calibration Toolbox (www.vision.caltech.edu/bouguetj/calib_doc/), we triangulated the three-dimensional positions of the markers from our two camera views. We then calculated the roll angle of head and body relative to the orientation of the ground for each time point. Only those recordings from which the roll could be reconstructed over the full recording time were used for further analysis. Data from animals contributing fewer than three recordings were discarded.

To compensate for any individual offsets caused by the position of the markers, we calculated the average head and body roll for each animal for the reference condition and, while assuming an upright head and body orientation, used the resulting values as calibration values for the experimental conditions. Hence, the reference head and body roll is 0 deg by definition.

To assess the accuracy of our reconstruction, we calculated the distance between the two markers placed on the head and assessed their variability. The mean distance between head markers is 0.8973 mm, with a mean standard deviation of 0.0194 mm over a run, showing that the reconstruction is sufficiently reliable and unlikely to significantly affect the determined orientations.

Head and body orientation as a function of cue orientation

To identify the contribution of each cue to the frame of reference for head and body orientation of the flies, we developed a simple model by describing the orientation as the weighted sum of the different cues available to the animal.

We use a weighted sum to combine the expected orientations for all cues:

$$O_\mathrm{p} = w_\mathrm{g} O_\mathrm{g} + w_\mathrm{f} O_\mathrm{f} + w_\mathrm{l} O_\mathrm{l} + w_\mathrm{s} O_\mathrm{s}, \tag{1}$$

with O_p being the prediction for the resulting orientation, O_g, O_f, O_l and O_s the expected orientations indicated by gravity, the floor, the lights and target bar, and the stripes on the walls, respectively, and w_g, w_f, w_l and w_s the corresponding normalized weights (i.e. w_g+w_f+w_l+w_s=1).

The optimal weights were estimated by random variation minimizing the mean square difference between the orientation predicted and the median orientation measured under each of our experimental conditions.

For those conditions in which the stripes on the walls were absent we applied the same approach to predict an orientation from the cues available only (i.e. w_s=0). We tested the robustness of our model by 20 times randomly selecting two-thirds of the data set and recalculating the predicted values. The predicted values were very robust.

RESULTS AND DISCUSSION

Different cues are integrated to modulate head orientation

A strong role of gravity in the head orientation of walking flies can be detected if all other cues oppose the frame of reference indicated by gravity. In such cases the head deviates slightly from the other cues in favor of gravity (Fig. 1C, condition 5; Fig. 1D, condition 8). Gravity perception in walking insects has previously been described as a consequence of a proprioceptive mechanism measuring the differential load on the legs (Horn and Lang, 1978; Horn, 1982). Although with tethered flies walking on an unsupported ball, the experimental paradigm differed from our free walk paradigm, the flies in both setups most likely experienced similar mechanosensory leg stimulation. Indeed, we observed a 5–15 deg roll towards gravity when the walking surface was tilted by 30 deg (Fig. 1C, condition 5; Fig. 1D, condition 8), similar to the one observed by Horn and Lang (1978). Our results show that the reflexes described by Horn and Lang (1978) can also be observed during free walking under the influence of gravity.

The overall direction of the light sources and the orientation of the target bar also have a significant influence on head orientation, as they align the head with both cues (Fig. 1C, conditions 4 and 5, $P<0.005$). There is only limited research on the role of vertical bars on head orientation (Hengstenberg, 1993), and previous investigations on the role of dorsal light in blowflies have not quantified the head rotation elicited by a light source held at any particular orientation relative to the head (Hengstenberg, 1993; Schuppe and Hengstenberg, 1993). In other insects, such as crickets (Tomioka and Yamaguchi, 1980), where head roll was quantified, a light source rotated by 30 deg with respect to the dorsal position has been shown to elicit a head reorientation of similar magnitude as observed here, i.e. a roll of approximately 5 deg relative to the remaining cues (see Fig. 1D, condition 6). Because the possible impact of a target on head orientation is unclear and the effect of a static light source has been described, but not quantified, we believe that the effect observed on head orientation is – at least partially – caused by the dorsal light response with a possible contribution of the orientation of the target.

The effect of floor orientation differs significantly from that of the target bar and the light sources. When comparing situations in which only the floor or only the bar and light sources oppose the remaining cues, the floor causes a much bigger head roll of approximately 15 deg relative to gravity (Fig. 1C, conditions 1 and 3, $P<0.001$). The surface contains two separate cues: the visual horizon, as a contrast edge between the dark ground and the white walls of the arena, and the physical orientation of the ground, which affects head orientation at least by restricting body orientation. The effect of a visual horizon was addressed by Horn and Knapp (1984). Their work revealed that a horizon rotated by 30 deg around the roll axis elicited a head roll of 10 deg. Thus, we conclude that, in addition to the influence of the visual horizon, the orientation of the head is controlled or constrained by the orientation of the body.

Stripes on the vertical walls (Fig. 1C) do not lead to a statistically significant difference in the flies' head orientation, irrespective of stripe orientation with respect to the ground (Fig. 1C, conditions 1 and 2, $P=0.435$, and conditions 3 and 4, $P=0.082$). As stripes seem to play little role in affecting head orientation, we also recorded head orientation in the absence of the stripes, thus providing the animal with fewer visual cues in the surroundings (Fig. 1D,F). We find significantly more alignment with the floor than with the light source and the target bar (Fig. 1D, conditions 6 and 7, $P<0.001$), confirming the greater importance of the floor. No significant change in head orientation is found when changing the orientation of the target bar and light sources alone (Fig. 1D, conditions 7 and 8, $P=0.105$). In the absence of the stripes, a change in the orientation of the light source and the target failed to elicit a significant change in head orientation (Fig. 1D, conditions 7 and 8) in contrast to the situation with stripes (Fig. 1C, conditions 4 and 5). Hence, the availability of particular visual cues affects the integration of other cues.

Body orientation is mainly controlled by gravity and ground orientation

Body orientation is almost unaffected by the orientation of the light sources relative to the animal and the orientation of the target bar (see Fig. 1E,F, conditions 1 and 6, compare conditions 4 and 5, $P=0.412$, conditions 7 and 8, $P=0.105$).

By contrast, the orientation of the walking surface has a big impact on body orientation, aligning itself much more towards the same than towards the target bar and the light sources (Fig. 1E,F, conditions 1 and 3, $P<0.001$, conditions 6 and 7, $P<0.001$). Although we cannot exclude the influence of the visual horizon on body orientation, we consider the strong alignment of the body with the orientation of the surface to be likely due to the constraints of walking, i.e. limits in the leg posture restricting body roll.

A contribution of gravity is also observed, but its effect is small compared with the one of the walking surface (Fig. 1E, condition 5; Fig. 1F, condition 8). It has been shown that locomotion along a tilted surface can cause roll of the body as a consequence of the change of the gravity vector relative to the surface (Diederich et al., 2002). Thus, although a mechanism to compensate for gravity cannot be excluded, we consider the small effect of gravity observed in our experiments most likely to be due to the physical constraints of walking along a tilted surface.

The orientation of visual cues presented in the form of stripes in the surroundings of the animal appears to have only a minor effect on body orientation. They do not cause a significant effect when walking on level surfaces (Fig. 1E, conditions 1 and 2, Wilcoxon rank sum test, $P=0.238$), but seem to cause a significant change when the fly walks on tilted surfaces (Fig. 1E, conditions 3 and 4, $P=0.001$), though this change is small in magnitude.

Linearity and adaptability of integration

To analyze the relative contribution of the different cues to head orientation, we performed a simple linear fit and estimated the relative weights of the different cues we manipulated for the experimental conditions with stripes and without stripes. Our model allows us to account for head and body orientation based on the orientation suggested by the cues available to the animals (Fig. 1C–F).

In the presence of stripes, gravity ($w_g=0.27$) and floor orientation ($w_f=0.52$) are the major factors controlling head orientation, but the orientation of the light sources and target bar ($w_l=0.15$) as well as the stripes ($w_s=0.07$) still contribute to head orientation, with the stripes playing the smallest role.

In the absence of stripes (fixed setting of $w_s=0$), we find that the relative weights of light sources and target bar ($w_l=0.14$) and of the floor ($w_f=0.51$) are almost unchanged, while a more substantial change occurs in the relative weight of gravity ($w_g=0.34$). This suggests that in the absence of additional visual cues, gravity gains a bigger impact on head orientation.

For the body, in the presence of stripes, the orientation is mostly controlled by the orientation of the surface ($w_f=0.81$) and gravity ($w_g=0.15$), while orientation of light sources and target bar ($w_l=-0.03$) as well as orientation of the stripes ($w_s=0.07$) only contribute weakly. Body orientation in the absence of stripes confirms that the orientation of the surface ($w_f=0.85$) and gravity ($w_g=0.18$) are major contributors, while the contribution of the orientation of light sources and target bar ($w_l=-0.02$) is negligible.

Previous research has shown that the integration of visual and gravitational cues is linear to some extent (Horn and Knapp, 1984). This is confirmed by our linear model, which is able to account for head and body orientation with a reasonable accuracy (Fig. 1C–F).

The integration shows some signs of adaptability. In the absence of stripes, the normalized weights of the light source and the target stripe and of the floor remain almost unchanged ($w_l=0.15$ to 0.14 and $w_f=0.52$ to 0.51, respectively). Instead, only the weight of gravity increases ($w_g=0.27$ to 0.34). This may explain the lack of any significant effect of the light sources and the target bar in absence of stripes in the surroundings (Fig. 1D, conditions 7 and 8), as the change may become too small to be functionally significant. This finding suggests that in some way the animals evaluate the availability of visual cues and compensate for their absence by giving more importance to gravity.

Open questions

Walking blowflies evaluate the availability of different types of visual cues, such as the direction of light sources or the orientation of environmental features. If such cues are lacking, the relative role of gravity in head orientation increases. How this is accomplished, however, is still an open question. We also remain in the dark on how the different cues are integrated, though both previous results (Horn and Knapp, 1984) and the accuracy of our model suggest at least some degree of linearity. It is also unknown where the integration takes place in the nervous system, but research on the neck motor neurons (Strausfeld and Seyan, 1985) has revealed connections between cervical neurons and visual neurons at the level of the prothoracic ganglion, suggesting that some degree of integration takes place there.

We can only speculate about why the animals integrate the orientation of different cues into a final head orientation instead of choosing to align themselves according to a specific cue. One possibility is that instead of using a more computationally complex procedure, blowflies might just perform a simple weighted sum of the different orientations detected and accept the possible deviations from the optimal orientation as a trade-off. It is worth mentioning that, despite rotating their head, and thus their eyes, as a compromise between the orientation of the walking surface and a target bar, walking blowflies are able to detect and approach their targets. This indicates that the mechanisms by which this behavior is achieved are robust with regard to rotations of the visual system.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: J.M., J.P.L., M.E.; Methodology: J.M., J.P.L., M.E.; Software: J.M., J.P.L.; Formal analysis: J.M.; Investigation: J.M.; Data curation: J.M.; Writing - original draft: J.M.; Writing - review & editing: J.M., J.P.L., M.E.; Visualization: J.M.; Supervision: J.P.L., M.E.; Project administration: J.M., J.P.L., M.E.; Funding acquisition: J.M., J.P.L., M.E.

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