Head movements in freely walking blowflies

Introduction

It is generally assumed that the visual system is optimised, through evolution and development, to the processing of natural visual input (review: Simoncelli and Olshausen, 2001). Most of the early studies of visual processing used simple stimuli like spots, bars, and sinusoidal gratings, mainly because these experiments were relatively easy to perform and analyse. Recently, however, studies of the visual system using natural stimuli have become more common (van Hateren, 1997; Stanley et al., 1999; Kern et al., 2001; Lewen et al., 2001). It is therefore important to investigate the determinants of the natural visual input of the animal.

The natural visual input is determined by the natural environment and the natural movements of the animal. In this chapter the latter will be studied. The movements of the head and thorax determine the orientations and angular velocities of the fly, which in turn determine the visual input, optic flow and Coriolis forces acting on the halteres. Rotations of the thorax are sensed by the halteres which give feedback for stabilisation of the head and thorax (Nalbach, 1993). Muscles in the neck control the orientation of the head relative to the thorax (Strausfeld et al., 1987). Because the difference between head and thorax is lower than \( \pm 20 \) degrees in yaw and pitch and \( \pm 90 \) degrees in roll (Hengstenberg, 1991), thorax rotations necessarily have
a considerable influence on head rotations. The movements of the head determine the visual input of the fly and the corresponding optic flow. The optic flow is composed of a rotational component, determined by the angular velocities of the head, and a translational component, determined by the translation in space. The translational optic flow can be used to extract the three-dimensional structure of the environment (Koenderink, 1986); the presence of the rotational optic flow complicates this task. Another adverse effect of the rotational optic flow on vision is the blurring which occurs during fast rotations (van Hateren, 1992).

Movements of the head and thorax of flies can be studied through several paradigms: open loop, where flies are restrained, and their actions do not modify their visual input; virtual open loop, where flies walk freely and the visual surround is modified accordingly, such that the fly always sees the same image (Strauss et al., 1997); artificial closed loop, where the own actions of flies, either fixed on a torque meter or observed by a wing beat analyser, are measured, and the surround is modified accordingly; natural closed loop, where flies move freely. The natural closed loop has been used on freely walking flies (Götz, 1980), freely flying flies (Schilstra and van Hateren 1998b), flies walking on a ball (Götz and Wenking, 1973), and tethered flying flies which can rotate only about the vertical axis (Mayer et al., 1988). Each of these paradigms is useful for the study of particular characteristics of the visual and mechanosensory systems. However, the most natural choice for the study of natural input and its processing is the natural closed loop, with a freely flying or walking fly. Most of the available techniques for measuring the movements of the fly under these conditions have at least one of the following limitations: limited temporal resolution (commonly 50 Hz), limited spatial resolution, not allowing the reconstruction of all 3 coordinates of the orientation of the thorax, not resolving the orientation of the head of a freely walking or flying fly. Although they give an indication about the natural movements of the animal, the fine structure of the movements, and especially the fine structure of head movements, cannot be detected. Recent advances like pan-tilt cameras (Fry et al., 2000) and the use of two cameras (Tammero and Dickinson, 2002) improved the performance significantly, but still do not allow a complete reconstruction of the visual input of a freely moving fly. To deal with the limitations of the methods, some of the following approximations are usually made: the head is glued to the thorax or is supposed to have the same orientation as thorax;
the orientation of the thorax is supposed to be tangent to the walking trace; pitch and roll angles are ignored. We will evaluate in this chapter the effect of several of these approximations by comparing recordings of high-resolution head orientation, high-resolution thorax orientation, and low-resolution (interpolated) thorax orientation.

Although much is known now about flying flies, much less is known about walking flies. Flies walk a significant proportion of their time when looking for food or a place to lay eggs (Dethier, 1976). Because of the importance of walking and because it is relatively easier to record the movements of walking flies than those of flying flies, walking is much studied in flies. Horn and Mittag (1980) found that blowflies turn their thorax by two types of rotations, one type frequent and small (6-8 degrees) and the other less frequent and larger (28-65 degrees). In Chapter 3 we showed that the small rotations are saccadic rotations of the thorax, and the less frequent movements are the complex manoeuvres used during turning (which consist of many small saccades). Turning manoeuvres in *Drosophila* were described in detail by Wannek and Strauss (1996) and Strauss and Heisenberg (1990). However, knowledge about head movements during walking is quite limited. In this chapter we investigate natural head and thorax movements using the search coil technique used earlier for flying flies (Schilstra and van Hateren, 1998a). Furthermore, we analyse several of the consequences of these movements to the visual system.

**Methods**

**Experimental setup**

The position and orientation of the head and thorax of blowflies were measured, using the technique described by Schilstra and van Hateren (1998a). The experiments were performed in a measuring volume surrounded by 3 magnetic coil pairs. AC currents of three different frequencies were driven through each of the coil pairs, generating two homogenous magnetic fields (50 kHz and 68 kHz) and one gradient field (86 kHz). Two tiny coils triplets sampled these magnetic fields and each coil in a coil triplet was connected to three lock-in amplifiers (each tuned to one of the three frequencies of the
magnetic fields), thus there were nine lock-in amplifiers for each coil triplet. The outputs of the amplifiers were digitized at 1 kHz with an A/D-converter (16 bit, Microstar DAP2416e) and stored for subsequent analysis. The intensities and orientations of each of the three magnetic fields with respect to the sampling coil triplet could be calculated from the output of the nine lock-in amplifiers. By using two coil triplets (corresponding to 18 lock-in amplifiers), it was possible to reconstruct the position and orientation of head and thorax simultaneously.

The walking arena consisted of a cylinder of 225 mm diameter and 80 mm height, with the side wall covered by a pattern of black and white squares (50% probability). The squares subtended 10 degrees when viewed from the centre of the cage, and their edges were slightly blurred. The bottom of the arena consisted of a dark grey background with grey squares (side length 5 mm, 0.5 squares/cm²). The ceiling was transparent, giving a clear view of the opaque ceiling, 18 cm above, of the surrounding cage (opaque white with dark grey squares). Mean luminance was 150 cd/m² at the walls and 800 cd/m² at the ceiling.

**Flies and coils**

The experiments were performed on first and second generation female blowflies bred in the laboratory: *Calliphora vicina*, *Lucilia cuprina* and *Lucilia caesar*. For experiments on *Calliphora vicina* we used coil triplets of 2 mm diameter with 40 windings for the head and 80 windings for the thorax. Van Hateren and Schilstra (1999) performed control experiments on flying *Calliphora vicina* with the same type of coil triplets (2 mm and 40 respectively 80 windings), and concluded that the effect of the coils on the normal movements of the flies was negligible. Because the angular accelerations of walking flies are lower than those of flying flies, we expect that the effect of the coils on walking flies is negligible as well. For *Lucilia*, which are lighter than *Calliphora vicina*, we chose lighter coils (see Table 4.1). The diameter of the head coil for *Lucilia* was 1 mm, because a 2 mm coil would touch the thorax coil.
Table 4.1. Fly species and coil choice

<table>
<thead>
<tr>
<th></th>
<th>Calliphora vicina</th>
<th>Lucilia cuprina</th>
<th>Lucilia caesar</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Head</td>
<td>Thorax+ Abdomen</td>
<td>Head</td>
</tr>
<tr>
<td>Weight (mg)</td>
<td>6</td>
<td>124</td>
<td>6</td>
</tr>
<tr>
<td>Total weight (mg)</td>
<td>130</td>
<td></td>
<td>45</td>
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<tr>
<td>Coil diameter (mm)</td>
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<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Windings</td>
<td>40</td>
<td>80</td>
<td>40</td>
</tr>
<tr>
<td>Triplet weight (mg)</td>
<td>0.8</td>
<td>1.6</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Table 4.1. Fly species and coil choice

Preparation, experiment and data processing

The preparation of the experiments was similar to that described in van Hateren and Schilstra (1999), with the difference that, for walking experiments, the tips of the wings of the flies were clipped. The flies were fixed in a holder with two soft pads which prevented movements of the animals while allowing access to the dorsal side, and the tips of the wings were clipped. Care was taken that the legs and wings were not damaged by clamping. Subsequently the hairs on the dorsal side of the head and thorax were cut in order to allow the attachment of coils. First, the head coil triplet was attached with cyanoacrylate on top of the head, its wire was allowed to make a loop and was connected to the top of the thorax. Second, the thorax coil triplet was attached on the dorsal side of the thorax, and the two wires were connected to the last segment of the abdomen, leaving a small reserve in order to allow the abdomen to move freely. The coil triplets were attached in alignment with the three main axes (longitudinal, transverse and vertical) of the insect’s head and thorax. Subsequently the flies were fed with water and sugar, were released in the walking arena, and the recording was started. The flies were fed again every two to three hours and the wires were checked for loops which would have hindered free walking.
Although the coil triplets were attached as much as possible in alignment with the three main axes of the head and thorax, respectively, they could not be perfectly aligned. Small offsets of coil triplets’ orientations were corrected by centring the roll and pitch distributions of the thorax on zero, choosing the thorax yaw offset such that the distribution of the transverse velocity centred on zero, and centring on zero the distribution of the relative head yaw in the thorax reference system. These corrections were smaller than 10 degrees. The reconstructed positions and orientations of the head and the thorax were subsequently low-pass filtered with a two-sided exponential filter, with a time constant of 15 ms for position, 5 ms for head orientation and 3 ms for thorax orientation.

We defined as “walking” the episodes having a velocity (low-pass filtered with a double sided exponential, time constant 150 ms) greater than 0.8 cm/s. For the analysis in this chapter we used only the data recorded during walking on the floor of the cage, excluding walking on the walls or ceiling. We obtained approximately 75 minutes of walking from 3 Calliphora vicina, 29 minutes from 2 Lucilia cuprina and 8 minutes from Lucilia caesar.

Angular coordinates

The orientation of an object in a three-dimensional space can be represented by a sequence of three rotations about each of the three orthogonal axes of a reference system, starting from a reference orientation (see Haslwanter, 1995). The reference systems can be divided in two types. In active reference systems, the axes of the reference system remain fixed (i.e. a fly rotates by an angle $a_1$ about the $z$ laboratory axis, then by an angle $a_2$ about the $y$ laboratory axis, and finally by an angle $a_3$ about the $x$ laboratory axis). In passive reference systems, the axes rotate together with the object (i.e. the fly rotates by an angle $a_1$ about its vertical axis, then by an angle $a_2$ about its resulting transverse axis, and finally by an angle $a_3$ about its resulting longitudinal axis). The resulting orientations using the two reference system types above are generally different, even if the angles and the order of rotations are the same. The sequence of rotations is also important: in the same reference system, an object rotated by an angle $a_1$ about axis 1, then $a_2$ about axis 2 and $a_3$ about axis 3 has generally a different final
The most natural reference system for the study of moving insects is a passive reference system; with a good choice of the sequence of rotations, each of the three angles has a consistent meaning. We chose the Fick-gimbal (which is a passive reference system) using the normal right-handed rule for the computations. For figures we used the more common aeronautical sign convention (which changes the sign of yaw and pitch). An orientation in this reference system is the result of an ordered sequence of rotations starting from a reference position: first a rotation about the vertical axis of the fly to the right (designated as yaw), followed by a rotation about the transverse axis upwards (pitch) and ended by a rotation about the longitudinal axis to the right (roll). In this reference system, the angles have a clear meaning: the yaw represents the heading, the pitch is the angle between the longitudinal axis and the horizontal plane, and the roll is the angle between the symmetry plane and the vertical plane which intersects it on the longitudinal axis.

Simple time differentiation of the yaw, pitch and roll yields “coordinate velocities” (e.g. velocity of pitch change), not angular velocities about the own axes (e.g. angular velocity about the transverse axis). However, the velocities and accelerations about the own axes are the most useful for the study of rotational optic flow components or torques rotating the fly. The angular velocities can be calculated from the rotation matrices from the reference orientation to the current orientation for each measured sample, using equation A4 from Haslwanter (1995). Subsequently, the rotation matrix from one sample to the next (differential rotation matrix) can be calculated by multiplying the inverse of the rotation matrix of the sample with the rotation matrix of the next sample. The yaw, pitch and roll velocities can be easily calculated by identifying the yaw, pitch and roll changes in the own system between successive samples (using the same equation A4 from Haslwanter, 1995), and dividing them by the time interval between samples (i.e. 1 ms). Angular accelerations are obtained by time differentiation of the angular velocities. The total angular velocity (about the momentary axis of rotation) can be calculated from the differential rotation matrix by using equations 22 and 23 from Haslwanter (1995).
Results

Figure 4.1 presents one second of walking of a *Calliphora vicina*. The curled line shows the trace described by the thorax and the short line segments show the yaw orientation of the head (red) and thorax (black), with a time interval between successive segments of 10 ms. The intersection between the line segments and the trace indicates the position of the thorax. The fly starts walking from the top right of the figure, and proceeds via the bottom left to the top left. To a first approximation, the head and thorax appear to have the same orientation, while being differently oriented than the direction of walking. The difference between the orientation of thorax and the direction of walking was discussed in the previous chapter; the present chapter concentrates on the relationship between head and thorax movements.

Thorax orientation during turns changes saccadically both in flying flies (Schilstra and van Hateren, 1998b) and in walking flies (chapter 3). The saccades of the thorax occur with a frequency of 5-10 Hz and between saccades the orientation is relatively stable. We found the saccades of the head and thorax from the peaks of their total angular velocities (in their own reference systems) and marked their positions in Figure 4.1 with large dots (head) and small dots (thorax). It is apparent that each saccade of the thorax has a corresponding head saccade, and head saccades reach their peak velocity earlier than the corresponding thorax saccades.

Figure 4.2 depicts the yaw, pitch and roll of the head and thorax for the short walk shown in Figure 4.1. Thick lines indicate head orientations and thin lines correspond to thorax orientation. Large changes in the orientation angles (yaw, pitch and roll) of the head and thorax are synchronized, with a frequency of approximately 10 Hz. These saccadic changes are abrupt, and between saccades the orientation is relatively steady. The difference between head and thorax orientation is usually small. While yaw, pitch and roll changes in flying flies occur in specific sequences - depending on the manoeuvre performed (Schilstra and van Hateren, 1999), the pitch and roll of walking flies appear to be uncorrelated with the yaw. Moreover, changes in pitch and roll are small compared with yaw changes, therefore we will concentrate here on the investigation of yaw.
From the total angular velocity of the head (in its own reference system) we detected the saccades of the head and averaged the yaws and yaw velocities in the 100 ms windows centred on the maxima of the angular velocity of the head. Averaged results from saccades to the right with sizes between 10-20 degrees in walking flies and 20-40 degrees in flying flies are shown in Figure 4.3. The results are based on 1550 saccades from walking *Calliphora vicina*, 667 from walking *Lucilia* and 176 saccades from flying *Lucilia*. The results from walking *Lucilia cuprina* and *Lucilia caesar* are pooled because the
average saccades from each individual fly measured from these two species were similar. Saccades to the left, and saccades of different sizes were similar (mirrored, respectively scaled). It is apparent that head saccades have higher velocities and shorter durations than thorax saccades, across species and for walking as well as flying.

In walking *Calliphora* and *Lucilia*, the head and thorax start rotating simultaneously, with the head turning faster than the thorax. The head reaches its maximum angular velocity approximately 5 ms earlier than the thorax, and has a higher peak angular velocity than the thorax. The head finishes its saccade earlier, and in the last part of the saccade the thorax still rotates.
while the head maintains its final orientation through a counter rotation with respect to the thorax. In flying *Lucilia cuprina*, the average saccade is similar to the saccades described in flying *Calliphora* by van Hateren and Schilstra (1999): the times of the maximum angular velocities of the head and thorax coincide, and at the beginning and end of the saccades the thorax rotates while the head is kept stable, thus the head then rotates with respect to the thorax. The main difference between saccades during walking and flying is that head and thorax saccades are symmetrical during flight.

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**Figure 4.3.** Average yaw and yaw velocity during saccades. Averages are calculated on saccades of 10-20 degrees in walking flies and 20-40 degrees in flying flies. (A-C) Head (h) and thorax (t) yaw for walking *Calliphora* (A), walking *Lucilia* (B) and flying *Lucilia* (C). (D-F) Yaw velocity of head (h) and thorax (t) for walking *Calliphora* (D), walking *Lucilia* (E) and flying *Lucilia* (F). Note that yaw velocity peaks are aligned in flight, while in walking the peak velocity of the head occurs earlier than the peak velocity of the thorax.
(their maximum angular velocities are aligned), while during walking they are asymmetrical (they are aligned by the starts of the saccades).

Movements of the head and thorax have consequences for the functioning of the fly’s visual system. Two factors determine the movements of the eyes: first, thorax movements, which induce rotational and translational components of optic flow corresponding to the simplified case of a walking fly with its head fixed to the thorax, and second, head movements superimposed on thorax movements, which induce a (supplementary) rotational optic flow. The rotational optic flow in walking flies is mainly due to yaw rotation because pitch and roll changes are small and have lower angular velocities than yaw changes.

It is possible to evaluate the effect of the thorax saccadic behaviour on the optic flow in walking *Calliphora* by comparing the measured thorax yaw velocities of a fly with hypothetical yaw velocities of its thorax while walking on the same path and turning smoothly through the same orientations. The non-saccadic yaw can be constructed from the measured thorax yaw by finding, in the middle of each yaw plateau, the moments and yaws halfway between the times of two successive saccades. The non-saccadic yaw can be subsequently interpolated by a cubic spline. Figure 4.4A illustrates an example of measured thorax yaw (thick line), the yaw angles (dots) found halfway between successive saccades, and the non-saccadic yaw (thin line). The non-saccadic yaw velocity can be obtained through time differentiation of the non-saccadic yaw angle. It is apparent from Figure 4.4A that, compared with the corresponding non-saccade yaw velocities, the saccades of the thorax introduce periods of lower yaw velocities (during the yaw plateaus) and higher yaw velocities (between yaw plateaus). The result can be observed in Figure 4.4B, representing the probability density functions of measured (thin line) and non-saccadic (dashed line) yaw velocities: some of the middle non-saccade yaw velocities (20 – 200 degrees/s) are pushed either to lower or to higher velocities. Movements of the head relative to the thorax cause a further reduction of yaw velocities in the range of 40 – 450 degrees/s.

A consequence of this is that it becomes possible to divide walking episodes in two groups, one consisting of the periods around saccades, and the other consisting of periods between saccades. This separation can be obtained as
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Figure 4.4. (A) Thorax yaw (thick line); circles indicate yaw values midway between successive saccades; a non-saccadic yaw can be constructed from these values through cubic spline interpolation. (B) Probability densities of yaw velocities of the head (h), thorax (t) and non-saccadic thorax (tns). Note that through thorax and head saccades the probability of low velocities is increased. (C) Probability densities of yaw velocities of the head (h) and thorax (t) during saccades. (D) As in (C), between saccades; the scales are different. (E) Cumulative probability of yaw velocities of head (h), thorax (t) and non-saccadic thorax (tns), obtained from data shown in (B).
follows: for each head saccade detected from the total angular velocity, we find the times when 10% and 90% of the head turn was completed, and we extend the resulting interval by 50% at the beginning and 100% at the end of saccades (different values are used because of the asymmetry of thorax and head yaw angular velocities). The episodes determined in this way will be defined as “during saccades”, and the remaining walking will be defined as “between saccades”. This algorithm yields a good approximation of the moments of onset and end of thorax orientation change. The proportion of time “between saccades” is slightly overestimated, because small saccades (below 2-3 degrees) cannot be reliably discriminated from the noise. The proportion of the walking time that was classified as “during saccades” was 21%, with the remaining 79% classified as “between saccades”.

The distributions of yaw velocities of the head and thorax for the two classes (during respectively between saccades) were calculated and the results are shown in Figures 4.4C and 4.4D. During saccades (Figure 4.4C) the yaw velocities reach values of 1500-2000 degrees/s (beyond the scale shown in the figure), with the head and thorax 90% of the time slower than 580 degrees/s and 500 degrees/s, respectively. Between saccades (Figure 4.4D) the yaw velocities are much lower than during saccades, with the head 90% of the time slower than 55 degrees/s and the thorax 90% of the time slower than 110 degrees/s.

Figure 4.4E shows the cumulative distributions corresponding to the probability density functions of Figure 4.4B. Shown are the distributions of the non-saccadic yaw velocities (tns) of the thorax (dashed line) and the yaw velocities for the head (thick line) and thorax (thin line). The result of pushing the yaw velocities towards higher and lower velocities is that, through saccades, the thorax keeps its angular velocities low (i.e., lower than approximately 50 degrees/s) for a higher proportion of time compared to a smoothly turning fly. Because of the mobile head, the proportion of time when the eyes can be held relatively steady increases even further.

Based on 5713 saccades detected from 3 walking Calliphora vicina, we calculated the average saccade duration versus saccade size and found that the duration of the saccades is approximately independent of the size of the saccades. We also found that yaw velocities of the head and thorax during saccades increase roughly linearly with the saccade size (Figure 4.5A). The
average angular velocities of the head and thorax for saccades between 0 and 5 degrees are somewhat higher; this can probably be explained by the fact that some of the small saccades cannot be distinguished from the noise. Figure 4.5B depicts the peaks of the yaw acceleration of the head and thorax (one peak corresponds to the first half of the saccade and the other to the second half). The angular accelerations of both head and thorax are higher during the first phase of the saccade (acceleration) than during the second phase (deceleration). The asymmetry is more pronounced in the thorax than in the head, and increases with the saccade size.

Discussion

Thorax orientation in flying tethered flies was found to change in a series of short, fast turns (Land, 1973; Wagner, 1986). The findings of Land (1973) were disputed by Geiger and Poggio (1977), but confirmed by Schilstra and van Hateren (1998), who showed clear evidence of the saccadic turns in freely flying flies by using a measuring technique with a high spatial and temporal resolution. We applied the same technique to walking flies, and we showed that also walking blowflies change the orientation of the thorax by...
using short and fast, saccade-like turns (see Chapter 3). By using saccades, walking flies in effect increase the proportion of time when the thorax has low angular velocities. By increasing the proportion of low angular velocities, two positive effects for vision are attained: the blurring due to photoreceptor integration times and the rotational component of the optic flow are reduced.

The three-dimensional structure of the environment can be reconstructed from the translational optic flow (Koenderink, 1986). Although the three-dimensional structure can still be reconstructed from a complex optic flow containing both rotational and translational components (Longuet-Higgins and Pradzny, 1980), the fact that blowflies increase the proportion of time with low angular velocities and thus low rotational optic flow makes it easier for the fly brain to process the optic flow. Rotations consume energy proportional to (a power of) the angular velocity due to the friction, and proportional to the squared angular velocity due to acceleration and deceleration. This energy is lost, thus saccadic changes of the orientation are less energy-efficient than corresponding non-saccadic changes would be. Apparently, this energy investment is justified by the resulting benefits for visual processing.

The eyes of the fly are fixed to the head. Although the photoreceptors can slightly move with respect to the facets, resulting in angular shifts up to a few degrees ( Franceschini and Chagneux, 1997), the corresponding angular velocities are small compared with the velocity of the turns. Therefore, the optic flow is almost completely determined by the movements of the head. The head can move with respect to the thorax, and its posture is controlled through different muscles (Straussfeld et al., 1987). In tethered flies, the head was found to compensate changes of thorax roll and pitch, and to perform saccadic movements in synchrony with the saccades of the thorax (Hengstenberg et al., 1986; Hengstenberg, 1992). This was also found in freely flying flies (Schilstra and van Hateren, 1998b), and the saccades of the head were found to be faster than those of the thorax.

Contrary to head rotations in flying flies, little was known about head rotations in walking flies. In this chapter we showed that head and thorax saccades occur at approximately the same time, and that the angular velocities of the head are higher than those of the thorax. The head consequently per-
forms a saccade in less time than the thorax. Immediately after the head saccade is completed and while the thorax still performs its saccade, the head is held stable with respect to the laboratory by effectively counter-rotating with respect to the thorax.

The supplementary movements of the head relative to the thorax increase even further the proportion of time during which the head rotates relatively slowly, thus further increasing the time available for the analysis of the visual surround. The overall effect of the combined thorax and head rotations during a saccade can be evaluated by comparing the head yaw rotations with the hypothetical non-saccadic rotation of the thorax: the probability of eye velocities under 20 degrees/s is substantially increased (Figure 4.4B), without decreasing the proportion of time with eye velocities lower than approximately 130 degrees/s (Figure 4.4E). This value is close to the characteristic velocity $v_c$ (van Hateren, 1992) above which vision is significantly blurred. The angular sensitivity of a single blowfly photoreceptor is 1.5 degrees (Smakman et al., 1984) and the integration time of the photoreceptors is approximately 10 ms at the light levels in our experiments, resulting in a $v_c$ of approximately 150 degrees/s. The effect of thorax and head saccades thus maximizes the probability of low head angular velocities, without increasing the proportion of time with significantly blurred images.

In flying *Calliphora vicina*, the peaks of the yaw velocities of the head and thorax during a saccade occur at precisely the same time (van Hateren and Schilstra, 1999). The saccade of the head is faster, and the head is kept stable, by counter-rotations of the head, at the beginning and end of the thorax saccades. We obtained similar results for flying *Lucilia*. In contrast, we found that in walking blowflies the peak of the thorax yaw velocity occurs approximately 5 ms later than the peak of the yaw velocity of the head. Furthermore, the thorax and head saccades are started simultaneously. Similar to flying flies, the head is held stable by a counter-rotation after the head completes its saccade and while the thorax still rotates. A possible reason for this difference between turns in walking and flying flies could be that in flying, turns are performed through a complex sequence of yaw, pitch and roll rotations (Schilstra and van Hateren, 1999). An early head saccade might mechanically destabilise the fly through the counter-yaw induced in the thorax, or at least complicate the turning sequence. In walking flies, at least three legs (in tripod coordination) or four legs (tetrapod coordination)
keep contact with the floor (Strauss and Heisenberg, 1990), thus the legs can transfer the momentum induced by head rotations immediately to the floor. Blowflies might take advantage of this stability by rotating the head immediately.

Between saccades, the head has a higher probability than the thorax of low yaw, roll and pitch velocities. There are many systems contributing to this stabilisation of the head during walking: feedback using the rotational optic flow (Egelhaaf and Borst, 1993; Krapp and Hengstenberg, 1996), feedback from the halteres (Nalbach, 1992), feedback from the prosternal organs (Preuss and Hengstenberg, 1992), and feedback from leg proprioceptors (Hengstenberg, 1992). The visual system is tuned to slow rotations and the haltere system is tuned to fast rotations (Drosophila: Sherman and Dickinson, 2003; Sherman and Dickinson, 2004; Frye and Dickinson, 2004). It is likely that between saccades the most important stabilisation system is the visual system. The halteres may mediate the stabilisation response of the head during the late phase of the thorax saccade in walking flies, and during both the early and late phases of the thorax saccade in flying flies. After the head saccade is completed and the thorax saccade is still finishing, the head remains stable by counter-rotating with respect to the thorax. A possible mechanism is that the walking saccade is initiated simultaneously in head and thorax and that the head stabilisation due to the haltere system is suppressed. When the head completes its saccade, the haltere stabilisation system becomes active and keeps the head stable while the thorax completes its saccade.

Angular velocities are lower during walking than during flying. A possible reason is that the translation velocity is much lower during walking than during flying, and therefore the flies do not need to react as fast. Using lower angular velocities decreases the energy consumption. Moreover, walking flies cannot use large single saccades, because the legs in contact with the ground normally only move the insect forward and the metachronal waves on either side of a walking fly cannot be decoupled (Strauss and Heisenberg, 1990). Therefore, large turns are performed in 2-phase and 3-phase manoeuvres. During these manoeuvres, the orientation is changed in a series of saccades (Chapter 3). The observed higher walking velocities during larger saccades might help to increase the velocity of turning.
The duration of saccades in walking and flying blowflies is comparable: in flying flies, the duration varies slightly with saccade size, between 20 and 30 ms (Schilstra and van Hateren, 1999), and in walking flies the duration of approximately 25 ms is independent of saccade size. The strong similarity between flying and walking saccades and saccade durations suggests that the same part of the blowfly brain controls the saccades in both flying and walking.

Studies of the visual processing of natural optic flow in walking or flying blowflies (e.g. Kern et al., 2001; Lewen et al., 2001) generally make one or more of the following simplifications: the fly rotates smoothly, the head is oriented similarly as the thorax, and the longitudinal axis of the thorax is considered tangent to the walking path. However, none of these simplifications are justified, and they significantly change the characteristics of the optic flow as received by the eyes. The orientation of the thorax is often misaligned with the walking path (Chapter 3), thus the optic flow is often eccentric and the visual system must be able to cope with this eccentricity. Furthermore, the saccades of the thorax and head push the angular velocities partly to high velocities as well as to low angular velocities. Consequently, the resulting optic flow is very different from the one resulting from a smooth trajectory of eye translations and rotations.

References


Chapter 4


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Chapter 4


