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The fine structure of honeybee head and body yaw movements in a homing task

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Honeybees turn their thorax and thus their flight motor to change direction or to fly sideways. If the bee's head were fixed to its thorax, such movements would have great impact on vision. Head movements independent of thorax orientation can stabilize gaze and thus play an important and active role in shaping the structure of the visual input the animal receives. Here, we investigate how gaze and flight control interact in a homing task. We use high-speed video equipment to record the head and body movements of honeybees approaching and departing from a food source that was located between three landmarks in an indoor flight arena. During these flights, the bees' trajectories consist of straight flight segments combined with rapid turns. These short and fast yaw turns ('saccades') are in most cases accompanied by even faster head yaw turns that start about 8 ms earlier than the body saccades. Between saccades, gaze stabilization leads to a behavioural elimination of rotational components from the optical flow pattern, which facilitates depth perception from motion parallax.

Keywords: vision; gaze stabilization; behaviour; bee; flight control; homing

1. INTRODUCTION

Honeybees vary their flight direction by combinations of roll, yaw and pitch rotations of their body. In a previous study (Boeddeker & Hemmi *in press*), it was shown that bees perform lateral movements by rapidly rolling their thorax and therefore their flight motor by up to 60°. If the bee's head were fixed to its thorax, such fast roll rotations would have great impact on vision, as the reference coordinate system of the visual system would keep changing rapidly and frequently (Hengstenberg 1993). Bees solve this problem by visually stabilizing gaze, keeping their head at a level orientation (Boeddeker & Hemmi *in press*). This shows that the control of locomotion requires precise interaction between sensorimotor subsystems and the flight control system. Here, we analyse the fine structure of head and body movements of honeybees during turns in the horizontal plane in order to find out how gaze and flight control interact. In bees and other insects, the direction of gaze is determined by the orientation of the head; they cannot move their eyes relative to the head capsule.

Only few studies have analysed gaze in freely flying insects by tracking the insects' head movements (Wehner & Flatt 1977; van Hateren & Schilstra 1999; Boeddeker & Hemmi *in press*). Blowflies have been shown to compensate rotations of the thorax in flight by counter rotations of the head relative to the thorax (Schilstra & van Hateren 1998; van Hateren & Schilstra 1999). Flies typically change their flight direction and concomitantly the direction of their gaze through a series of short, fast saccadic turns of their entire body and, in synchrony but at a higher angular speed, of the

head (Land 1973; Schilstra & van Hateren 1998). These stepwise rapid changes of gaze direction have been called, by analogy with human eye movements, saccades (Collett & Land 1975). Between saccades, gaze direction is kept largely constant, eliminating rotational optic flow on the fly's eyes. This coordinated flight and gaze strategy has been interpreted as an active behavioural means that facilitates the processing of spatial information (Boeddeker *et al.* 2005; Kern *et al.* 2005). Processing of depth information from motion parallax depends crucially on precise gaze stabilization against rotations as has been shown in locusts and blowflies (Collett 1978; Kern *et al.* 2006).

In flies, fast gaze stabilization is thought to be mainly achieved by mechanosensory input from halteres that act as gyroscopes (Sandeman & Markl 1980; Hengstenberg 1988). The halteres are sensitive to the angular velocity of the fly's thorax (Nalbach 1993; Dickinson 1999) and beat in antiphase to the forewings (Pringle 1948). The dynamics of body saccades are also to a large extent controlled by the fly's haltere system (Bender & Dickinson 2006). Honeybees, however, like many other insects, lack such specialized inertial sensors and to our knowledge whether and how they coordinate their head and body movements and, thus, shape their visual input have not yet been analysed. The question is whether head and body yaw orientation change in the same way or whether the bee's head counteracts, to some extent, body yaw movements, helping to stabilize gaze in a similar way as in flies (Land 1973; Schilstra & van Hateren 1998) and solitary wasps (Zeil *et al.* 2007).

We recorded head and body movements of honeybees during a homing task utilizing the bee's ability to memorize the spatial location of places (reviews, Collett *et al.* 2006; Zeil *et al.* 2009). Bees and also wasps acquire visual

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memories during systematic learning flights on their first departures from the goal and update them whenever approaches to the goal have been difficult (review, Zeil *et al.* 2008). Bees use cues derived from the image motion for a variety of behavioural tasks (review, Srinivasan & Zhang 2004) and we have recently found that they also use motion parallax to acquire spatial information cues in a navigation task (L. Dittmar *et al.* 2010, unpublished data). Here, we investigate how honeybees shift gaze during their learning and return flights and discuss the impact of structured gaze movements on visual motion processing.

2. MATERIAL AND METHODS

(a) *General procedure*

Honeybees (*Apis mellifera*) were maintained according to standard beekeeping practices. Up to 20 bees per day were trained to collect sugar solution from a transparent feeder, which was located in an indoor flight arena. Bees that continued to visit the feeder regularly were individually marked with acrylic paint on thorax and abdomen. These bees were then trained to associate the food reward with a constellation of three cylinders we will refer to as landmarks. The whole setup, the training and the recording procedures were similar to those used in a parallel study, where the performance of honeybees in locating the feeder was probed by targeted modifications of landmark texture and the landmark–feeder arrangement (L. Dittmar *et al.* 2010, unpublished data).

(b) *Experimental setup*

The circular flight arena (diameter of 1.95 m) was located in a windowless room about 10 m away from the hive. The side wall of the arena was 500 mm high and covered with the same red–white Gaussian blurred random dot pattern as the arena floor. Honeybees entered the flight arena via a plastic tube that led them through a small hole in the wall.

Landmarks had a height of 250 mm and a diameter of 50 mm. They were placed at different distances (100, 200, 400 mm) around the feeder, at angles of 120° to each other with the feeder in their centre. Every landmark was covered with either solid red paper or paper with the same Gaussian blurred random dot pattern as the arena floor and walls. A drop of sugar solution was provided on the feeder which was made of an upright Perspex cylinder (100 mm high, 20 mm diameter) carrying a Perspex disc (5 mm high, 40 mm diameter) on top. A dome of white cloth surrounded and covered the upper part of the flight arena to prevent the bees from seeing external visual cues. Indirect illumination was provided by eight Dedo-Lights (DLH4; 150 W each) placed outside the cloth around the arena and by nine 50 W halogen lamps from above. All lights ran on DC power and were positioned symmetrically with respect to the arena centre.

(c) *Recording sessions*

Departing and approach flights were recorded from a distance of about 2 m above the flight arena with three synchronized high-speed digital video cameras. The visual field of the cameras did not cover the whole arena (see inset figure 1*d*). For recording, we therefore shifted the feeder–landmark arrangement to a position directly below the three cameras. Two of the cameras (Redlake MotionPro500) were used as a stereo camera system. They were positioned above the arena and allowed us to measure the position and orientation of the body length axis at 250 frames s⁻¹ with a resolution of

1024 × 1024 pixels in each view. The optical axis of one of the two stereo cameras was levelled with respect to gravity and pointed straight down. The third camera (LightningRDT) was levelled and orientated the same way and also located above the arena running at the same frame rate as the other cameras. This camera was used to resolve head movements and therefore equipped with a macro-lens that provided a magnified view of the area close to the feeder with a size of about 425 × 340 mm resolved at 1280 × 1024 pixels. Video sequences were stored as uncompressed 8-bit image files in tiff format on computer hard disk for off-line processing. With these parameter settings, the maximum recording time was restricted by the onboard memory of our video cameras to 16 s. Recordings were done on 6 days with different bees on each day.

(d) *Data analysis*

The position of the bee and the orientation of its body length axis were automatically determined in each video frame by custom-built software. This was done for both cameras of the stereo video camera system. We determined the bee's body yaw angle from the levelled camera that viewed the flight arena from above (top view). For camera calibration and three-dimensional stereo triangulation, we used the Camera Calibration Toolbox for MATLAB by Bouquet (1999). Three-dimensional coordinates and the yaw body orientation of the bee were then low-pass filtered (second-order Butterworth filter) with a cut-off frequency of 20 Hz.

We also used our custom-built computer program to measure the bee's head position and yaw orientation in the image sequences that were recorded by the third (macro) camera. The centre of the bee's head was manually marked by clicking on it in every frame of the sequence. A region of interest (ROI, size 90 × 90 pixels) was then automatically defined around the centre of the head. A new image was generated on the computer screen from this ROI and rotated by moving the computer mouse until the bee's head appeared straight on the computer monitor. The inverse of the angle, which was used to straighten the image, then gave the yaw orientation of the bee's head relative to the orientation of the camera. Orientation measurements were greatly facilitated by this method and errors were easy to detect this way. We checked the positional precision of our methods using markers with known positions in the flight arena. We analysed differences of orientation measurements of the bee's head that were done by two different observers in a given image sequence. These differences were on average smaller than 1°. We also compared manual and automatic measurements of the bee's body orientation and found that differences were also smaller than 1°.

3. RESULTS

During the initial sections of departing flights from the sucrose feeder, the bee faces the goal while backing away from it. This 'turnback-and-look behaviour' (TBL) has an important function for the learning of a novel food site, as bees prevented from performing TBL flights never come back (Lehrer 1991). Our close-up high-speed recordings reveal a consistent temporal fine structure of coordinated head and body rotations during TBL and return flights. While the bee is pivoting around the goal location in increasing arcs, it frequently moves sideways in short straight flight segments keeping

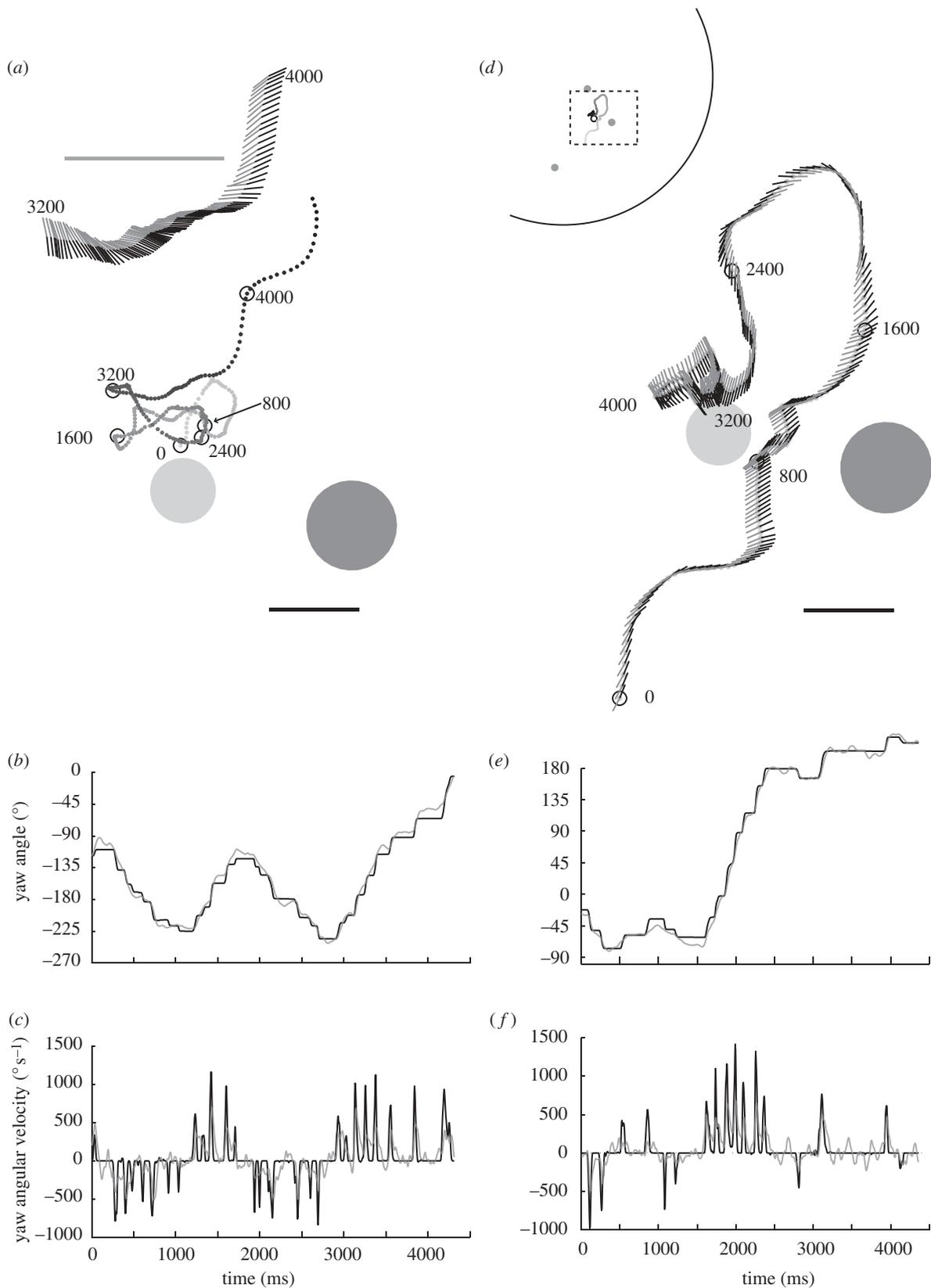


Figure 1. Examples of TBL and return flights. (a) Top view of the flight trajectory of a bee departing from the feeder (light grey circle). The position of the bee's head is shown every 16 ms. During the initial sections of this TBL flight, the bee is facing the goal while backing away from it. The closest of the three landmarks visible is shown in the inset in (d). The inset in (a) provides a magnified view for time from 3200 to 4000 ms and illustrates that the bee's head orientation (black) can deviate considerably from the yaw orientation of its body (grey). Scale bar, 50 mm. (b) Head yaw angle (black) and body yaw angle (grey) for the flight shown in (a). The head usually turns with the thorax but at a higher angular speed, starting and finishing slightly earlier. (c) Head (black) and body (grey) yaw angular velocity for the same flight. (d–f) Format as in (a–c). (d) Scale bar, 50 mm. Return flight trajectory of the same bee after about 5 min. (e) Head yaw angle (black) and body yaw angle (grey) for the return flight. (f) Head (black) and body (grey) yaw angular velocity for the return flight.

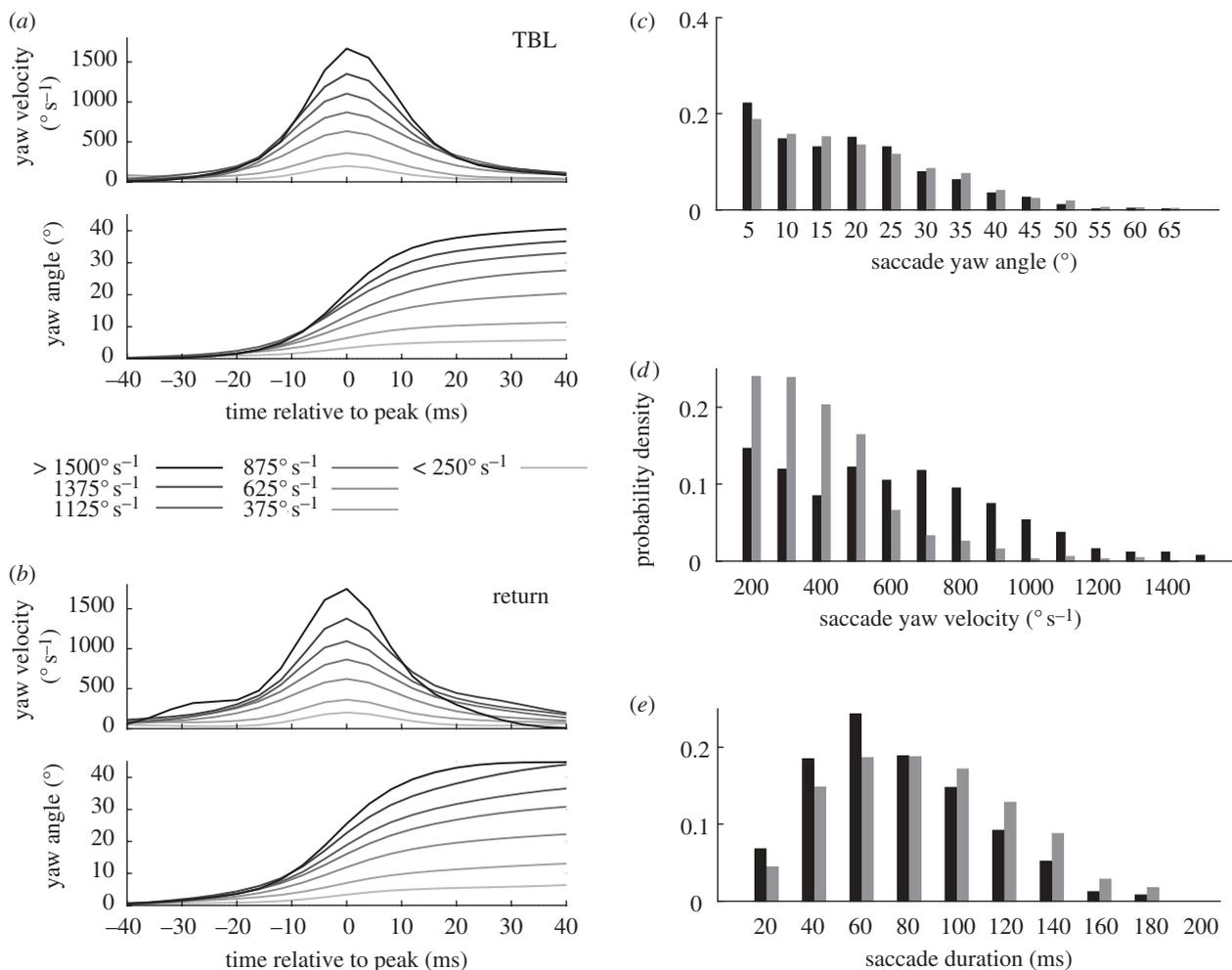


Figure 2. (a) Saccade velocity amplitudes for TBL flights (top) and angular velocity profile (bottom) from a total of 752 saccadic head movements for different head saccade size classes. Saccades were detected as peaks in yaw angular velocity (see (d) for the distribution of head saccade velocities). (b) Format as in (a). Angular velocity and amplitude distributions for return flights. (c–e) Histograms for the amplitude, velocity and duration of body and head saccades. Each data plot is normalized to sum up to one. Head saccades have the same amplitudes as body saccades but are on average faster and shorter. Black bar, head $n = 752$; grey bar, body $n = 810$.

head orientation constant in space. During these segments, the bee's body yaw direction is also kept nearly constant except for brief periods when fast yaw orientation changes take place. Such yaw body turns ('body saccades') are often accompanied by even faster head yaw turns ('head saccades'). Flights can thus be divided into two characteristic phases: 'saccades', when angular velocities of the head reach up to $2000^{\circ} \text{ s}^{-1}$, and 'between saccades', when the yaw orientation of the head is stabilized. Flight direction, body yaw orientation and head yaw orientation can differ noticeably during some phases of the flight (magnified flight sections in figure 1*a,d*). The bee's head orientation sometimes deviates considerably from the yaw orientation of its body. From 3200 to 4000 ms in figure 1*a*, for example, head and body orientation are not in line in several instances. The time course of body and head yaw orientation is very similar, with the difference that head orientation angle changes in a more step-like manner and varies less than body yaw orientation between these steps (figure 1*b*). The head usually turns in synchrony with the thorax but at a higher angular speed, starting slightly earlier (figure 1*c*). When the same bee returns to the feeder after about 5 min, its return flight (figure 1*d–f*) has similar characteristics: gaze

changes are fast and saccadic, which leads to periods of predominantly translational movements between saccades.

The two examples illustrate that honeybees employ a saccadic flight strategy. To what extent are the different parameters characterizing head and body saccades similar for TBL and return flights and how stereotypical are they across different bees? In the following, we analyse and quantify several saccade parameters. There is a tight relationship between the angular velocity and the angular amplitude of saccadic head yaw turns during TBL flights (correlation coefficient: 0.81 for all head saccades; see also figure 2*a*). Although saccade velocity amplitudes range from below $250^{\circ} \text{ s}^{-1}$ to $1500^{\circ} \text{ s}^{-1}$, the angular velocity profile of saccadic head movements is very similar for different head saccade sizes (figure 2*a*). This relationship is similar for return and TBL flights (see angular velocity and amplitude distributions in figure 2*a,b*).

To further compare the characteristics of head and body saccades, we calculated histograms for the amplitude, velocity and duration of body and head saccades. Head saccades have the same amplitudes as body saccades (figure 2*c*) but are on average faster (figure 2*d*) and shorter (figure 2*e*). Head saccade velocities have a narrower peak than body saccades (figure 3*a*). More

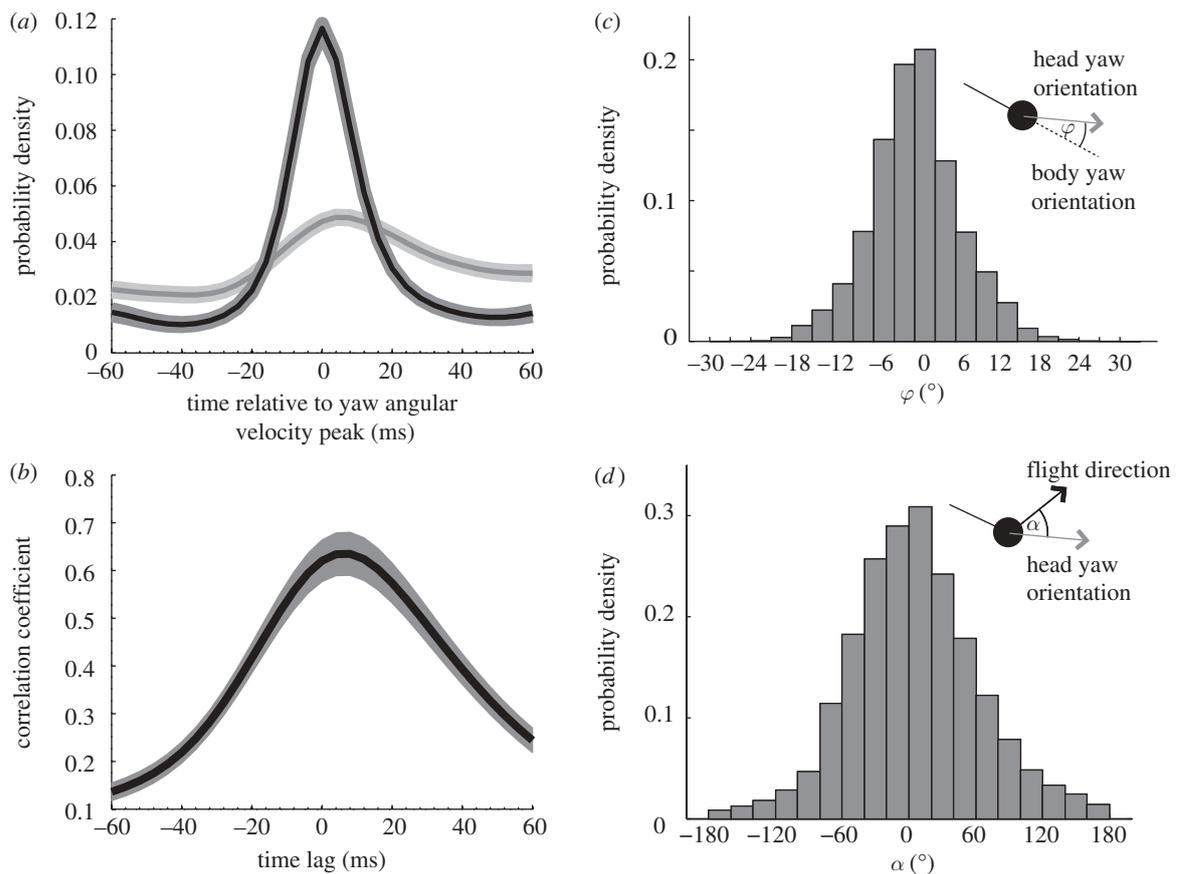


Figure 3. (a) Normalized mean head (black) and body (grey) saccade velocities ($n = 752$ each). The peak head velocity is the reference point for the timescale. Grey areas denote the standard error of the mean. (b) Cross-correlation between head and body yaw velocity from a total of 132 s of learning and return flights. (c) Frequency distribution of the difference between head and body orientation (φ , see inset) from 132 s of learning and return flights (mean 0.01° , s.d. 6.5°). (d) Frequency distribution of the angle between head orientation and flight direction (α , see inset). From the considerable width of this distribution, it can be seen that all other combinations of flight and viewing direction are possible (mean 3.4° , s.d. 56.2°) and that bees sometimes also fly backwards ($\alpha = 180^\circ$).

than 90 per cent of head saccades are followed by a body saccade, which is also reflected by a correlation coefficient of 0.65 between head and body yaw velocity (figure 3b). The cross-correlation peak lies at a time lag of about 8 ms, which indicates that head saccades are closely followed by body saccades.

Body orientation can be measured automatically from each frame in the image sequences, but does it give a reasonable estimate of gaze direction? We measured the difference between head and body orientations (φ , see inset in figure 3c) from a total of 132 s of learning and return flights. The frequency distribution of angles between the orientations of head and body shows that body orientation and gaze direction are often aligned (mean 0.01° , s.d. 6.5°) but can differ by up to 20° .

The consequence of saccadic head movements is that there are frequent periods of stable gaze. During these periods, the bee's flight direction and head yaw orientation can deviate considerably from each other. We calculated the angle between head orientation and flight direction for all flights (α , see inset in figure 3d). The maximum of the α angle histogram (figure 3d) is close to 0° which indicates that bees often look in the same direction as their flight direction. The shape and width of this distribution is similar for TBL (mean 7.5° , s.d. 52.2°) and return flights (mean 1.6° , s.d. 58.8°). This

indicates that there are no pronounced differences with respect to lateral movements between TBL and return flights. All combinations of flight and viewing direction are possible and the bees sometimes also fly backwards ($\alpha = 180^\circ$).

4. DISCUSSION

We found that honeybees perform fast saccadic head and body yaw orientation changes during flight. Between these manoeuvres, they stabilize their head against yaw rotations even though the bee's body yaw axis orientation shows considerable variation in orientation between saccades. We hypothesize that these highly structured movements indicate an active vision strategy that helps bees navigate using translational optic flow (L. Dittmar *et al.* 2010, unpublished data). The specific pattern of optic flow moving animals experience is determined by both the layout of the environment and by the animal's behaviour (Gibson 1950; Lappe 2000). Depending on their flight style, honeybees can experience two basic types of image motion patterns, one is due to rotations of the eyes (rotational optic flow) and one is due to translations (translational optic flow) (review, e.g. Taylor & Krapp 2007). The rotational optic flow component is generated by orientation changes of the eye; image

displacements have uniform directions across the visual field and amplitudes are independent of the distance to objects. In contrast, optic flow generated by a pure translation depends on the direction and speed of the movements and on the distance of objects in the world. The pattern of optic flow during translational movements therefore contains range information as images of close objects move faster across the retina than those of more distant objects. Optic flow is therefore shaped by the organization of behaviour and there are several examples which suggest that the specific mode and pattern of movement facilitates visual information processing, creating favourable conditions for image analysis (Zeil *et al.* 2008). We find that bees experience mainly translational optic flow between saccades, which can help them extract depth cues. There are frequent instances where the bee's flight direction and head yaw orientation deviate considerably during TBL and return flights. During these flight manoeuvres, honeybees experience translational optic flow in their frontal field of view. This flight style is likely to be useful for the detection of landmarks in front of the bee and provides spatial information about the goal location (L. Dittmar *et al.* 2010, unpublished data). The bee's sideways movements might therefore have a similar function as the scanning movements found in other invertebrates (Collett & Paterson 1991; Kral & Poteser 1997). Bees and other insects are known to use the apparent velocity of nearby surfaces to detect objects during locomotion (Collett 1988; Kimmerle *et al.* 1996; Lehrer 1996) and honeybees can even be trained to distinguish camouflaged figures by using motion parallax as a cue (Zhang *et al.* 1995; Lehrer & Campan 2005).

The flights of honeybees analysed here share several characteristics with the flight behaviour of other insects and birds. Especially saccadic body yaw turns have been recorded in several freely flying animals (Hedrick *et al.* 2009). Saccadic eye, head or body movements are also similar across different taxonomic groups (reviewed by Land 1999). In the case of blowflies, these gaze changes involve coordinated head and body movements that are in many aspects similar to the head and body movements we describe here for honeybees. During cruising flights of blowflies, the orientation of the head changes at regular intervals abruptly at high angular velocity while between these changes in gaze direction the head is stabilized around the three rotational axes of rotation (Schilstra & van Hateren 1998, 1999; van Hateren & Schilstra 1999). However, the relative timing of head and thorax yaw turns is slightly different in bees and flies. In blowflies, thorax saccades are accompanied by faster saccades of the head, starting later and finishing earlier than the thorax saccades (Schilstra & van Hateren 1998). We show here that—as in flies—the honeybee's head orientation usually turns in synchrony with the thorax, but that it starts and finishes slightly earlier than the thorax. Despite these differences in their temporal fine structure, head saccades in both species maximize the periods of stable gaze and compress the visual system's exposure to rotational optic flow into very brief moments in time. Why is it so important for flying animals to control the orientation of the optic flow field? We assume that one important reason is the facilitation of depth perception from motion parallax, because

visual mechanisms that exploit the translational components of optic flow for odometry or depth perception, for instance, break down if contaminated by strong rotational optic flow.

What are the sensory cues that bees use to control the orientation of the head and how do they manage to coordinate head and body movements? A recent study shows that flying honeybees visually stabilize head roll orientation (Boeddeker & Hemmi *in press*). These experiments reveal that vision plays a dominant role in the control of head roll rotations because bees flying through an oscillating, patterned drum align their head with respect to their visual environment causing head orientation to diverge from the horizontal. It is yet unclear how visual information might serve the bees in coordinating head and body rotations and what other sensory and neuronal mechanisms assist in stabilizing gaze against roll (Boeddeker & Hemmi *in press*) and yaw rotations (this study) during flight. Visual motion stimuli evoke neural activity in the brain of flies with a delay of about 30 ms (Warzecha & Egelhaaf 2000), much of which is due to the slow process of visual transduction in photoreceptors (review, Hardie 1986). Mechanosensory control loops, in contrast, can be very fast as there often is a direct linkage between the activation of ion channels and membrane deformation of the mechanoreceptor; the latency measured in neck motor neurons from haltere deflection is only about 3 ms in blowflies (Sandeman & Markl 1980). Experiments by Hengstenberg (1993) and Sherman & Dickinson (2003, 2004) show that in flies, the visual system is tuned to relatively slow rotation whereas the haltere-mediated response to mechanical rotation increases with increasing angular velocity. It is not clear whether honeybees possess specialized inertial sensors. Our data show that head saccades in bees with their maximal yaw velocities around $1200^\circ \text{ s}^{-1}$ have slower dynamics than head saccades in flies where yaw velocities above $2500^\circ \text{ s}^{-1}$ are frequently reached (van Hateren & Schilstra 1999). These findings might indicate that fast haltere-mediated coordination helps flies to control their fast head–body coordination and thus enabling them to perform very rapid flight manoeuvres. In addition, pre-programmed motor commands might assist head–body coordination in both bees and flies. Such forward models predict the sensory consequences of action and are thought to play a crucial role for understanding motor control in vertebrates (Wolpert & Ghahramani 2000). There is recent evidence from invertebrates for the predictive modulation of sensory processes by motor output (Webb 2004). For head–body coordination in flying insects, it could thus be that information about when a saccade is generated and when rotational optic flow is expected is conveyed to neck muscles that keep the head levelled except for the brief periods of saccadic head orientation changes.

Although the bee's gaze direction depends on the orientation of its head rather than its body, it has been concluded from high-speed recordings in bumblebees that body orientation does give a reasonable estimate of gaze direction (de Ibarra *et al.* 2009). We find here that in honeybees, the general relationship between head and body orientation is very similar to bumblebees (figure 3c). Our analysis also reveals that the fine temporal details of body and head saccades differ, which can have

great impact on visual processing. It has been shown that the temporal differences in head and body rotations of blowflies are relevant for motion processing in the fly's visual system (Kern *et al.* 2006). Kern *et al.* (2006) show that if the fly's head was tightly coupled to the body, the resulting optic flow would not contain behaviourally relevant information. To reach conclusions about the coding properties of visual motion sensitive neurons, it is therefore desirable to get the behavioural dynamics right. As it is difficult to resolve head orientation in many experimental paradigms and because we find here that the relationship between head and body yaw saccades is relatively stereotyped, we are planning to develop an algorithm that transforms yaw body orientation measurements into an estimate of head orientation in a similar way to the method of Kern *et al.* (2006). This algorithm is likely to be useful, because it is relatively easy to automatically resolve body orientation from videos, whereas measuring head orientation has to be done manually, which is very time-consuming.

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