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Neural Mechanisms of Visual Course Control in Insects

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Chapter 18

Neural Mechanisms of Visual Course Control in Insects

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1 Introduction

Visual orientation and course-stabilization of flying insects rely essentially on the evaluation of the retinal motion patterns perceived by the animals during flight. Apparent motions of the entire surrounding indicate the direction and speed of self-motion in space and are used as visual feedback signals during optomotor course-control manoeuvres. Discontinuities in the motion pattern and relative motions between pattern-segments indicate the existence of stationary or moving objects and represent the basic visual cues for flight-orientation during fixation- and tracking-sequences, and possibly also for the avoidance of obstacles, and the selection of landing sites.

Neurophysiological studies, carried out in the last three decades, have revealed a large variety of functionally different motion-sensitive interneurons in the visual systems of insects (for review see Wehner 1981). The problems tackled in these studies range from the uptake and peripheral preprocessing of visual signals, and the cellular mechanism of the elementary motion detector, to the subsequent processing of motion information in higher neuronal circuits, and the functional relevance of these circuits in flight-control. It is evident that the latter questions, in particular, can only be adequately studied in conjunction with behavioral analyses.

The visual system of the fly has proven to be particularly well suited for investigations on these topics. Its compound eyes, optic lobes and visuo-motor pathways have been the subject of numerous optical, physiological, and anatomical studies (reviews: Strausfeld 1976; Hausen 1977; Heide 1983; Laughlin 1984; De Voe 1985; Franceschini 1985; Hardie 1985; Järvilehto 1985) and it may not be exaggerating to claim that it is the most thoroughly investigated insect visual system at present. Furthermore, visually guided behavior has been extensively studied in various species of flies under both natural and laboratory conditions (reviews: Reichardt and Poggio 1976; Land 1977; Götz 1983; Buchner 1984; Heisenberg and Wolf 1984; Wehrhahn 1985; Reichardt 1986).

The present account, which reviews neuronal mechanisms of optomotor course-control and the detection and fixation of objects, will therefore be mainly concerned with studies in flies. We will first discuss the results of recent behavioral investigations which have been of major relevance for the electrophysiological analysis of motion-computation in the fly visual system. The general architecture

of visuo-motor pathways, and the anatomy, physiology and functional role of identified interneurons in the control of visual behavior are topics of the following sections. Related studies on other insect species will be considered briefly at the end of the paper.

2 Motion-Induced Behavior in Flies

2.1 Visual Course-Stabilization

Flies stabilize their flight direction by following, and hence reducing the global movements of the retinal image induced by involuntary deviations from their flight course. For example, rotatory retinal motions, which indicate rotations of the body with respect to the environment, elicit syndirectional torque responses around the three body axes. Translatory motions in vertical and horizontal directions, which indicate deviations from the flight altitude and changes of the flight velocity, induce corrective modulations of the translational flight forces (lift and thrust).

The motor activity of the flying animal during these maneuvers is complex and far from being fully understood. The generation of yaw torque, and of thrust and lift, results mainly from differential and covariant changes of the beat amplitudes of both wings, respectively (Götz 1968; Götz et al. 1979; Zanker 1987). Differential changes of wing pitch on both sides may be involved at least in the generation of roll responses (Hengstenberg et al. 1986). In addition, changes of the plane of the wing-stroke and active rudder movements of hindlegs and abdomen play a prominent role during steering maneuvres (Götz 1968; Götz et al. 1979; Zanker 1987).

The neural computations underlying these complex motor responses have been extensively investigated in the last decades. One of the first, and most important, results of these studies was the finding that the motion detectors involved in the control of optomotor responses are of the so-called correlation type (Hassenstein and Reichardt 1956; Reichardt 1957, 1961, 1987). A motion detector of this kind basically performs a multiplication of input signals received by two retinal sampling stations (Fig. 1a). Prior to multiplication, one of the signals is delayed by low-pass filtering, whereas the other remains unaltered. Due to these operations, the circuit responds preferentially to visual stimuli moving in one particular direction. By connecting two of them with opposite directional selectivities as excitatory and inhibitory elements to an integrating output stage, one gains a bidirectional elementary movement detector (EMD) having a preferred and a null direction.

The preferred direction of an EMD depends on the spatial arrangement of the sampling stations in the compound eye. In the visual system of the fly, individual EMD's receive input mainly from contiguous points of the hexagonal ommatidial lattice (Fig. 1a). This sample scheme holds true at least for *Drosophila* (Götz 1968, 1983; Buchner 1976; Götz et al. 1979), and there is some evidence for a similar organization in the larger flies *Musca* and *Calliphora* (Zaagman et al. 1977). The situation seems, however, somewhat more complex in the latter species, since

EMD's having enlarged and horizontally or vertically aligned sampling bases have been also demonstrated (Kirschfeld 1972; Riehle and Franceschini 1984).

Apart from its directional selectivity, an EMD of the correlation type is characterized by the fact that its average output depends on the contrast frequency of a motion stimulus (i.e., the ratio of angular velocity and wavelength of its spatial Fourier components) rather than its actual velocity. Behavioral studies have demonstrated that the amplitudes of the optomotor responses controlled by these motion detectors are indeed strongly dependent on the contrast frequency of motion stimuli (for a detailed discussion of this point see Buchner 1984; see also Reichardt and Guo 1986).

Two further functional aspects of the detector shall be briefly mentioned. The first one regards the time constant of the filter in the input channel, which was recently found to depend on the actual stimulus conditions. It has been shown that prolonged stimulations with high contrast frequencies can shorten the time constant considerably (Maddes and Laughlin 1985; de Ruyter van Steveninck et al. 1986; Borst and Egelhaaf 1987). The result of this adaptive process is an effective increase of the temporal operating range of the motion detector, which is reflected in the broad peak of the contrast frequency function of the optomotor system (1–10Hz) as found in behavioral investigations (Götz 1964; McCann and MacGinitie 1965; Eckert 1973; Wehrhahn 1986; Borst and Bahde 1987; Hausen and Wehrhahn 1987a), and in electrophysiological studies (Mastebroek et al. 1980; Eckert 1980; Hausen 1981, 1982b; Eckert and Hamdorf 1981; Maddess and Laughlin 1985).

The second aspect concerns the role of spatial integration processes in motion computation. Studies on the dynamic properties of motion detectors have revealed that their transient responses to motion are strongly influenced by the spatial structure of the stimulus (Reichardt and Guo 1986; Egelhaaf and Reichardt 1987). For particular classes of motion stimuli, this may even lead to an inversion of the detector-response and, thus, to incorrect signals with respect to the actual direction of motion. Ambiguities of this kind are certainly fatal for a flight-control system relying essentially on motion information and can be avoided by integrating the outputs of extended arrays of EMD's. As will be discussed below, such spatial integration does indeed play an important role in the motion-detection circuits of the fly.

Whereas the above studies revealed basic functional properties of the EMD, further series of behavioral investigations elucidated the spatial organization of the EMD networks in the visual system and their functional connections to the motor system. Under natural conditions, optomotor responses are usually induced by binocular motions of the environment. Labboratory experiments have demonstrated, however, that monocular stimulation of arbitrary small areas of the retina, and even stimulation of individual EMD's is sufficient to elicit measurable motor responses (Götz 1964; Kirschfeld 1972). This shows that the entire retina is subserved by dense networks of EMD's, each ommatidium representing an input channel to the various directional types of EMD's described above.

Optomotor yaw torque responses are selectively induced by horizontal motions (Fermi and Reichardt 1963; Götz 1968; Wehrhahn 1986; Hausen and Wehrhahn 1987a) and, hence, must be controlled by EMD's having sampling bases

parallel to the horizontal axis of the eye lattice (h, Fig. 1a), or by pairs of EMD's having symmetrically arranged sampling bases with respect to this axis (x and y, Fig. 1a), the outputs of which are added. Monocular stimulation with progressive (front to back) motion leads to a simultaneous decrease of the ipsilateral and an increase of the contralateral wing beat amplitude and thus to generation of yaw torque turning the animal in the same direction as the perceived motion. Regressive (back to front) motion is less effective but leads also to syndirectional torque

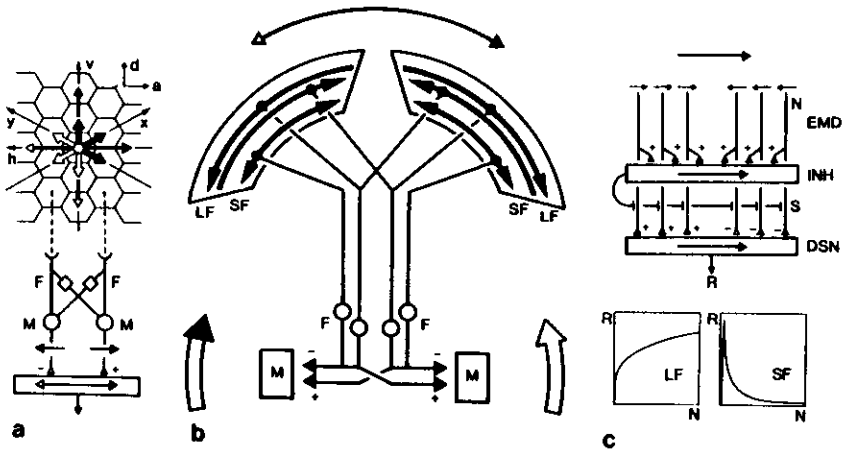


Fig. 1.a-c. Motion computation circuits in the visual system of the fly. *a* Retinal sampling stations and organization of elementary motion detectors (EMD's). The wiring diagram in the lower part of the figure shows a bidirectional EMD consisting of two subunits. Each subunit has two input channels derived from the retina, one containing a low-pass filter (*F*), and a multiplication stage (*M*); it responds preferentially to motion across the retinal sampling stations in the direction indicated by an *arrow* in the output channel. The bidirectional EMD has a preferred and null direction as indicated by the *black and white arrowhead* in the summation stage at the bottom of the circuit. The *upper graph* shows the sampling stations of presently known EMD's in the ommatidial lattice of the compound eye (*thick black and white arrows*). h, v, x, y: axes of the hexagonal ommatidial lattice; *d,a* dorsal, anterior. *b* Model of neural circuits controlling motion-induced yaw torque responses. Horizontal motions activate two motion sensitive systems behind each eye, which integrate the outputs of arrays of EMD's, and which are specifically tuned to large-field motion (*LF*-system) and small-field or object motion (*SF*-system). The LF-system is activated by ipsilateral front-to-back motion and contralateral back-to-front motion, and induces syndirectional yaw torque responses of the fly by simultaneous excitation and inhibition of the contralateral and ipsilateral flight motor (*M*), respectively. The SF-system is activated by ipsilateral horizontal motion of small objects in both directions and induces turnings towards the stimulus. The output channels of the LF- and SF-system contain different frequency-filters (*F*). The SF- and LF-system dominate in torque-control under stimulation with high-frequency and low-frequency oscillatory motion, respectively. *c* Model of gain-control mechanism underlying the spatial tuning of the LF- and SF-system shown in *b*. The outputs of excitatory and inhibitory arrays of EMD's sensitive to front-to-back motion and back-to-front motion are integrated by a direction selective element (*DSN*), which represents an output element of the LF- or SF-system. The EMD-outputs are also integrated by an inhibitor (*INH*) which shunts the individual EMD-channels (*S*) peripheral to the DSN. Depending on the transfer characteristics of the output synapses of the EMD's, the output (*R*) of the DSN increases with the number (*N*) of EMD's activated by a motion-stimulus (*LF*-tuning, *left curve*), or reaches a maximum when only few EMD's are excited and declines subsequently (*SF*-turning, *right curve*). (*a* After Reichardt 1961; Kirschfeld 1972; Buchner 1976; Götz et al. 1979; *b,c* after Reichardt et al. 1983; Buchner 1984; Egelhaaf 1985c)

responses. We must hence assume functional connections between the networks of elementary motion detectors and the flight motor of the fly as sketched in Fig. 1b, which are termed large-field system (LF). Corresponding systems, which shall not be discussed in detail, control roll and pitch responses (Götz 1968; Wehrhahn and Reichardt 1975; Srinivasan 1977; Götz and Buchner 1978; Buchner et al. 1978; Wehrhahn 1978; Götz et al. 1979; Blondeau and Heisenberg 1982; Zanker 1987).

2.2 Discrimination and Fixation of Objects

Freely flying flies frequently display a pursuit behavior, in which two flies follow each other (Land and Collett 1974; Wehrhahn 1979; Wagner 1986a). This demonstrates that the animals are able to detect, fixate, and track a moving object in a structured environment even when the retinal image of the environment is also moving. Behavioral and electrophysiological studies have revealed that the evaluation of relative motion between object and background plays a key role in the neural control of this behavior, and that the cellular circuits performing this computation are closely interrelated with those controlling optomotor course stabilization.

In the early experimental investigations of fixation behavior (Reichardt 1973; Reichardt and Poggio 1976; Heisenberg and Wolf 1984), tethered flying flies were positioned in the centre of a bright panorama and were stimulated with a single dark stripe. The stripe was oscillated horizontally around arbitrary positions and the yaw torque responses of the flies were recorded. The measurements revealed that the average torque responses were consistently directed towards the moving stimulus, indicating that the flies attempted to fixate it. The amplitudes of these responses were found to be strongly dependent on the stimulus position, being largest for frontal stimuli.

The mechanism underlying fixation behavior was originally thought to rely on the fact that yaw torque responses induced by progressive motion are not only of opposite polarity but also larger than those induced by regressive motion (see above). An oscillating stimulus will consequently elicit a net response towards the target and thus lead to the observed fixation behavior (Reichardt 1973; Wehrhahn and Hausen 1980). In an alternative hypothesis, it was proposed that fixation responses are controlled by flicker detectors in the visual system rather than by motion detectors (Pick 1974).

In subsequent studies (Virsik and Reichardt 1976; Reichardt and Poggio 1979; Poggio et al. 1981; Reichardt et al. 1983; Egelhaaf 1985a,b,c), the yaw torque responses of tethered flies were measured under stimulation-conditions more closely resembling the complex retinal motion pattern encountered by freely moving animals. In these experiments the flies were stimulated by a textured stripe (figure or object) moving in front of a textured moving panorama (ground). Figure and ground had the same texture and were oscillated horizontally with the same frequency and amplitude, but with a certain phase difference. Hence, the only visual cue for the discrimination of the figure was the relative motion between both patterns. The experiments clearly demonstrated that flies are able to detect and fixate a figure under these conditions, and that, hence, motion detection and not flicker detection is the essential process underlying this behavior. However, the

hypothesis that fixation is simply caused by the response asymmetry for progressive and regressive motion turned out to be insufficient to explain the dynamic properties of the torque responses recorded in these experiments.

The analysis of these transient yaw torque components and related electrophysiological studies of the motion computation circuits in the optic lobes of the fly revealed that optomotor course stabilization and fixation behavior are jointly governed by two control systems (Reichardt et al. 1983; Egelhaaf 1985a,b,c, 1987). The first one is the aforementioned LF system, which is sensitive to motion of the entire environment, and which induces syndirectional torque responses. The second system, which will be called small-field (SF) system (Fig. 1b), evaluates horizontal motion of small objects. It induces turning responses towards an object irrespective of its actual direction of motion and is inhibited, when the size of the object increases, or when the background moves in the same direction as the object. Due to these characteristics, the relative influence of both systems on torque generation depends critically on the actual stimulus condition: e.g., oscillatory motions of the entire surrounding, which greatly inactivate the SF-system elicit syndirectional optomotor following responses, whereas oscillatory object-motions activate predominantly the SF-system and hence will lead to torque oscillations with a strong component directed towards the target. The contributions of both control systems to the final motor output vary with the oscillation frequency, the LF-system dominating at low and the SF-system at high frequencies. It is assumed that these temporal characteristics are due to different frequency filters in the output channels of the two control systems (Egelhaaf 1987).

The different spatial sensitivities of the LF- and SF-system can both be modelled by the circuitry shown in Fig. 1c (Poggio et al. 1981, Reichardt et al. 1983; Egelhaaf 1985a,c). It consists of two arrays of EMD's sensitive to regressive and progressive motion, an integrative inhibitory element (INH) and an integrative directionally selective output element (DSN). The EMD's represent the entire arrays of motion detectors sensitive to horizontal motion behind one eye and are for clarity separated into two groups according to their directional selectivity. The output element DSN may be regarded as one of the output elements of the LF-system shown in Fig. 1b, or as one of several directionally selective output elements of the SF-system having opposite preferred directions. The latter are shown as a single bidirectional element in Fig. 1b, since they induce turning tendencies into the same direction. Under stimulation with motion, the inhibitory element integrates the signals of the EMD's and inhibits them individually in a shunting-operation (S). The strength of this inhibition depends thus on the number (N) of EMD's stimulated and hence on the size of the stimulus. The output element subsequently integrates the reduced signals of the EMD's. Depending on the transfer characteristics of the output synapses of the EMD's, stimulation with a motion stimulus of increasing size will either lead to an increasing signal amplitude in the output element, as is characteristic for the LF-system, or to a peak response at small stimuli and a subsequent response decay, as is found in the SF-system. Hence, the principle difference between both systems lies in the synaptic efficiencies of the EMD-terminals on the integrating output elements. Further differences concern the actual neuronal realization of these circuits in the optic lobe of the fly, which will be discussed below. The computations performed by this

inhibitory network have been mathematically formulated and investigated in computer simulations (Reichardt et al. 1983). The graphs in Fig. 1c show the simulated responses of an LF-and an SF-output element as function of the number of stimulated channels and illustrate the spatial integration properties of the two systems.

The interplay of the two systems in flight control is illustrated in Fig. 2a which shows the yaw torque response of a fly to stimulation with motion of a textured figure and background. As indicated in the stimulus trace at the bottom, the

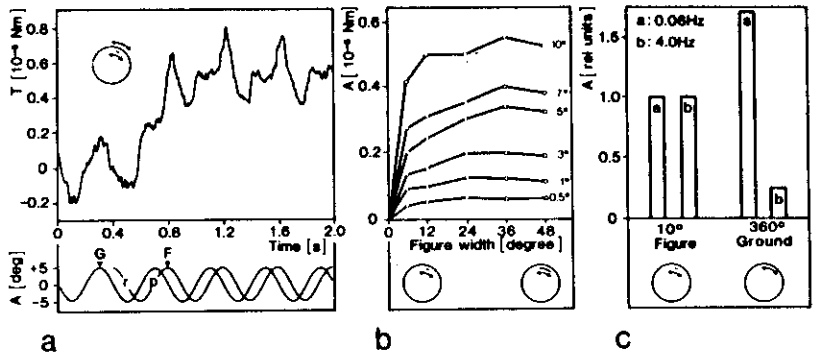


Fig. 2.a-c. Yaw-torque responses of a tethered flying housefly (*Musca*) to horizontal motion. *a* Averaged transient responses T recorded under stimulation with horizontal motion of a narrow stripe (figure *F*) in front of a moving panorama (ground *G*). The stimulus situation is shown in the inset, and the motion of figure and ground are indicated at the bottom of the figure. The figure is positioned in the equatorial, frontolateral visual field of the right eye and has an angular width of 12°. Progressive and regressive motion of the figure are marked with *p* and *r*. Figure and ground have identical textures (random dot patterns) and are oscillated with the same amplitude (10°) and frequency (2.5 Hz); both are first moved in synchrony and later with a phase difference of 90°. Synchronous motion induces zero-symmetric optomotor yaw torque fluctuations, which are syndirectional to the stimulus motion. Relative motion between figure and ground elicits strong torque responses towards the figure, indicating that the fly is attempting to fixate it. The complicated transient response pattern reflects the influence of two torque control systems on the motor output: a large-field (LF) system, which is tuned to large motion-stimuli, and a small-field (SF) system, which responds selectively to small motion stimuli (see text). *b* Response dependency on the size of the stimulus. The curves show the amplitudes *A* of yaw torque responses of the fly as function of the width of a figure, oscillating horizontally with a frequency of 2.5 Hz within a stationary panorama (see *insets*). Parameter in the experiment is the oscillation amplitude of the figure. Each value plotted is derived from 100 measurements. Under all conditions the response amplitudes increase first steeply and reach later a plateau. This is compatible with the hypothesis that torque generation is jointly controlled by the SF- and the LF-system. *c* Response dependency on the stimulus size under different oscillation frequencies. The histogram shows the amplitudes A of yaw-torque responses to oscillations of a small figure (width: 10°) and the entire ground (360°). Responses to both stimuli were measured at two oscillation frequencies (*a* 0.06 Hz; *b* 4 Hz). The values plotted were obtained from 32 (0.06 Hz) and 52 (4 Hz) flies; they were normalized using the response to figure motion under each condition as reference. At low oscillation frequencies the responses to motion of the ground are large as compared to those induced by the figure. The opposite situation is found under at high frequencies. This shows that the influence of the LF-system, dominating in torque control under stimulation with large patterns, decreases with increasing oscillation frequencies, and indicates different frequency-filtering in the output channel of the LF- and SF-system (*a,b* From Reichardt et al. 1983; *c* from Egelhaaf 1987)

experiment starts with synchronous oscillations of figure and ground. The fly shows a normal corrective optomotor response: clockwise motion (from $A = -5°$ to $A = +5°$) induces a positive torque response which indicates intended clockwise turning of the fly, whereas counterclockwise motion leads to a negative response. Obviously, the figure is not detected under this condition. When the figure starts moving relative to the background, the response of the fly changes considerably. It shifts to positive values and shows conspicuous peaks. The positive response level indicates that the figure is now detected and that the fly attempts to fixate it. The ongoing torque fluctuations reflect the activity of both control systems. Large response peaks occur, when the figure moves with maximal speed in progressive direction, while the ground velocity is transiently zero. In these instants, the SF-system is maximally stimulated by progressive motion of the figure and is simultaneously released from the inhibition caused by background-motion.

Figure 2b shows the dependency of the torque amplitudes induced by oscillatory figure motion as a function of the size of the figure, while the ground is held stationary (see Reichardt et al. 1983). The oscillation frequency is chosen such that the LF- and SF-system are about equally effective in torque control. Parameter in this experiment is the oscillation amplitude of the figure. In all cases the torque responses increase steeply initially and remain then rather independent of the stimulus size. This is in accordance with the concept that the response consists of an increasing LF-controlled component and a simultaneously decreasing SF-component (compare with Fig. 1c).

The relative influence of both systems under different oscillation frequencies is illustrated in Fig. 2c, which shows the responses to oscillation of the figure and the ground, measured at a very low and a high oscillation frequency. It can be seen that in agreement with the proposed filter characteristics in the output channels of the LF- and the SF-system, the responses to ground motion become small compared to the figure-induced responses at high oscillation frequencies and large at low frequencies (Egelhaaf 1987).

Thus, the behavioral data compiled in Fig. 2 can at least qualitatively be interpreted in terms of the two control systems proposed in the model. More convincing are simulations of the model output which show a high similarity to the behavioral data. We will consider these simulations later and discuss first the basic neural architecture of the visual system of the fly and the neuronal motion computation circuits in the optic lobe.

3 Visuo-Motor Pathways in the Nervous System of the Fly

The visual system of the fly consists of the ocelli, the compound eyes, the optic lobes, and the visual tracts and projection centres in the brain (Strausfeld 1976). Each compound eye scans about one hemisphere of the environment and samples the light-intensity distribution in the optical axes of the ommatidia. The signals of the compound eye are conveyed by receptor axons into the optic lobe, which consists of successive visual neuropils (lamina, medulla, lobula, lobula plate) and two chiasms. The basic blueprint of all visual neuropils is similar: each is composed of

retinotopically arranged columns and superimposed layers. Columns are built up by parallel centripetal and centrifugal small-field neurons (columnar cells), the axons of which project through the chiasms and establish the retinotopic connections between the neuropils. The columnar cells mediate, in addition, local interactions between adjacent columns. In contrast, layers are dense synaptic regions within the neuropils, which are oriented orthogonally to the columns, and which contain the arborizations of large interneurons (tangential and amacrine cells). The latter elements are the structural substrate of long-range interactions and spatial integration processes within the columnar array. Output connections from the optic lobe to the brain are established by both columnar and tangential cells (Fig. 3). Columnar cells leave the highest-order visual neuropils lobula and lobula plate as dense bundles and terminate in visual centers of the ventrolateral brain termed optic foci. Tangential output neurons of the optic lobe originate from all neuropils except the lamina. Some of them connect both optic lobes, others project also into the optic foci.

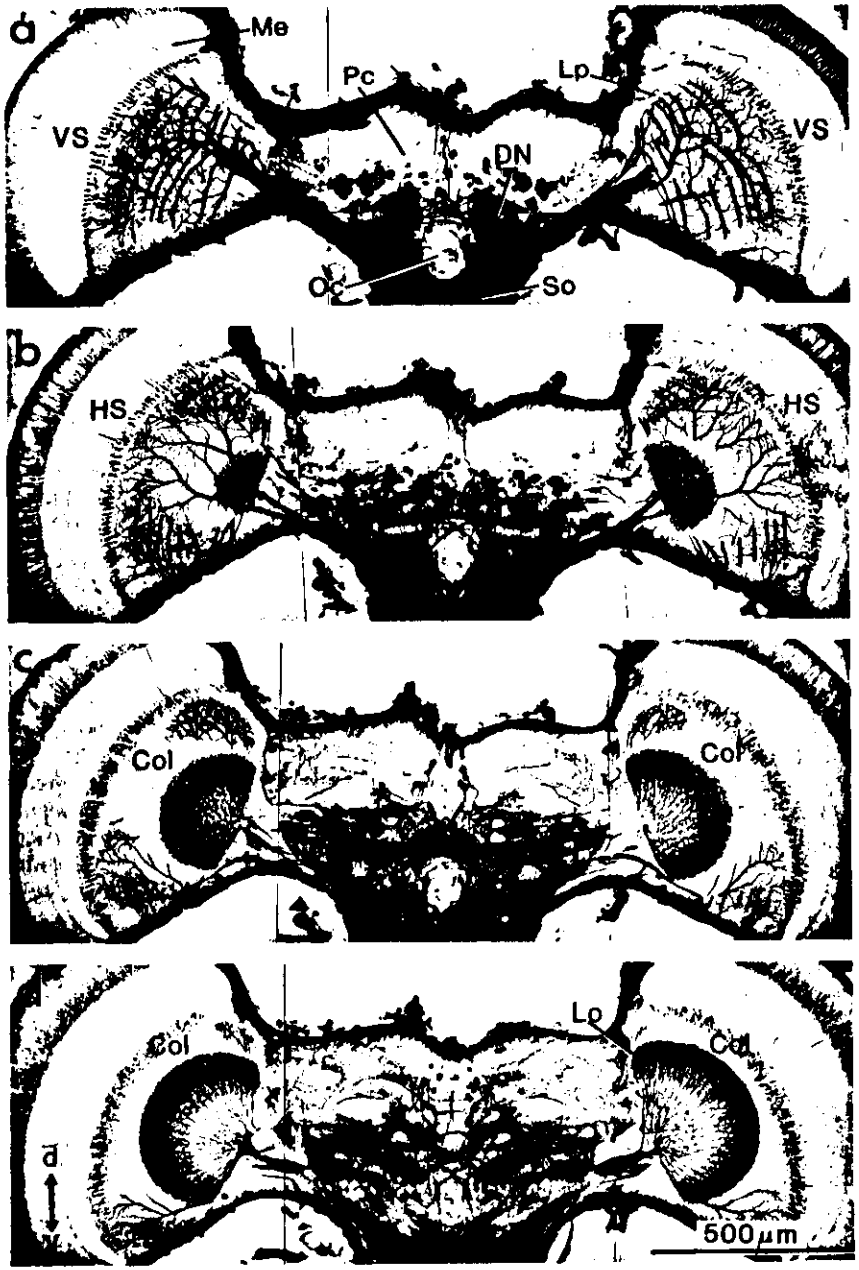
The optic foci can be regarded as major sensory integration areas for the motor control in the brain. Apart from the optic lobes, they receive visual input from the ocelli, and mechanosensory inputs from antennae and halteres (Strausfeld and Bacon 1983; Strausfeld et al. 1984). The output elements of these areas are descending neurons, which pass through the cervical connective and terminate in the motor neuropils of the thoracic ganglion. Intensive path-tracing studies employing transsynaptic cobalt stainings have revealed evidence for connections between output neurons of the optic lobe, descending neurons and motor neurons of the neck muscles (Strausfeld and Seyan 1985; Strausfeld et al. 1987; Milde et al. 1987), the leg musculature (Strausfeld and Bassemir 1985a), and the indirect flight muscles, which play a major role in torque generation during steering maneuvres (Hausen and Hengstenberg 1987).

In short, the major visuo-motor pathways between compound eye and motor system consists of a sequence of retinotopic visual neuropils, the output elements of which converge together with other sensory tracts onto descending neurons. The latter represent the bottle neck of the pathway and in the thoracic ganglion establish divergent connections to the motoneurons of various groups of muscles. The direct neuronal chain between eye and, e.g., the flight muscles consists of about six to seven cells.

The main motion computation centre in the whole pathway is the lobula plate, the structural organization of which shall be described in some detail.

4 Cellular Architecture of the Lobula Plate

The lobula plate receives input from columnar cells derived from the medulla and lobula. The retinotopic order of these elements is such that the lateral and medial columns of the neuropil subserve the frontal and caudal parts of the ipsilateral visual field, whereas the dorsal and ventral columns subserve the dorsal and ventral regions, respectively. The complicated network of columnar inputs to the lobula plate is not yet fully analyzed. Best investigated are three classes of neurons, namely



the Y-cells, which are putative GABA-ergic elements (Meyer et al. 1986) originating from the medulla and terminating in both lobula and lobula plate; the T4-cells, which occur as twin elements in each medulla column and terminate at two different levels in the lobula plate; and the T5-cells of the lobula, which are also columnar twin elements showing a similar terminal organization in the lobula plate. Since the terminal of each T4- and T5-cell is bilayered, one finds four discrete input layers in the lobula plate (Strausfeld 1984).

The large interneurons of the lobula plate have been the subject of numerous anatomical studies (Dvorak et al. 1975; Hausen 1976, 1981, 1982a,b, 1984, 1987; Pierantoni 1976; Eckert and Bishop 1978; Hausen et al. 1980; Eckert 1981; Bishop and Bishop 1981; Hengstenberg 1982; Hengstenberg et al. 1982; Egelhaaf 1985b; Strausfeld and Bassemir 1985a,b). A recent account on the structural organization of this network lists about 50 identified neurons (Hausen 1987). The individual cells can be classified anatomically as anaxonal amacrine cells, and as tangential cells having a separate input and output region connected by an axon. The latter group of cells can be further subdivided into centripetal output cells of the lobula plate projecting into the brain, centrifugal feedback cells terminating in the lobula plate and heterolateral connection elements between the lobula plate and neuropils of the contralateral optic lobe. Examples of these cell types are compiled in Fig. 4.

Typical output elements of the lobula plate are two classes of giant neurons termed the horizontal system and the vertical system (HS, VS; see also Fig. 3). The horizontal system consists of three elements, the dendritic arbors of which are located near the anterior surface of the neuropil and cover the dorsal, medial and ventral region of the neuropil. According to these dendritic locations the three cells are termed north, equatorial, and south horizontal cell (HSN, HSE, HSS). The axons of the HS-cells project into the ipsilateral ventrolateral brain. Dye or cobalt injections into HS-cells lead to transneuronal lalls lead to transneuronal labeling of descending neurons, indicating synaptic couplings between both types of cells (Hausen 1987). Two of these descending neurons are shown together with the reconstruction of the horizontal system in Fig. 4. Further synaptic contacts of horizontal cells to a bundle of descending elements have recently been demonstrated (Strausfeld and Bassemir 1985b).

The vertical cells are a class of 11 output neurons (VS1–11) which lie serially arranged at the posterior surface of the lobula plate and which have narrow vertical dendritic domains. The axons of the VS-cells project centrally and terminate near the oesophageal channel at the posterior surface of the brain. Like those of the HS-cells, the axon-terminals of the VS-cells show numerous presynaptic

Fig. 3. a–d. Cobalt-stained output neurons in the lobula complex and descending neurons of the brain in the blowfly (*Calliphora*). The figure shows serial sections (30 µm thick) in a sequence from posterior (*a*) to anterior (*d*) through the brain and the proximal parts of the optic lobes. Giant output elements of the optic lobe are the cells of the vertical system (*VS*) and the horizontal system (*HS*), showing large dendrites at the posterior and anterior surface of the lobula plate, respectively. Columnar output elements of the optic lobe are the Col A-cells (*Col*) of the lobula. The axons of the cells project into the ventrolateral brain, which is heavily invested by dendrites of descending neurons (*DN*). The latter project through the cervical connective into the motor centres of the thoracic ganglion. *Me* medulla; *Lo* lobula; *Lp* lobula plate; *Pc* protocerebrum; *So* suboesophageal ganglion; *Oc* oesophageal channel; *d,v* dorsal, ventral

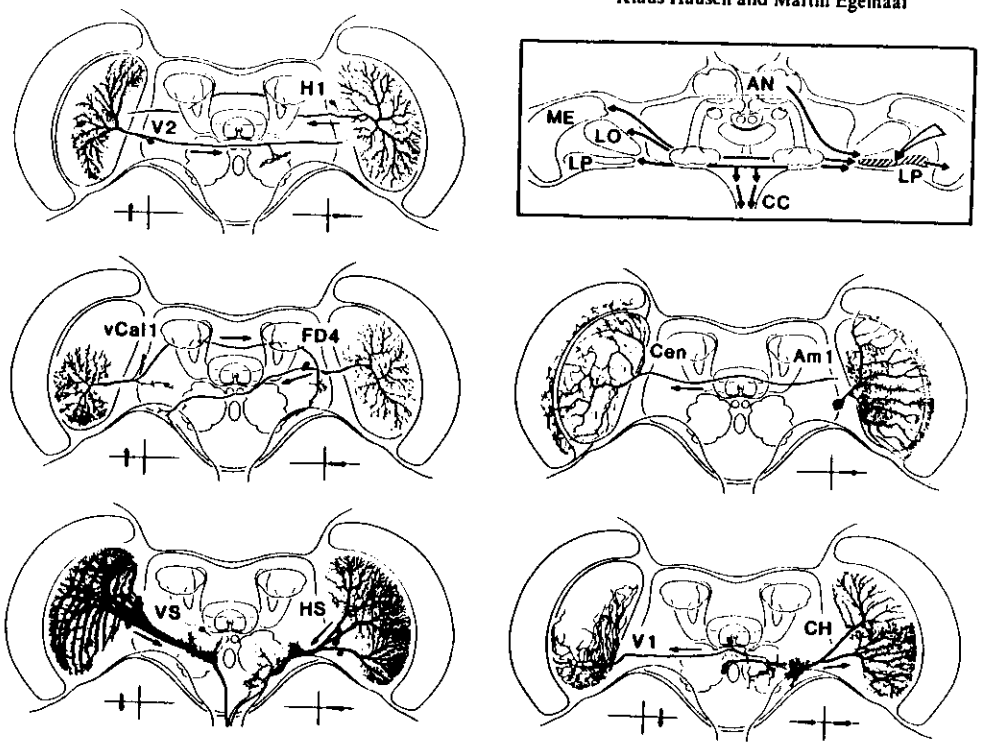


Fig. 4. Tangential and amacrine neurons of the lobula plate (*Calliphora*). The figure shows examples of the different anatomical types of cells in the lobula plate reconstructed after cobalt or Lucifer stainings from frontal serial sections as shown in Fig. 3. Homo- and heterolateral output elements of the lobula plate are the HS- and VS-cells, and the cells vCal1 and FD4, respectively. All cells of this type show large dendrites in the lobula plate and project into the ventrolateral brain. Examples of heterolateral connection-elements between both lobula plates are the cells V2 and H1. The CH-cells and the V1-cell represent centrifugal elements, which originate in the ventrolateral brain and give rise to extended terminal arborizations in the lobula plate. Further centrifugal connections to the medulla are established by the amacrine cell Am 1 and the cell Cen. The polarities of the individual neurons are indicated by arrows at the axons. All neurons shown are motion-sensitive elements, the directional selectivities of which are indicated by arrows in cross-diagrams representing the left and right, and the dorsal and ventral hemispheres of the visual field. The inset shows a summary diagram of the axonal pathways of lobula plate cells in the brain. AN: antennal lobe, *CC* cervical connective; *ME* medulla; *LO* lobula; *LP* lobula plate. (From Hausen 1987; reconstruction of the FD4-cell from Egelhaaf 1985b)

specializations (Hausen et al. 1980; Bishop and Bishop 1981) and are coupled to descending neurons (Hengstenberg et al. 1982). A detailed investigation of the synaptic connectivity in this region has so far revealed two major pathways between VS-cells and the motor system (Strausfeld and Bassemir 1985b): the cells VS2-3 are directly coupled to motoneurons of particular neck muscles , whereas the cells VS4-9 are coupled to descending neurons, which project into the thoracic ganglion. One of these descending neurons is shown in the VS-reconstruction of Fig. 4.

Whereas the HS- and VS-cells are examples of output neurons of the lobula plate terminating in the ipsilateral part of the brain, a second group of output neurons projects into the contralateral part and terminates in close vicinity to the axon terminals of the contralateral HS-cells. Examples of such heterolateral elements are the cells vCal1 and FD4 shown in Fig. 4. Although detailed connectivity studies are still lacking, it is likely that these cells are also synaptically coupled to descending neurons.

Centrifugal cells project from the brain back into the lobula plate. Homolateral neurons of this kind are the dorsal and ventral centrifugal horizontal cell (CH), which show small dendritic arborizations at the HS-terminals and project into the dorsal and ventral half of the ipsilateral lobula plate, respectively. The V1-cell is a heterolateral centrifugal element arising from the termination area of the VS-cells and projecting into the contralateral lobula plate. More complex centrifugal connections are established by elements like the amacrine cell Am1 and the tangential cell Cen, which project from the lobula plate back into the medulla.

The last group to be mentioned are the heterolateral connection elements, which establish direct pathways between the lobula plate and the contralateral optic lobe. Figure 4 shows two cells of this kind, the H1 and the V2, both having large dendritic domains in one lobula plate and large terminals (not shown) in the contralateral lobula plate.

The inset in Fig. 4 summarizes schematically all connections established by the groups of cells discussed above. The open arrow in the right internal chiasm represents the retinotopic visual input of the lobula plate. Thin arrows indicate the bidirectional pathways between lobula plate and the ipsi- and contralateral projection areas in the ventrolateral brain and the visual neuropils of the contralateral optic lobe. Unidirectional pathways link the lobula plate to the ipsilateral antennal lobe and the ipsilateral medulla.

Finally, it should be mentioned that the tangential cells of the lobula plate show extraordinary structural constancy: the position, size, and layer of their arborizations within the lobula plate, as well as their axonal pathways, are nearly identical from animal to animal. In contrast to the lobula, which shows a remarkable sexual dimorphism (Hausen and Strausfeld 1980; Strausfeld 1980), this holds true for both sexes (Hausen 1984, 1987). The anatomical invariance of the tangential cells is paralleled by physiological similarity between individual cells of the same type in different animals, which has considerably facilitated the electrophysiological analysis of the lobula plate.

5 Functional Architecture of the Lobula Plate

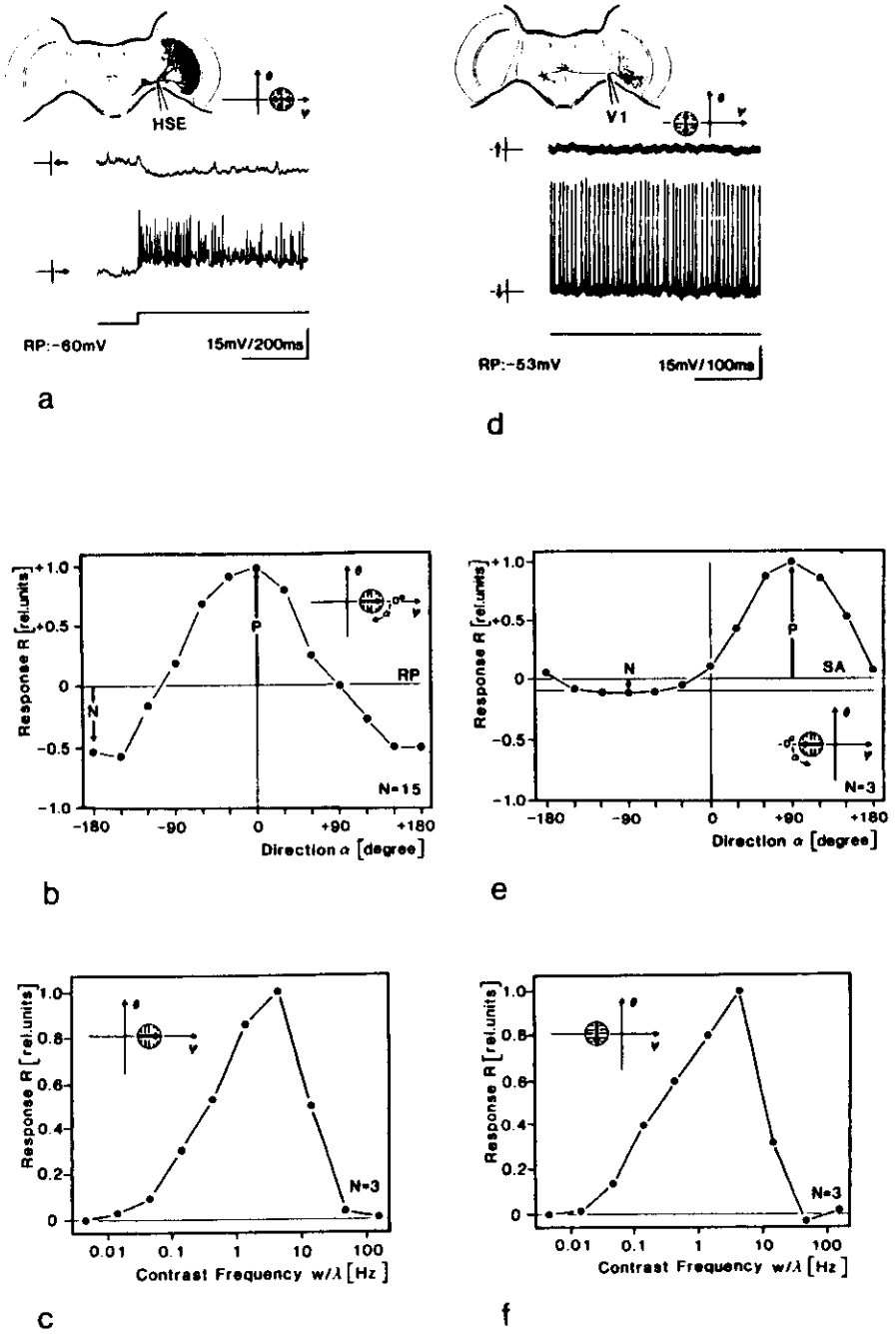
5.1 Response Characteristics and Input Organization of the Tangential Cells

All tangential cells of the lobula plate investigated so far are motion-sensitive elements differing physiologically from each other with respect to their directional selectivities and receptive fields, and their particular response properties resulting from interactions with other tangential cells of the ipsi- and contralateral optic lobe.

The response characteristics of individual tangential cells have been reviewed in detail previously (Hausen 1981, 1984). We will therefore discuss only briefly the functional properties of the equatorial horizontal cell HSE and the V1-cell as representative examples of the homolateral output cells and the heterolateral centrifugal cells (Fig. 5).

The HSE responds selectively to progressive motion and is inhibited by motion in the opposite direction. As demonstrated by the recordings shown in Fig. 5a, the responses to motion consist of graded potentials and superimposed irregular action potentials. This type of signal is characteristic for all three horizontal cells and also for the vertical cells, which selectively respond to vertical motion. Common anatomical features of both classes of cells are their rather short and thick axons, which allow virtually decrement-free transmission of graded dendritic potentials into their terminals (Eckert 1981; Hausen 1982b). The significance of the action potentials in the signal transmission of these cells is still an open question (for discussion of this point see Hausen 1982b). Therefore the graded responses are used to characterize their functional properties. A quantitative evaluation of the directional selectivity of the HSE (Fig. 5b) demonstrates that the graded response amplitudes decrease in cosine-like fashion from the peak values obtained under motion in the preferred and null direction (P,N). The latter are opposite to each other and are parallel to the horizontal lattice axis h of the ommatidial mosaic (see Hausen 1982b). The measurements show further that the cell does not respond to vertical motion. The dependence of the HSE's response on the contrast frequency of a moving periodic stimulus is shown in Fig. 5c. The lower and upper response thresholds lie at about 0.01 Hz and 50 Hz, respectively, and the response optimum is located between 1–10 Hz. More detailed measurements have revealed that the response curve is nearly flat in the peak range (Hausen 1982b), which can be explained by the adaptation of the time constants in the motion detectors (see Sect. 2.1). These basic response characteristics are identical in all three horizontal cells.

Fig. 5a-f. Response characteristics of the HSE-cell (*a-c*) and the V1-cell (*d-f*) of the lobula plate (*Calliphora*). The cells were recorded intracellulary in the right optic lobe, and were stimulated with moving periodic gratings of dark and bright stripes placed in the equatorial plane of the right and left visual field at $\psi = +40°$ and $\psi = -50°$ (see insets; ψ and θ denote azimuth and elevation in the spherical visual field of the fly). The gratings had diameters of 39° and were moved with a contrast frequency of 1.5 Hz in *a,b* and *d,e*. *a* Signals of the HSE. The HSE shows graded responses to motion. It is inactivated (hyperpolarized) by regressive motion and activated (depolarized) by progressive motion in the ipsilateral visual field. The depolarizing graded responses are accompanied by irregular spike activity. *b* Response dependency on the direction of motion α. The graded response amplitudes of the HSE depend in cosine-like fashion on the motion-direction. Preferred (*P*) and null (*N*) direction are antiparallel. The data are normalized values from N = 15 measurements. *c* Response dependency on the contrast frequency of the grating moving in preferred direction (progressive). The graded response amplitudes are maximal under stimulation with contrast frequencies of 1–10 Hz. N = 3 measurements. *d* Signals of V1. The cell responds to motion in the left visual field with modulation of its axonal spike frequency. The cell is inhibited by upward motion and excited by motion in the opposite direction. *e* Response dependency on the direction of motion α. As in the HSE, the response curve shows a cosine-like slope; the modulation under stimulation with motion in null-direction (*N*) is small because of the low spontaneous activity (*SA*) of the cell. Null and preferred direction (*N,P*) are antiparallel. N = 3 measurements. *f* Response dependency on the contrast frequency of motion in preferred direction. The responses of the V1 are almost identical to those of the HSE. N = 3 measurements. (From Hausen 1982b, 1984)



Responses of the V1-cell are shown in Fig. 5d-f. As is typical for all heterolateral tangential cells of the lobula plate having long and thin axons, the V1 transmits information by modulating its axonal spike frequency. The cell responds preferentially to downward motion and is inactivated by upward motion. In contrast to the graded response pattern of the HSE, which allows bidirectional potential modulation around the resting value, the response-modulation of the V1 under stimulation with motion in the null direction is limited by the low resting activity of the cell (about 10 spike/s). The orientation of the preferred and null direction of the V1-cell are, again, antiparallel, but aligned in this case with the v-axis of the ommatidial lattice. The contrast frequency dependence of the V1-responses resembles closely that of the HSE.

The response properties of the two cells are typical for all tangential cells of the lobula plate so far investigated: all of them show the same velocity characteristics and have antiparallel preferred and null directions, which are aligned either with the h-axis or the v-axis of the ommatidial lattice. Exceptions from this latter characteristic are found in only a few cells (e.g., the VS1 and VS7-9), the receptive fields of which are subdivided into compartments with different preferred directions (Hengstenberg 1982). Some elements show also two preferred directions within the same area of the receptive field (Hausen 1981).

These common characteristics indicate that all tangential cells receive excitatory and inhibitory input from arrays of functionally identical elementary motion detectors of the correlation type, which differ only with respect to the orientation of their sampling bases in the retina. The location and cellular structure of these EMD's has remained an unsolved problem so far. There is physiological evidence that the tangential cells receive input from individual EMD's rather than peripheral integrating elements, and that the actual process of motion detection does not take place directly at their dendrites (Hausen 1982b; see also Hausen et al. 1980). It cannot be decided, however, whether the EMD's are located in the lobula plate or in the medulla. The most plausible guess which can be made at present is that the columnar input elements of the lobula plate, the T4-, T5- and Y-cells, are parts of the motion-detection circuits. Direct synaptic connections betweeen T4-terminals and tangential cells have been demonstrated electron microscopically (Strausfeld 1984). For simplicity, we will assume in the following that there are eight arrays of retinotopic EMD's, two for each of the four preferred directions, which feed as excitatory and inhibitory input elements into the assembly of tangential cells. Deoxyglucose studies, in which motion-induced activity in the lobula plate was visualized by radioactive labeling (Buchner et al. 1979, 1984), and combined electrophysiological and light microscopical investigations (Hausen 1987) have revealed that the neuropil of the lobula plate is composed of four directionality layers, which contain (in a sequence from anterior to posterior) the tangential cells responding to progressive, regressive, upward and downward motion. It is tempting to assume that these four layers represent the terminal areas of the arrays of EMD's having the respective preferred directions. Interestingly, the four terminal-strata of the T4- and T5-cells seem to accord to these layers (Strausfeld 1984).

Comparisons of the location and size of the receptive fields of individual tangential cells and their dendritic organizations show that the receptive fields are directly determined by the position and extent of their dendritic domains within the retinotopic columnar array of the lobula plate. Furthermore, the spatial sensitivity distribution in the receptive fields of the cells can be correlated with local variations of the arborization densities in their dendritic domains (Hausen 1981, 1982a,b). This indicates again that the dendrites of the tangential cells receive input from individual retinotopic EMD's, and suggests, in addition, that the local synaptic density accounts for the local gain of signal transmission between EMD's and tangential cells.

In summary, motion is evaluated in the visual system of the fly by retinotopic arrays of EMD's, which have different preferred directions and seem to terminate in the four directionality layers of the lobula plate. The tangential cells gain their individual directional selectivity by investing a particular layer in the lobula plate and contacting excitatory and inhibitory EMD's having opposite preferred directions. The position, size and density of the dendritic arborization within the layer determines the receptive field of a cell and its local sensitivity to motion.

5.2 Gain Control Mechanisms in Tangential Cells

From the foregoing it is evident that the basic operation performed by the tangential cells of the lobula plate is the spatial integration of local motion information. There are two functional categories of tangential cells, the spatial integration properties of which differ significantly: cells of the first group respond to stimulation with moving patterns of increasing size with increasing response amplitudes (Hausen 1981, 1982b; Egelhaaf 1985a), whereas cells of the second group show peak responses under stimulation with small patterns (Egelhaaf 1985b). The measurements on the HSE and the so-called figure-detection cell FD1 shown in Fig. 6 illustrate these response characteristics.

Figure 6a shows the response amplitudes of a HSE as function of the angular extent of a progressively moving periodic pattern. Parameters in the experiment were the mean luminance of the pattern (compare curves 1, 3 and 4) and the contrast frequency of motion (curves 2, 4). The data demonstrate that the response amplitudes of the cell increase under all conditions with increasing stimulus size. The same behavior is observed under a different experimental condition (Fig. 6b), in which the response dependency on the width of a textured figure oscillating horizontally around the animal was evaluated. In contrast, the FD1-cell (Fig. 6b) responds selectively to a small pattern and becomes almost insensitive to motion when the pattern grows large.

These spatial integration properties of the two cells can be fairly well modeled by the inhibitory gain control mechanism for the LF- and SF-system outlined already in Sect. 2.2 and shown in more detail in Fig. 7. Experimental evidence, which will not be discussed here (see Reichardt et al. 1983), indicates that the inhibitory element INH in the gain control circuitry of the HSE-cell is activated by progressive and regressive motion in the ipsilateral visual field. In case of the FD1-cell, the inhibitory element must be assumed to be sensitive to contralateral regressive and ipsilateral progressive motion (Egelhaaf 1985b,c). If these inhibitory elements are implemented in the model circuits and the respective synaptic

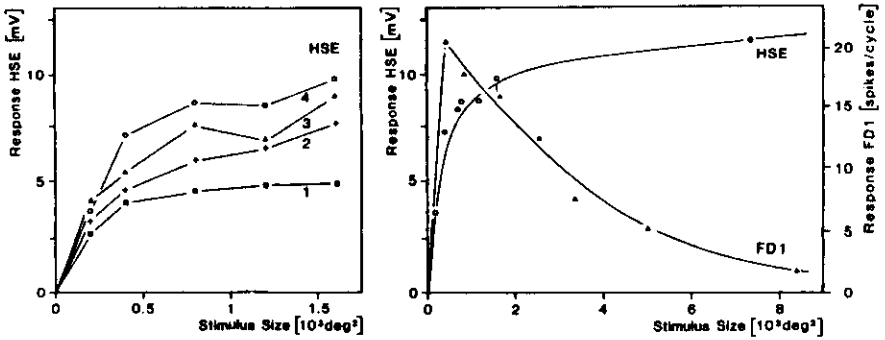


Fig. 6a,b. Spatial integration characteristics of the HSE-cell and the FD1-cell (*Calliphora*). *a* Response amplitudes of the HSE as function of the angular size of a periodic grating moving in progressive direction. Parameters in the experiment were the contrast frequency and the mean luminance of the pattern. In experiments 1,3, and 4 the contrast frequency was kept constant (1.5 Hz) and the mean luminance was varied (1:7 cd/m², 3:20 cd/m², 4:70 cd/m²), in experiments 2 and 4 the mean luminance was constant (70 cd/m²) and the contrast frequency was changed (2:0.45 Hz, 4:1.5 Hz). The values plotted are means of 3 measurements. The cell responds preferentially to large stimuli in all cases. In addition, even under large-field stimulation complete saturation does not occur, since different response levels are reached under the different stimulus conditions. This indicates the existence of a gain control mechanism. *b* Response amplitudes of the HSE and the FD1 as function of the size of a textured figure oscillating horizontally in a panorama. Maximal width of figure: whole panorama, oscillation frequency: 2.5 Hz, oscillation amplitude: 10°. Values plotted are averages of 20 measurements (HSE *filled circles; open circles* show the values of curve 4 in *a* for comparison), and 24 measurements (FD1). The *curves* demonstrate that the HSE and FD1 are tuned to large and small stimuli, respectively. (*a* From Hausen 1982b; *b* after Hausen 1982b; Reichardt et al. 1983; Egelhaaf 1985c)

efficiencies of the EMD's are chosen appropriately (see Reichardt et al. 1983; Egelhaaf 1985a,c), the experimental data of Fig. 6 are closely fitted by the corresponding model simulations shown in Fig. 7.

The different spatial integration properties of the HSE and FD1 are representative for a number of further tangential cells investigated in this respect. Large-field characteristics were also found in the cells of the VS-system (Hengstenberg 1982) and in the heterolateral connection element H1 (Egelhaaf 1985a); further small-field elements are the cells FD2–4 (Egelhaaf 1985b). Thus, the experimental evidence available so far strongly suggests that the assembly of tangential cells in the lobula plate is subdivided into two groups with LF- and SF-tuning.

5.3 Synaptic Interactions Between Tangential Cells

Although synaptic interactions in the lobula plate have been thoroughly studied (Hausen 1981) the inhibitory circuits mediating gain control in the cells sensitive to large-field motion are not yet identified. There are several possible explanations for this. First of all, it cannot be excluded that the gain control operation takes place

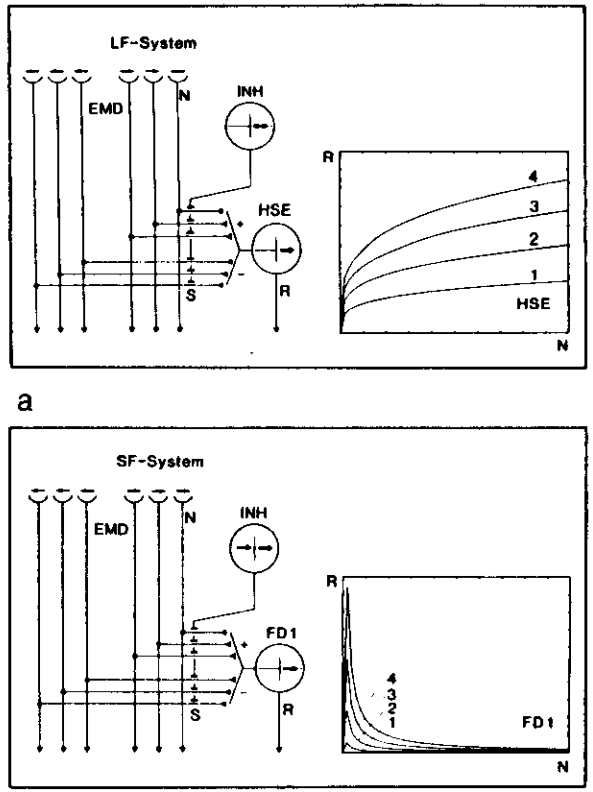


Fig. 7a,b. Models of the gain control mechanism in the HSE-cell and the FD1-cell. The inhibitory circuits shown in *a* and *b* are basically identical to the gain control circuit of the LF- and SF-system shown in Fig. 1c. The HSE and FD1 integrate the outputs of excitatory EMD's sensitive to progressive motion and of inhibitory EMD's sensitive to regressive motion. The individual EMD's are shunted by an inhibitory element INH. There is experimental evidence that in case of the HSE, the inhibitor shows monocular sensitivity to horizontal motion in both directions, whereas the inhibitor in the input network of the FD1 shows binocular sensitivity to clockwise horizontal motion. Implementation of these different inhibitors into the circuits leads to spatial integration characteristics in the output elements (HSE, FD1) which are in close agreement with the measurements shown in the previous figure. The curves show the simulated responses (R) of the two output elements as function of the number (N) of EMD's stimulated. Parameter in the simulations are the signal amplitudes of the EMD's, which depend on stimulus properties like contrast frequency or mean luminance. (After Reichardt et al. 1983 and Egelhaaf 1985a,c)

peripheral to the lobula plate in the medulla, which has not been investigated in this respect. Alternatively, elements of the model circuitry like, for example, the bidirectional inhibitor shown in Fig. 7a, may in fact consist of two or more unidirectional cells, having opposite preferred directions. Various elements of this kind are known; it is still unclear, however, whether they interact with EMD's. These problems deserve further investigation.

The large-field cells of the lobula plate exhibit another type of synaptic interaction, which is of major significance for their functional role in the control of motion-induced behavior. These interactions are based on direct synaptic contacts between tangential cells of both lobula plates and lead to enhanced sensitivities of the cells to particular binocular motion stimuli. Examples of these synaptic connections are compiled in Fig. 8.

The HS-cells (except for the South Horizontal Cell) are postsynaptic to the H2-neuron of the contralateral lobula plate, which responds selectively to regressive motion in its receptive field (Hausen 1976, 1981; Eckert 1981). Due to this excitatory synaptic input the HS-cells gain binocular sensitivity and respond selectively to horizontal rotatory motion (Fig. 8, yaw). Under natural conditions, rotatory retinal motion patterns arise from self-rotations of the animal in space, and one can thus interpret the HS-system as a visual yaw-monitor, specifically designed for the control of course-stabilizing yaw torque generation by the motor system.

A similar situation is found in the VS-system (Fig. 8, roll). The medial vertical cells VS2-6 respond to downward motion within their receptive fields, which are located in the frontolateral part of the ipsilateral visual field. Some, if not all of them, respond additionally to upward motion in the lateral part of the contralateral visual field (Hengstenberg 1981, 1982). It is most likely that this contralateral input is mediated by the V2-cell (Hausen 1981). The resulting rotational sensitivity of

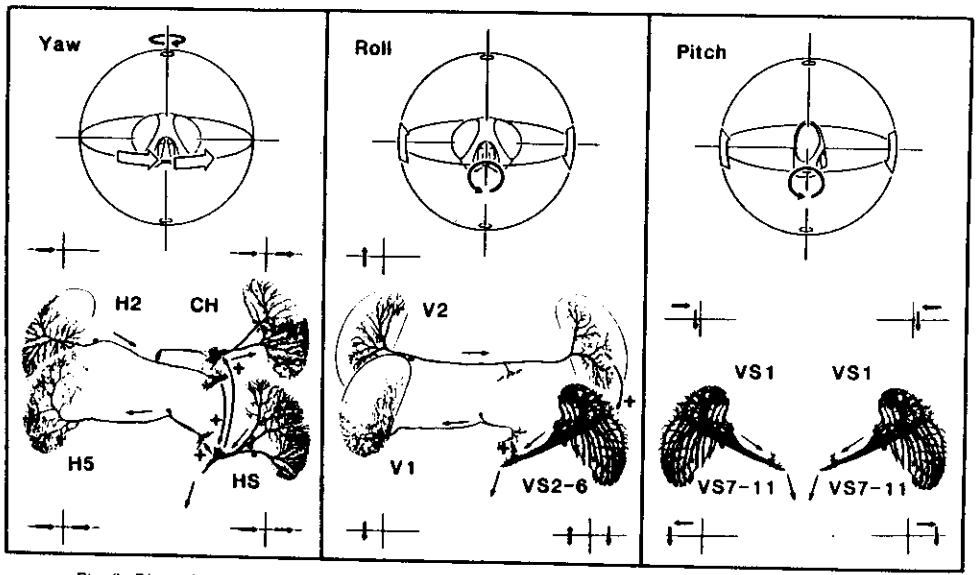


Fig. 8. Binocular interactions between tangential cells of the lobula plate showing large-field tuning (*Calliphora*). The monocular and binocular directional selectivities of the cells are indicated by arrows. The excitatory synaptic interactions indicated lead to high sensitivities of the cells to rotatory retinal motion patterns. Under natural conditions, such patterns result from self-rotations of the animal in space (*upper graphs*). The cells thus code the information necessary to control optomotor course-stabilization maneuvres. (After Hausen 1981, 1987)

the VS-cells indicates, again, that they are particularly well suited to signal self-rotations of the animal with respect to the environment, in this case around the longitudinal body axis.

A remarkable combination of directional sensitivities is found in the most lateral VS-cell VS1, which scans the dorsal and a narrow frontal region of the ipsilateral visual field, and in VS7-9, which also scan the dorsal and, in addition, the caudal region of the visual field. VS1 and VS7-9 respond to regressive and progressive motion in their dorsal fields, respectively, and to downward motion in the other parts of their receptive fields (Hengstenberg 1981). This particular combination of preferred directions leads to specific sensitivities of these cells to pitch movements of the animal (Fig. 8, pitch). It should be noted that, in contrast to the situation during yaw and roll, visual detection of pitch movements does not require binocular information. This may be the reason why these cells show purely monocular responses.

In conclusion, a number of large-field output cells of the lobula plate are particularly sensitive to the binocular and monocular retinal motion patterns arising during rotations of the animal around the three body axes. They thus code the information necessary to control course-stabilizing torque responses.

We will now consider the response behavior of the HS- and FD-cells under stimulation with relative motion between a stripe and a panorama as used in the behavioral experiments on object fixation (Sect. 2.2). Experiments of this kind were performed on the HSE-cell and the FD-cells in order to investigate their potential role in fixation and tracking behavior (Reichardt et al. 1983; Egelhaaf 1985a,b,c).

Figure 9 shows the responses of HSE- and FD-cells to three characteristic stimuli of this kind: progressive motion of a single figure (A), and simultaneous motion of figure and ground in the same and in opposite direction (B,C). In the HSE, the largest response is found under ipsilateral progressive and contralateral regressive motion (B). There is also a considerable response of the cell to progressive motion of the small figure, which is compatible with the steep increase of the response curves shown in Fig. 6. The response to antiparallel motion of figure and ground (C) results from the simultaneous excitatory and inhibitory inputs to the cell activated by the progressive figure-motion and the regressive ground-motion, respectively. The response amplitude under this stimulus condition depends critically on the relative weight of both inputs, and thus on parameters like size and velocity of the stimuli.

A comparison of this response pattern to that of FD-cells demonstrates again the basic functional difference between the two types of cells. Both FD-cells shown in Fig. 9 respond to progressive motion within their receptive fields but are subject to different inhibitory influences. As already discussed, the inhibitory element in the gain control circuitry of the FD1 is sensitive to binocular horizontal rotatory motion. In contrast, the inhibitor of the FD4 shows bidiretional sensitivity in the contralateral visual field (see, however, Egelhaaf 1985b,c). The response histograms of the two cells demonstrate clearly the preferential sensitivity of both cells to the figure motion and the response inhibition during simultaneous motion of the large, binocular ground. Whereas the response depression under stimulus B results evidently from the activation of the inhibitory inputs to the cells, the reason for the

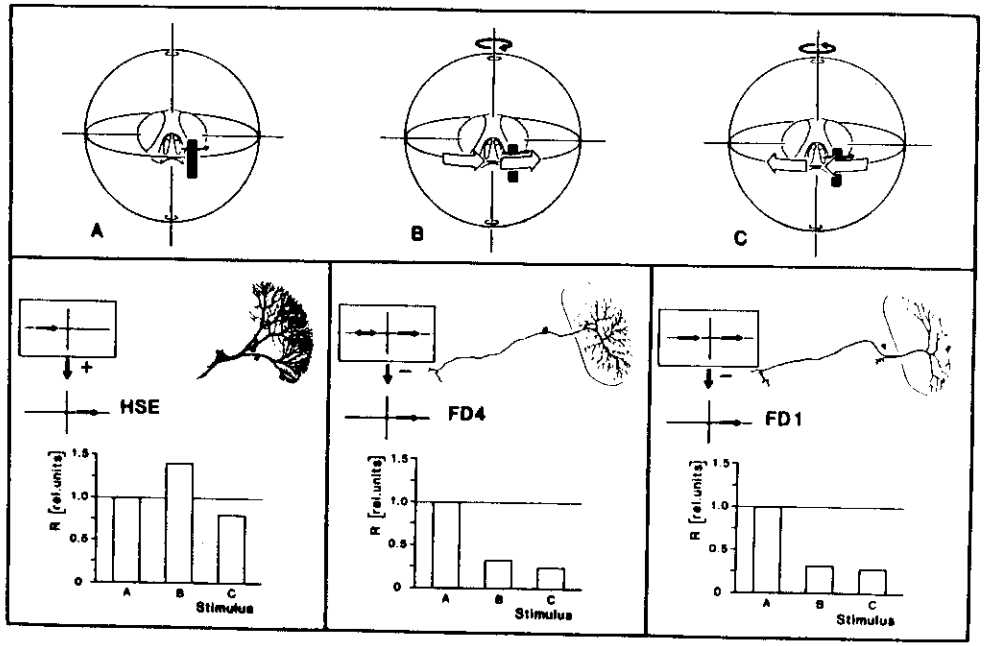


Fig. 9A-C. Responses of the HSE-cell and FD-cells under stimulation conditions which represent object motion (*A*) and simultaneous self and object motion (*B,C*). The experimental data shown in the three histograms were obtained from recordings of the cells in tethered animals (*Calliphora*), which were stimulated by a texture stripe (figure) oscillating horizontally in a textured panorama (width of stripe: 10° (HSE), 6° (FD1),24° (FD4), oscillation frequency: 2.5 Hz). Response-values *A,B,C* are normalized average responses measured during progressive motion of the figure, and during syndirectional and antidirectional motion of figure and binocular ground, respectively. The responses of the cells reflect the illustrated binocular excitatory and inhibitory interactions within their input circuitries. The HSE shows maximal responses under syndirectional figure and ground motion in the preferred direction of the cell (*B*). Both FD-cells are maximally excited by the motion of the figure (*A*), and are inhibited during motion of figure and background in the same and in opposite directions. The latter two stimuli arise, under natural conditions, during turnings of the animal towards or against a moving object. FD-cells are hence inactivated in both situations. (After Reichardt et al. 1983 and Egelhaaf 1985b)

low response amplitudes measured under stimulus C is less obvious. They are conceivable, however, if one takes into account that the cells, like the HSE, receive direct input from excitatory and inhibitory EMD's when figure and ground move in opposite direction.

Stimulation conditions B and C resemble the motion patterns seen by a fly turning away from or towards an object, which moves independently from front to back through the visual field. In particular the latter situation (C) is frequently encountered by the animals during the initial phase of object fixation and tracking in free light. The response histograms demonstrate that the FD-cells, although highly sensitive to motion of small objects, can be strongly inhibited during such self-motions. This appears to be an undesired but inevitable consequence of the small-field tuning of the FD-cells. There is no other mechanism preventing these cells from firing in response to extended moving patterns which can be as easily

implemented as their inhibition by a directionally selective element sensitive to large-field motion.

The cellular components of the gain control circuitry of FD-cells have also not yet been identified. However, the CH-cells (see Fig. 8) are likely candidates for the inhibitor elements of the FD1 and FD4. This is suggested by anatomical evidence, as well as the directional selectivity of these cells shown in Fig. 8, which fits to the directional selectivity of the inhibitor at least in the case of the FD1. The finding that the CH-cells may be GABA-ergic (Meyer et al. 1986), and thus very probably inhibitory elements, supports this view. The other FD-cells known so far (FD2, FD3), which are sensitive to regressive motion might be inhibited by the H5-cell, which has the opposite directional selectivity to the CH-cells (Fig. 8).

The discussion in the last two sections has demonstrated that the large-field cells and the FD-cells of the lobula plate show the functional characteristics of the LF-system and the SF-system deduced originally from the results of behavioral analyses: the spatial integration properties of both groups of cells can be simulated with the proposed gain control circuitry, and the particular combinations of binocular directional selectivities found in the different cells suggest functional significance of the elements in the control of torque generation about the different body axes. We will now consider the transient responses of tangential cells to stimulation with motion and compare them to respective computer simulations performed on the basis of the proposed model network.

Figure 10a shows the signals of the HSE and the FD4 recorded under oscillatory horizontal figure motion, ground motion and relative motion between figure and ground (phase difference:90°). The responses obtained under the first two stimulus conditions reflect characteristics discussed above: both cells are selectively activated by progressive motion but respond differentially to the stimulus size. In contrast, the responses recorded to simultaneous motion of figure and background are rather complex. The FD4-signals obtained under this stimulation are particularly interesting. The cell generates large response-peaks which occur, after a certain response delay, in those instants, in which the figure moves in progressive direction while the ground motion is transiently zero.

Figure 10b shows computer simulations of the output signals of LF-and SF-elements of the model circuitry, in which the particular excitatory and inhibitory interactions of the HSE and FD4 as shown in Fig. 9 were implemented. The simulations demonstrate that the model describes not only the spatial integration properties but also the complex transient response behavior of the HS-cells and the FD-cells under stimulation with relative motion.

6 Motor Control by the Lobula Plate

The electrophysiological data and the computer simulations discussed in the last section suggest strongly that the HS-cells and the FD-cells are the neural correlates of LF-and SF-system controlling motion-induced yaw torque generation. When implementing the particular binocular input organization of both groups of cells into the model-circuitry of Fig. 1b it is indeed possible to simulate the complex transient yaw torque responses which are generated by tethered flying flies under

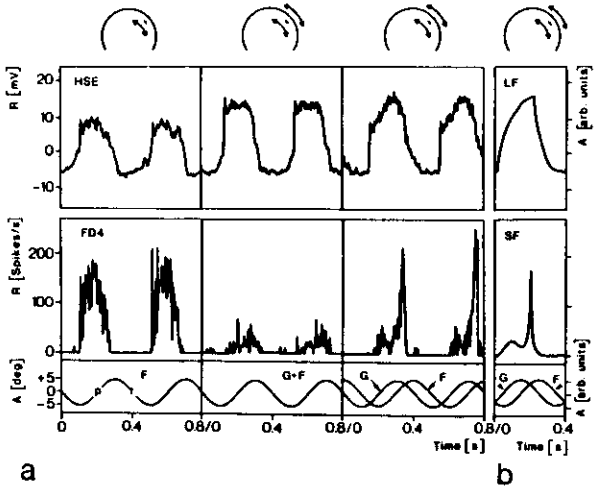


Fig. 10a,b. Transient responses of the HSE-cell and the FD4-cell to oscillatory horizontal motion of a textured stripe (figure *F*) and a textured panorama (ground *G*), and computer simulations of the response patterns of the two cells. *a* The response traces show the motion-induced graded responses (R) of the HSE and PST-histograms of the responses of the FD4 (*Calliphora*). Stimulus conditions are indicated by insets and the stimulus traces. Textures of figure and ground random dot pattern; width of figure: 10° (*HSE*), 24° (*FD4*); oscillation-frequency: 2.5 Hz; oscillation-amplitude A: 10°; p, r: progressive and regressive motion of the figure, placed in the fronto-lateral part of the right visual field of the test-fly. The data are averages of 29 (HSE) and 16 (FD4) measurements. The three recordings in each cell show the responses to figure motion in front of the stationary ground panorama, to syndirectional motion of figure and ground, and to relative motion of both stimuli (phase difference: 90°). The responses of the two cells under the first two conditions reflect the preferred directions and the spatial tuning of the two cells: the HSE shows large response-amplitudes under clockwise synchronous motion of figure and ground whereas the FD4 responds preferentially to progressive motion of the figure. The response patterns of the cells under stimulation with relative motion of figure and ground is complex and results from superposition of excitatory and inhibitory response components. The response of the FD4 under this condition shows characteristic peaks, which occur when the figure moves progressively while the ground motion stops (note that there is a certain response delay of the cell. *b* Computer-simulations of the responses of the HSE and FD4 to relative motion of figure and ground (phase difference: 90°)) performed with the gain control circuits of the LF- and SF-system shown in Fig. 7. For better comparison, the simulations were shifted on the time-axis according to the response-delays of the cells. The simulations are in close agreement with the experimental data. (From Reichardt et al. 1983 and Egelhaaf 1985b,c)

stimulation with horizontal motion of a ground and a small figure (Fig. 11; Egelhaaf 1985c). The close agreement between the simulation and the torque response is indirect, but rather compelling evidence that the HS- and FD-cells are in fact the major control elements for torque generation under this stimulation, and that the model is a basically correct representation of the neural computations underlying course stabilization and object fixation in flies.

More direct evidence for the functional role of the cells in torque control was gained by lesion experiments, in which the axonal pathways of HS- and FD-cells of flies were microsurgically cut and the torque responses of the treated animals were subsequently measured (Hausen and Wehrhahn 1983, 1987b). Results of

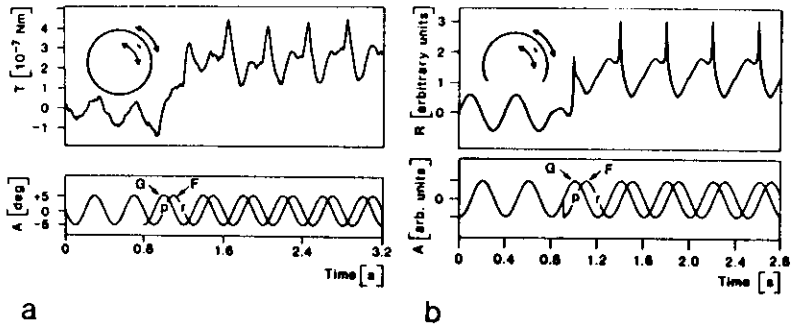
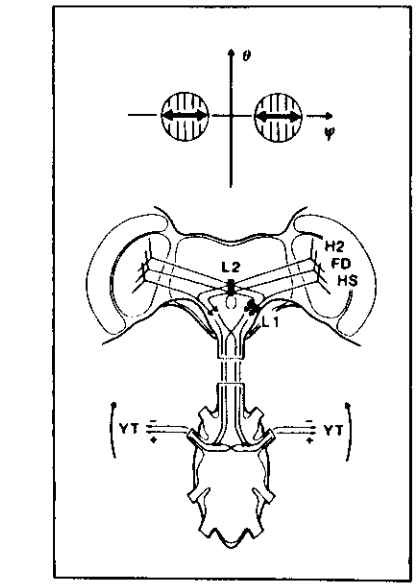


Fig. 11a,b. Transient yaw torque responses of a fly (*Calliphora*) to stimulation with oscillatory horizontal motion of figure (F) and background panorama (G), and computer simulation of the output of the LF- and SF-system. *a* Torque response-pattern of a tethered flying fly positioned in the center of the experimental setup sketched in the inset. The fly detects and attempts to fixate the figure, when it is moved relative to the background. Stimulus condition and response pattern are virtually identical to those shown in Fig. 2a. The response trace represents the average of 100 sweeps. *b* Simulation of the yaw torque responses to stimulation with oscillatory motion of figure and ground. The simulation was performed on the basis of the torque control model shown in Fig. 1b. It was assumed that the LF-system consisted of the HSE-cell, and that the SF consisted of the cells FD1–4. The particular binocular excitatory and inhibitory interactions within the input circuitries of the individual cells were implemented in the model. (From Egelhaaf 1985a,c)

such experiments are shown in Fig. 12. The first graph shows the locations and the effects of the lesions: the terminals of the right HS-cells and the left FD-cells in the right ventrolateral brain were destroyed by lesion L1; the axonal pathways of the FD-cells and the H2-cells in the central protocerebrum were cut by lesion L2. Torque responses of the operated animals were recorded under monocular and binocular stimulation with horizontally moving gratings, placed in the frontolateral visual fields of the eyes. A stimulus size was chosen which elicited comparable responses in the FD-cells and HS-cells. The stimulus combinations in the different experiments are indicated below the torque traces.

The traces in the first row of Fig. 12b and c show the response behavior of intact control flies. Monocular stimulations with progressive motion in front of the left and right eye induce strong negative and positive torque responses, which represent intended turnings of the flies to the left and right side, respectively. Under monocular stimulation with regressive motion the measured torque responses are only weak or even absent. This response difference can be understood on the basis of the differing output connections of the HS- and FD-cells as shown in Fig. 12a; the torque components induced by the HS- and FD-cells are of the same sign only under stimulation with progressive motion, whereas regressive motion induces torque components of opposite sign, which more or less cancel each other. Under binocular stimulation, significant torque responses are only induced by rotatory motions, whereas the response components induced by translatory motions cancel each other for symmetry reasons.

The response pattern of lesioned animals shows a number of characteristic differences, only two of which will be discussed here. We will first consider the response to monocular stimulation with progressive motion in the right visual field



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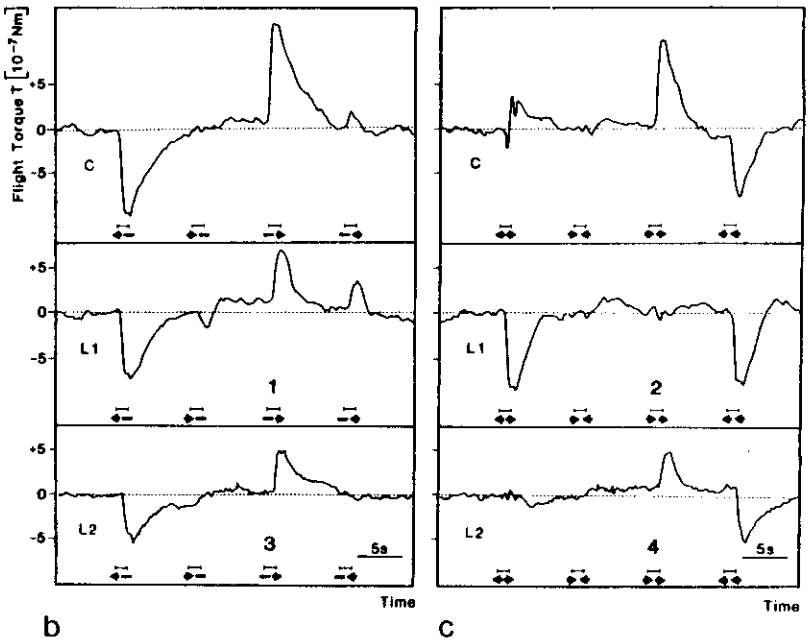

(1) in animals with lesion L1. In this case, the right HS-cells are cut and the recorded positive response can be induced only by the right FD-cells sensitive to progressive motion. When displaying simultaneously regressive motion as a second stimulus in the left visual field (2), the response vanishes completely. This is consistent with the fact that FD-cells are inhibited by contralateral motion. Additional response components induced under this stimulus condition by the regressive-sensitive FD-cells of the left lobula plate do not occur, since their terminals are destroyed also by the lesion L1.

In contrast to the situation in (1), the positive response to monocular progressive motion recorded in animals with lesion L2 (3) reflects the activity of the right HS-cells, since in this case only the central axonal pathway of the FD-cells is cut. Accordingly, the response is not suppressed when regressive motion is simultaneously displayed in the contralateral visual field (4). These examples illustrate that the specific alterations of the response patterns in lesioned animals are fully consistent with the concept of torque control by HS- and FD-cells illustrated in Fig. 12a, which is equivalent to the initial model circuitry shown in Fig. 1b.

Further evidence for a joint control of torque generation by two separate neural systems showing LF- and SF-tuning was gained in behavioral investigations on flies, the HS-cells of which were eliminated by laser-ablation of their precursor cells in an early larval stage (Geiger and Nässel 1982), and also in detailed behavioral studies on *Drosophila* mutants, which lack the HS- and VS-cells of the lobula plate (Heisenberg et al. 1978; Heisenberg and Wolf 1984; Bausenwein et al. 1986). In all cases the torque responses to motion of large patterns were found to be strongly impaired, whereas responses to small moving patterns or objects could still be observed.

In summary, there are several lines of evidence which demonstrate convincingly that yaw torque generation during course stabilization maneuvers and fixation sequences is controlled by the HS- and FD-cells, which gain their particular spatial tunings and binocular sensitivities from inhibitory and excitatory interactions within their input circuitries. Although the cellular components of

Fig. 12a-c. Lesion experiments, demonstrating the importance of the HS- and FD-cells in yaw torque control (*Calliphora*). *a* Flies were operated at sites in the brain marked lesion L1 and lesion L2. The terminals of the right HS-cells and the terminals of their presynaptic elements H2 originating from the left lobula plate were destroyed by L1 in a first group of animals. The central axonal pathway of the FD-and the H2-cells was cut by L2 in a second group of animals. The sketch of the output connections of the HS- and FD-cells to the motor system (YT: yaw torque) accords with the model circuitry of Fig. 1b and is in agreement with the results of the experimental data shown in *b* and *c*. Operated and normal control animals were stimulated with periodic gratings placed in the equatorial plane of the left and right frontolateral visual field, and moving horizontally with a contrast frequency of 1.5 Hz. The size of the patterns was such that the HS-cells and the FD-cells were stimulated about equally strongly. *b* Yaw torque responses of control animals (C) and operated animals (L1, L2) to monocular stimulation with motion as indicated below the stimulus traces. Positive and negative deflections in the response traces indicate turning tendencies to the right and left side, respectively. *c* Yaw torque responses to binocular stimulation with motion. All response traces are averages obtained from at least 200 stimulation sequences in 10 flies. The data show characteristic differences between the response behaviors of the operated and normal flies, which demonstrate directly the functional role of the HS- and FD-cells in torque-control. See text for further explanation. (Hausen and Wehrhahn 1987b)

these circuits are not yet completely identified, it is evident that they are at least in part constituted by the homo- and heterolateral centrifugal cells and the heterolateral connection cells between both lobula plates, which are sensitive to horizontal motion. It seems likely that respective bilateral gain-control circuits exist between the tangential cells sensitive to vertical motion.

Two final aspects of this control system warrant discussion. As shown in the wiring diagram of Fig. 1a, the HS- and FD-cells elicit torque components of the same sign under stimulation with monocular progressive motion, but are assumed to have antagonistic effects on the motor system under stimulation with regressive motion (see Egelhaaf 1985c). This has the consequence that selective stimulation of the horizontal system by horizontal large-field motions in both directions (or by respective self-motions of the animal in space) leads to syndirectional turning responses and, thus, to a course-stabilization maneuver. In contrast, selective stimulation of the FD-cells by horizontal object motions in both directions might lead to turnings towards the stimulus and, thus, to a fixation response. Another interesting point concerns the different efficiencies of the two systems in torque control under stimulus oscillations at low and high frequencies, as discussed above. Under free-flight conditions, slow changes of the direction of the perceived motion can arise during passive course deviations due to turbulences in the air or can result from asymmetries in the flight motor; they are compensated by corrective steering maneuvers dominated by the HS-system. On the other hand, houseflies do not change course smoothly in free flight, but in sequences of rapid turns which inevitably lead to retinal large-field motion of continually changing sign (Wagner 1986b). Under this condition, the LF-system contributes to the turning response with only a relatively small gain and thus does not counteract the active turns, while the SF-system is still operational (Egelhaaf 1987). Both aspects illustrate the high adaptation of the torque-control system to the particular demands of course stabilization and fixation under natural conditions.

This review has been mainly concerned with the neural mechanisms underlying the visually induced yaw torque responses in the fly. The neural control of the torque responses about the other body axes and the control of the additional steering movements like abdominal and hindleg deflection are less well analyzed. There is accumulating evidence, however, that they are also governed by the lobula plate. Very recent studies have revealed, in addition, that the tangential cells of the lobula plate are the major sensory elements controlling motion-induced head movements (Hengstenberg 1984; Milde and Strausfeld 1986; Milde et al. 1987; Strausfeld et al. 1987).

7 Motion Computation in the Visual System of Other Insects

The computation of motion is evidently not a peculiarity of the fly visual system, but appears to be of widespread importance throughout the animal kingdom and, in particular, in the various insect groups (for an exhaustive literature review see Wehner 1981). However, it is hard to gain a coherent view on motion computation in insects in general, due to paucity of evidence.

Nevertheless, the existence of control systems mediating optomotor course stabilization is vital for all insects and, particularly, for the fast-flying ones. Accordingly, directionally selective units sensitive to large-field motion have also been found in different nondipterous insect groups like *Odonata* (Olberg 1981a,b), *Orthoptera* (Burtt and Catton 1954; Horridge et al. 1965; Kien 1974, 1975), *Lepidoptera* (Collett and Blest 1966; Collett 1970, 1971a; Rind 1983), and *Hymenoptera* (Kaiser and Bishop 1970; DeVoe et al. 1982). The fact that at least some of these neurons receive input from both eyes and are sensitive to rotations of the entire surrounding underlines their potential involvement in the optomotor turning response.

There is much less uniformity among the different insect species with respect to the functional properties of neurons which are selectively tuned to retinal small-field motion (Palka 1969, 1972; Collett 1971b, 1972; Collett and King 1975; O'Shea and Rowell 1975; Frantsevich and Mokrushov 1977; Rowell et al. 1977; Pinter 1977; Olberg 1981a, 1986). Although in most of these examples there is no experimental evidence on the functional significance of these units in orientation behavior, it can be speculated that this diversity might be due to the different behavioral contexts in which small objects moving relative to the eye have to be detected. For instance, the stimulus conditions in flying and in walking or even stationary animals differ considerably and, consequently, impose quite different constraints on the neuronal mechanisms underlying figure-ground discrimination (e.g., compare Collett 1971a; Egelhaaf 1985b,c and O'Shea and Rowell 1975; Rowell et al. 1977). Moreover, even in flying insects, different pursuit strategies inevitably lead to different temporal characteristics of retinal image motion and are likely to be reflected in the functional properties of the respective control systems (compare, e.g., syrphid flies, Collett 1980, and the houseflies, Wagner 1986a,b). Without thorough analyses at both the behavioral and the neuronal level it is not possible, however, to relate – in more than a superficial way – the electrophysiological findings in other insect species to what is known in flies on the detection and fixation of objects and the underlying neuronal circuits.

8 Conclusions

The results discussed here have clearly revealed that in the fly the visual stabilization of the flight course and the detection and fixation of objects essentially depend on the evaluation of motion and relative motion from the retinal image flow. This is mainly achieved by two control systems which are selectively tuned to large-field and small-field motion, respectively. They reside in the lobula plate which, therefore, represents a prominent motion computation center in the fly's brain. Although there remain many problems to be solved in this context, the principle mechanisms underlying these tasks can now be understood, at least in outline. These mechanisms might be of importance beyond the detection and fixation of stationary and moving objects as measured in our behavioral paradigms. Relative motion between objects and their background might also be the decisive cue in other tasks which require knowledge on the three-dimensional

layout of the visual surround, such as the avoidance of obstacles and predators, or the control of landing.

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