Chapter 6

Flight behavior and head movements of hoverfly and honeybee: a preliminary analysis

INTRODUCTION

It is interesting to compare head motion strategies between different species of flying insects. The visual system of each species receives its own particular visual input determined by the properties of its flight behavior, head movements and its visual environment. It is highly probable that during evolution these visual systems have become tuned to the expected properties (statistics) of this visual input, for example to optimize information transfer in the visual system (e.g. van Hateren, 1992). Therefore, characteristics of flight behavior may partly explain properties of the visual system, and vice versa (e.g. O’Carroll et al., 1996; O’Carroll et al., 1997). In this chapter, the methods used before on the blowfly (Chapters 3-5) are applied to two other species: hoverflies (Eristalis tenax) and honeybees (Apis mellifera).

The hoverfly is an interesting species to compare with the blowfly for two reasons. First, its kinematics and dynamics are quite different from that of the blowfly, since it often flies sideways and backwards, and hovers for prolonged periods of time (Collett and Land, 1975; Collett, 1980). Second, hoverflies were found to perform body saccades, at least in the horizontal plane. As it was suggested that the head remains fixed with respect to the thorax (Collett and Land, 1975), the question is how much the thorax, and thus the head, rolls during flight.

Honeybees have been used extensively for behavioral experiments on, for instance, pattern discrimination (e.g. van Hateren et al., 1990) and navigation (e.g. Collett, 1996; Lehrer, 1996; Srinivasan et al., 1996). Little is known, however, about the kinematics and dynamics of free flight. Still, it is interesting how honeybees control body and head orientation, because they belong to the Hymenoptera, which lack the halteres found in Diptera. In Diptera, only the halteres are fast enough to establish effective stabilization of the head (Chapter 5). The lack of halteres may thus have important consequences for the kinematics of head motion in honeybees and therefore for their visual system.
A series of experiments on hoverflies and honeybees was performed in order to obtain answers to the above questions. The results below present a first, preliminary analysis of the experiments. A more extended analysis is currently in progress.

**MATERIALS AND METHODS**

*Position and orientation measurement*

Position and orientation of flying hoverflies (female *Eristalis tenax*) and honeybees (*Apis mellifera*, worker) were measured with the method described in Chapter 2 of this thesis. The insects carried sensor coil systems on both head and thorax, which enabled position and orientation measurements of both. The sensor coil systems used were the same as those used on blowflies (see Chapters 4, 5). The hoverflies and honeybees used in the experiments had a mass of 100-125 mg and 90-100 mg, respectively. Therefore, the relative masses of the sensor coil systems were similar as in the case of blowflies. Since the added masses did not significantly influence the movements of head and thorax of blowflies (Chapters 4, 5), we assume that they do not influence those of the hoverfly and honeybee either.

*Preparation and flight recording*

Hoverflies and honeybees were caught in the wild in July and August. Preparation of the insects was basically identical to that of blowflies. Hoverflies and honeybees have more hairs than blowflies on both head and thorax, which had to be removed since they hinder mounting of the sensor coil systems. Head coils were mounted on top of the head, blocking the ocelli. This probably does not hinder normal head and thorax motion, since the role of ocelli in controlling head and body orientation of both hoverfly and honeybee is small (review: Mizunami, 1994), just like in blowflies. Honeybees were cooled to about 5 °C before and during preparation to prevent them from stinging.

Both species of insects flew in a 40×40×40 cm³ cage with walls covered with photographs of natural scenes. The ceiling was covered with brightly-lit frosted paper onto which gray squares at semi-random distances were printed. This provided the insects with depth clues, preventing them from accidentally flying into the ceiling. The bottom of the cage was covered with black paper onto which gray squares were printed with the same dimensions and distances as those printed on the ceiling.

Both hoverflies and honeybees were cooled for 25 minutes at 3 °C before being released in the flight cage, to prevent them from escaping immediately after release, with the entrance of the cage still open. Hoverflies usually started flying within a few minutes after release, while honeybees needed at least 30 minutes. Behavior was essentially the same as that of blowflies (Chapter 4). However, when walking on the bottom of the cage, both hoverflies and honeybees occasionally became entangled in
the cable lying there. This is probably caused by the hooks on their legs, which are much larger than those of blowflies. The flights performed by hoverflies had a duration approximately equal to those of blowflies (Chapter 4), while honeybees tended to perform longer flights of up to several minutes. The results presented below are typical for measurements obtained in three hoverflies and three honeybees.

RESULTS

Hoverfly flight track

Figure 1 shows a horizontal projection of a typical hoverfly flight path of 1400 ms. The orientation of the lines show the orientation of the body (yaw) for every 20 ms. The filled circles symbolize the head. The fly is climbing from 0 to around 540 ms, stays approximately level until 840 ms, then descends until 1040 ms, after which it climbs again. Independent of vertical motion the hoverfly is able to fly sideways and backwards. Hoverflies can perform turns while the body orientation is kept at a constant angle for seconds, independent of the flight direction. However, on average hoverflies have a preference to fly forward, as was reported before (*Syritta pipiens*: Collett and Land, 1975). The yaw angle of the body changes with saccade-like steps while the yaw angle remains relatively constant between the saccades, just like in the blowfly *Calliphora vicina* (Chapter 5; Wagner, 1986) and in the hoverfly *Syritta pipiens* (Collett and Land, 1975; Collett, 1980).

![Figure 1](image-url)

**Figure 1.** Example of a 1400 ms track of hoverfly flight, projected on a horizontal plane. Lines indicate body (yaw) orientation while filled circles indicate head position. The position is shown every 20 ms.
Hoverfly saccades

Figure 2 shows an example of the angular motion of the head (fat line) and thorax (thin line) of the hoverfly. Shown are the yaw, pitch and roll angles as defined in Fig. 1A in Chapter 4 (see also Haslwanter, 1995). The saccades in the yaw are clearly visible in both thorax and head. Like in Calliphora, head and thorax perform saccades simultaneously, while the head starts to perform the saccade around 10 ms later than the thorax. In addition, it also ends earlier, thus shortening the head saccade compared with the thorax. Between saccades, the yaw angles of both head and thorax are held stable, again just like in Calliphora. The typical interval between two saccades is 200-300 ms. The pitch angle of the head is seen to follow that of the thorax, though the head is held more horizontally than the thorax. Neither head nor thorax show saccades in the roll angle. The head roll follows the thorax roll, but lags by about 20 ms. Overall, the head of a hoverfly mostly follows the motion of the thorax, though it is not strictly fixed to the thorax as was suggested earlier (Collett and Land, 1975).

![Figure 2](image-url)

**Figure 2.** Yaw, pitch and roll angles of head (fat line) and thorax (thin line) during 700 ms of hoverfly flight. Angles are defined as in Fig. 1A in Chapter 4.
To elucidate the characteristics of the head roll further, Fig. 3 shows head (fat line) and thorax roll (thin line) during three seconds of flight. Here, it is even more clear that the head roll follows the thorax roll. Both for small and large roll angles the delay of the head is about 20 ms. There is no stabilization of head roll as in Calliphora (Chapter 5). Furthermore, an oscillation of about 25 Hz, having an amplitude of 5-10°, can be distinguished both for the thorax and the head. The large roll angles which occur typically every 300 ms (corresponding to an oscillation of about 3 Hz) are not all associated with saccades. However, when a saccade occurs it is generally accompanied by a large change in the roll angle.

Honeybee flight track

Figure 4 shows a horizontal projection of a typical 2 s flight path of a honeybee. Lines indicate the thorax orientation (yaw) for every 20 ms while the filled circles indicate the head. Honeybees flew often close to the ceiling of the cage (mostly within 5 cm) which was also the case for the flight track shown here. As far as the amount of sideways and backwards motion is concerned, flight behavior of honeybees resembles that of blowflies (Chapter 4). However, honeybees show more periods of (nearly) hovering, once or twice a second, lasting about 200 ms. This can be seen in Fig. 4 between 220 and 580 ms, and between 1540 and 1760 ms. They also perform more U-turns and more zigzag manoeuvres than blowflies. The yaw angle of the honeybee thorax remains fairly constant between turns, but it does not show the truly saccadic behavior of the blowfly and the hoverfly.

Figure 3. Roll angle of head (fat line) and thorax (thin line) during 3000 ms of hoverfly flight.
Honeybee angular motion

Figure 5 shows 500 ms traces of yaw, pitch and roll angles of both head (fat line) and thorax (thin line) with angles as defined in Fig. 1A of Chapter 4. The head of the honeybee flight, projected on a horizontal plane. Lines indicate body (yaw) orientation while filled circles indicate head position. The position is shown every 20 ms.
Hoverfly and honeybee

honeybee shows saccade-like motion in the yaw direction, typically every 200 ms. However, only the onsets are sharply defined, after which the yaw movement fades away slowly. The stability of the head yaw between saccades is relatively poor compared to that of blowfly and hoverfly. The thorax yaw does not show saccadic behavior: the thorax yaws faster during a head saccade, but also yaws with appreciable speed between head saccades.

The pitch of both head and thorax does not show saccades like that of the blowfly (Chapter 5), and it is also not really stable. Just like the pitch angle, the roll angles of both head and thorax are not very stable and do not show saccadic behavior. The thorax roll angle tends to be large during a head saccade, similarly as during the banked turns performed by blowflies.

**Honeybee head and thorax roll**

Although the roll of the head is not very stable, it is usually smaller than the roll angle of the thorax. Figure 6 shows 2 s traces of head (fat line) and thorax (thin line) roll angle. The head roll angle is, on average, about half of the thorax roll angle. Occasionally, an oscillation of about 60 Hz with an amplitude of about 3° is superimposed on the slow head roll motion, which is not seen in the thorax roll.

**DISCUSSION**

Although the high manoeuvrability of hoverflies might suggest otherwise, it appears that the force vector of a hoverfly has at least a partly fixed direction. As a result, the roll motion associated with turns resembles the banked turns of blowflies (Chapter 4). Hoverflies also roll on their side when flying sideways, though not as much as blowflies.

Hoverflies exhibit saccadic changes in the yaw angle for both thorax and head. The hoverfly head turns later and faster than the thorax, comparable to blowflies (Chapter 3, 5). Furthermore, the yaw angles of both head and thorax are quite stable in between saccades. The frequency of saccades is lower than for blowflies, though, while the frequency of turning (with or without making a saccade) is comparable.
This partly explains the abundance of sideways and backwards flights. The frequently measured sideways and backwards movements are in agreement with earlier measurements on a different species of hoverfly, *Syritta pipiens* (Collett and Land, 1975).

The head and thorax motion in the yaw direction may be similar to that of the blowfly, the pitch and roll motion are quite different. The head does not compensate for thorax roll motion. In fact, the roll of the head resembles the motion produced by a passive, damped mass-spring system connected to the thorax, lagging behind because of the inertial moment of the head. The 25 Hz oscillation is probably caused by the thorax and transferred to the head via the neck, because changes in oscillation amplitude are correlated with changes in head oscillation about 20 ms later. Since *Eristalis* has a wing beat frequency of 170-180 Hz (Ennos, 1989) the 25 Hz oscillation is probably an actively produced movement, and not a side-effect of the wing beat, in contrast to the head pitch oscillation of the blowfly (Chapter 5). The movements of the head with respect to the thorax in all angular directions show that the head is not entirely fixed to the thorax during flight, as was assumed earlier for *Syritta* (Collet and Land, 1975).

As far as the occurrence of sideways and backward flight is concerned, honeybee flight shows appreciable resemblance with blowfly flight. Furthermore, honeybees also perform banked turns and roll movements when flying sideways, suggesting a fixed direction of the force vector. However, in contrast to blowflies, honeybees do not make real thorax saccades, although the thorax tends to yaw and roll faster during head saccades. The start of a head saccade is similar to that of a blowfly saccade, reaching yaw velocities of up to several thousand deg/s. However, the yaw velocity decreases slowly, leaving the end of the saccade ill-defined.

The particular structure of honeybee head saccades may be explained by the absence of halteres. First, at the onset of the saccade, a voluntary movement of the head is made, during which the optomotor reflex (the compensating mechanism driven by input from the visual system) is temporarily suppressed or overruled. After some time, the optomotor reflex starts to stabilize the head again. Since the visual system of honeybees is slower than the haltere system in Diptera, the stabilization of the head is slower than in Diptera. In the roll direction, the honeybee head does not show saccadic behavior like the blowfly head. Nevertheless, the head roll is reduced compared to the thorax roll by a factor of about two, a reduction similar to that found in the blowfly. Apparently, the visual system of the honeybee is able to cope with the remaining rotational optic flow both in the yaw direction (during the end part of head saccades) and in the roll direction.

REFERENCES


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