Gaze control in the blowfly *Calliphora:* a multisensory, two-stage integration process

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Flies move their eyes by turning their heads either spontaneously or in response to unexpected disturbances of their preferred flight attitude. They use several visual and mechanosensory cues to keep flight balance and to stabilize their eyes relative to the surroundings by compensatory head/eye movements. The various sensory subsystems have different speed characteristics and cooperate autonomously to provide the fly with fast and accurate visual stabilization. Head and trunk are coordinated by neck sense organs affecting head posture as well as flight torque. The functional structure of the fly's gaze control system changes its input-and output configuration when the fly alternates between flight and walking.

Key words: blowfly *Calliphora* / eye movements / fly gaze / insect oculomotor system / multisensory integration

FOR FREELY MOBILE animals it is vital to keep balance, i.e. to establish and maintain a distinct orientation relative to the vertical. This equilibrium orientation also determines the average alignment of sense organs, such as the eyes, with the surroundings. The retinae and visual nervous systems have evolved under the constraints of gravity and probably work best in their 'normal orientation' .

Visual perception may be degraded by different kinds of disturbances: if the retinal image moves too fast, the limited temporal resolution of the photoreceptors prevents the resolution of fine spatial detail; when objects of interest are imaged an inappropriate parts of the retina (e.g. extrafoveal), they are seen less well than when correctly centered; familiar objects are less well recognized when seen in an unfamiliar orientation.[1-3] Thus, best visual perception requires upright stabilization of the eyes whereas high manoeuverability, as in a flying animal may require fast movements and oblique postures. This conflict of interest can be partly solved by mobile eyes which may be stabilized temporarily an the visual scene

during locomotion. Stabilizing eye movements have been extensively studied in humans,[3] other vertebrates,[4] molluscs[5,6] and crustacea[7,8] but, until recently, very little in insects.[9] Here I illustrate that the blowfly *Calliphora,* despite having a very small brain (< 1 mg), has a sophisticated gaze control system and achieves good performance in this difficult task which is of general biological significance.

The fly's eyes and gaze movements

Insects have two kinds of eyes: the pair of large lateral compound eyes, suited to resolve spatial detail, and three small dorsal ocelli that detect overall brightness changes.[9-11] All are part of the head capsule and are thus moved in rigid conjunction with the head. The neck joint is formed by the articulated sclerites and soft folds of the neck cuticle. Head movements are effected by 21 pairs of neck muscles, with a single motor neuron innervating each muscle.[12-14] In the blowfly *Calliphora,* the range of head turns is $\pm 20°$ both horizontally (yaw) and vertically (pitch), and $\pm 90°$ for rotations about the line of sight (roll) which roughly corresponds with the main body axis. Here, head movements are interpreted exclusively as eye movements but, of course, they also affect other head sense organs and may serve other purposes, for example as one component of flight steering.[15-17]

Insect head movements are very difficult to observe in free flight, but can be recorded in tethered flight. A fly mounted horizontally on a very light vertical pivot shows fast 'saccadic' yaw turns of its head towards visual objects, followed by slower body turns.[18] When mounted vertically on the pivot, the fly rolls quasi-randomly about its body axis and simultaneously rolls its head in the opposite direction.[19] In both situations the fly tries to stabilize its head in space while performing self-induced body turns.

Unexpected changes of the fly's flight attitude, such as those caused in free flight by air turbulence, can be generated in tethered flight in a wind tunnel (Figure la): the fly, attached by its back coaxially

to a servomotor, flies in a fixed position inside a cylinder which accommodates various patterns (Figure lb). Fly and pattern can be rolled independently; head movements are observed by a macro video camera (Figure 1c) and evaluated by measuring the angular positions of the fly's head (HP), its trunk (TP) and the pattern (PP) and by calculating head roll relative to the trunk (HR = HP - TP, Figure 1d). Pitch- and yaw-turns can also be generated and studied by mounting the fly appropriately.

If a fly is rolled, for example, sinusoidally at 1 Hz through ± 90° in optically structured surroundings (Figure 2a), it generates a phase-locked head roll that counteracts the imposed roll stimulus (Figure 2b). In free flight, this response would reduce the eye's misalignment caused by an unexpected change of flight attitude. The response amplitude is, in most
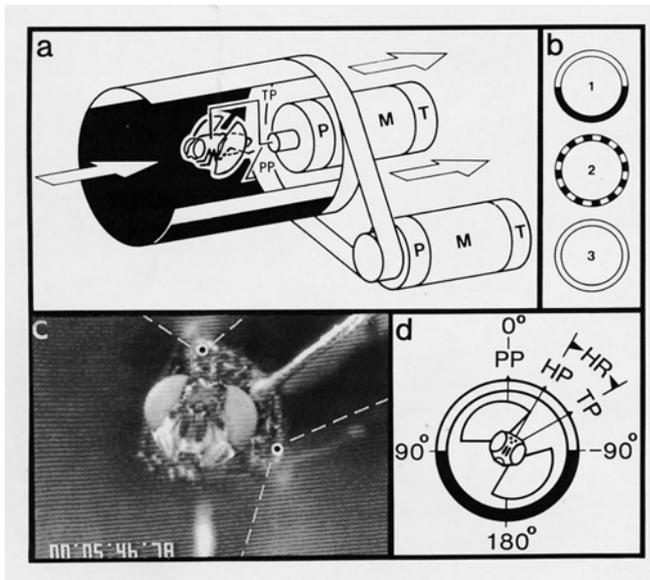

Figure 2. Compensatory head roll of *Calliphora* in tethered flight. (a) Sinusoidal roll stimulus (± 90°, 1 Hz) (b) Rolling the fly in the sky-and-ground pattern elicit an antiphasic head roll compensating for about 66% of the imposed misalignment. (c) Rolling the pattern with the fly held stationary elicits a head-following response in phase with the stimulus resulting from visual roll perception. (d) Rolling the fly in visually homogeneous surroundings elicits an antiphasic head roll due to body motion perception.

Figure 1. Observation of insect head/eye movements. (a) A fly, fixed coaxially to the shaft of a servomotor (M), is flying stationarily in an airstream (arrows) in a suctiontype wind tunnel that consists of an aerodynamic nozzle (not shown), an opaque cylinder and an electric fan (not shown). The cylinder accommodates different patterns (b) that are diffusely illuminated from outside. The fly and/or pattern cylinder can be tilted or turned arbitrarily with feedbacks to control angular position or angular velocity. (c) The fly is observed by a macro-video camera through the entrance nozzle of the wind tunnel. The angular positions of the pattern (PP) and of the fly's trunk (TP) are indicated by pointers (see a,c). These and the fly's head position (HP) relative to the vertical are measured in still-frame mode. (d) Head roll (HR) is calculated relative to the fly's trunk (HR = HP - TP).
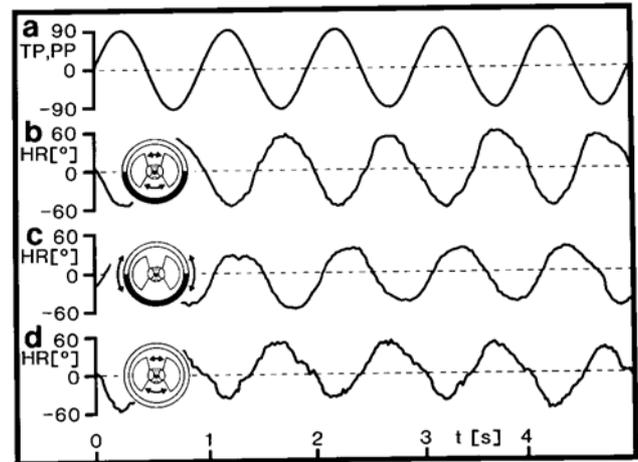
cases, smaller than required for an actual stabilization of the eyes with respect to the surroundings. Simultaneously, however, flies produce a compensatory flight-steering response which contributes to the overall realignment of the eyes during free flight.[1]

Sensory mechanisms and dynamic complementation

The response of Figure 2b could be due to visual roll perception or to body motion perception or both. Which mechanism is used by the fly? The wind-tunnel/stimulator enables us to separate the components of the complex roll stimulus: a phaselocked head roll can be elicited by sinusoidal movement of the pattern while the fly is held stationary, (Figure 2c) proving that roll can be perceived visually. Conversely, rolling the fly in bright, visually homogeneous surroundings elicits a phase-locked response as well (Figure 2d), proving that *Calliphora* also uses body-motion perception to control its head posture. Both response components tend to stabilize the eyes against unexpected roll.[20] Similar mechanisms are used to control pitch- and yaw-turns of the fly's head. [18,21,22]

Which are the characteristic cues, sense organs and neural mechanisms that *Calliphora* uses to perceive its particular orientation or motion with respect to an external frame of reference? Specific stimulation combined with selective elimination of sense organs has been used to isolate different response components. Figure 3 characterizes four visual and four mechanosensory subsystems used for roll perception by name, sense organ and a pictogram indicating the procedure used to define the respective response (refs 19-23; R. Hengstenberg, unpublished results).

Visual mechanisms

The *pattern motion response* (Figure 3a) is elicited by coherent roll motion of arbitrary patterns as long as the texture of the patterns can be resolved by the compound eyes. Interestingly, this response is also elicited by monocular vertical motion stimuli in the lateral visual field, which can be considered as an ambiguous component of one of two unambiguous binocular flow patterns: when the fly rises or falls (translation) the image flow is in the same direction in the two eyes, whereas when the fly rolls (rotation) the image flow is in opposite directions in the two eyes, relative to the fly's sagittal symmetry plane (see Figure 3a, arrows). The fly does not seem to need to resolve the apparent ambiguity of the visual motion stimulus, for example, by an AND-operation,

to generate a head stabilizing response. The *edge orientation response* (Figure 3b) is elicited by contours in the frontal visual field. The housefly *Musca* prefers, as estimated by its flight torque, to align itself with vertical contours[24] whereas *Calliphora* tends to align its head with horizontal edges, for example the horizon (R. Hengstenberg, unpublished results). It is not known whether this is a true species difference or whether the flies behave differently in the two experimental situations. The *dorsal light response* (Figure 3c,d) results in insects turning their backs towards the center of brightness of the surroundings; normally this is the sky, so they turn usually upwards.[9-11] The roll component of this response depends upon the difference of the mean brightness in the left and right hemifields (R. Hengstenberg, unpublished results), and is strongly stimulated when one eye is illuminated while the other is occluded. This can be used to separate the contributions of the fly's two types of eyes. The compound eyes mediate the *tonic dorsal light response* (Figure 3c): after the light is switched on, the fly rolls its head gradually towards the illuminated side, within 2 s reaching a steady state head angle that is maintained as long as the light is on.

The ocelli mediate *a phasic dorsal light response* after light on (Figure 3d), which is a transient head roll in the same direction as the tonic response but disappearing within a few seconds during maintained asymmetrical illumination of the ocelli. In *Calliphora* this response
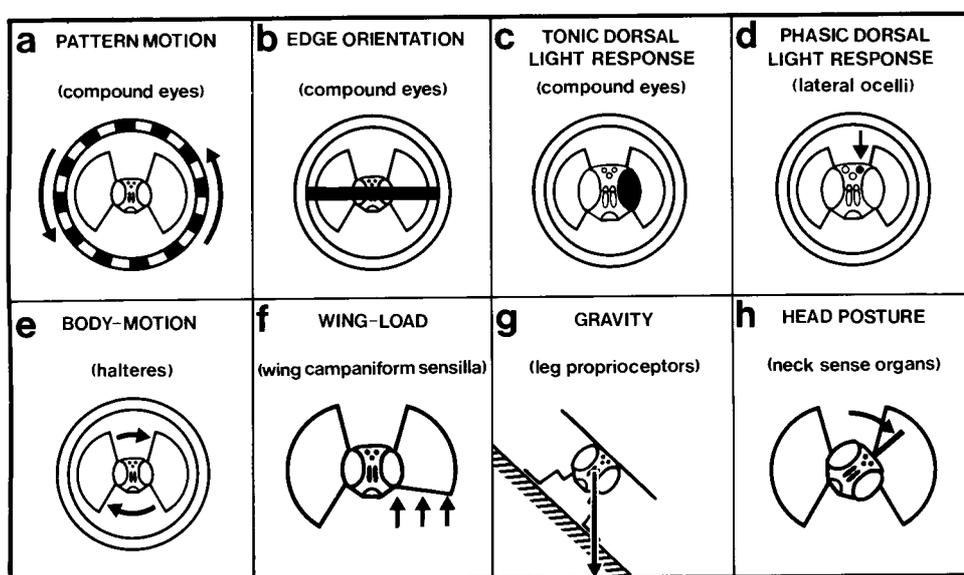

Figure 3. Cues and sense organs for roll perception in *Calliphora*. Four separate visual (a-d) and four mechanosensory (e-h) response components have been identified by applying specific stimuli and by eliminating particular sense organs. Gravity is effective only in the walking fly. Most other cues also influence the flight torque and some the walking posture.

is small relative to the tonic component (R. Hengstenberg, unpublished results), and compared with that in other insects.[9]

Mechanosensory mechanisms

The mechanosensory mechanisms for roll perception are more varied among different insect orders than the visual ones.[9] In the highly evolved flies, *body rotations* (Figure 3e) are perceived through the halteres, unique sense organs for rotation, which evolved by transformation of the hind wings and which oscillate during flight in antiphase with the wings. Halteres measure angular velocity by sensing the periodic Coriolis force that acts upon the oscillating haltere when the fly rotates. Frequency and phase of the two haltere signals, relative to the wingbeat cycle, provide unambiguous information about the direction and speed of rotation.[20,25-28] Thus, the physical principles of haltere function are entirely different to those of statocysts or semicircular canals used by other animals. *A difference in wing-load* on either side (Figure 3f), which may be caused by a tilt to one side or during generation of a roll torque, elicits a transient head roll. Wing load is probably sensed by campaniform sensilla, sense organs in the wing base which respond specifically to directional strain in the cuticle of the wing veins.[20] *Gravity is,* it seems, not sensed by flies or any other insect during flight[20,29] but it does passively stabilize the upright flight position.[30] In walking flies (Figure 3g), gravity influences the head posture through the load distribution among the legs.[21] Finally, the head posture affects itself (Figure 3h) through *neck sense organs*[9,23] (see below).

Calliphora may use additional, more sophisticated cues to control the orientation of its head, but even the list of responses shown in Figure 3 is sufficient to suggest that for a fly, keeping its eyes aligned with the vertical is an

Kinetic and dynamic complementation of subsystems

What is the specific advantage of using both visual and mechanosensory mechanisms to stabilize eye position in the fly? In crustacea, molluscs and vertebrates, eye stabilization is also controlled bimodally:[3-8] statocysts and semicircular canals are commonly believed to be directionally selective by virtue of their structure and are thus best suited to respond quickly though not very precisely to fast

movements; visual mechanisms, on the other hand, are considered to be slow because they require several stages of processing to achieve directional specificity. This seems to be true also for the fly.

If *Calliphora* is rolled stepwise (90° at *2000° s^{-1}*) during flight in sky-and-ground surroundings, it rolls its head after a short latency (10 ms) with high speed *(1200° s^{-1})* against the imposed misalignment and maintains this response, minus some adaptation, continuously (Figure 4a). When the fly is rolled by the same amount in the absence of visual cues, it still responds after a short delay with high speed, but the response vanishes completely within 5 s (Figure 4b). If the fly is held stationary and the pattern is displaced at the same speed through the same angle, the fly responds only after 30 ms and much slower (450° s^{-1}) but the response is maintained indefinitely (Figure 4c). It appears that the initial phase of the head-roll step response of *Calliphora* is predominantly under control of the mechanosensory subsystems (Figure 3e-h), whereas the steady-state response is exclusively due to the visual subsystems (Figure 3a-d). At intermediate times, all systems contribute to the momentary response, each to a time-dependent extent.

If *Calliphora* is rolled back and forth through ± 90° at constant angular velocity inside the sky- and ground pattern, its steady-state head posture depends upon the angular velocity of the stimulus (Figure 4d): with a steady misalignment (trunk velocity TV = 0° s^{-1}), the fly shows a steady compensatory head roll; the response increases with angular velocity up to about 1000° s^{-1}, and declines again, because at very high speeds the head cannot follow the rapidly reversing stimulus motion. Mechanosensory roll perception, through the halteres and wings (Figure 3e,f) is ineffective below TV = 50° s^{-1} but elicits strong responses at higher roll speeds (Figure 4e). Pattern motion yields maximum responses at intermediate speeds, depending on the spatial wavelength of the pattern (Figure 4f). The dorsal light response is observed when the fly is steadily illuminated from the side (Figures 3c, 4g; pattern velocity PV = 0° s^{-1}). Shifting the center of brightness, without directional motion, by counterphase brightness modulation in the receptive fields of the two eyes, elicits a response up to an illusory speed of PV = 500° s^{-1} (Figure 4g).

These findings demonstrate a striking functional similarity between the fly's gaze control system and the oculomotor systems in other phyla: fast disturbances are predominantly detected and controlled by mechanosensory systems whereas slow drift and
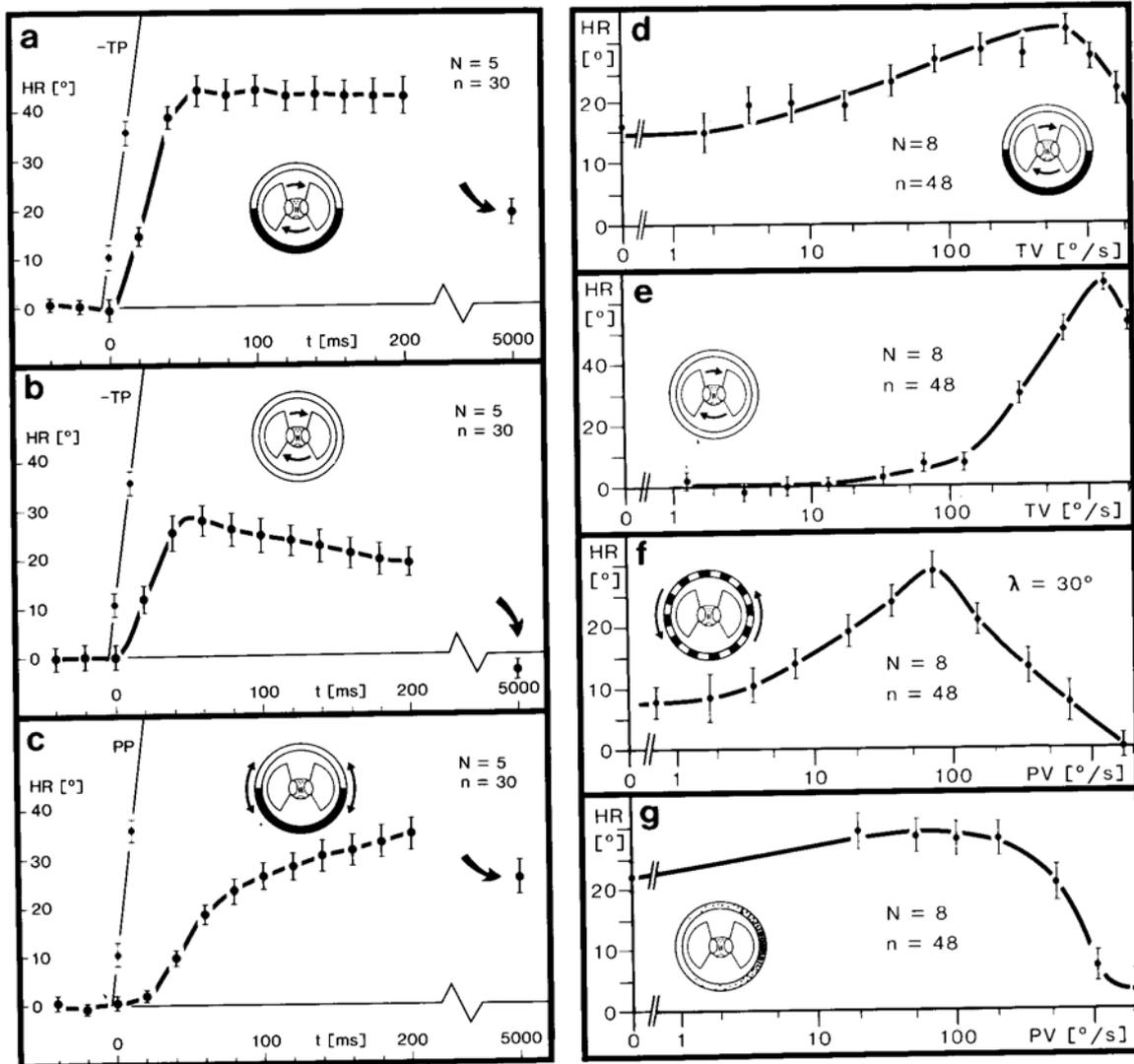
Figure 4. Kinetics and dynamics of sensory subsystems. (a-c) Time course of head roll in response to angular step stimuli (90°, 2000° s⁻¹). (a) A fly tilted by - 90° in the sky-and-ground pattern generates, after a short delay, a fast head roll which is maintained for seconds. (b) Tilting the fly in visually homogeneous surroundings elicits, after a short delay, a fast head roll which disappears in less than 5 s. (c) Stepwise displacement of the pattern elicits a head roll after a much longer delay which rises slowly to a maintained level. (d-g) Angular velocity dependence of the responses of sensory subsystems. (d) A fly, rolled in visually structured surroundings, responds over a very wide range of angular velocities. (e) Body motion (TV) in the absence of visual cues is perceived only above TV= 50° s⁻¹ and best at comparatively high speeds. (f) Pattern motion (PV) is optimally perceived at intermediate speeds, depending on the spatial frequency (1/λ) of the pattern. (g) The dorsal light response is elicited over a wide range of apparent angular velocities (see text); most important, however, is its contribution at zero speed, the fly's only measure of absolute orientation during flight. The two experiments demonstrate that *Calliphora* combines fast mechanosensory responses and slower visual responses in roll control. The weighting of the response components varies with the angular velocity at which the fly is rolled.

steady misalignments are perceived visually.

At intermediate angular velocities all sensory subsystems cooperate to achieve optimal stabilization of the eyes. Such 'kinetic and dynamic complementation' requires autonomous operation of all subsystems. The experiments discussed above, which identify the response components in Calliphora (Figure 3), prove that this condition is fulfilled.

Functional organization of roll control

Small, voluntary body turns can be compensated by the neck motor alone (see above). Large, unexpected deviations from the correct flight attitude, however, also require corrective flight manoeuvres to regain balance. For flight control, *Calliphora* uses essentially the same sensory mechanisms as for head realignment. [18,22,27] The neck- and flight motors are thus controlled in parallel by roll-specific signals (Figure 3). The movements produced by the two motors, however, act in series on the fly's eyes because the head is carried by the body.

On the ground, the orientation of the trunk is largely determined by the slant of the substrate. Walking flies nevertheless try to align their head and body vertically by appropriate postural responses (ref 29; R. Hengstenberg, unpublished results). So far this field has barely been studied but qualitative observations show that *Calliphora,* when walking, uses at least pattern motion (Figure 3a), the dorsal light response (Figure 3c, e) and gravity (Figure 3g) to control stance and head posture,[21,31] (R. Hengstenberg, unpublished results). These observations show that flies use two motor stages to shift gaze: one turns the head and the other turns the trunk. The latter has two configurations: depending on the locomotor state, body turns are effected by wing- or leg muscles. In each configuration, neck- and trunk motors are simultaneously activated by common roll-specific signals.

Head/trunk coordination

Because of imperfections, the fly's head motor tends to accumulate a positional error that drives the head towards its end of range. This can be prevented either passively if the neck acts as a rotary spring or actively by means of neck sense organs monitoring head position. *Calliphora* has two types of proprioceptive sense organs associated with the neck: a pair

of prothoracic chordotonal organs whose specific function is still unknown and a pair of prosternal organs[32] that are selectively stimulated by pitch- and roll motions of the fly's head and elicit a response returning the head to its neutral position. [21,23]

On the other hand, neck sense organs also influence the fly's flight torque: imposed head yaw elicits a torque in the same direction which fails if the sense organs are destroyed. [15] In free flight the fly's trunk follows the yaw movement of its head, which may be guided by visual cues. It is not clear which type of sense organ is involved, and whether pitch- and roll-torques are controlled in the same way. These results, which at first sight are contradictory, illustrate how the fly's head is poised between an 'extrovert' orientation towards the visual world and an 'introvert' orientation with reference to itself. It may well be that the fly is free to chose its frame of reference from moment to moment.

Signal flow for roll control in Calliphora

The signal flow diagram shown in Figure 5 summarizes our present knowledge of roll control in *Calliphora:* there are two visual and three mechanoreceptive cues, perceived through six kinds of sense organs that feed into neural circuits extracting roll-specific signals. These are distributed in turn on to the three motor control centers that coordinate the activity of neck, leg and flight muscles. Compensatory movements physically reduce the roll error signal. Switches opened by different locomotor states (F = flight, W = walking, S = standing) disable the input from mechanoreceptive sense organs and the inappropriate motor outputs.

This diagram (Figure 5) also serves to identify areas that are poorly understood and to guide the physiological studies required to characterize particular sensory subsystems. The diagram can be expanded to accommodate neuroanatomical findings (see below) or condensed to facilitate modelling and dynamic simulation. To produce a complete functional diagram of gaze control in the fly, elements for the specific control of pitch and yaw turns need to be added, and a representation of the fly's spontaneous behaviour is also lacking.

The neural basis of gaze control

Diptera have a highly condensed central nervous system.[33] The 'brain' comprises the cerebral and
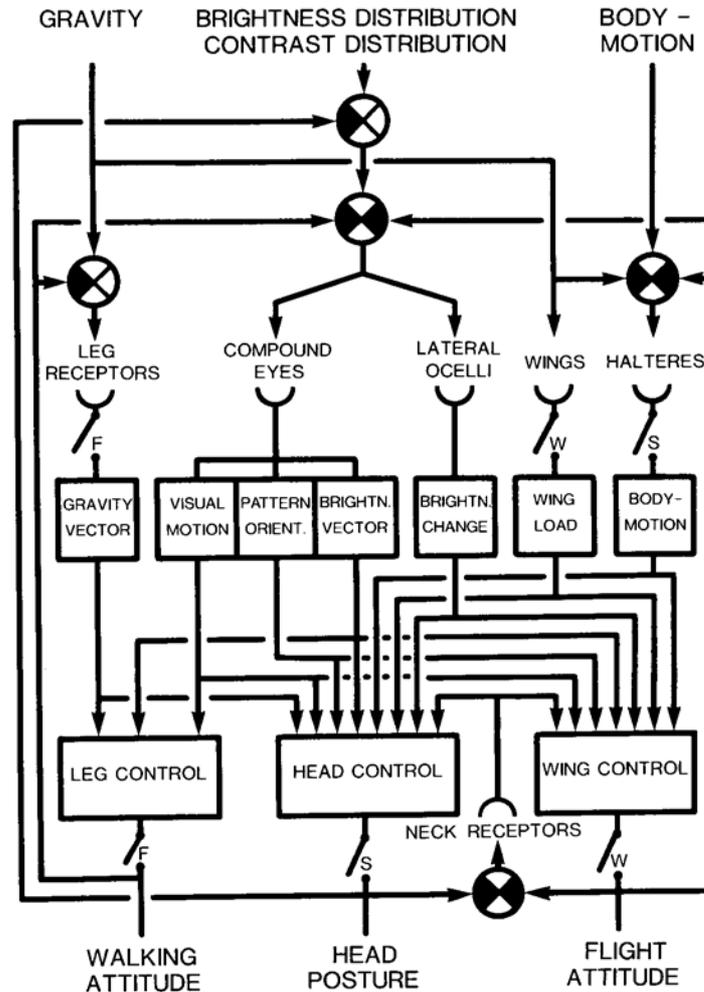
Figure 5. Signal flow diagram of roll control in Calliphora illustrates the effective cues, the sense organs involved, the signal processing stages that can be logically separated, the distribution of signals on motor control centers, and the compensatory effect (black sectors at signal summation points) of motor actions an input signals. Switches are opened by the locomotor states (F, flying; W, walking; S, standing) to prevent the simultaneous operation of conflicting pathways.

subesophageal ganglia and the 'thoracic compound ganglion' consists of the fused thoracic and abdominal ganglia. Nevertheless, the original segmentation of the insect ventral nerve cord can still be distinguished by the shape of the thoracic neuropiles known as neuromeres (Figure 6). The arborization of the motor neurons of neck, leg, and flight steering muscles have been displayed in detail using silver-intensified cobalt labelling.[34,36] Each of these three groups consists of a small number of motor neurons (< 50 pairs), each of which is individually recognizable by its distinct location of the cell body which is functionally unimportant, its arborization, which occupies a characteristic part of the neuropile and the particular nerve through which its axon leaves the thoracic ganglion (Figure 6).

The arborization of leg motor neurons mainly lie in ventral areas of the thoracic neuromeres, restricted to the side and segment of the leg they innervate (R. Hengstenberg, unpublished results). Arborizations of flight steering muscle motor neurons are concentrated in the dorsal mesothoracic neuro pile,[35,36] whereas some neck motor neurons are found in the subesophageal ganglion and some in the prothoracic ganglion; their arborizations are mostly located in the dorsal neuropile. Twenty-one out of 26 pairs of neck motor neurons have their cell bodies and most of their arborizations ipsilateral to the muscle they innervate. Some, however, have contralateral arborizations.[12,13]

The general layout of sensory projections on to motor neurons is well known in the commonly
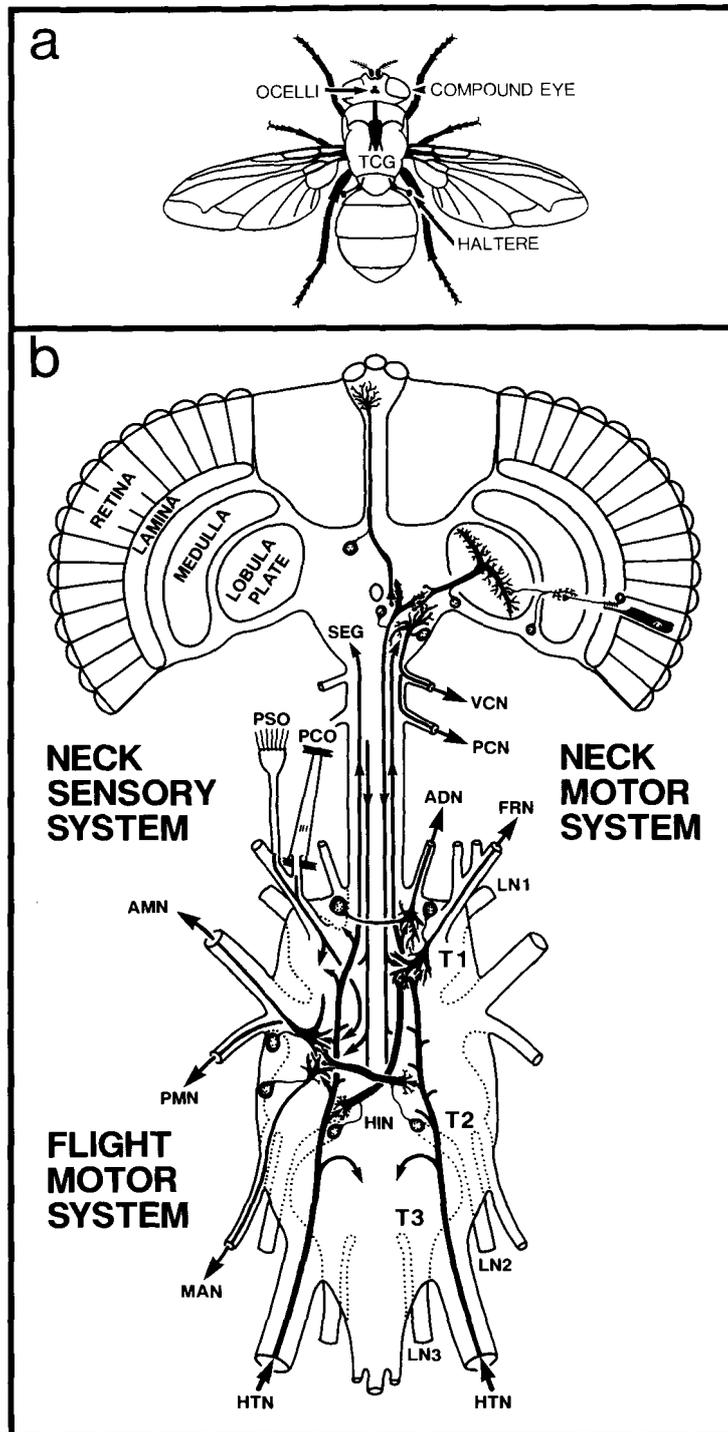
studied fly families[12-14,32-36,48,52] and in a few other insects, particularly locusts[11,37-39] This paragraph summarizes briefly what is known about the two motion sensitive systems of the fly-the halteres and the visual system.

Body motion perception (Figure 3e) in the fly is mediated by the halteres which are equipped with about 450 mechanoreceptors, arranged in seven precisely ordered groups. The haltere nerve (Figure 6) carries the receptor axons anteriorly into the thoracic compound ganglion, where it projects as a solid bundle through the ipsilateral side of all three thoracic neuromeres, before ascending through the fused cervical connectives to the ipsilateral side of the subesophageal ganglion. [12,35] In each thoracic neuromere the receptor axons give off collaterals that contact ipsilateral wing and neck motor neurons and interneurons that project to the contralateral side, where they converge on the wing and neck motor neurons of the other side of the body. Most remarkably, these pathways have been demonstrated by the passage of cobalt ions across one or even two contiguous neurons.[12,35] In other neurons in the fly, this cell-specific transneuronal cobalt labelling is associated with gap junctions,[40] another indication that the haltere pathway is a particularly fast one (see Figure 4).

Visual motion perception (Figure 3a) is mediated through the compound eyes and requires a nonlinear interaction between two adjacent inputs.[41,42] The spatial arrangement of the two inputs determines the directional specificity of the local movement signal. To perceive motion in arbitrary directions at one point in the visual field, there are thought to be a set of probably six unidirectional movement detectors for each element of visual space.[43] The neurons performing these operations have not been identified but this process is likely to take place in the second visual neuropile, the medulla (Figure 6b). Directionspecific, small field motion information is carried, again by unidentified small neurons, to the third visual neuropile, the lobula plate, where it is sorted according to its preferred direction into a stack of four retinotopic maps, one for each of the principal directions of motion in the visual field (left, right, up, down).[44] A few, individually recognizable, tangential neurons in the lobula plate collect and integrate local movement signals over large areas of the visual field by picking specific small-field motion information from the motion maps at distinct locations.[45-48] At this stage, information about the location in visual space is discarded and information about global coherent motion is generated. Widefield motion information from the contralateral eye also converges at this level on particular tangential neurons conferring on most of them maximal sensitivity to rotations of the whole animal.[44,45]

Positional information, signalling the location of objects, is represented at different levels of the visual nervous system in retinotopic arrays of small field neurons but little is known about their physiology and position-specific processing.[44] Output neurons of the optic lobe converge either directly on neck motor neurons[12,13] or, in most cases, on descending interneurons, which may receive additional input from other brain regions and sense organs.[48,49] Visual descending neurons project through the cervical connectives, which contain several thousand

Figure 6. Neural basis for gaze- and flight control. (a) Dorsal aspect of *Calliphora* illustrating the major sense organs and the location of the thoracic compound ganglion TCG, part of the central nervous system. (b) Cerebral ganglia (top) and thoracic compound ganglion (below), which consists of the fused thoracic (T1-T3) and abdominal ganglia. Neuron classes are illustrated by a realistic cartoon of one cell for each class and projection pathways by solid lines. For clarity, elements of the neck sensory system and of the flight motor system are shown on the left side only and elements of the visual pathways and of the neck motor system are shown on the right. All elements are, of course, bilaterally symmetrical. Visual information converges, after specific preprocessing in the optic lobe, either directly on neck motor neurons in the subesophageal ganglion (SEG) or an descending neurons. They project through the fused cervical connectives into the TCG, and send axon collaterals into the arborization areas of neck, leg and wing motor neurons in the respective segments. Mechanosensory information provided by wing and haltere receptors enter the nervous system through the wing nerve (AMN) and the haltere nerve (HTN). Receptor axons ascend ipsilaterally to the SEG and give off collaterals which contact ipsilateral wing and neck motor neurons in T2 and T1. Haltere information reaches contralateral wing and neck motor neurons through heterolateral interneurons that cross the midline (HIN). Head position information is detected by neck sense organs (PSO, PCO) and routed through the frontal nerve (FRN) to the ipsilateral neck- and wing motor neuropile. The arborizations of motor neurons occupy distinct areas in the segmental neuropiles of T1 and T2; motor axons leave the CNS through various nerves: VCN, PCN, ADN and FRN supply neck muscles: AMN, PMN and MAN supply wing muscles, and LN1-LN3 supply leg muscles (for abbreviation, see below). Multisensory integration takes place on at least two levels: an descending interneurons and mainly on motor neurons. In flies the physiology of these interactions is still largely unknown.

descending and ascending fibres, to the thoracic motor centers, where they branch in dorsal neuropile areas shared by motor neuron arborizations. Their response characteristics have only partially been determined and for a small proportion of cells.[50-52] Similarly their interactions with premotor interneurons and motor neurons have not yet been studied in flies. Nevertheless it appears that, compared with the haltere pathway, many processing stages are required to extract a signal encoding the direction and velocity of the fly 's motion in space from the temporally varying spatial pattern of brightness that is received by the retina.

Prospects and significance

The blowfly *Calliphora* clearly has a highly developed oculomotor system: it can turn its head in all three directions either voluntarily, or involuntarily in response to extrinsic disturbances. It uses several mechanosensory and visual mechanisms to stabilize both its body in space and its direction of sight and the alignment of its eyes with the vertical. The various sensory mechanisms, which differ with respect to their kinetic and dynamic characteristics, operate independently but complement each other. It will be necessary to characterize the components of this system (Figures 3, 5, 6) quantitatively before attempting model simulations of its performance. The mechanisms for controlling pitch and yaw turns of the head and trunk must also be studied in detail. As the sensory and motor mechanisms concerned with the fly's principal axes are not necessarily orthogonal, making them linearly independent, oblique measuring axes and motor crosstalk must be considered.[27] The biggest challenge, with present techniques, is the identification and functional characterization of neural elements of the orientation control system. As with most insect preparations, the principal pathways contain only a small number of neurons, each with a precise location and characteristic shape: evidence obtained from different experiments can thus be attributed to neurons that are recognizable from one preparation to the next, an increasingly detailed picture of their particular functions can be built up.[44-51]

How does the study of the fly's gaze control system contribute to the general understanding of motor systems for gaze control? The insects are phylogenetically only very distantly related to crustacea, molluscs and vertebrates and the sensory, neural and motor systems they use for gaze control have evolved independently and differ radically from those in other phyla. Nevertheless there are striking functional similarities between phyla in the use of position- and motion-specific mechanisms to control eye position; the use of visual and mechanosensory mechanisms to control gaze; the dynamic range fractionation between different sensory components; and even the general arrangement of control mechanisms, i.e. mobile eyes are equivalent to the fly's head, they are carried on a platform (the head or, in the fly's case, the trunk) which is under fast mechanosensory control of the labyrinth or the fly's halteres. It seems to me that such similarities tell us much about the problems to be solved by any gaze control system and about the biological mechanisms needed to implement a particular solution. Comparing the differences between the systems may well serve to provoke new ideas about both the general organisation of gaze control systems as well as the detailed mechanisms of specific systems.

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