

Chapter 5

Blowfly flight and optic flow: head movements during flight

SUMMARY

The position and orientation of the thorax and head of flying blowflies (*Calliphora vicina*) were measured using small sensor coils mounted on thorax and head. During flight, roll movements of the thorax are compensated by counter rolls of the head relative to the thorax. The yaw turns of the thorax (thorax saccades) are accompanied by faster saccades of the head, starting later and finishing earlier than the thorax saccades. Blowfly flight can be divided into two sets of episodes: 'During saccades', where high angular velocities of up to a few thousand degrees per second are reached both by thorax and head, and 'Between saccades', where the thorax and in particular the head are well stabilized in orientation. Between saccades, the angular velocities of the head are approximately two times lower than those of the thorax, and lie mostly in the range of 0-100 °/s for any rotation (yaw, pitch, and roll). These velocities are low enough to keep the visual blur attributable to rotation limited. It is argued that the split in periods where either rotational optic flow dominates ('During saccades') or translatory optic flow ('Between saccades') is helpful for processing optic flow when signals and neurons are noisy.

INTRODUCTION

Blowflies are well-known for their agility during flight, performing fast and acrobatic flight manoeuvres. This flight behaviour must have important consequences for vision. First, fast turns can lead to motion blur, impairing vision of spatial details (Srinivasan and Bernard, 1975). Second, turns interrupt the pattern of optic flow that reveals the three-dimensional structure of the surroundings during translation (Koenderink, 1986). In principle, these adverse effects of flight behaviour can be alleviated by compensating eye movements (Carpenter, 1988; Land, 1973, 1975; Steinman and Collewijn, 1980).

For blowflies, with their compound eyes fixed to the head, these eye movements

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correspond to head movements. The head of blowflies has appreciable freedom of movement, because the neck is flexible and controls head posture via an elaborate system of muscles (Strausfeld *et al.* 1987; Hengstenberg, 1992). Experiments on tethered flies show that head movements can indeed be used to partly compensate thorax rotations (roll: Hengstenberg, 1986, 1992; yaw: Land, 1973, 1975). In the study of Land (1973, 1975), thorax rotations in the yaw direction (rotation around a vertical axis) occurred in fast steps (called thorax saccades). Between the saccades, the thorax and in particular the head were more stable. These experiments were subsequently challenged by Geiger and Poggio (1977), who argued that the saccadic behaviour was an artifact attributable to the appreciable mass and inertial momentum added to the animal by the tether. With a more light-weight tether, they were unable to repeat Land's observations. Subsequent measurements on insects in free flight, however, gave support to the existence of at least thorax saccades (*Syritta*: Collett, 1980; *Musca*: Wagner, 1986). Unfortunately, with the available techniques (video and film), these experiments could not resolve head movements, gave no or only limited information on roll movements, and had a rather low temporal resolution (typically 20 ms).

With the development of a modified search coil technique suitable for measuring position and orientation in (almost) freely flying blowflies (Schilstra and van Hateren, 1998a,b, 1999), it has now become possible to readdress this question of how the head and thorax move during flight. The new technique was specifically developed to give information on the spatiotemporal input received by the blowfly eye during normal flight: this input can be reconstructed from the stimuli on the walls of the flight cage, and the measured eye positions and orientations. The statistical properties of this input play an important role in recent theories of early visual processing (see e.g. van Hateren, 1992a,b). A full analysis of this input is beyond the scope of the present article, however. Instead, it will concentrate on the detailed properties of the head movements occurring during thorax saccades (see the accompanying article, Schilstra and van Hateren, 1999). It is shown that free flight behaviour of blowflies can indeed be separated into two sets of episodes ('during saccades' and 'between saccades'), which have strongly different patterns of rotational optic flow.

MATERIALS AND METHODS

Position and orientation measurement

Position and orientation of flying blowflies were measured as described in the accompanying article (Schilstra and van Hateren, 1999; see Schilstra and van Hateren, 1998a, for further details on the method). Briefly, pairs of coils surrounding the flight cage (40×40×40 cm³) generate magnetic fields that induce voltages in small sensor coils attached to a blowfly (female *Calliphora vicina*). These voltages are transferred via a thin cable, hanging down from the fly's abdomen, to amplifiers, and can be used to infer the fly's position and orientation at a rate of 1000 readings

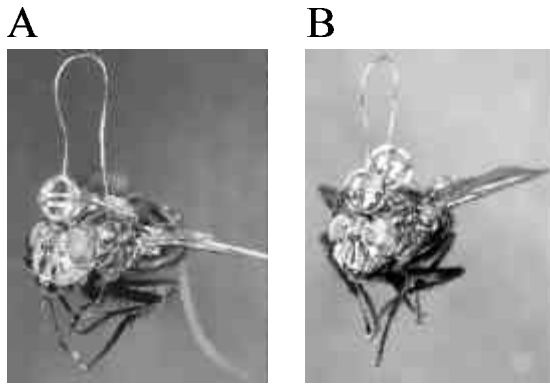


Figure 1. (A) Blowfly with coils mounted on the head. The wire loop provides freedom of movement for the head. The wire runs via thorax and abdomen to the bottom of the flight cage. (B) Blowfly with coils mounted on head and thorax. All 2×6 degrees of freedom are measured simultaneously using two sets of 9 lock-in amplifiers each.

per second. Whereas in the accompanying article coils were attached to the thorax, they are here either attached to the head only (Fig. 1A), or to both thorax and head (Fig. 1B) whilst using two sets of sensor coils and amplifiers. The coils attached to the head are lighter (0.8 mg, 40 windings of 2 mm diameter) than those attached to the thorax (1.6 mg, 80 windings of 2 mm diameter). The size of the head coils was chosen as a reasonable compromise, which still gives an adequate angular resolution (signal-to-noise ratio) without disturbing the head motion significantly (see Results for control experiments). As shown in Fig. 1, the cable goes from the head coils to the thorax via a loop of 8-10 mm height, which is flexible enough to enable virtually unrestrained head movements (see Results for control experiments). As in the accompanying article, the walls of the flight cage were covered with photographs of natural scenes, and the luminance was 150 cd/m² for the walls and 800 cd/m² for the ceiling.

Preparation and flight recording

Preparations for attaching the coils to the head are similar as described for the thorax (Schilstra and van Hateren, 1999). On the dorsal side of the head, hairs hindering mounting of the coils were cut away, and the coils were glued with a tiny amount of (viscous) cyanoacrylate. The position of the coils is such that only a small part of the field of view of the compound eyes is restricted. This restriction appears to induce no measurable changes in thorax and head movements, as indicated by experiments with different coil sizes (1, 2, and 3 mm), restricting different amounts of the field of view. The coils restrict the field of view of the ocelli (3 single lens eyes on top of the head) more severely, though not completely. The influence of this on thorax and head movements is probably also small: first, because we did not find differences in (thorax) flight behaviour between flies with or without head coils, and second, because the role of the ocelli for head posture appears to be negligible (Schuppe and Hengstenberg, 1993).

The orientation of the coils was estimated, and deviations from the standard orientation were corrected in the final reconstruction. This yielded angles relative to an orthogonal coordinate system fixed to the head. This system is defined by a plane parallel to the chitinous surface at the back of the head capsule, and the plane of

symmetry of the head. Position of the head is calculated as the origin of the head coordinate system, a point approximately midway between the compound eyes.

The cable forming the loop coming from the head coils was glued to the thorax, led to the abdomen, and was glued to either the last or last but one segment. For experiments with a second set of coils (on the thorax), the second cable was also glued to the abdomen. The two cables running to the bottom of the cage were loosely twisted in order to keep them together during flight.

For most of the analysis below, the results of experiments on 4 flies with coils on both the head and thorax were used. The head movements measured in these experiments were consistent with experiments on 13 flies where only head movements were measured. Moreover, control experiments were performed (with various coil configurations) on another 17 flies. For the averages and histograms of Figs. 4-6, only flights of at least 2 seconds duration were selected, yielding a total flight time of 703 seconds containing 6697 (detected) saccades.

Angular coordinates

Angles are defined according to a Fick system (see Haslwanter, 1995), where the orientation of an object is given by a rotation matrix, formalizing an ordered sequence of yaw, pitch, and roll rotations of the object (Fig. 3, inset). The rotation matrix describes the orientation of an object relative to a fixed, external coordinate system, which will be called the laboratory system below. Apart from this, the angular orientation of the head is in several places also given relative to the thorax. This is calculated by multiplying the inverse of the thorax rotation matrix with the head rotation matrix (Haslwanter, 1995). Angular velocities are not calculated in the laboratory coordinate system, but in the coordinate systems rotating with either the thorax or the head. These velocities are obtained from the (differential) rotation matrix describing the rotation of, e.g., the thorax from one millisecond to the next. Once this rotation matrix is obtained, the yaw velocity, pitch velocity, and roll velocity are easily calculated (with Eq. A4 of Haslwanter, 1995). From the differential rotation matrix it is also possible to calculate the rotation velocity vector (analogous to Eqs. 23 and 25 of Haslwanter, 1995), which then yields the total angular velocity (analogous to Eq. 22 of Haslwanter, 1995). Finally, from the angular velocities in the thorax and head coordinate systems one obtains the corresponding angular accelerations by time differentiation.

RESULTS

Mounting coils on the head rather than on the thorax increases the risk of artifacts. Not only is the mass ratio worse (coils : head = 0.8 : 8 mg, coils : thorax = 1.6 : 80 mg), also the extra load on the neck muscles due to the loop connecting head and thorax may be a problem. Therefore, a series of control experiments was done to assess the extent of the mechanical disturbance attributable to the coils and loop.

Below, these experiments are presented first, and subsequently the results of the free-flight experiments are described.

Control experiments

Two types of experiments were designed to estimate the effects of the sensor coils and cable loop on the head motion of the fly. The first experiment determines whether the stiffness of the cable loop running from the head to the thorax affects the head motion. The second experiment investigates how much mass can be added to the head before normal head motion is significantly disrupted. Both experiments were based on measuring the compensating head roll reflex of blowflies: when the thorax is suddenly rolled, the head rolls partly back after a short delay (Hengstenberg, 1986, 1992). A tether was glued to the dorsal part of a fly's thorax, and the fly was suspended such that it could be rotated around its long axis without changing its position. The fly was placed inside a perspex cylinder (diameter 6 cm, length 18 cm), of which the lower half was covered with black paper and the upper half with frosted paper, brightly lit from the outside. Despite the tether, flies usually tried to fly for periods of variable duration. During such flight, the fly was occasionally subjected to an abrupt roll of 90°.

In the first experiment, the head and thorax were both recorded on video at a rate of 50 fields (=half-frames) per second. Compensating head rolls were recorded for a series of thorax rolls, both with and without the cable loop running from the head to the thorax, but without any additional mass (i.e., no coils). Segments of the video were digitized, and subsequently analyzed field by field using a public domain graphics browser (Paint Shop Pro). From these measurements, the thorax roll (relative to the laboratory) and the compensating head roll (relative to the thorax) were determined. Figure 2A shows an example of a measurement. First, no loop was present (open circles, average of 5 rolls), second, a loop was attached to the head and thorax of the same animal, and the experiment was repeated (plusses, average of 10 rolls), and finally, the loop was removed (crosses, average of 4 rolls). As can be seen, the presence of the loop has no discernable effect on the compensating roll reflex: both with and without loop, the head compensates about 50% of the thorax roll, with a delay of a few video fields (of 20 ms each). The head roll reflex we find here is similar to that reported by Hengstenberg (1986, 1992). We performed this experiment on two other flies, and found consistently no effects of the loop on the head roll reflex. Furthermore, we observed that manually moving the (loosened) thorax end of the loop over realistic distances had negligible effect on the head position. We conclude that the stiffness of the loop is small enough for the present purpose.

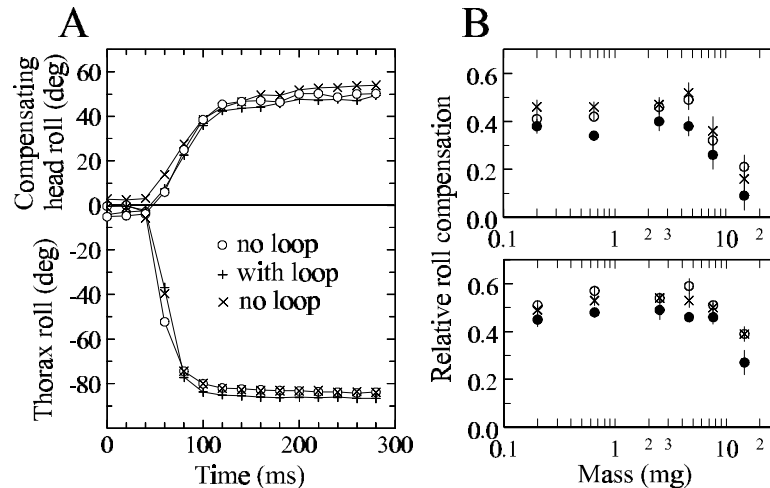


Figure 2. Control experiments for checking the influence of coils and loop on normal head movements. (A) Imposed thorax roll (relative to the laboratory) and compensating head roll (relative to the thorax), measured by an analysis of video recordings of tethered flies. The open circles show the response when the head is completely free, the pluses with a loop connecting head and thorax (but no coils present), and the crosses after the loop was removed. (B) Relative roll compensation (size of compensating head roll divided by size of thorax roll) as a function of mass mounted on the head. Measurements were done with light-weight sensor coils; the symbols show the roll compensation at different times after the thorax roll: 50 ms (filled circles), 150 ms (crosses), and 450 ms (open circles). Upper graph: rolls to the right, lower graph: rolls to the left. See text for further explanation.

In the second control experiment, the head orientation was (again in tethered flies) measured at a rate of 1 kHz with a very light-weight system of sensor coils, made of coils with 20 windings and a diameter of 1 mm. The total system had a mass of approximately 0.2 mg (*cf.* 8 mg for the head). Movements were also recorded on videotape, enabling a post-hoc visual check on the head roll reflex and on when the fly had been flying. Small pieces of metal with different masses were subsequently attached to the head by sticking them to a tiny amount of grease, and the compensating head roll was measured. Figure 2B shows the results for rolls of approximately 90° to the right (upper panel, average of 20-40 rolls) and to the left (lower panel, average of 20-40 rolls). The relative roll compensation (=size of compensating head roll divided by size of thorax roll) is given at three particular times after the start of the thorax roll: 50 ms (filled circles), 150 ms (open circles), and 450 ms (crosses). The difference between leftward and rightward compensation lies within the normal variation one finds for the roll compensation: this varies somewhat between flies, and even for a single fly it may vary as a function of time or roll direction. As can be seen from the roll compensation as a function of the added mass, the roll reflex is only disturbed for the largest masses (7.6 mg and 14.5 mg). In these cases, we also observed, in the traces with 1 ms resolution, transient artifacts immediately after the initiation of the thorax roll. For the smaller masses (0.2, 0.65, 2.5, and 4.6 mg), the compensating head rolls were free from this artifact, and all similar. It thus appears that the blowfly head has a certain amount of mechanical reserve to carry and move loads that go beyond its own mass (8 mg). For rotation, it is not just the mass, but rather the added inertial momentum that is

important. Because the coils are mounted on top of the head, this problem is larger for roll and pitch movements than for yaw movements (because in the latter case the axis of rotation goes approximately through the centre of mass of the coils, minimizing the effective inertial momentum). From the fact that the roll movement is only affected for larger masses, we conclude that the mass of the standard coil system used for the head (0.8 mg) is not expected to have a large influence on head rotations. Nevertheless, we show below (see the section 'Head pitch oscillations') that there are subtle effects on the small head oscillations in the pitch direction that are induced by the wing beat.

Angular motion of head and thorax

Head and thorax rotations during a typical blowfly flight are shown in Fig. 3. The upper panel shows the saccadic behaviour of both the thorax (thin line) and the head (fat line). At a rate of about 10 times per second, the yaw (a rotation around a vertical axis, see inset) changes abruptly. The size of the steps in yaw varies; most of the steps are small (up to several tens of degrees), but occasionally larger steps of up to 90° occur (Schilstra and van Hateren, 1999). The head saccades are generally faster than the accompanying thorax saccades (Schilstra and van Hateren, 1998b), starting later and finishing earlier (see insets for examples, see below for averages).

The middle panel of Fig. 3 shows the pitch (up-down rotations). Steps in pitch usually occur simultaneously in the thorax and head. Between steps, the pitch is slightly more stable for the head than for the thorax (see e.g. the traces around time 1000 ms). Furthermore, the head is held more level than the thorax; the latter is kept at a pitch of approximately 30° during flight. Much of the variation in thorax pitch has to do with varying the direction of the flight force, thus producing variations in forward and vertical speed.

The lower panel of Fig. 3 shows the roll (rotations around the length axis of the animal). The thorax makes fast and large roll movements during flight, because those are required to make turns (similar to the roll an aeroplane has to make when changing course; see further Schilstra and van Hateren, 1999). The head roll, on the other hand, is quite modest for most of the time, because most of the thorax rotation is effectively compensated by counter rolls of the head relative to the thorax (for similar results on tethered flies see Hengstenberg *et al.* 1986; Hengstenberg, 1992; for results on blowflies in free flight see Schilstra and van Hateren, 1998b). Only large thorax rolls can (but not always do) give some residual roll of the head.

Saccades can be detected from peaks in the total angular velocity of the head. Figure 4 was obtained by subsequently averaging the various angles and angular velocities over a stretch of 100 ms surrounding the detection point; this was done here for saccades with a yaw of 20° - 30° to the right. Figure 4A shows the resulting yaw for the thorax (t), the head (h), and the head relative to the thorax (h_t). The yaw of the thorax starts to change first, whilst the head is kept stable by a counter rotation of

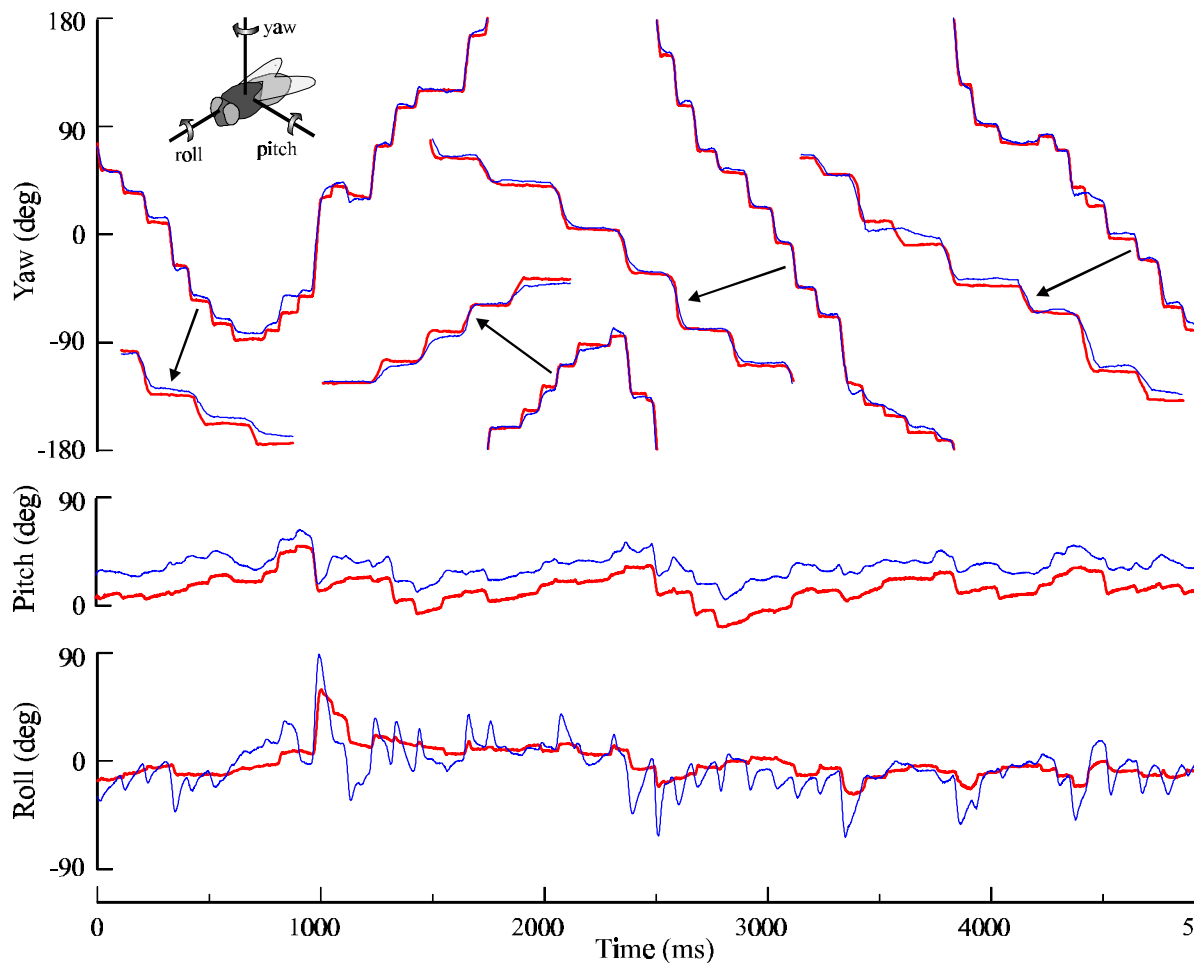


Figure 3. Angles during a typical blowfly flight. Thin lines denote thorax movement, and fat lines the corresponding head movement. Yaw, pitch, and roll are defined as shown in the inset. Further insets show enlarged views of yaw saccades (2.5× horizontally, 1.5× vertically). Note that the head saccades are generally shorter than the corresponding thorax saccades, and that the roll of the head is typically much smaller than the roll of the thorax. A movie showing a reconstruction of thorax and head movements can be found at http://hlab.phys.rug.nl/demos/flying_eye.

the head relative to the thorax. After about 10 ms, the head starts to move, faster than the thorax, and reaches its final orientation well before the thorax. This is accomplished during the final stages of the turn by again a counter rotation of the head relative to the thorax.

The pitch (Fig. 4B) changes, on average, only little during a saccade (note the difference in scale of B and A). The residual movement of the head is typically concentrated at the time when the yaw speed is high. The roll (Fig. 4C) has an entirely different behaviour than the yaw. Here, the head is not working with, but against the thorax. The head performs a counter rotation (h_t , head relative to thorax) effectively compensating the thorax rotation (t), leading to only small residual roll movements of the head relative to the outside world (h).

The angles for h and t in Fig. 4A-C are given relative to the laboratory coordinate system. For the flight control as performed by the fly's sensors and muscles, however, the coordinate systems defined by the thorax and the head are at least as important. These coordinate systems are fixed to the thorax and head, respectively, and move and rotate along with them. A yaw in the thorax coordinate system implies a torque produced by the wings around a well-defined axis of the thorax. Therefore, it can be produced, at least in principle, by a fixed program of muscular activity. The coordinate system of the head is identical to the coordinate system of the compound eye. This is the preferred system for assessing the blur caused in the compound eye by the various rotations. Furthermore, this system clarifies the visual consequences of rotational optic flow for the various visual interneurons.

Since the thorax and head coordinate systems are continuously changing in orientation, they can not yield absolute values for the yaw, pitch, and roll coordinates themselves (there is no fixed scale for these coordinates). What can be calculated unambiguously, however, are differential measures, i.e., angular velocities and angular accelerations. The current yaw velocity of the thorax, for example, is then defined as the yaw rotation per millisecond needed to rotate the thorax from its coordinate system one millisecond ago to the present thorax rotation. The yaw acceleration is the time derivative of the yaw velocity; it is proportional to the torque that must have been present around the yaw axis of the thorax (because torque=inertial momentum×angular acceleration). Figure 4D shows an example of the yaw velocities of the thorax (t, in the thorax coordinate system), the head (h, in

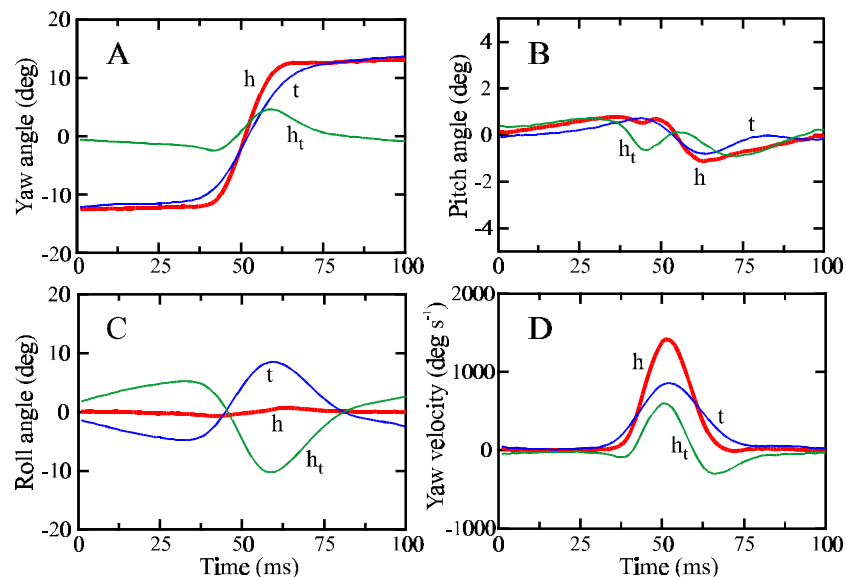


Figure 4. Average angles and angular velocities of 620 saccades to the right, with a yaw between 20° and 30°. (A) Yaw of thorax (t), head (h), and head relative to thorax (h_t). (B) As (A), for the pitch. (C) As (A), for the roll. (D) Yaw velocity of the head (h, differentially measured relative to the head coordinate system), of the thorax (t, relative to the thorax coordinate system), and of the head relative to the thorax coordinate system (h_t; this is the rotation per unit of time required to go from the previous head orientation relative to the previous thorax orientation to the current head orientation relative to the current thorax orientation).

the head coordinate system), and of the head relative to the thorax (h_t , in the thorax coordinate system). Again, we see that the head rotates shorter and faster than the thorax.

Angular velocities and accelerations during a saccade

Average angular velocities and accelerations are shown in Fig. 5 for yaws (to the left) of 10° - 20° (A and B), 30° - 40° (C and D), and 60° - 70° (E and F). Yaws to the right give similar results, and yaws of intermediate sizes give intermediate curves. The broken lines denote thorax movements, and the continuous lines head movements. The yaw (y) of the head starts later, stops earlier, and reaches higher speeds than the yaw of the thorax. For small saccades, this difference in speed is approximately a factor of two, which implies that the neck muscles contribute about as much to the angular speed of the head as is contributed by the flight muscles, rotating the thorax. For larger saccades, the increased angular speed and acceleration of the head are exclusively produced by an increase in thorax speed and

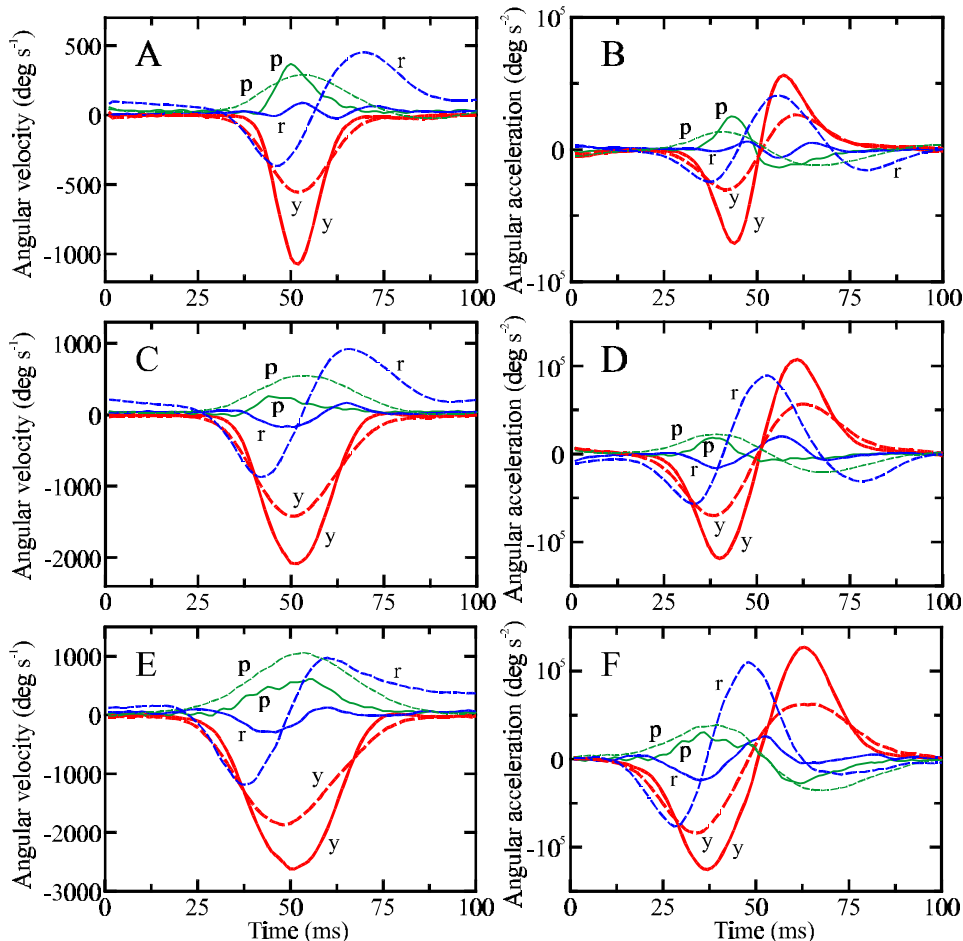


Figure 5. Angular velocities and accelerations of the head (continuous lines) and thorax (broken lines); for the head this is measured relative to the head coordinate system, for the thorax relative to the thorax coordinate system; y=yaw, p=pitch, r=roll. (A), (B) Average of 722 saccades with a yaw of 10° - 20° to the left. (C), (D) Average of 449 saccades with a yaw of 30° - 40° to the left. (E), (F) Average of 112 saccades with a yaw of 60° - 70° to the left.

acceleration. The yaw velocity of the head relative to the thorax is approximately constant (684 ± 92 °/s, mean \pm s.d.) for saccades larger than 20° . Also the yaw acceleration of the head relative to the thorax reaches a plateau for saccades larger than 20° ($5.1 \pm 0.6 \times 10^4$ °/s²).

Whereas the pitch (p) velocity of the thorax increases with increasing saccade size (Schilstra and van Hateren, 1999), the pitch velocity of the head is more variable. The duration of pitch movements of the head is generally shorter than that of the thorax. As can be seen in Fig. 5, the pitch movement of the head shows a clear ripple, with a frequency close to the wing beat frequency (between 120 and 170 Hz in blowflies). This pitch ripple will be further discussed below.

The roll (r) velocity and acceleration of the head are much reduced compared to those of the thorax. The roll velocities of the head relative to the thorax increase along with the roll velocities of the thorax to values of 1000-1200 °/s for large saccades. The maximum acceleration of the head relative to the thorax ($8.6 \pm 0.6 \times 10^4$ °/s²), is almost as large as that reached by the thorax during large saccades (about 10^5 °/s², see Schilstra and van Hateren, 1999).

Stabilizing gaze

The thorax and head movements made by blowflies during flight have consequences for the functioning of the fly's visual system. It is useful to distinguish two different sets of episodes, the first consisting of the periods surrounding the point where the thorax makes a saccade, and the second consisting of the periods between saccades. From for example Fig. 3 it is clear that such a distinction can be made: the saccades are sharp and short, and demarcate periods of more stable angular orientation. Between saccades, this stability is higher in the head than in the thorax for all three angles, and during saccades head stability is highest for the roll. To assess this quantitatively, we calculated probability densities of the velocities and accelerations of the yaw, pitch, and roll for the two sets of episodes (Fig. 6). Head saccades were detected from peaks in the total angular velocity of the head. Integrating this angular velocity over the entire saccade gives the length of the angular trajectory traversed by the head during the saccade. Subsequently, the times when 10% and 90% of this trajectory was completed were computed. Finally, the period between these two times was extended by 25% both at the onset and end, to include the early and late phases of both the head and thorax saccade. This then defines a period classified as 'during saccades'. Visual inspection of a large number of traces showed that this (somewhat heuristic) algorithm gives, independent of saccade size, a good estimate of the period during which the saccade unfolded. All other times (63% of the total flight time) are then defined as 'between saccades'.

Figure 6A shows that during saccades, the yaw velocity of the head and the thorax reach high values of a few thousands degrees per second. Yaw velocities between saccades (B) are much lower, in particular for the head relative to the surroundings (fat line). This is accomplished by yaw velocities of the head relative to the thorax (thin line) with a similar distribution as those of the thorax (broken line). This is also true for the pitch and roll velocities between saccades (D and F): the residual head angular velocities are mostly lying in a range of 0-100 °/s, significantly lower than those of the thorax. During saccades, the yaw, pitch, and roll velocities (A, C, and E) are much higher than between saccades. Whereas the yaw and pitch velocities of the thorax and head are similar during saccades (A and C), this is different for the roll velocity (E). In the roll direction, the head is always better stabilized than the thorax, even during saccades.

The lower row of Figure 6 gives the accelerations corresponding to the upper row. As expected, the yaw acceleration of the head is much larger during saccades than that of the thorax. The reverse is true for the roll: head accelerations are smaller than thorax accelerations, both during and between saccades. Note that the accelerations of the head relative to the thorax are in general similarly distributed as the accelerations of the thorax. This matching of effective neck muscle performance to effective flight muscle performance is a necessary requirement for an effective gaze stabilization.

Head pitch oscillations

Single traces of the pitch of flying blowflies always display an oscillation with a frequency between 120-170 Hz, and with an amplitude that varies somewhat, but

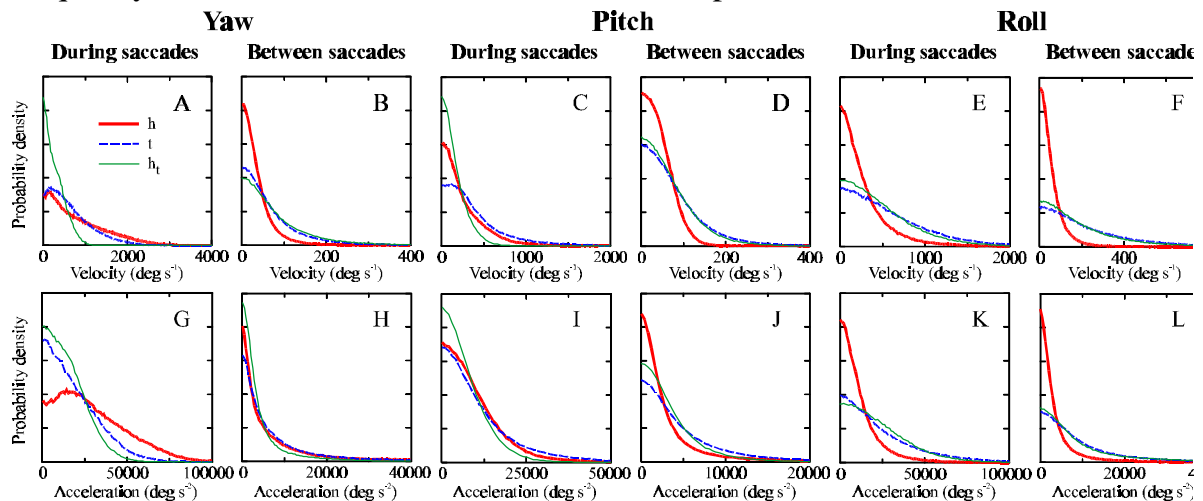


Figure 6. Probability densities of the angular velocities and accelerations of the head (h, fat line), the thorax (t, broken line), and the head relative to the thorax (h_t, thin line). The total flight time was divided into two sets of episodes, 'During saccades' and 'Between saccades'; see text for further explanation. Full scales are: (A) $3 \cdot 10^{-3} \text{ deg}^{-1}\text{s}$, (B) $2.5 \cdot 10^{-2} \text{ deg}^{-1}\text{s}$, (C) $5 \cdot 10^{-3} \text{ deg}^{-1}\text{s}$, (D) $1.5 \cdot 10^{-2} \text{ deg}^{-1}\text{s}$, (E) $3.5 \cdot 10^{-3} \text{ deg}^{-1}\text{s}$, (F) $1.5 \cdot 10^{-2} \text{ deg}^{-1}\text{s}$, (G) $5 \cdot 10^{-5} \text{ deg}^{-1}\text{s}^2$, (H) $2.5 \cdot 10^{-4} \text{ deg}^{-1}\text{s}^2$, (I) $10^{-4} \text{ deg}^{-1}\text{s}^2$, (J) $3.5 \cdot 10^{-4} \text{ deg}^{-1}\text{s}^2$, (K) $8 \cdot 10^{-5} \text{ deg}^{-1}\text{s}^2$, (L) $3 \cdot 10^{-4} \text{ deg}^{-1}\text{s}^2$.

generally lies around 0.5° (peak-to-peak, see Fig. 7A). The frequency matches the wing beat frequency of *Calliphora*, and it appears that these are vibrations that are somehow transferred from the flight motor in the thorax to the head. The yaw and roll often show similar oscillations, but smaller and more variable. As the pitch oscillation is not as obvious in the thorax movement as it is in the head, we investigated the possibility that it is an artifact caused by the coils on the head or the loop connecting thorax and head.

One possibility is that the loop transfers (small) vibrations from the thorax; these vibrations might be amplified if the stiffness of the loop forms a resonator with the mass of the head. We tested this possibility in tethered flies by mechanically driving the (loosened) thorax end of the loop (by attaching it to a small loudspeaker) with frequencies in the range of the wing beat frequency. We observed no significant movement, nor resonance, of the head, and conclude that the loop is not causing the head pitch oscillations.

The only other way the oscillations generated by the flight motor can be transferred to the head is through the neck. Pitch oscillations of the head may be produced by pitch oscillations of the thorax, but also by small oscillatory displacements of the thorax. For example, if the thorax oscillates slightly along its length axis (superimposed on its overall movement, similar to the intermittent forward motion of a rowing boat), this might cause a pitch movement of the head. This happens if the resulting force vector, as transferred through the neck, is not going right through the centre of mass of the head. As the mass of the coils is expected to shift the centre of mass slightly upwards, the head oscillation may thus be a function of the coil mass. We tested this possibility by varying the mass of the coils, and measuring the amplitude of the pitch oscillation from the surplus of power observed at about the wing beat frequency in the power spectrum of the pitch. The right side of Fig. 7B shows the results of 13 blowflies (small filled circles) with coils of 1.6 mg (80 windings, diameter 2 mm), 0.8 mg (40 windings, 2 mm), and 0.4 mg (20 windings, 2

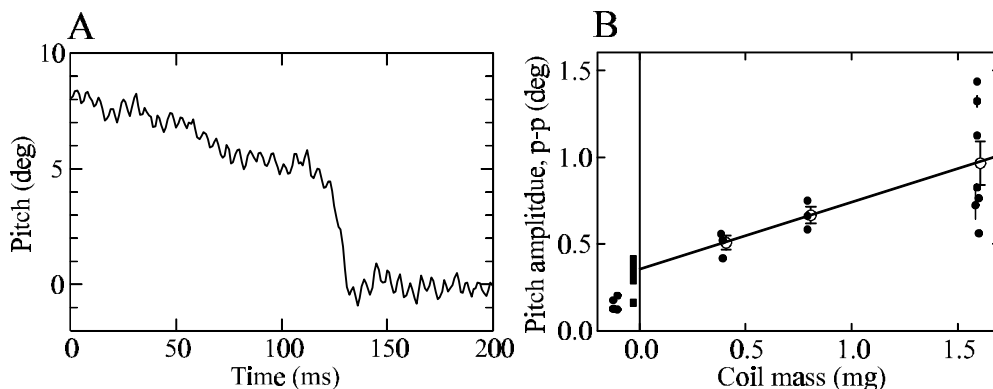


Figure 7. (A) Example of the pitch oscillation observed in the head during free flight. (B) The peak-to-peak amplitude of the pitch oscillation as a function of total coil mass. To the right, measurements on the head of 13 flies are shown (dots), to the left on the thorax of 4 flies (dots). The lower vertical bar shows the average and standard error of the thorax oscillation amplitude, the upper vertical bar the linear extrapolation to coil mass zero of the head oscillation amplitude.

mm). Still smaller coils give too much noise to reliably estimate the amplitude of the pitch oscillations. The open circles and bars show the averages and standard errors of these measurements. These averages lie close to a straight line; the continuous line is a least squares fit to the averages. The vertical bar to the left denotes the average and standard deviation of this fit for coil mass zero. Thus if we assume that such a linear extrapolation is justified, this analysis predicts that without coils, the amplitude of the pitch oscillation of the head would be $0.35^{\circ} \pm 0.08^{\circ}$ (peak-peak). On 4 other flies, with coils mounted only on the thorax, we observed that pitch oscillations also occur in the thorax (4 data points to the left), but these are smaller than those of the head. The small vertical bar denotes the average and standard error of these measurements: $0.15^{\circ} \pm 0.02^{\circ}$. This is significantly different from zero, but also significantly smaller than the estimated head oscillation. Some of the head oscillation may indeed be generated by oscillatory displacements of the thorax: we observed peak-peak amplitudes of 50-100 μm in all directions (again determined from peaks in the power spectrum of the various displacements). However, as the dorsal part of the thorax (where the coils are mounted) is likely to move in a somewhat different way than the neck (driving the head), no further conclusions about the thorax-head mechanics can be drawn at this stage.

DISCUSSION

During flight, head rotations of blowflies are effectively compensating part of the thorax rotations, which results in improved conditions for vision. Between saccades, stabilization of the head in all angular degrees of freedom (yaw, pitch, and roll) is about twice as good as that of the thorax (Fig. 6). During saccades, the head compensates most of the thorax roll, and the yaw movement of the head is shorter than that of the thorax (Figs. 4 and 5). As a result of these head movements, blur in the visual system is significantly reduced. Furthermore, by minimizing the duration of head rotations, rotational optic flow is kept to a minimum. The optic flow due to translation will then dominate. This type of optic flow yields, contrary to rotational optic flow, information about the three-dimensional structure of the visual environment (through motion disparity, i.e., differential visual speeds of objects at different distances). Unfortunately, the simultaneous occurrence of rotational and translatory optic flow is potentially confusing to the visual system, and rotational optic flow is unavoidable when turns must be made when changing course. Although untangling the two types of optic flow is possible in principle (Longuet-Higgins and Pradny, 1980; Koenderink, 1986), this may not always be feasible if there is noise in the signals, and if the neurons are noisy and have a limited dynamic range available for their responses. Then the strategy followed by the blowfly may be a superior one: the rotational optic flow is concentrated at specific points in time (the saccades), whilst the remaining time can be used for analyzing the structure of the visual environment on the assumption of translatory optic flow only.

The shortening of the yaw saccade of the head compared to that of the thorax can be viewed as a further specialization to increase the time available for scene analysis (Schilstra and van Hateren, 1998b). The saccade becomes effectively almost as short (for the smallest saccades only a 15-20 ms period of significant visual blur) as the integration time of the photoreceptor (10 ms for the conditions of the experiment). Saccades much shorter than the integration time are disadvantageous, because they do not reduce visual blur further, and cost more energy because of the higher accelerations (~forces) required.

Between saccades, several systems are acting to stabilize the gaze (Hengstenberg, 1992), such as the prosternal organs on the thorax (Preuss and Hengstenberg, 1992), visual feedback through optic flow analysis (Egelhaaf and Borst, 1993; Krapp and Hengstenberg, 1996), and a mechanical system of gyroscopic sensors attached to the thorax, the halteres (Nalbach and Hengstenberg, 1994; see Chan *et al.* 1998 for a recent overview). The visual system, however, is too slow to explain the angular stability of the head at the onset and end of a saccade (e.g., the latency of just the photoreceptors is already 8 ms at the light levels of the experiment). It is possible that the thorax and head movements during a saccade are entirely preprogrammed, based on predicted flight dynamics. A more likely possibility, however, is that the head stabilization at early and late stages of the saccade is controlled by the halteres. This analogue of the vestibulo-ocular reflex (VOR) in vertebrates (see e.g. Tabak *et al.* 1997) has been shown in experiments where mechanical stimulation of the halteres yields head movements (Sandeman and Markl, 1980), with a minimum latency of approximately 5 ms (Hengstenberg *et al.* 1986). We propose the following scheme: early in the saccade, the haltere-head reflex (HHR) causes the head rotation that compensates for the early stages of the thorax saccade. Subsequently, the HHR is suppressed or overruled, and the head makes its saccade (with the size and direction under control of the brain, which also initiated the preceding thorax saccade). Finally, the HHR becomes dominant again towards the end of the head saccade, producing the final counter rotation of the head.

The oscillations found in the pitch of the head appear to be genuine, although influenced by the mass of the coils mounted on the head. The amplitude of the oscillation ($0.35^{\circ} \pm 0.08^{\circ}$ peak-to-peak) is much smaller than the angular sensitivity of single photoreceptors (approximately 1.5° FWHM, Smakman *et al.* 1984). This amplitude will nevertheless produce a significant intensity modulation when an edge or bar happens to cross the visual field of the photoreceptor. The frequency of this modulation (typically 120-170 Hz) is rather high for blowfly photoreceptors (with an integration time of 7 ms in very bright light), which significantly reduces the resulting modulation. Thus the pitch oscillation will not have a strong visual effect on single photoreceptors. This is different, however, for wide-field neurons: as the head oscillation affects the entire visual field at the same time, a noticeable effect is expected when the signals of many photoreceptors converge. This assumes that the contributions of brightness increments and decrements over the visual field do not

cancel, because this is prevented by nonlinearities in the signal pathways before they converge.

The present method records head movements, and infers gaze position from the head. Although the facet lenses of the compound eye are fixed to the head, the photoreceptors in blowflies are not completely fixed relative to the facets. Via several muscles, small movements of up to a few degrees can be made by the photoreceptors relative to the head (Hengstenberg, 1971; Franceschini and Chagneux, 1997). A visual function for these movements has been suggested (Franceschini and Chagneux, 1997). As the movements are generally small and slow compared to the saccadic head movements presented here, we believe that these internal retinal movements are at most a second-order effect compared to the head movements during saccades.

The histograms in Fig. 6 show that angular velocities of the head between saccades are generally lower than 100-200 °/s. This is well matched to the velocity where blur in the photoreceptors becomes important. This so-called characteristic velocity (van Hateren, 1992a; see also Glantz, 1991) is $v_c = \Delta\rho / \Delta t \approx 200$ °/s, with $\Delta\rho \approx 1.5^\circ$ the full width at half maximum of the photoreceptor angular sensitivity, and $\Delta t \approx 7$ ms that of the photoreceptor impulse response. Nevertheless, this is only part of the story, because this analysis only gives the blur attributable to rotation. The blur attributable to translation has to be accounted for as well. This blur can be determined from a reconstruction of the complete spatiotemporal input to the eye, taking into account the animal's time-varying position and orientation, and the visual stimuli on the walls of the cage. Such a study is currently under way.

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