CHAPTER 13

Multisensory control in insect oculomotor systems

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1. Introduction

Many studies on the visually guided orientation behavior of insects have revealed a wealth of fascinating mechanisms which enable these small animals to make their way with usually much less than one milligram of brain (see Chapter 11). However, only a few studies have been devoted to insect eye movements although it is clear that most insects can turn their head, and thus their eyes relative to the body.

Since there is no review available on the subject, I will first briefly describe insect eyes and oculomotor systems, and then address stabilizing eye movements relative to the surroundings. I will mainly describe roll-stabilization, using the blowfly as an example (Hengstenberg, 1992), and mention common or distinctive features of other insects where advisable.

2. Insect oculomotor systems

Most insects have two kinds of eyes: three ocelli and two compound eyes (Fig. 1). Ocelli are small, have a single, underfocussed wide-angle lens and a few hundred photoreceptors converging upon very few second-order neurons. Ocelli are well suited for overall brightness measurement and less well suited for the resolution of fine spatial detail. The receptive fields of ocelli can either be centered along the horizon as, for example in locusts and dragonflies, or they can be directed upwards into the sky as in honey-bees and flies (review Goodman, 1981). Highly developed compound eyes consist of several thousand "ommatidia", each with a small lenslet, looking essentially at a 1-3 deg patch of the world, 8-9 photoreceptors sharing this receptive field, and in the visual system a cascade of small field neurons processing the local information in various ways (see Chapter 3). The overall receptive field of a compound eye usually approximates the ipsilateral hemisphere with a narrow zone of overlap along the sagittal plane. Thus compound eyes are well suited to process spatial details from all over the unit sphere (review Wehner, 1981).

The lenses of ocelli and compound eyes are part of the head capsule. Hence eye movements are made in rigid conjunction by moving the head about a single neck joint. This is formed by thickened, articulating parts of the neck cuticle, and thin, highly flexible parts. Head movements are effected by ca. 20 neck muscles per side, each consisting of one or a few motor units (Shepheard, 1973; Strausfeld et al., 1987, Honegger et al., 1984). Head mobility depends in detail upon an insect's shape and life style (compare dragonfly, grasshopper, praying mantis, cockroach, plantlouse, butterfly, blowfly, cockchafer). The blowfly, for example, can turn its head about the dorsoventral axis (yaw) and transverse axis (pitch) each by ±20 deg, and about the body axis (roll) by ±90 deg. The neck joint only allows for minute translations. Larger translatory head movements, for example to utilize parallax cues, are made by appropriate body movements (Collett, 1978).
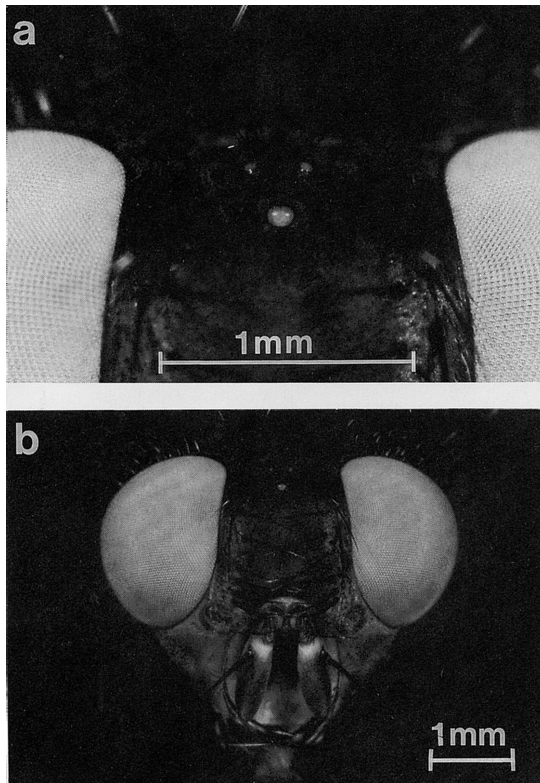
Fig. 1. Eyes of the blowfly *Calliphora.* View of the fly's head, seen from ahead and from 45 deg above. (**a**) Three small ocelli on top of the head provide a wide-field low-resolution view of the dorsal hemisphere. (**b**) Two large lateral compound eyes provide spatial resolution, each for the ipsilateral hemisphere, by 6000 small facet eyes.

Head turns shift all sense organs of the head (antennae, wind hair fields, tactile bristles, gustatory sensilla). In many instances, it is clear that head movements are made to shift gaze; for example, in robber flies fixating and tracking a flying prey before starting to catch it (Kirmse and Lässig, 1971). Similarly, stabilizing head movements reported below only make sense when interpreted as gaze-stabilizing movements.

3. Observation of insect head movements

Insect head movements are difficult to observe during free locomotion. They can, however, be continuously measured during stationary walk on a treadmill (Moorhouse et al., 1978; Buchner, 1976; Horn and Lang, 1978) and in tethered flight, either attached to a pivot allowing the fly to turn about one axis (Fig. 2a; Mittelstaedt, 1950; Goodman, 1965; Land, 1973), or rigidly fixed to a Stimulation device (Fig. 2b; Tracey, 1975; Sandeman and Markl, 1980; Hengstenberg, 1984). Head movements are recorded by miniature angle transducers in larger insects (Koch and Elliot, 1983; Miall and Hereward, 1988) or by film or videography in smaller ones (Fig. 2d). For roll turns, the angular positions of the fly's head (HP), its trunk (TP) or the pattern (PP) are referred to the external world i.e. the vertical, and head roll (HR = HP-TP) is referred to the fly's trunk.

4. Types of insect head/eye movements

Insect gaze movements can be classified by the phenomenological categories used for other animals. The eyes may be moved voluntarily or in response to a stimulus: Flies shift gaze and flight course spontaneously in perfectly static surroundings (Land, 1975; Hengstenberg et al., 1986). Gaze shifts may be directed towards an object of interest (Mittelstaedt, 1952; Kirmse and Läsig, 1971) or may be made to align the eyes with the surroundings. Head/eye movements can be made to catch sight of an object or to hold gaze on target, even if either the object or the observing insect is moving (Land, 1975; Rossel, 1980). The head can be turned smoothly or in a saccadic manner, sometimes alternately (Rossel, 1980). Horizontal eye movements (yaw) are mostly directed towards an object; pitch movements may be referred either to an object (usually near the horizon) or to space. Roll movements are closely related to equilibrium control, and therefore refer to the vertical, and provide the eyes on average with their normal, upright orientation relative to the external co-ordinate System.

5. Compensatory head roll in the blowfly
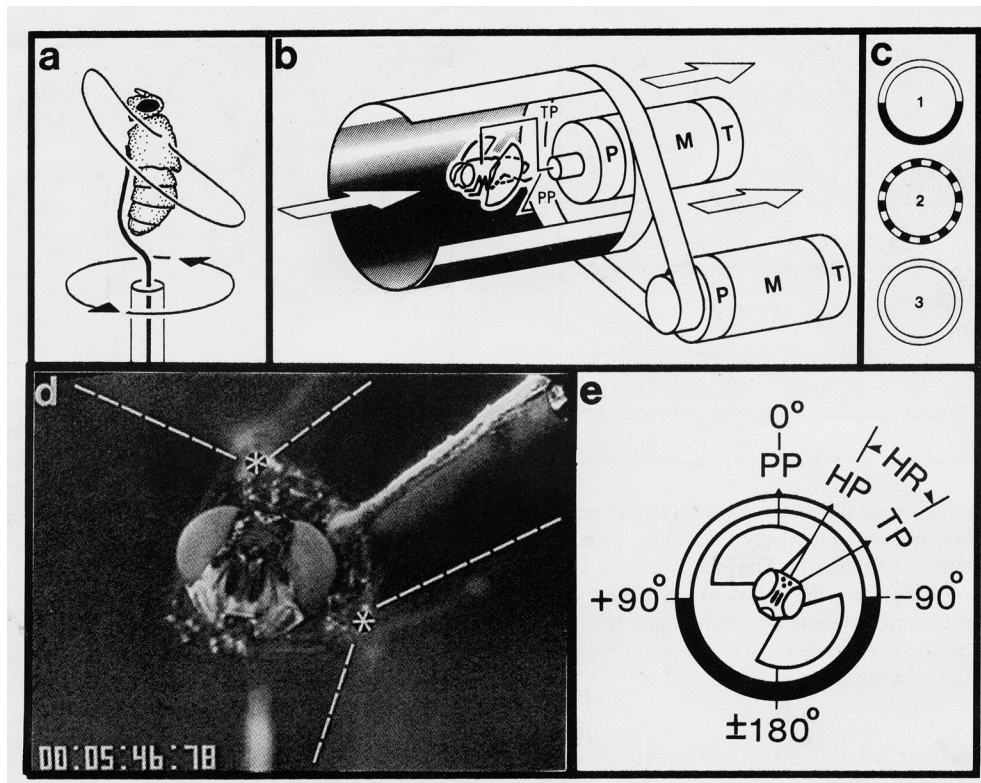
When a blowfly is mounted with its back upright

Fig. 2. Observation of insect head movements. (**a**) A fly, fixed to a lightly pivoted crank, can roll about its body axis and turn its head in all directions. (**b**) Suction wind tunnel with a fly mounted within a pattern cylinder which is diffusely illuminated from the outside and can be fitted with various patterns (**c**). The fly or the patterns can be tilted or turned by servomotors, and head movements are recorded by a macro-videocamera through the entrance nozzle of the wind tunnel. (**d**) Sample video record, illustrating the fly's eyes (dorsal ocelli, compound eyes) and a stabilizing head roll during flight, caused by an imposed roll to the fly's left in the "sky-and-ground" pattern shown in (**e**). The fly is held by a piece of cardboard, glued to its back, indicating a body angle of TP = -55 deg. The fly's wings are blurred and out of focus; their joints are marked by asterisks. (**e**) defines the angular scale, the angular position of the fly's head (HP), its trunk (TP), and of the pattem (PP) as indicated by a pointer, visible also in (**d**). Head roll (HR = HP-TP) is the angle between head and body sagittal planes.

in a windtunnel, displaying sky, ground and horizon in their familiar orientations (Fig. lb), it will fly for up to two hours if its feet do not touch ground. When its normal alignment with the surroundings is disturbed, for example, by an imposed sinusoidal body roll of ±90 deg at 1 Hz (Fig. 3, trace TP), it will generate an antiphasic head roll (Fig. 3a) compensating for most of the imposed disturbance, thus stabilizing the fly's head in space (Fig. 2d). Pictograms characterizing the experimental situation are derived from Fig. 2e which also specifies the angles to measure head roll (HR [deg]). When the fly stops flying in

mid-air, the compensatory response is suppressed (Fig. 3b), proving also that the head movement in Fig. 3a is not simply a passive, inertial motion. When the fly is given a small styrofoam ball, flight is inhibited, and the fly will walk on the ball intermittently (Fig. 3, trace LM). While it walks, it generates a somewhat shaky but still anti-phasic head roll in response to an imposed sinusoidal body roll (Fig. 3c). Simultaneously with the head movements, flies generate synergistic steering responses when flying (Hengstenberg et al., 1986), and appropriate postural responses when walking (Gaffron, 1934). Similar stabilizing re-
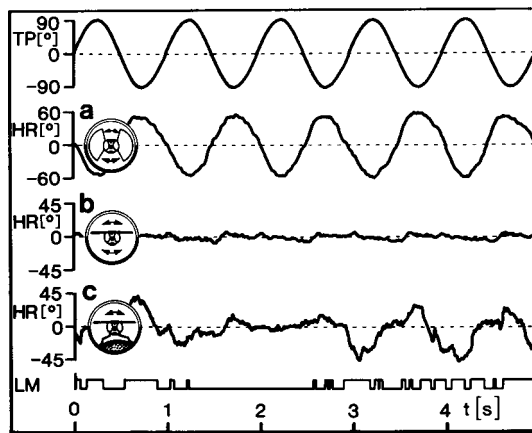
Fig. 3. Compensatory head roll in the blowfly *Calliphora.* In response to an imposed sinusoidal body roll (1 Hz, ±90 deg). The uppermost trace (TP) shows the body angle relative to the vertical. The lower traces show the fly's head roll relative to its body, (**a**) during flight, (**b**) during immobility, and (**c**) while walking intermittently on a styrofoam ball. Trace LM indicates walking (high) and standing (low) episodes.

Fig. 4. Visual and mechanosensory head stabilization. Roll responses are decomposed into a visual component (**b**) by rolling the pattern (**a**, PP) sinusoidally (1 Hz, ±90 deg) while the fly is held stationary, and into a mechanosensory component (**c**) by rolling the fly (**a**, TP) in visually homogeneous surroundings.

sponses have been observed in different insects usually in somewhat different experimental situations (Goodman, 1965; Horn and Lang, 1978; Horridge et al., 1984; Mittelstaedt, 1950; Stange and Howard, 1979; Taylor, 1981a; Tomioka and Yamaguchi, 1980).

6. Sensory mechanisms for roll stabilization

By modification of the roll stimulus one can show that the stabilizing response is mediated by angular position signals as well as by angular motion (Hengstenberg et al., 1986). Rolling the pattern, instead of the fly, shows that visual signals elicit a stabilizing head roll (Fig. 4b). Conversely, rolling the fly in visually homogeneous surroundings demonstrates that mechanosensory signals about body-rotation are also used to stabilize the fly's head (Fig. 4c). Further modification of the stimuli, combined with specific manipulations of sense organs, revealed that in *Calliphora* eight distinct sensory processes control the fly's head roll (Hengstenberg, 1988 in preparation). They are illustrated in Fig. 5, and briefly characterized
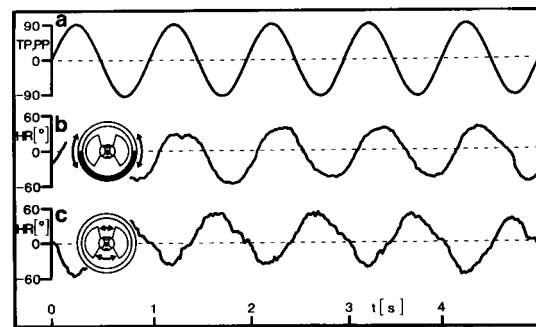
below. References are given whenever the same process has been described for other insects.

6.1. Visual pattern motion

Coherent roll motion of an arbitrarily textured extended pattern is sensed via the compound eyes (Hengstenberg, 1982; Chapter 3), and elicits a head roll which initially compensates for up to 80% of the stimulus velocity. With continued pattern motion, the fly's head reaches a steady state roll angle of up to 90 deg, which is close to the mechanical limits of the neck joint. Weaker motion stimuli elicit a smaller steady state head roll, suggesting a balance between a continuous pattern motion response and head returning processes discussed later (Section 7). *Calliphora* generates occasional roll-"saccades" but never a roll-"nystagmus" (Hengstenberg et al., 1986). Pattern motion is an effective means of head stabilization in many insects and in all directions of head rotation. (Horridge et al., 1984; Mittelstaedt, 1950; Thorson, 1966; Varjú and Bolz, 1980). Some insects show a clear head nystagmus, preferentially with horizontal pattern motion but this is certainly not an universal feature of insects (Land, 1975; Kien and Land, 1978; Rosses, 1980; Von der Grün, 1989).
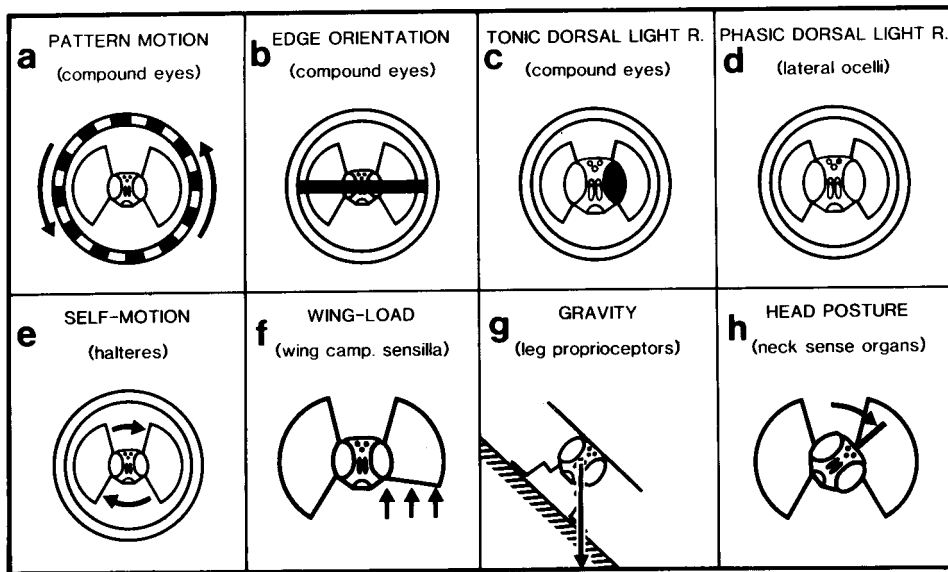
Fig. 5. Sensory subsystems for roll control in *Calliphora*. Pictograms illustrate the experimental conditions defining cues and sense organs used by the fly to keep its head aligned with the vertical. There are four visually induced roll responses (**a- d**) and four mechanosensory ones (**e-h**); gravity is perceived only by pedestrian flies.

6.2. Alignment with pattern contours

In textured optical surroundings many insects exhibit a tendency to tum towards prominent contours, to stabilize this course for a while and then to change their heading by rapid yaw turns towards something else (review Wehner, 1981; Reichardt, 1973; Land, 1973; Götz, 1989; Götz et al., 1979; Heisenberg and Wolf, 1984). From this behavior one expects that insects prefer to see elongated objects vertically in the frontal part of their visual field. Srinivasan (1977) has demonstrated this to be true by a closed loop arrangement where the roll speed of frontal patterns was controlled by the roll torque produced by house flies in tethered flight. *Calliphora,* when faced with a single bar or a parallel grating at a roll orientation of 45 deg tends to turn its head such that the bar is seen horizontally (Fig. 5b: Hengstenberg, unpublished). This is a comparatively weak component of the roll control system of *Calliphora,* but the contradictory results obtained with two closely related genera need clarification.

6.3. Dorsal light response (DLR)

Many animals up to the lower vertebrates have a tendency to turn their back towards the center of brightness (review Meyer and Bullock, 1977; von Buddenbrock, 1915). This has also been shown in some insects for the alignment of the head with respect to the overall brightness distribution (review Wehner, 1981). The DLR can, in principle, be controlled by the compound eyes and/or the ocelli (Section 2, Fig. 1). In dragonflies and locusts, where the ocelli are directed towards the horizon, significant head and steering responses could be elicited by unequal illumination of the ocelli (Stange and Howard, 1979; Stange, 1981; Taylor, 1981a; Rowell, 1988). Previous studies on the same species, however, had shown that the dorsal light response is predominantly elicited via the compound eyes (Mittelstaedt, 1950; Goodman, 1965; Tomioka and Yamaguchi, 1980).

Dorsal light responses can be elicited in *Calliphora* during flight in visually featureless surroundings when either a compound eye or a

lateral ocellus are occluded, and the illumination of the surroundings is suddenly switched on. Thereby a drastic difference of mean brightness in the visual fields of the left and right eyes is created which seems to indicate to the fly that the occluded eye is looking down on a dark ground and the other eye up into the sky. This stimulus may elicit a "righting" roll turn of the head. Occluding a compound eye yields a large tonic head roll with slow rise and fall, the "tonic dorsal light response" (Fig. 5c). Occluding a lateral ocellus yields a small, transient head roll, the "phasig-dorsal light response" (Fig. 5d). This suggests that *Calliphora* uses its ocelli predominantly for purposes other than roll stabilization.

6.4. Gravity sensation without graviceptors

Specific graviceptors have, so far, not been found in insects (review Markl, 1974). Walking honeybees use their head and abdomen as statoliths and mechanoreceptive hair fields to sense the direction of gravity (Lindauer and Nedel, 1959). Ants use their abdomen in a similar way (Markl, 1962) and many insects use leg proprioceptors to compute, from the distribution of the body weight on the legs, the direction of gravity (Fig. 5g, Markl, 1974). When *Calliphora* is suspended by its back, and given a styrofoam ball of its own weight, it will hold it and walk along as if it were walking, back down, on the ceiling. Holding the fly at different roll or pitch angles elicits compensatory head turns depending on the size of the tilt angle (Fig. 6a: dots; Horn and Lang, 1978). If the ball is pivoted so that the fly can still walk on it but does not have to carry its weight, no such response is elicited (Fig. 6a: triangles). This proves that leg proprioceptors are used to sense the direction of gravity.

In flying insects front and middle legs are tightly folded below the body, and the hind legs are used as trailing rudders (Camhi, 1970; Götz et al., 1979). Consequently the graviceptive function of legs is disabled in flight. When *Calliphora* is held during flight at a body roll angle of TP =60 deg
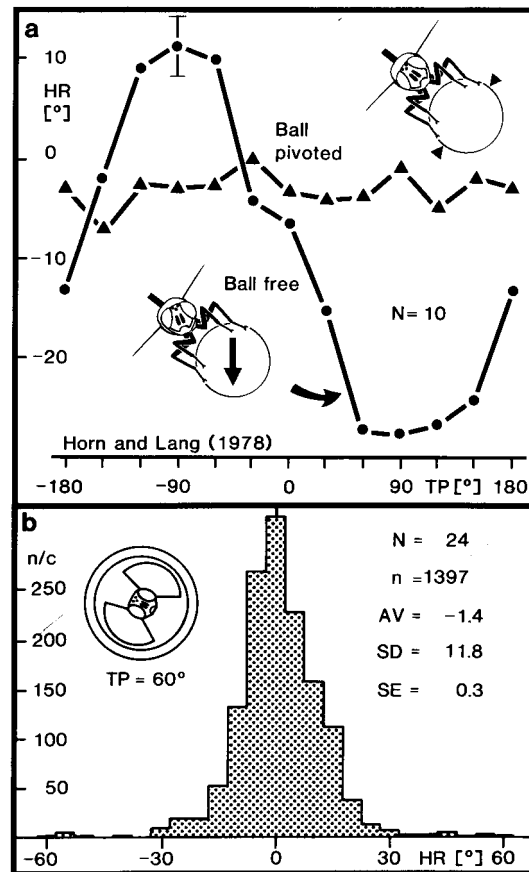

Fig. 6. Gravity sensation in walking and flying flies. (a) Walking flies generate a righting head roll towards the vertical when they have to carry their weight (ball); the response depends upon body orientation (TP) in the gravity field (dots). The lack of a response, when the ball is suspended on bearings, i.e., when the legs are not loaded (triangles), proves that leg proprioceptors are used to measure the direction of gravity. (b) Flying flies roll their head frequently in conjunction with spontaneous flight manoeuvres. When their body is held at TP = 60 deg in visually homogeneous surroundings, and head posture is measured every second, the mean value of the distribution is nearly zero. Hence gravity is not used for head realignment in tethered flight.

in homogeneous visual surroundings the head is on average aligned with its body and no trace of a compensatory gravity response can be found (Fig. 6b; Hengstenberg, 1988).

It could be argued that in free flight where insects must carry their weight by the wings, tilt to one side might lead to a difference in wing

load, indicating a deviation from the vertical. Application of a wing load difference actually elicits a small compensatory head roll (Fig. 5f) but it is transient and therefore not suited to indicate the absolute orientation relative to the vertical.

It appears from these findings that flying insects have no sense of gravity in flight. This appears reasonable if one considers the high centrifugal accelerations, generated by even moderate turns, that would cause frequent misindications of the vertical by any graviceptor. On the other hand, to maintain an upright flight attitude, and the correct alignment of the eyes with the surroundings, an active "knowledge" of the vertical is not necessary. Most technical flight machines (e.g., balloons, parachutes, glider planes) are designed to have passive stability. Many insects, especially those which can glide, seem to have this feature too (Hengstenberg and Bayer, 1988).

6.5. Halteres, the "gyroscopic" sense organs of Diptera

Calliphora generates stabilizing head movements when sinusoidally rolled in featureless visual surroundings or in darkness (Fig. 4c). This response is abolished when the "halteres" are eliminated. The ancestors of Dipteran flies have transformed their hind wings into special sense organs for rotations, the halteres. They are small, pendulumlike organs, buried in the cleft between thorax and abdomen (Fig. 7a). A haltere consists of a distal knob, a thin stiff stalk, and a basal swelling, attached to the body wall via a hinge joint (Fig. 7b). The knob carries ca. 15 mechanoreceptive hairs and the base contains about 350 cuticular strain receptors, organized in five distinct fields, and two internal stretch sense organs (Pflugstaedt, 1912). In flight, the halteres oscillate vertically about their hinge and in antiphase with the wings. The rotating mass of the haltere tends to conserve its angular momentum, and to oppose any change of its plane of oscillation. If the fly rotates about

any axis, other than that of the haltere oscillation, a complex periodic force is generated which acts upon the haltere's center of mass. The coriolis component of this force encodes the direction and angular velocity of the fly's rotation by its frequency, amplitude and phase relative to the wing beat (Pringle, 1948; Nalbach, 1991). Thereby, halteres measure angular velocity directly, and not by integration of an angular acceleration like statocysts and semicircular canals. The fact that the two halteres do not oscillate in the same plane enables the halteres to measure rotations of the fly about arbitrary axes (Pringle, 1957; Nalbach and Hengstenberg, 1986). The halteres are particularly sensitive to high angular velocities (Fig. 11b) and elicit head turns with very short latencies (Sandeman and Markl, 1980; Hengstenberg, 1992).

6.6. The dragonfly head: an angular accelerometer

Dragonflies can fly artistically and catch prey on the wing. During rapid banked turns, they stabilize their eyes passively by the inertial
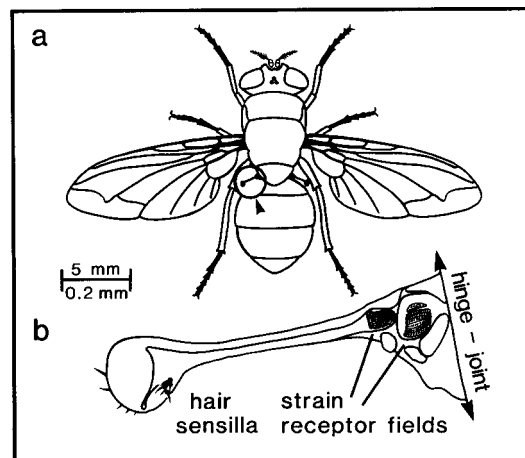

Fig. 7. Halteres of Dipteran flies. Halteres are homologues of hind wings, transformed into sense organs to perceive body rotations. (**a**) Halteres are situated between thorax and abdomen of the fly (circle). (**b**) A haltere consists of an end knob, a thin stiff stalk and a basal swelling carrying most mechanoreceptive organs. In flight, halteres oscillate, vertically and in antiphase with the wings, about a proximal hinge joint within the body wall.

their large head (Fig. 8; Mittelstaedt, 1950). At rest, dragonflies latch their head rigidly to the body. When preparing for flight, they unlatch the neck joint and put their head near its center of mass an a tiny, almost frictionless pin-bearing. This way the dragonfly's head can maintain for a short time its initial orientation when the insect executes a voluntary or unexpected banking (Fig. 8). The neck cuticle consisting, as usual, of rigid joint sclerites and soft bending areas, contains four fields of mechanosensory hairs to monitor head roll relative to the body. These sense organs have two functions: they elicit a change in wing pitch that in free flight leads to a compensatory flight steering manoeuvre (Fig. 8). Their second action is a feedback influence an head position: unilateral elimination of these organs yields a steady head position error as long as the neck is unlatched (Mittelstaedt, 1950; see next paragraph). Head/eye stabilization by means of inertia works, of course, best for brief, abrupt roll turns. At low but longer accelerations, the head turns with the body, and alignment with the vertical has to be achieved by other means.
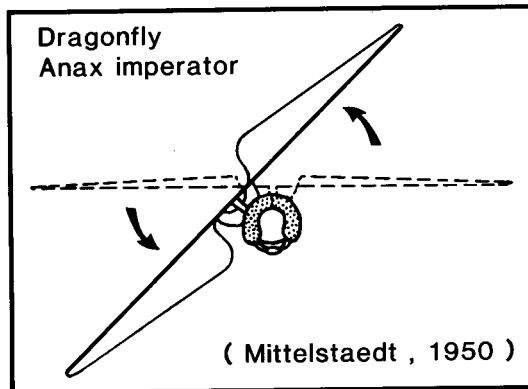

Fig. B. Inertial head stabilization in the dragonfly. *Anax* can latch its head to the thorax when resting. In flight, the head is lightly suspended, near its center of mass, an a delicate pin bearing. The heads inertial momentum causes transient stabilization against unexpected body roll (arrows). Neck sense organs, monitoring the misalignment, elicit compensatory steering (see differential wing pitch) and head realignment.

The brief survey of sensory mechanisms, employed by various insects to align their head and eyes with the vertical, is certainly still very fragmentary. It suggests, however, some degree of uniformity of visual mechanisms among different insect families, whereas the mechanosensory mechanisms appear quite diverse.

7. Head/body-alignment

The insect head is, an the one side, tied to the trunk by the neck. On the other side it is tied to the surroundings, by visual links. This, and internal drifts tend to drive the head eventually towards the boundary of its mobility range. This can be prevented by various means: A neck whose stiffness increases with head excursion would return the head to its middle position as soon as the neck muscles relax. Conversely, symmetrical activation of neck muscles could generate a reset saccade repositioning the head to its symmetrical middle position. Finally, head position sense Organs could be used to measure and control the posture of a lightly mobile head.

Neck sense organs are known in many insects. Their specific function, however, has only been worked out in a few cases or for particular aspects (Lowne, 1895; Mittelstaedt, 1950; Goodman, 1959; Shepheard, 1973; Thurm, 1963; Liske, 1989). The dragonfly, for example, has 10 distinct patches of mechanoreceptive hairs, four of which are used to monitor head roll, and to elicit the respective steering responses of the wings (Mittelstaedt, 1950). In the praying mantis, two hair fields are known to respond to head yaw (Liske, 1989). In locust, one pair of hair plates is excited by head roll. The significance of these hair fields for head posture control has not yet been studied, and their role in flight steering is still controversial (Goodman, 1959, 1965; Hensler and Robert, 1990; Miall, 1990).

Calliphora has two different types of neck sense organs: a pair of hair fields, called prosternal organs (Fig. 9a; Lowne, 1895; Peters, 1962), and a pair of internal stretch sense organs, the

prothoracic chordotonal organs (Vater, 1961). The hairs of the prostemal organs are bent by contact sclerites when the fly turns its head. The degree and number of bent hairs varies in the two hair fields in the same sense with head pitch, and in opposite sense with head roll (Fig. 9a). Creating an imbalance of bent hairs by shaving one hair field results in a steady head roll in the expected direction (Fig. 9b; Preuß and Hengstenberg, 1990).
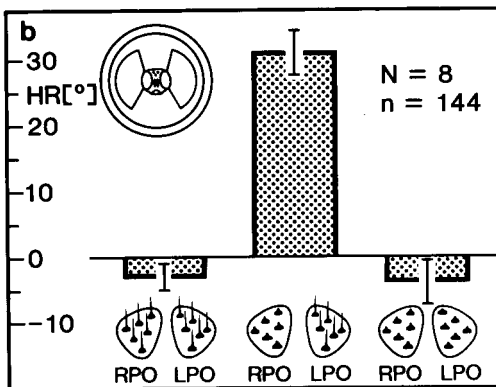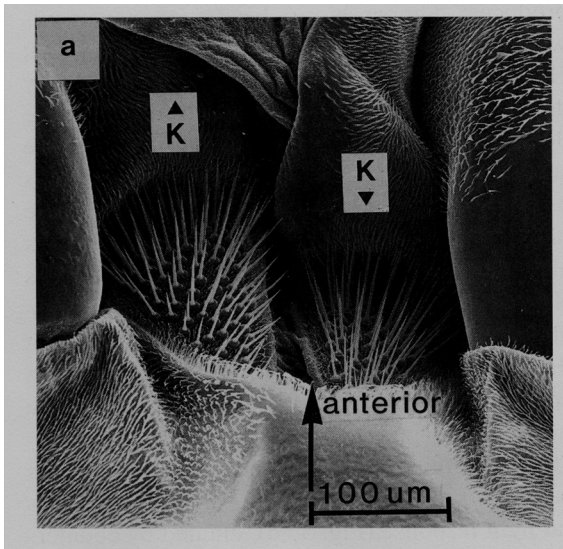

Fig. 9. Head/trunk alignment by neck sense organs. (**a**) *Calliphora* has a pair of mechanoreceptive hair fields on the ventral side of its neck. With head roll the number of hairs bent by contact sclerites (*K*) in the two fields is changed differentially. (**b**) If a difference in excited hair sensilla is created by shaving one field, a steady head offset is elicited in the expected direction.

In *Calliphora* too, the neck sense organs influence flight steering (Liske, 1977, 1978). However, the specific roles of the two types of neck sense organs for the control of head position, and of flight torque, each concerning three axes, are still incompletely understood.

There is an interesting aspect of head/trunk co-ordination by neck sense organs associated with equilibrium control in two different flight situations. When a fly is tilted to one side by turbulent air, it generates corrective head and body turns simultaneously and in the same direction. (Hengstenberg et al., 1986). This leads to a transient excitation of neck sense organs until both, head and body, are realigned with the vertical. Conversely, when the fly performs a banked turn in still air, its head stays more or less aligned with the vertical while the body banks to keep balance (Hengstenberg, 1992; Wagner and Wehrhahn, 1985). Here again, the neck sense organs are transiently excited until the turn is completed. Interestingly, in the two flight situations, the cause of banking is different; the sequence of events during realignment, however, is qualitatively the same. In this way, the fly's central nervous system does not need to recognize its momentary flight situation in order to generate the appropriate motor actions.

8. Kinetic and dynamic aspects

In gaze-stabilizing systems of Crustacea, higher Molluscs and Vertebrates, it is well known that visual and vestibular subsystems have different dynamic characteristics. Roughly speaking, vestibular systems are fast but inaccurate with respect to angular position, and visual systems are slow but more precise. Our present knowledge about insects suggests a similar relationship: the dragonfly's angular accelerometer is specifically suited to monitor fast movements and not at all to measure angular position. Similarly, the Coriolis force exploited in fly halteres is proportional to angular velocity, and elicits responses only above a threshold at ca. 50 deg/s (Fig. 1lb). Thus the

rapidity of mechanosensory responses seems to arise from the physical principles used and from the degree of specificity built into the sense organs. Visually elicited responses are commonly believed to be slower because more neural processing stages are required to generate a specific control signal. This is probably true in a general way but not necessarily in all instances. Locusts, for example, do not seem to have a mechanosensory system specialized to sense body rotations. Hence their visual mechanisms must be fast enough for effective stabilization, and it seems that the ocelli represent the fast channel (Wilson, 1978; Taylor, 1981b; Rowell and Pearson, 1983; Rowell, 1989).

In *Calliphora,* the kinetics of compensatory head roll has been measured in response to an angular step displacement (Fig. 10). When the fly is rolled within the sky-and-ground pattern, it produces after a short latency (ca. 10 ms) a rapidly rising response that is maintained much longer than 5 s (Fig. 10a). When the fly is equally rolled in visually featureless surroundings, the response has again a short latency and fast rising phase but decays within less than 5 s (Fig. 10c). Displacing instead the pattern, elicits after a much

longer latency (ca. 30 ms) a visual response, rising gradually to a nonzero steady state level (Fig. 10b). Apparently, *Calliphora* corroborates the general notions about the dynamic characteristics of visual and "vestibular" systems.

When *Calliphora* is rolled back and forth through ±90 deg in the sky-and-ground pattern and the angular velocity of the stimulus is varied between 0 deg/s and more than 2000 deg/s, the fly produces compensatory head/eye movements with a maximum at about 500 deg/s (Fig. 11a; Hengstenberg et al., 1986). The angular velocity dependence of the major partial responses can be demonstrated by application of the appropriate stimuli (Fig. 5) at varying angular velocities. This reveals that the perception of body roll via the halteres (Fig. 5e) is significant only at roll speeds above 50 deg/s and saturates at about 1000 deg/s (Fig. 11b; the decline beyond 1000 deg/s is probably due to the short stimulation time of 90 ms at this speed). Motion of a striped pattern with a spatial wavelength of $\lambda = 30$ deg (Fig. 5a) elicits a maximum response at a pattern velocity of PV = 70 deg/s, and smaller responses at pattern speeds below and above this optimum (Fig. 11 c). The dorsal light response (Fig. 5c,d), elicited by counter
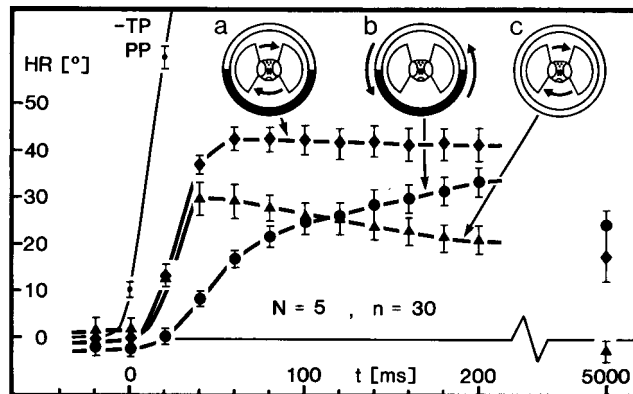

Fig. 10. Kinetics of head roll with angular step stimuli. Initial and steady state head roll of *Calliphora* in response to an angular step displacement (90 deg; 2000 deg/s) of (a) the fly within the sky-and-ground pattern eliciting, after short delay, a fast maintained head realignment. (b) Displacement of the pattern elicits, after a longer delay, a slower rising maintained head roll. (c) Displacing the fly in homogeneously bright surroundings elicits, after short delay, a fast rising but transient head roll. Thus, the initial phase (t < 100 ms) of the response to the combined stimulus is largely determined by mechanosensory signals, and the steady state level of the response (t ≥ 5 s) by visual signals.

phase flicker in the left and right half of the visual field, elicits a head roll up to an equivalent angular velocity of 500 deg/s, and, most significantly at 0 deg/s, that is to say, at a steady misalignment with the overall brightness distribution (Fig. 11 d). Interestingly, the arithmetic sum (Fig. 11e) of the three component responses (Fig. 11b-d) is, except for an amplitude factor, very similar to the response curve obtained with complex roll stimulation of the fly (Fig. 11 a). This suggests that in the head motor system of *Calliphora* the integration of different sensory signals may be quite simple.

9. Architecture of the insect gaze control system

To stabilize its eyes with respect to the vertical, *Calliphora* makes use of a variety of cues and sensory mechanisms (Fig. 5). Some of them, with appropriately different directional specificity, are also available to control pitch- and yaw-turns (Land, 1975; Meyer, 1978; Nalbach and Hengstenberg, 1986; Kirschfeld and Baier-Rogowski, 1987). Insect gaze movements are the sum of head- and body turns. The sensory mechanisms, illustrated above, act simultaneously on both the head- and the body-motor. Since head turns stimulate neck sense organs which in turn elicit specific body turns, the latter are also affected indirectly by sensory signals causing a head turn. (Geiger and Poggio, 1977). Finally, the whole setup is modified, when an insect switches from walking to flight or vice versa: the eyes seem to operate independent of the locomotor state, but some mechanosensory organs are useless in flight (e.g., leg load receptors), or useless on the ground (e.g., wing load receptors). Finally, the result of sen-
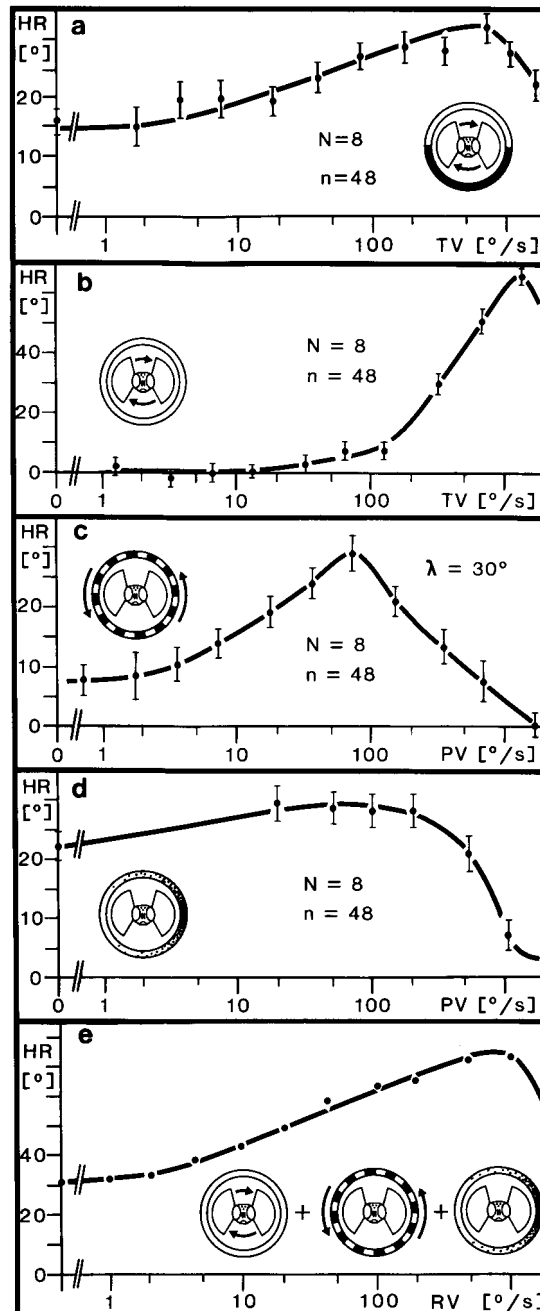

Fig. 11. Angular velocity characteristics of sensory subsystems. Head roll in *Calliphora* elicited by steady motion stimuli of varying angular velocity. (**a**) Flies rolled within the sky-and-ground pattern from 0 deg/s to more than 2000 deg/s respond with a maximum at about 500 deg/s. (**b**) Body roll as sensed by the halteres is effective only above 50 deg/s and saturates beyond 1000 deg/s (see text). (**c**) The pattern motion response peaks at 70 deg/s with a pattern wavelength of λ = 30 deg, and declines to zero at lower and higher angular velocities. (**d**) The dorsal light response yields a true steady state response at 0 deg/s extending, however, up to considerable angular velocites of about 500 deg/s. (**e**) The arithmetic sum of the response components **b-d** is very similar to the response to the combined stimulus (**a**).

sory processing must be routed to the correct motor output system (legs, wings), and suppressed in the other one, depending upon the momentary locomotor state.

The signal flow diagram shown in Fig. 12 summarizes qualitatively what we presently know about the roll-stabilizing system of *Calliphora*. There are five cues, received by six different sense organs and processed by appropriate networks to generate roll-specific signals. These are distributed to three motor output systems. Switches enable or disable input from the sensory subsystems, or output to the control muscles, depending upon the fly's locomotor state. Error

signals are reduced physically by compensatory movements.

10. Concluding remarks

It is now evident that at least some insects have a quite elaborate oculomotor system. It enables them to shift and stabilize their gaze in a similar manner as other highly visual animals, i.e., Crustacea, Molluscs and Vertebrates. Motion of the retinal image or its misalignment with the retinal co-ordinates cause a degradation of vision, irrespective of the particular design of the eyes. Preventing these disturbances by effective stabilization of the eyes in their normal orientation prevents their deleterious effects on the visual information gained at the different levels of processing. This may be particularly advantageous for insects having really small brains
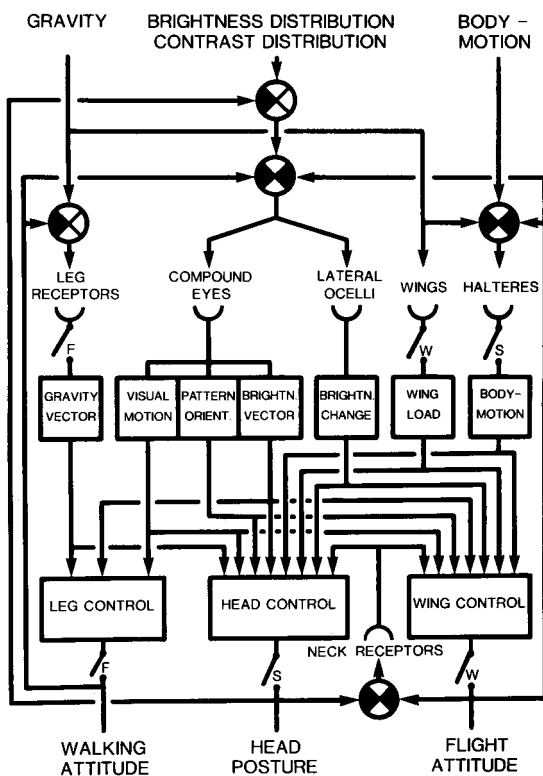
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Fig. 12. Roll control in the blowfly *Calliphora*. Signal flow diagram showing identified sensory cues, sense organs and neural processing stages for the generation of roll-specific signals and their projections to motor output stages. Switches, opened by various locomotor states (F = flight; W = walking; S = standing) gate inputs and outputs appropriately. Stabilization of the eyes in space prevents visual degradation at its origin and minimizes the need for "mental" image realignment.

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