The Head-Neck Sensory Motor System

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Movement and Orientation of Insects in Space

A flying insect has all six degrees of freedom to move in space; translations (due to lift, sideslip, and thrust) determine its location in space, and rotations (yaw, pitch, and roll) change its orientation relative to external coordinates. In cruising flight insects have, on average, a preferred flight attitude with their back directed upward. This flight attitude is continuously modified by voluntary flight manoeuvres, and by eddies of turbulent air. Flying over a sizeable distance thus requires continuous control of body orientation in order not to crash.

In walking insects, pitch turns and roll turns are restricted by the contract with the ground. However, the substrate may have any orientation relative to the vertical, for example, the surface of rocks, plants, and the like. Most insects can walk easily on slanted surfaces, even upside down, as a fly does on a ceiling. On more or less horizontal surfaces, however, insects adjust their body posture relative to the vertical, very much like quadrupeds or bipedes. Posture control during locomotion is made to keep balance in the gravity field and it stabilizes a preferred orientation relative to the surroundings.

The Eyes of Calliphora

The blowfly, like most other insects, has five eyes: three ocelli on top of the head and two compound eyes at the sides (Fig. 5-1). Ocelli have a single astigmatic wide-angle lens. Their combined field of view covers essentially the dorsal hemisphere. The ocellar retinas comprise a few hundred photoreceptors whose light-sensitive structures lie well inside the focal distance of the lens. Photoreceptors converge upon very few second-order neurons. Therefore, ocelli are believed to act as widefield brightness sensors, and are not suited to perceive fine spatial details (see review in Goodman, 1981). The compound eyes of Calliphora consist of about 6,000 "ommatidia," each with its own narrow-angle lens. They are arranged to overlook the ipsilateral hemisphere of the surroundings. Each lenslet focuses upon eight photoreceptors, which in turn are connected to a small set of second-order neurons. They represent a minute part of the visual surrounding in a retinotopic array of repeating "columnar" neurons. Several such neuronal "maps" of the surrounding are stacked in the optic lobes of insects to allow spatial analysis of the Image perceived via the compound eye (Strausfeld, 1976; Wehner, 1981; Buchner, 1984; Heisenberg and Wolf, 1984). The visual field of Calliphora covers almost the whole surroundings of the fly. Only a small backward and downward part, obscured by the fly's own body, cannot be seen (Burkhardt et al., 1966). The visual fields of the two compound eyes overlap in a narrow zone along the sagittal plane. It has not, however, been demonstrated that flies have true stereoscopic vision, and the functional significance of visual field overlap is not known. A narrow zone of the surrounding, aligned with the dorsal sagittal meridian, is seen simultaneously by all five eyes. At present, no functional significance can be attributed to this multiple sampling.

Oculomotor System of Calliphora

The lenses of all five eyes of an insect are part of the head capsule. Hence they cannot grosso modo, be moved independently. Higher Diptera, however, have an internal eye muscle that displaces the retina along the focal plane, thus causing small horizontal shifts of the optical axes of ventrofrontal ommatidia (Hengstenberg, 1971). Calliphora can turn its head relative to the thorax about all three body axes: yaw ±20°, pitch ±20°, and roll ±90°. Head movements are effected by a set of 19 muscles per side, each consisting of only one motor unit; all act in concert upon the neck skeleton (Milde et al., 1987; Strausfeld et al., 1987; see also Chapter 7, this volume). Head movements of course affect more or less all sense organs on the head, for example, the antennae. The main function of head movements, however, is probably to turn the eyes.

Why should an insect move its eyes at all if it sees the whole surroundings anyway? Degradation of visual perception by blurring during self-motion is principally similar in all types of eyes.

The transfer of high spatial frequencies can be maximized by minimization of retinal slip, using the appropriate compensatory eye movements. Further, the neural networks processing spatial information are not as isotropic as the surface of the compound eyes may suggest. Physiologic properties of wide-field visual interneurons in Calliphora indicate that they only operate correctly if the eyes have their proper alignment with respect to the vertical (Hengstenberg, 1982; Hausen, 1984).

How to Study Head-Eye Movements in the Fly

Flies are small, move fast, and perform unbelievable aerobatics. It is therefore very difficult to observe their head-eye movements in free flight (Wagner and Wehrhahn, 1985; see Fig. 5-3). Fortunately they fly stationarily in a wind tunnel (Fig. 5-2). There, either the fly or its visual surroundings can be rotated by servomotors, either by a fixed angle or at constant angular velocity or both according to external time functions. The behavior of the flies is observed by a macro video camera, recorded on tape, and evaluated frame by frame.

This chapter reviews studies on roll movements of the fly's head that have partly been reported previously (Hengstenberg et al., 1986; Hengstenberg, 1988). Other studies have dealt with yaw turns of the fly's head (Land, 1975; Liske, 1978; Sandeman and Markl, 1980).
Voluntary Head-Eye Movements in Flight

The orientation of a flying insect may change either voluntarily, when it performs a banked turn in still air, or involuntarily, when it passes through eddies of turbulent air. High-speed movies of freely flying houseflies show that they actually bank up to 90° when turning rapidly (Fig. 5-3). Magnified film frames further suggest that flies keep their head aligned with the vertical during such maneuvers. Even in the best film scenes (Fig. 5-3), however, head orientation cannot be measured precisely.

Measurement of head orientation is made possible when a fly is mounted coaxially to a small crank, freely rotating in a low-friction bearing. The crank is mounted in a wind tunnel with its axis adjusted vertically so that the fly is held in a vertical, head-up position. When the optical surroundings are homogeneously white, the fly changes its body orientation by spontaneous roll torque fluctuations. At the same time, the fly rolls its head in the opposite direction, which tends to stabilize the orientation of its eyes in space against the self-induced body roll (Fig. 5-4). This is as expected, and in contrast to the head-trunk coordination observed during unexpected roll turns imposed on the fly.

Compensatory Head Movements with Involuntary Roll

Calliphora stabilizes its head in space when its normal orientation is unexpectedly disturbed. This can be demonstrated when the fly is mounted upright in a horizontal wind tunnel with the
visual surroundings simulating a dark ground below, a bright sky above, and a horizon at its usual elevation (Fig. 5—2). If a fly is rolled sinusoidally (1 Hz, ±90°) during flight, it produces a smooth, almost sinusoidal head roll in antiphase to the imposed motion (Fig. 5—5a). This response is switched off when the fly stops flying and does not walk (Fig. 5—5b). Walking in flies is an intermittent means of locomotion wherein short bouts of walking are interspersed with short periods of rest (Fig. 5—5c, trace LM). When a fly is rolled while it walks on a small styrofoam ball, it generates somewhat jerky head movements in antiphase to the stimulus; no such movements occur while it is mostly resting (Fig. 5—5c). Head movements against an imposed motion clearly tend to stabilize the fly's head in space. Apparently, such stabilization is most important during flight.

Compensatory Flight Maneuvers

Head movements mostly do not fully compensate an imposed misalignment. Head position relative to external coordinates, however, depends also on movements of the body that carries the head. The stimuli used above to study compensatory head movements elicit flight steering responses at the same time. By independent modulation of the amplitude and pitch of the two wings the fly can probably generate yaw torque and roll torque independently. The responses can be used to counteract involuntary body turns. Since both the compensatory head roll and the compensatory flight manoeuvre are made in the same direction and at the same time, the effective speed and angle of head realignment is increased accordingly during free flight. Note that the coordination of head and flight movements differs from that during banked turns (Figs. 5—3 and 5—4).

Mechanisms of Roll Control

The fly's alignment with the vertical could be stabilized either by orientation toward an indicator of roll angle (gravity, horizon) or by suppression of roll motion. The laurier mechanism is bound to drift and therefore appears insufficient for long-term stabilization. Calliphora's ability to perceive its roll orientation is demonstrated if a fly is mounted in a wind tunnel as shown in Figure 5—2, held in this position for control measurements, and then rolled to the side and held in the oblique position. Comparison of the frequency distribution of head posture in the two situations shown that Calliphora makes use of the angular position cue and tries to realign its head with its subjective vertical. On average it compensates about half of the imposed misalignment (Fig. 5—6a,b).

Calliphora's ability to perceive roll motion is demonstrated by mounting the wind tunnel vertically to eliminate gravity as a position indicator, and by replacing the sky-and-ground pattern by one made of equally spaced stripes. When the fly is rolled at constant angular velocity to the left, it rolls its head to the right, initially compensating for most of the imposed motion (Fig. 5—6c). The response saturates near the mechanical limit of head roll (between -90° and +90°), and declines later on by adaptation. Generally, flies do not show a nystagmus in response to roll motion stimuli.

Cues and Sense Organs for Roll Perception

The previous experiments were made by rolling the fly in optically structured surroundings in order to simulate free flight situ-
Comparative Aspects of Head-Neck Movement System

There, the stimulus always contained mechanical and visual components. To reveal if *Calliphora* uses visual and/or mechanosensory information to control its head posture, stimuli were modified appropriately. Visual roll perception was demonstrated by holding the fly stationary and rolling its optical surroundings sinusoidally; the fly's head followed the pattern motion (Fig. 5—7b). Body motion perception was demonstrated when the optically structured surroundings were replaced by a homogeneously white cylinder, and the fly was rolled sinusoidally; the fly rolled its head in antiphase with the stimulus (Fig. 5—7c). Obviously, *Calliphora* uses visual as well as mechanosensory information to control its head posture.

For both sensory modalities several effective cues have been characterized by specific modification of the roll stimulus. Sense organs receiving these cues were identified by selective elimination. A series of pictograms (Fig. 5—8) summarizes the sensory cues presently known to be used by *Calliphora* for roll control.

The visual system provides four roll-specific signals (Fig. 5—8, upper row). Coherent roll motion of an extended and well-textured pattern is perceived by compound eyes in their entire receptive field (Fig. 5—8a). The orientation of prominent contours in the frontal visual field is also seen by the compound eyes (Fig. 5—8b). The overall brightness distribution, represented by the average brightness difference between left and right eyes, is utilized via the compound eyes (Fig. 5—8c) and the lateral ocelli (Fig. 5—8d), with complementary dynamics and with very low gain of the ocellar component. In the absence of visual cues, body motion of the fly is perceived via the halteres (Fig. 5—8e). A difference in wing load, as measured presumably by campaniform sensilla in the main vein of the wing, elicits a transient head roll (Fig. 5—8f). Walking flies perceive a roll misalignment via leg proprioceptors (Fig. 5—8g; Horn and Lang, 1978). Finally, head position is sensed by proprioceptive neck sense organs, enabling the fly to align its head relative to its body (Fig. 5—8h). The
surprising wealth of sensory information taken up and processed by the fly stresses the importance of stabilizing its eyes during flight in a more or less complex visual environment.

**Modifications in Different Locomotor States**

The visual systems of *Calliphora* are equally responsive in each of its locomotor states: flying, walking, or standing still. Some of the mechanoreceptive systems, however, are disabled in one or the other mode of locomotion. Gravity, for example, acting on the body of a fly, is perceived by pedestrian flies via leg proprioceptors. In flight, however, no active response to a misalignment in the gravity field can be demonstrated. Halteres perceive self-motion during flight and possibly during walking. In the resting fly, however, the haltere signal is not generated. Similarly, wing load can only be measured in flying flies and not in pedestrians. Consequently, the roll control system of *Calliphora* has different configurations, depending upon the fly’s momentary locomotor state.

Conversely, roll control affects different motor output systems when flying and when walking. This requires a considerable amount of routing of sensory information, involving "enable gates" and "disable gates"; visual pattern motion signals, for example, reach certain flight steering muscles only during flight (Heide, 1983) and certain leg muscles only when the fly is walking. These processes, especially their central nervous substrates, are at present very little understood. The neck motor neuron is, of course, the same in all modes of locomotion. The response gain, however, for any particular sensory cue is largest during flight (R. Hengstenberg, unpublished data). This emphasizes again that vertical stabilization of the fly's head and eyes is probably most important during flight.

**Head-Trunk Alignment by Neck Sense Organs**

Eyes, as part of the head, may perceive more or less roll than the mechanoreceptive organs located on the fly's thorax. Consequently, each type of sensory information is routed in parallel to the respective head motor and locomotor systems. However, this would not prevent drift between the two. The large range of head roll in *Calliphora* (+90°) could then lead to intolerable misalignments. This is prevented by mechanoreceptive sense organs associated with the neck joint: a pair of prothoracic chordotonal organs, about which little is known, and a pair of prosternal organs. They seem to be symmetrically activated by head pitch, and differentially by head roll. Thus, by appropriate central processing, prosternal organs should be useful to control both axes of head posture. Creating a functional asymmetry by blocking one of the two prosternal organs elicits a steady state roll-offset of the fly's head (Fig. 5-9). Prosternal organs have also been proposed to influence the fly's yaw torque in flight (Liske, 1978), illustrating that their functional characteristics are not yet fully understood.

**Dynamic Complementation of Sensory Subsystems**

It is well known in crustaceans, molluscs, and vertebrates that visual and vestibular subsystems have different dynamic characteristics: vestibular systems act rapidly but may be inaccurate with respect to angular position; visual systems act slowly but more accurately. In *Calliphora* the neural subsystems are very differently organized, and the halteres even use an entirely different principle of mechanosensory motion perception—evaluation of the coriolis force created in the oscillating haltere by rotations of the fly (Pringle, 1948). Nevertheless, the above functional distinction holds true also in flies. If a fly is turned at 2000 °/s through 90° in visually homogeneous surroundings, and is held in this position, it turns its head after a short latency (<10 ms).
Fig. 5–10. Instantaneous (<50 ms) and steady state (>5 s) responses to an angular step displacement (±90°; 2,000°/s) of a fly in visually structured surroundings (○), in homogeneous surroundings (▲), and during pattern movement with the fly held stationary (●). Notice the different latency, response speed and maintained response with visual (○) and mechanosensory (▲) stimulation.

Fig. 5–11. Function diagram summarizing effective cues, sense organs involved, and the distribution of roll-specific information on different motor output systems. Switches are activated by locomotor states: flight (F), walking (W), and rest (R). Error signals are reduced physically by compensatory motions.
Stabilizing Head-Eye Movements in the Blowfly

Concluding Remarks

Figure 5—11 shows the surprisingly elaborate function diagram of roll control in Calliphora. One may ask why such a small creature, having a central nervous system of less than 1 mg, devotes so much effort to keep its head and eyes aligned with the visual world. Motion and misalignment of the retinal image cause degradation of vision on all levels of processing, and in many different perceptual tasks. Preventing the two disturbances automatically eliminates all their deleterious effects. This is true independent of brain size, but it may be particularly useful if one has a particularly tiny brain.

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rapidly (700 °/s) in the opposite direction (Fig. 5—10, triangles). This response to body motion vanishes within five seconds. If, instead, the pattern is displaced in the same way, and the fly is held stationary, it turns its head after a longer latency (30 ms) and slower (450 °/s) in the direction of pattern displacement. With the sky-and-ground pattern, this response is maintained indefinitely (Fig. 5—10, circles). If the visual and mechanosensory components are combined by turning the fly in optically structured surroundings, the time course of the response (Fig. 5—10, diamonds) matches that of the step stimulus much better than with either of the component stimuli alone. This demonstrates that in flies also the visual and mechanosensory systems to perceive self-motion have characteristically different dynamic characteristics. They operate autonomously and complement each other.