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# MULTISENSORY CONTROL OF HEAD/EYE MOVEMENTS IN AN INSECT

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**Orientation in space:** The blowfly *Calliphora* has a preferred posture relative to the vertical when flying, walking or resting. In flight, it can turn through arbitrary angles about each of its body axes (yaw, pitch, roll). In pedestrian flies, pitch and roll turns are restricted by the contact with the substrate. Posture control means in essence, to keep balance while moving in the gravity field.

**The fly's oculomotor System:** *Calliphora* can also turn its head relative to the thorax (yaw, pitch: ± 20°, roll: ± 90°). Any head movement turns the three ocelli and the two compound eyes by the same angle in the same direction, because all eyes are part of the head capsule. This forced conjugation simplifies the insect oculomotor control system: only one joint, the neck, has to be considered (see Strausfeld et al 1987).

**Gaze control in flight:** The fly's orientation is changed either voluntarily during a banked turn in still air, or involuntarily when passing through turbulent air. In both situations, its eyes lose their proper alignment with the surroundings, and have to be readjusted by compensatory head movements. Their coordination with the respective flight manoeuvres is different in the two situations. Since the fly's head is carried by its body, the ultimate direction of gaze, and the alignment of the eyes with the vertical, are determined by the sum of head and body movements.

**Compensatory head roll in flight:** Insect head movements are difficult to observe in free flight, and analysis is hampered by the complexity of inputs and outputs. Tethered flight in a wind tunnel allows to isolate visual from mechanical inputs, and to separate head/eye movements from reactive body movements. Figure 1 shows the basic experiment: a fly is suspended vertically in a visual environment displaying sky, ground and horizon in their normal orientation. When the fly is sinusoidally rolled by its thorax around its body axis (TP, 1Hz, ± 90°), it rolls its head (HR) in the opposite direction compensating most of the imposed body roll. This response can be caused by fixation and tracking of a cue for angular Position or by perception of angular motion.

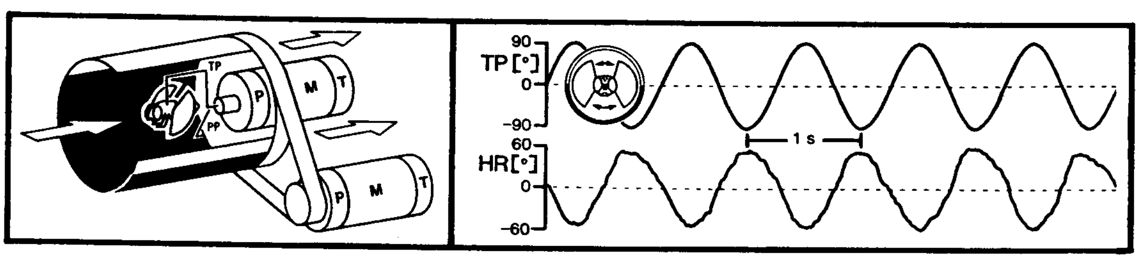


*Figure 1: Compensatory head roll (HR) of Calliphora elicited by imposed sinusoidal roll of the fly (TP, 1Hz, ± 90°) during tethered flight. Video recordings were made through the entrance nozzle of the suction wind tunnel.*

**Cues and sense organs:** Sensory cues eliciting compensatory head roll were identified by tilting or turning either Calliphora or its optical surroundings, which may consist of various patterns. Sense organs were identified by selective elimination. It was shown that Calliphora uses visual as well as mechanosensory cues to stabilize its head in space:
(1) Coherent roll motion of extended, textured patterns is perceived via the compound eyes.
(2) The orientation of elongated objects in the frontal visual field is also effective via the compound eyes.
(3) An uneven spatial brightness distribution elicits a tonic dorsal light response, again via the compound eyes.
(4) A change in the spatial brightness distribution elicits a small phasic dorsal light response via the lateral ocelli. In flight, Calliphora perceives
(5) its self-motion mainly via the halteres, and
(6) roll, less effectively, by a difference in wing load.
(7) Gravity is totally ineffective as an orienting cue during flight, but in walking flies it affects head posture via leg proprioceptors (Horn and Lang 1978). The most effective cues for roll (1),(3),(5) are also used to control yaw- and pitch turns, if presented in the respective directions (Land 1975, Meyer 1978, Nalbach and Hengstenberg 1976, Kirschfeld and Baier-Rogowski 1987, Hengstenberg unpublished).

**Head/trunk-coordination:** Head posture is monitored by various neck sense organs (Vater 1961, Strausfeld and Seyan 1985). Their physiology is only partially known. They have a feedback influence on head posture (Horn and Lang 1978) and a forward influence on the wingbeat (Liske 1978). Thus flight control by a particular sensory cue is effected indirectly via head turn and neck receptors as well as directly (Geiger and Poggio 1977).

**Locomodifications:** Mechanosensory cues are not equally available for flying, walking, or resting flies, because sense organs of legs, wings, halteres are inoperative in one or the other locomotor state. When present, each cue controls a complex set of motor outputs (head, wings, legs, abdomen; see Götz et al 1979) according to the prevailing locomotor — state. The overall orientation control system of Calliphora has to accommodate all these modifications appropriately.

**Advantages of multisensory control:** Multisensory control of head/eye movements increases the accuracy with which Calliphora perceives the direction and the velocity of rotation. It provides the fly with an extremely wide range of motion perception (0°/s to beyond 3000°/s) because the sensory subsystems (1), (3) and (5) have complementary angular velocity characteristics, and operate essentially independent from one another.

**Advantages of visual stabilization:** Compensatory head/eye movements reduce degradation of vision during locomotion an different levels of processing: (a) Contrast transfer by photoreceptors, especially at high spatial frequencies is preserved by reduction of retinal image velocity. (b) Image analysis may be facilitated when the image is localized in appropriate parts of the eye. (c) Objects may be recognized more readily when seen in familiar orientation. (d) Analysis of the optical flow pattern in the eyes may only be possible after elimination of the rotatory components. It will have to be shown that Calliphora actually makes use of these advantages.

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