J Comp Physiol A (1988) 163:373–388

Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology
© Springer-Verlag 1988

Reafferent control of optomotor yaw torque in *Drosophila melanogaster*

M. Heisenberg* and R. Wolf
Institut für Genetik und Mikrobiologie, Röntgenring 11, D-8700 Würzburg, Federal Republic of Germany

Accepted February 4, 1988

Summary. In the flight simulator the optomotor response of *Drosophila melanogaster* does not operate as a simple feedback loop. Reafferent and exafferent motion stimuli are processed differently. Under open-loop conditions responses to motion are weaker than under closed-loop conditions. It takes the fly less than 100 ms to distinguish reafferent from exafferent motion. In closed-loop conditions, flies constantly generate torque fluctuations leading to small-angle oscillations of the panorama. This reafferent motion stimulus facilitates the response to exafferent motion but does not itself elicit optomotor responses. Reafference control appears to be directionally selective: while a displacement of the pattern by as little as 0.1° against the 'expected' direction leads to a fast syndirectional torque response, displacements in the 'expected' direction have no comparable effect. Based on the behavior of the mutant *rol sol*, which under open-loop conditions is directionally motion-blind but in closed-loop conditions still performs optomotor balance, a model is proposed in which the fly's endogenous torque fluctuations are an essential part of the course control process. It is argued that the model may also account for wild type optomotor balance in the flight simulator.

Introduction

Being blindfolded enables one to realize how much one relies on vision for orientation. Little, however, is known about how the visual information is actually used. As a comparative approach and in an attempt to reduce the complexity of this problem, experimental studies of visual orientation in insects began early this century (e.g., Rádl 1903; Brun 1914; Kühn 1919). Here, we will discuss one of the most intensely studied single parameters of orientation behavior: optomotor yaw torque of flies in stationary flight (Götz 1980; Reichardt 1970; Heisenberg and Wolf 1984).

For measuring optomotor yaw torque the animal is glued by its thorax to a wire or piece of cardboard and the head is immobilized with respect to the body. The animal is then attached to a so-called yaw torque compensator that provides an on-line analog signal of the torque produced by the fly. An important feature of this paradigm is that it allows for 'open-loop' experiments in which the behavior, in this case flight and yaw torque, does not interfere with the stimulus, i.e., the experimentally provided visual motion reaching the eyes.

The paradigm has been exploited in many directions. On the input side optomotor behavior serves to assess the transfer functions of compound eyes and to deduce computational properties of early visual processing in the optic lobes. On the output side it has been used to show that flies generate yaw torque by the differential modulation of wing beat amplitude (Götz 1983). The question to be addressed here is how visual motion input and yaw torque output are linked.

We suggested earlier that in the fly *Drosophila melanogaster* visual information in general cannot be understood as a complex mixture of 'sign stimuli' releasing certain motor patterns. Rather, sensory data resemble long-term dispositions in that they modify the probability of activation of various items of the behavioral repertoire. While there is ample evidence supporting this view (Heisenberg and Wolf 1984), the most thoroughly investigated behavior in flies, optomotor yaw torque, seemed to be an exception. It is one of the most reliable, sturdy, and enduring responses ever encountered

* To whom offprint requests should be sent

in behavioral research (e.g., Götz 1983). In this case input and output appear to be firmly linked.

On the other hand, one may wonder how much of the structure of behavior would show in the optomotor response, considering that recording under open-loop conditions would reveal little more than a correlation between the motion stimulus and the fly's yaw torque. The first torque compensators were too 'noisy' to allow for the evaluation of single yaw torque traces of *Drosophila*; however, with improved recording equipment it soon became apparent that individual yaw torque traces did not simply echo the stimulus. Even under steady stimulus conditions yaw torque was continuously modulated over the whole response range. Furthermore, in these traces so-called torque spikes corresponding to body saccades in free flight were discovered. This raised the possibility that the modulations are not just the internal noise of the flight control system but reflect active behavior.

Working with the house fly *Musca domestica*, Reichardt and Wenking (1969) developed the so-called closed-loop paradigm of optomotor yaw torque simulating, at the torque compensator, free flight with respect to rotations in the horizontal plane. In this set-up the analog signal of yaw torque drives the panorama in the direction opposite to that in which the fly would turn, had it not been tethered. Thus, the fly is now in control of the motion of the panorama and the only instantaneous information the fly has for executing this control is the visual motion stimulus. As expected from the open-loop experiments flies are able to stabilize the panorama. Reichardt (1973) showed that in *Musca* the open-loop responses quantitatively account for the behavior under closed-loop conditions if the spontaneous torque fluctuations are treated as noise independently feeding into the control loop. If optomotor behavior were indeed nothing but a motion (and position) servo loop it would be a strong counterexample to the ideas of the general organization of visual behavior described above.

In their famous paper on the 'principle of reafference', von Holst and Mittelstaedt (1950) outlined one of the most fundamental distinctions a moving animal has to make: the one between sensory information referring to the organism's own actions and information referring to the outside world. The authors took the active behavior of the organism rather than its responses to stimuli as the point of departure. They called the two kinds of sensory data reafference and exafference. As an example they suggested that a fly which was unable to distinguish exafferent and reafferent motion signals would be 'immobilized' by its own optomotor control circuits. The reafference model envisages the central nervous system as generating, for each behavioral action, a copy of the motor command, the so-called efference copy, which is to be matched with the incoming sensory data in order to eliminate the reafference from them. A similar scheme in the framework of electrophysiology was advanced at the same time by Sperry (1950) who coined the term 'corollary discharge' for what in the reafference model is called the efference copy. Both models are designed to prevent reafferent information from reaching higher centers in the brain and consider the exafference, the events in the outside world, to be the main concern of the organism.

In 1951 Mittelstaedt noted that the distinction between reafferent and exafferent information is not the only way the fly can escape its stabilizing control mechanisms for action. In fact, in torque compensator experiments with *Musca* in which the endogenous behavioral activity appeared as 'torque noise,' no indication for a distinction between reafference and exafference was observed (Reichardt and Poggio 1976).

The behavior of *Drosophila* in the closed-loop paradigm is quite different from that of *Musca*. We have provided direct and indirect evidence (Heisenberg and Wolf 1979, 1984; Wolf and Heisenberg 1986) that in *Drosophila* reafferent and exafferent visual motion data are processed differently. Using an improved closed-loop set-up we now extend these findings and give preliminary explanations for some of them. As it turns out, optomotor control in *Drosophila* conforms well to the general structure of behavior outlined above.

Materials and methods

Flies. The flies used throughout this study were 2- to 5-day-old females of the wild type strain Berlin and the double mutant *reduced optic lobes*^{KS221} *small optic lobes*^{KS58} (*rol sol*), glued to a small hook made of silver wire as described by Götz (1964). For preparation, the flies, immobilized by cooling, were placed on a tempered metal block in a stream of dry, cool air in order to avoid water condensation on the surface of the fly. To exclude head movements during the experiments, the silver hook carrying a small drop of glue (UV sensitive; Loctite) was positioned between the fly's head and thorax using a micromanipulator. The glue was then hardened by irradiation with UV light in less than 20 s.

Apparatus. A newly developed experimental set-up was used. The major components are an inductive force transducer (Fig. 1) which simultaneously measures the fly's yaw torque and thrust, and a microprocessor-controlled arena (Fig. 2) in which three concentric cylinders containing the visual stimuli

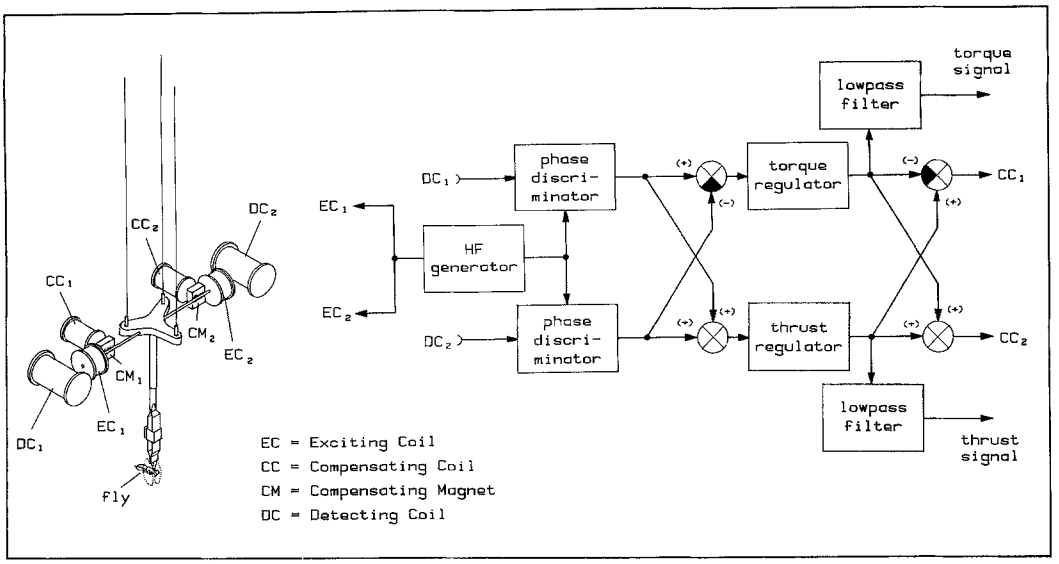

Fig. 1. Inductive force transducer for yaw torque and thrust. The fly is suspended on a swing carrying two coils (*EC1*, *EC2*) and two permanent magnets (*CM1*, *CM2*). The position of the swing is inductively monitored by the stationary coils *DC1* and *DC2*. A third pair of coils (*CC1*, *CC2*) compensates any displacements of the swing. The sum of the compensating currents is proportional to thrust, the difference to yaw torque

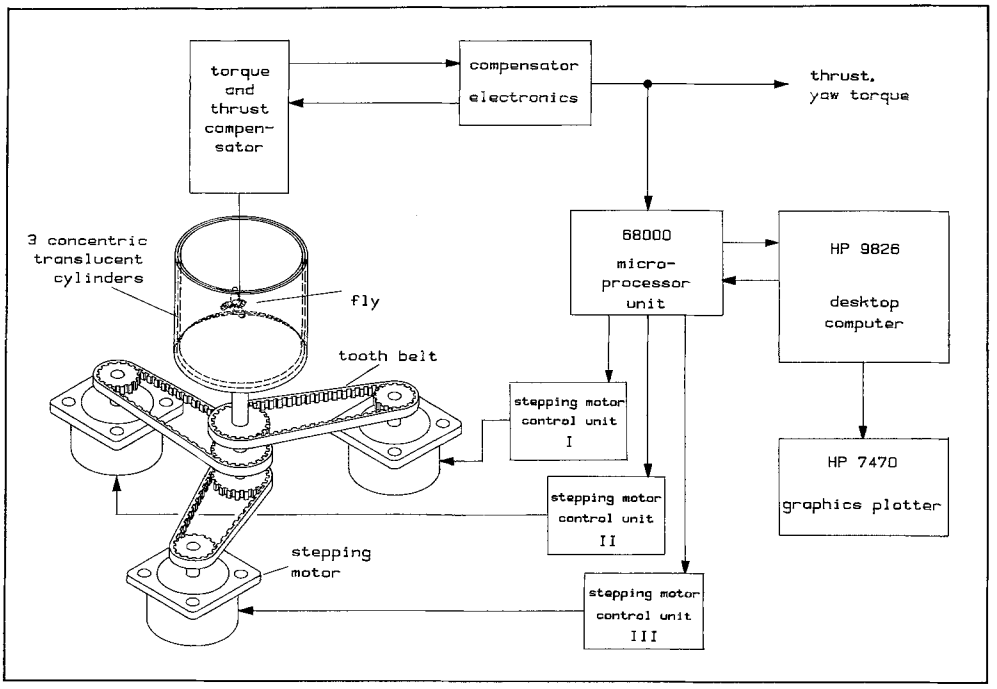

Fig. 2. Stimulus set-up and flight simulator (explanations in the text)

can be rotated, either synchronously or independently of each other, around the fly's vertical axis. In the present study only torque was recorded and only one cylinder was used.

The transducer's cut-off frequency for the torque signal lies at 32 Hz (−3 dB) with a corresponding phase shift of 180° (−15.5 ms). The cylinders are driven by three stepping motors (Berger RDM 564/50). Since the motors' stepping angle in the half-step mode amounts to 0.36°, a toothbelt reduction gear is used to reach a resolution of 0.1° per step. The motor control units need standard pulses as input signals and these are provided by a special processor unit containing a MC68000 microprocessor. The analog voltage from the force transducer is digitized by a 12-bit ADC and then stored in the microprocessor's memory. In free flight the fly's yaw torque is approximately proportional to the angular velocity of the fly (Reichardt 1973; Reichardt and Poggio 1976). Correspondingly, the microprocessor computes the theoretical angle between the fly's longitudinal axis and a fixed point in the visual surround every 50 µs. If not stated otherwise, the coupling coefficient (k) between torque and resulting angular velocity amounted to $11°/s/10^{-10}$

Nm (Heisenberg and Wolf 1984). In closed-loop experiments the rotation of the fly can be simulated by driving the visual pattern(s) to the actual calculated angular position. Up to an angular velocity of 2.000°/s, limited by the microprocessor's program which runs at 20 kHz, this set-up faultlessly transfers the angular steps with a maximum acceleration of 40000°/s^2. Since the visual pattern is simply guided by the computed angular value, no device for measuring angular position (e.g., ring potentiometer) is necessary. The fly's continuous flight angle and torque values are stored in a special area of the memory, this being controlled simultaneously by the MC 68000 microprocessor and a HP 9826 desk-top computer which records, computes, stores, and plots the data and, in addition, controls the experimental timing. Switching of the operating mode between open and closed loop (Fig. 7), inverse feedback (Fig. 11), several different coupling coefficients (Figs. 9, 10), rectified coupling (Fig. 13), or superimposition of rotatory bias can easily be realized by the corresponding software.

Using a steering mechanism with stepping motors instead of a servomotor control system has the advantage that even at low angular velocities no friction-dependent losses are encountered; these may result in a considerable angular error with increasing experimental duration. Therefore, if necessary, the three visual patterns can be synchronized to a high degree of precision.

As an additional feature the processor unit controls its own RAM (128 kByte). This allows the fly's torque or position signal to be stored on-line during a whole closed-loop experiment with high time resolution. If in a subsequent experiment the stored torque signal, instead of the fly's actual torque, is being used to compute the position signal, exactly the same sequence of pattern movements as in the previous closed-loop experiment will be reproduced in open loop (Figs. 4, 5).

Results

Difference between open- and closed-loop optomotor behavior

In the open-loop situation at the torque compensator *Drosophila* generates syndirectional yaw torque in response to being surrounded by a rotating pattern (e.g., Götz 1964). This behavior is called an optomotor response and is thought to be mediated by several lattices of elementary movement detectors which sample most of the visual field (Buchner 1976; Götz and Buchner 1978). Detectors with the appropriate directionality sum their activity in large pool cells which, in turn, control the flight motor system in the ventral ganglion (e.g., Hausen 1981). The optomotor response system consists of several perceptual subunits (Bausenwein et al. 1986) which for the present investigation need not be distinguished.

First, let us assume that in the closed-loop situation the optomotor response has the same properties as under open-loop conditions and operates as part of a simple feedback control loop as proposed for *Musca* (Fig. 3). This assumption can be tested since, at the torque compensator in both situations, input to and output from the optomotor controller may be continuously recorded at high resolution. Irrespective of whether the feedback loop is open or closed, the same input should lead to the same output. With the apparatus described in 'Material and methods' the position trace of a pattern recorded under closed-loop conditions can be displayed in open-loop conditions. However, the output of the controller can only be recorded after the noise is added to it (Fig. 3). Hence, each individual torque trace is different. Nevertheless, if the noise is independent of the output of the optomotor controller, the noise should become small compared to the input-dependent torque modulations in averages of many such torque traces.

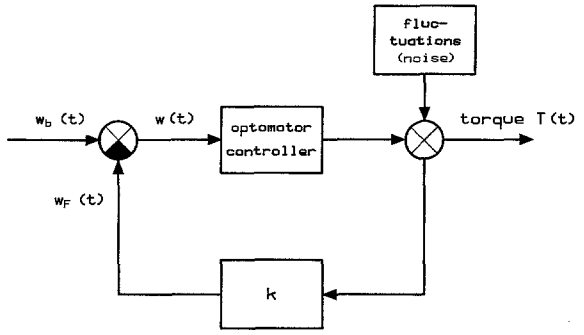

Fig. 3. Visual feedback loop as proposed for the optomotor response of *Musca domestica* (after Poggio and Reichardt 1973). Note that internal generation of 'fluctuations' is independent of the output of the optomotor controller. The constant k is the coupling coefficient linking the fly's yaw torque $T(t)$ to the angular velocity of the panorama. The final motion stimulating the fly (retinal slip w) is composed of the rotatory bias (w_b) and the motion generated by the fly (w_F), where $w = w_b - w_F$

In the experiment of Fig. 4 a sinusoidally modulated rotatory bias (w_b) was added into the (closed) loop at the position indicated in Fig. 3. The remaining difference between the injected disturbance and the fly's adjustments to the changing situation is the only available input which enables the optomotor controller to modulate its output. This position trace produced during the closed-loop experiment was subsequently displayed to the same fly under open-loop conditions (Fig. 4a).

The averaged traces from many flies (Fig. 4b) show that the input-dependent yaw torque output is different in the two situations. Under open-loop conditions the torque modulation is much smaller than in closed-loop conditions and, in addition, is phase-shifted by about 8 s with respect to the bias. Using angular pattern velocity as input, a standard optomotor controller (e.g., PID) would generate a very similar output in the open- and closed-loop cases. No phase shift would be ob-

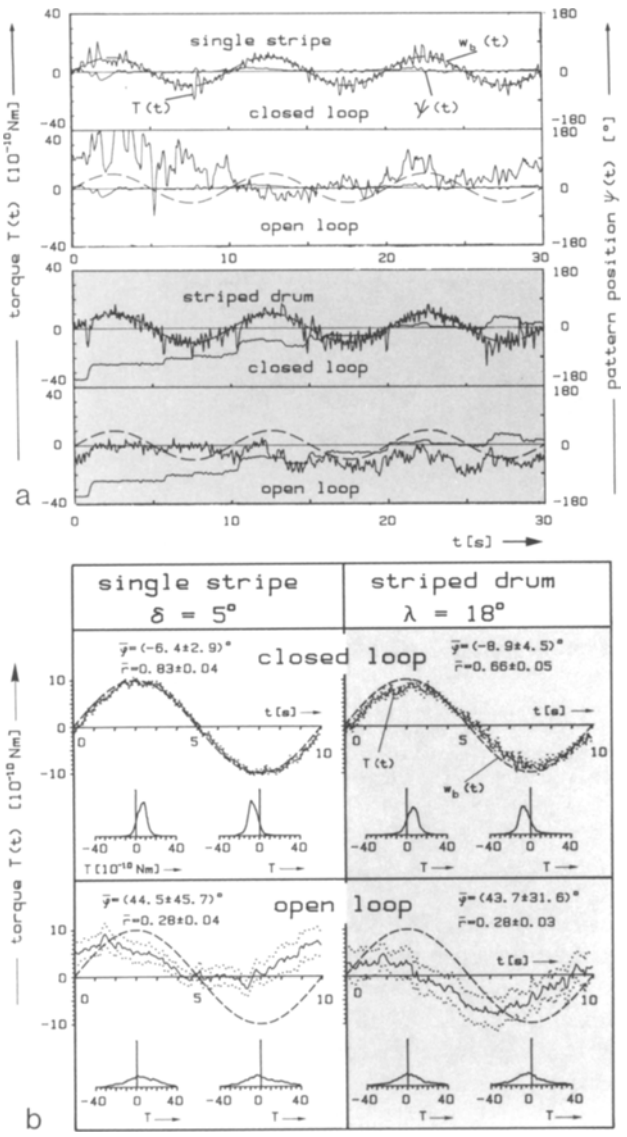

Fig. 4a, b. Different processing of exafferent motion stimuli in the presence and absence of reafferent motion. First, flies were in closed-loop conditions with a single vertical stripe ($\delta = 5°$) or with a striped drum (pattern wavelength $\lambda = 18°$; shaded area). A sinusoidally modulated rotatory bias (frequency $f = 0.1$ Hz) was added into the loop (upper traces). Pattern position as a function of time was recorded digitally and was subsequently displayed to the same flies under open-loop conditions (lower traces). **a** Short flight episodes from individual flies are shown; **b** averages of 120 periods of ten flies. In the closed-loop experiment dashed lines represent the theoretical torque level for perfect optomotor balance. Disregarding the noise, under open-loop conditions torque would follow the dashed lines if processing were the same as in closed-loop conditions. Insets are frequency distributions of torque during the first and second halves of the periods. Numbers in the insets give the mean phase angles ($\bar{\varphi}$) between the rotatory bias in closed-loop conditions and the torque responses fitted by regression sinus. $\bar{r}$ is the mean coefficient of correlation between the torque traces and the respective regression sinus. Mean phase angles and angular deviations were calculated according to Batschelet (1981). Confidence limits of traces and correlation coefficients are SEMs ($n = 10$)

served but the noise would cause a slight reduction of the torque modulation in the averaged trace. Considering that the operating range of yaw torque has an upper (and lower) limit one has to take into account that occasionally the torque noise drifts close to one of these limits, thereby clipping, on the 'outward' side, the response of the controller. The insets in Fig. 4b show separate torque histograms for the positive and negative half-cycles of the disturbance and demonstrate that during open-loop experiments torque fluctuates over a wide range (noise) whereas in closed-loop experiments it is sharply tuned to the level granting optomotor balance. The open-loop torque histograms allow us to estimate that only for less than 10% of the time is torque in the range of about $30–40 \cdot 10^{-10}$ Nm where a reduction of the response amplitude might be expected. This would maximally cause a 5% reduction of the open-loop modulation in the average trace whereas the observed reductions are 50% and 65%, respectively (Fig. 4b).

The difference in the responses in the open- and closed-loop situations is even more striking than can be shown in the average traces. It is known from other experiments (unpublished observations) that *Drosophila* has a tendency to generate torque spikes against the direction of a changing rotatory bias. These torque spikes produce large and abrupt displacements of the pattern in the closed-loop trace which change their angular direction with the same period as the disturbance. Angular pattern motion generated in this way provides a large proportion of the stimuli responsible for the torque modulations in the open-loop traces of Fig. 4b. The basis of this effect is shown in the experiment of Fig. 5. In this case the period of the rotatory bias oscillation was 30 s. Otherwise experimental conditions were the same as in the left part of Fig. 4b. After the experiment flies were ranked according to the modulation of their responses in open-loop conditions. The five 'responders' and the five 'nonresponders' differed significantly in the number of torque spikes they generated during closed-loop conditions. (Note that the phase relation between open- and closed-loop responses is not steady, indicating that the torque spikes occurred at variable points in the cycle.

The experiments show that the system under consideration operates differently in open- and closed-loop conditions, even if the inputs are made identical. The only possible way this can happen is that the so-called noise interacts with the optomotor controller. In the model of Fig. 3 the inter-

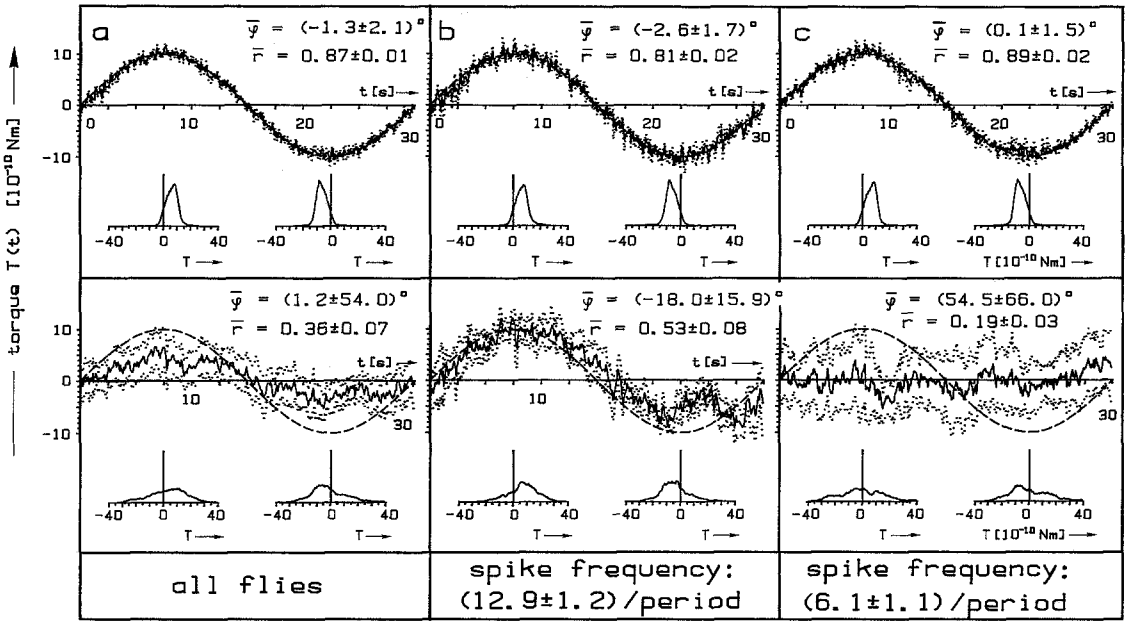

Fig. 5a–c. Same experiments as in Fig. 4 except that oscillation period was 30 s. **a** 40 cycles of ten flies are averaged. **b** Mean responses of the five flies with the largest open-loop response amplitudes are averaged; **c** mean responses of the remaining five flies. Numbers below each part of the figure indicate average numbers of torque spikes per cycle in the corresponding closed-loop part of the experiment (upper traces). Numbers in the insets indicate mean phase angles ($\bar{\varphi}$) between the rotatory bias in closed-loop conditions and torque responses fitted by regression sinus. $\bar{r}$ is the mean coefficient of correlation between regression sinus and actual torque traces. Confidence limits of traces and correlation coefficients are SEMs ($n=10$). Mean phase angles and angular deviations were calculated by circular statistics according to Batschelet (1981). Inset histograms indicate torque distributions during each half-cycle

action is a summation. However, as our data show, the model does not fully account for *Drosophila* optomotor behavior under open- and closed-loop conditions. The generator of endogenous yaw torque fluctuations and the optomotor controller must interact by more than just adding their output. Evidently, the nature of this interaction determines the different processing of reafferent and exafferent information, as first formulated in the specific model of von Holst and Mittelstaedt (1950).

Figures 4 and 5 demonstrate that the modulation of yaw torque in response to the sinusoidal oscillation of visual patterns is influenced by the frequency and polarity of body saccades and by the presence or absence of reafferent visual stimuli. A schematic input-output analysis using a continuum of oscillation frequencies and amplitudes would thus not lead to satisfactory characterization of the optomotor controller.

It has already been described (Heisenberg and Wolf 1984) that even under optimal stimulus conditions open-loop responses have a smaller amplitude than closed-loop responses. In the experiment of Fig. 6 each fly of a group of 10 was tested in a striped drum in four experimental conditions. A comparison of Fig. 6c and d again shows the larger response amplitude in closed-loop as compared to open-loop conditions. In Fig. 6c the rotatory bias (closed-loop motion stimulus) was slowly raised to a level which is just not fully stabilized. The difference between the dashed line and the torque trace gives the remaining average angular velocity if converted by the coupling coefficient. The effective stimulus sequence of Fig. 6c was played back to the fly in open-loop conditions (Fig. 6d). In Fig. 6a, a conventional optomotor stimulus of $w/\lambda=1$ Hz was applied in open-loop conditions. Finally, as a further control, a closed-loop experiment without rotatory bias in the striped drum was recorded (not shown) and the pattern motion of this experiment superimposed upon a continuous rotation as in Fig. 6a. This 'wiggly' rotation stimulates less yaw torque under open-loop conditions (Fig. 6b) than the smooth rotation. Thus, it is not the special noisy quality of the stimulus which the fly requires for a maximal response, but it is the temporal correlation between the reafferent visual stimulus and the motor output which matters.

In order further to characterize the open- and closed-loop processing modes we then tested how quickly the fly switches from one mode to the

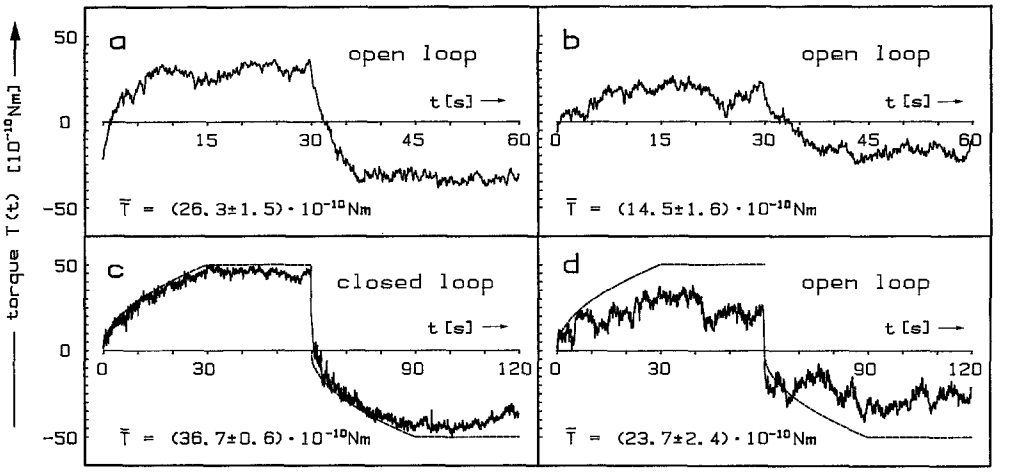

Fig. 6a–d. Yaw torque responses to a rotatory bias are larger under closed-loop conditions than responses to exafferent motion in open-loop conditions. Traces are each an average of ten experiments with the same set of ten flies. **a** The fly was in open-loop conditions. A striped drum (pattern wavelength $\lambda = 18°$; $w/\lambda = 1$ Hz) was rotated around the fly first clockwise for 30 s, then counterclockwise. For each fly the sequence was repeated once. **b** The hypothesis was tested that the fly might quickly lose 'interest' in the case of constant angular motion. The stimulus was the same as in **a** except that the angular fluctuations of a closed-loop experiment, performed in an interim period with the same striped drum, were added to the rotation of the panorama. **c** Flies were in closed-loop conditions with a striped drum ($\lambda = 45°$). Coupling coefficient $k = 5.5°/s/10^{-10}$ Nm. A rotatory bias was added to the closed-loop conditions, slowly increasing during the first 30 s to a final level of $w_b = +275°/s$. After another 30 s the bias was switched off and a bias with opposite polarity slowly built up. Dotted curve indicates torque level of perfect optomotor balance which, due to torque spikes, was not fully reached in the average trace. **d** The pattern movements of the experiments in **c** were displayed to the same flies under open-loop conditions immediately after the closed-loop experiment

other. As in the experiment of Fig. 6 the fly was confronted with a constant rotatory bias. During the onset of motion yaw torque was recorded. At the same moment at which motion started the experimental program could change from open- to closed-loop conditions or vice versa. How swiftly does the fly reach the new yaw torque value of optomotor balance if it was under open-loop conditions before? How quickly does it reduce the response probability to the level of the open-loop mode? In the closed-loop phases of the experiment (Fig. 7) coupling was lower than normal (1/55th of free flight conditions; 1/5th normal coupling). The rotatory bias of 20°/s was added for 1.1 s when the stripe happened to be at a lateral position in the visual field. The sign of the bias is such that the stripe was always driven towards the front. The low coupling coefficient was chosen in order to prevent the stripe from entering the very frontal part of the visual field where it would have elicited an object response (Bausenwein et al. 1986).

Under closed-loop conditions most flies respond with strong syndirectional yaw torque at some time during the first 250 ms (Fig. 7a, c) irrespective of whether the feedback loop had been opened or closed before the onset of exafferent motion. The main effect that the coupling conditions have during the period before the onset of the bias is on the plateau reached after the initial response. As close inspection of the data shows the average traces do not reach the new level of optomotor balance (i.e., the level at which the rotatory bias is cancelled) because of torque spikes against the direction of the bias. This well-known tendency (Heisenberg and Wolf 1984, Fig. 55) is stronger if flies have been under open-loop conditions before the onset of the bias. A comparison of the traces in Fig. 7b and d shows the same difference. In Fig. 7b and d the exafferent motion is presented under open-loop conditions. No immediate large syndirectional yaw torque response was observed. Thus, the presence or absence of reafferent motion exerts its effect on the processing of exafferent motion within 100 ms. In Fig. 7d, where the onset of motion was preceded by open-loop conditions, some flies initially responded to the stimulus. This quick torque deviation is seen more clearly in Fig. 10 (arrow) and in the results of a similar experiment with normal coupling conditions published earlier (Heisenberg and Wolf 1984, Fig. 85).

It might be argued that in the experiments of Figs. 7 and 10 the average motion of the stripe was not exactly the same under open- and closed-loop conditions and that this difference might have been responsible for the difference in the average response. This objection can be refuted: between the onset of the response and the moment at which

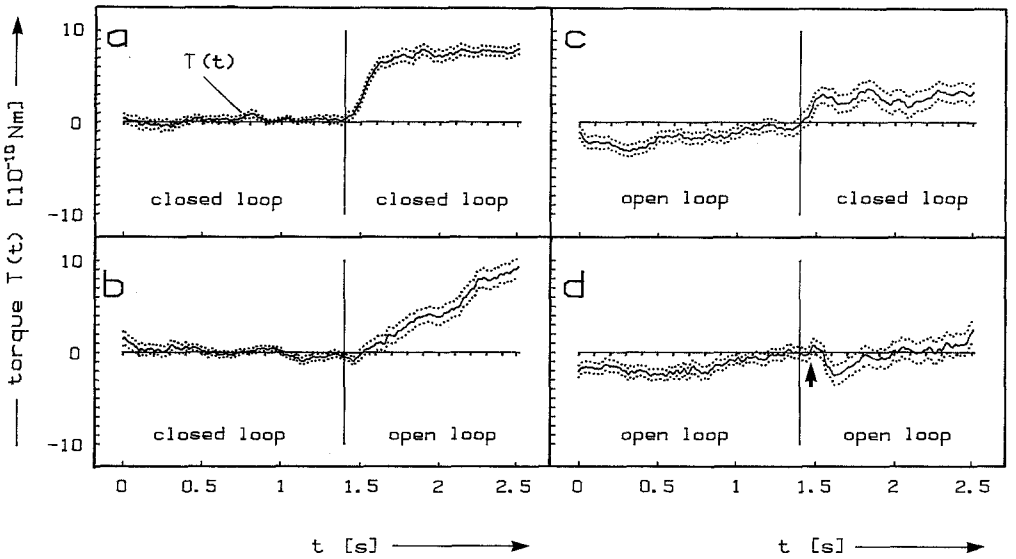

Fig. 7a–d. Optomotor behavior changes immediately when feedback loop is opened or closed. **a** Flies were in closed-loop conditions with a vertical black stripe ($\delta = 5°$) for the whole 2.5-s recording period. Coupling coefficient $k = 2°/s/10^{-10}$ Nm. After 1.4 s a rotatory bias of 20°/s moving the stripe from a lateral position towards the front was added into the loop. After a short delay flies responded with syndirectional yaw torque reaching a plateau after 250 ms. The average trace does not reach the new level of optomotor balance since the bias increases the probability of torque spikes against the direction of exafferent motion. **b** The experiments started as in **a** but with the addition of the rotatory bias at 1.4 s the feedback loop was opened. No fast response was observed but slowly torque drifted in the direction of the bias. **c, d** Flies were initially kept under open-loop conditions with a stationary stripe at variable lateral positions. After 1.4 s the bias was added with a simultaneous switch to closed-loop conditions in **c** and no switch in **d**. Irrespective of the first phase of the experiment, flies generated a fast syndirectional response under closed-loop conditions and, if anything at all, only a slow drift in the direction of the bias in open-loop conditions. The plateau in **c** is even lower than in **a** indicating an even higher probability of torque spikes against the direction of the bias in the case of open-loop conditions before the onset of the bias. The same effect is apparent if the traces of **b** and **d** are compared. In **d** a small fast syndirectional response (arrow) was observed which was turned off about 50 ms later. This initial response under complete open-loop conditions is more clearly shown in Fig. 10 and in results of a similar experiment published earlier (Heisenberg and Wolf 1984, Fig. 85). Starting positions of the stripe at the onset of rotatory bias (closed loop) or uniform motion (open loop) were sufficiently lateral to keep the stripe in the same visual hemifield during the recording period. Individual traces were highly variable. Traces shown are averages of 150 experiments each. Dotted envelopes indicate SEMs

the distinction becomes apparent lie about 30 ms (Fig. 10) or less (Fig. 7). The distance travelled by the stripe during that period in open- and closed-loop conditions differs by less than minimum step size of the motor driving the panorama. The distinction between open- and closed-loop conditions must be based on the perception of reafferent motion. It should be remembered that the propensity to respond does not increase when the angular noise produced by a fly's torque during a closed-loop experiment is displayed in open-loop conditions (Figs. 4–6).

The optomotor controller does not respond to reafferent motion in the 'expected' direction

The short delay of about 100 ms needed by the fly to distinguish open- from closed-loop situations implies that it is the so-called noise which conveys to the visual system the information for this distinction. Throughout flight at the torque compensator *Drosophila* generates yaw torque fluctuations which in closed-loop conditions lead to small perturbations of orientation. This also holds for flies in the thread paradigm (Mayer et al. 1988, this volume), irrespective of whether the head is glued to the thorax. Free flight motion pictures of *Drosophila* and larger flies so far are not detailed enough to distinguish such fluctuations from scatter in the evaluation of data. In this section the small torque fluctuations under open- and closed-loop conditions at the torque compensator are studied.

In Fig. 8 the Fourier spectra of short periods of yaw torque under different flight conditions are shown. The straight dashed lines indicate the amplitude limit above which the respective frequencies would generate motion of the cylinder (smallest step $\Delta\psi = 0.1°$). All three spectra are from the same fly and are each an average of 25 measurements. The data show that under closed-loop conditions (quiet flight mode without torque spikes; see Heisenberg and Wolf 1979, 1984) only frequen-

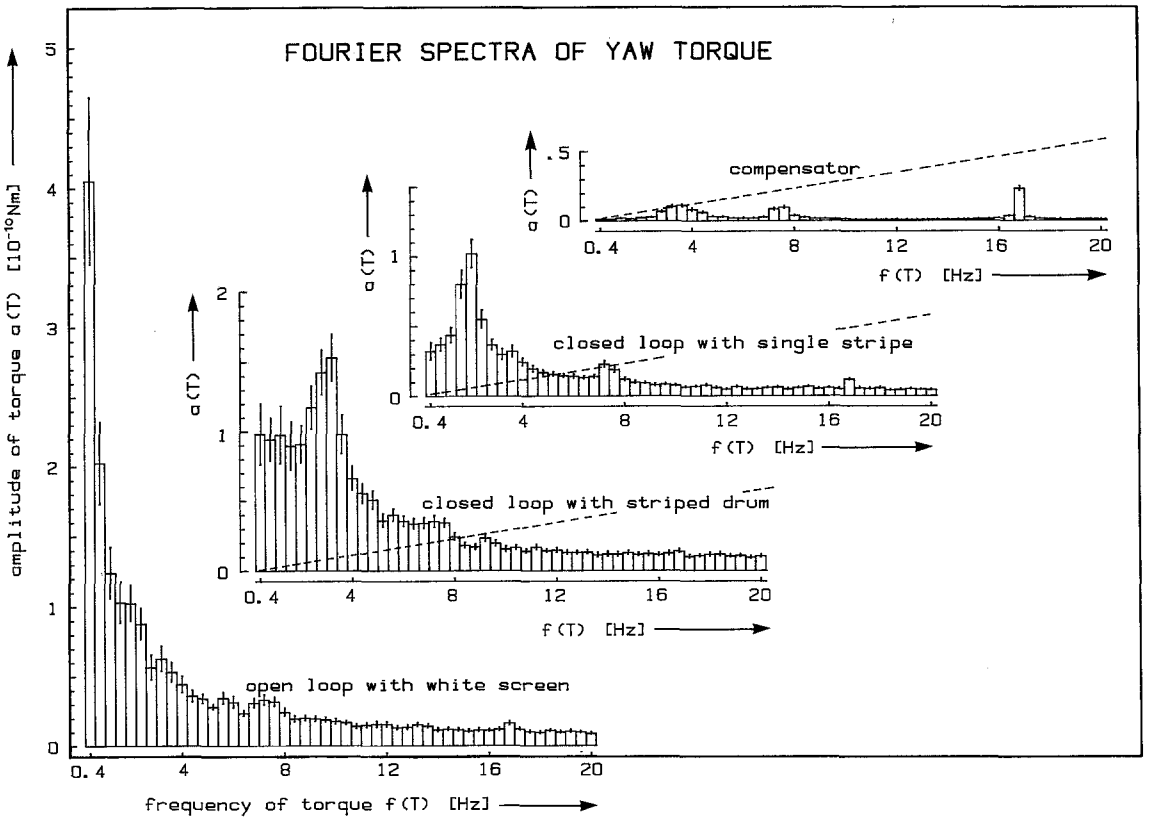

Fig. 8. Fourier spectra indicating the amplitudes by which the various frequencies contribute to yaw torque fluctuations. All data were obtained from one individual. Fourier spectra were calculated from 2.5-s recordings of yaw torque (sampling rate 200 Hz); 25 such spectra were averaged for each condition. Vertical lines in the columns indicate SEMs. Dashed lines show, for the respective frequencies, the amplitudes above which, in closed-loop conditions with $k=11°/s/10^{-10}$ Nm, the frequencies cause a displacement of the panorama (smallest step size $\Delta\psi=0.1°$)

cies below 8 Hz contribute to the motion of the panorama. With a single stripe the spectrum has a single distinct maximum at 2 Hz. When the loop is opened the amplitude of the 2-Hz component does not change significantly. The only substantial increase observed was in the amplitudes of low-frequency components.

In closed loop conditions the torque fluctuations depend upon the visual stimuli. With a striped drum fluctuations are often larger than with a single stripe and the maximum of the Fourier spectrum may be at a higher frequency ($f_{max}=$ 3.2 Hz). Nevertheless, opening the visual feedback loop seems to have little influence on the torque fluctuations in the frequency range above 1 Hz.

Under closed-loop conditions different coupling coefficients have surprisingly little effect on the torque fluctuations (Fig. 9). However, the transition to open-loop is gradual. If the coupling constant is lowered enough to immobilize the panorama with the normal 'closed-loop fluctuations' the fly adds low frequencies with sufficiently large amplitudes to generate small displacements of the panorama (Fig. 9).

The important finding of these observations and experiments is that the frequency components above 1 Hz do not change significantly with different coupling coefficients and between open- and closed-loop conditions, just as the shape of torque spikes is invariant with these experimental variations (Heisenberg and Wolf 1979, 1984). The optomotor controller seems not to generate responses to these self-induced small-angle oscillations of the panorama. Note, however, that in the previous section it was shown that the reafferent small-angle oscillations provide the means by which a fly distinguishes open- from closed-loop situations. Thus, the system is not insensitive to small-angle oscillations.

The optomotor controller is responsive to motion directed against the 'expected' reafferent motion

When a sudden rotatory bias is added to the closed-loop, the latency and steepness of the shift in yaw torque are highly variable, the shortest latency being 35 ms (Heisenberg and Wolf 1984, Fig. 87). In the experiment of Fig. 10 the coupling

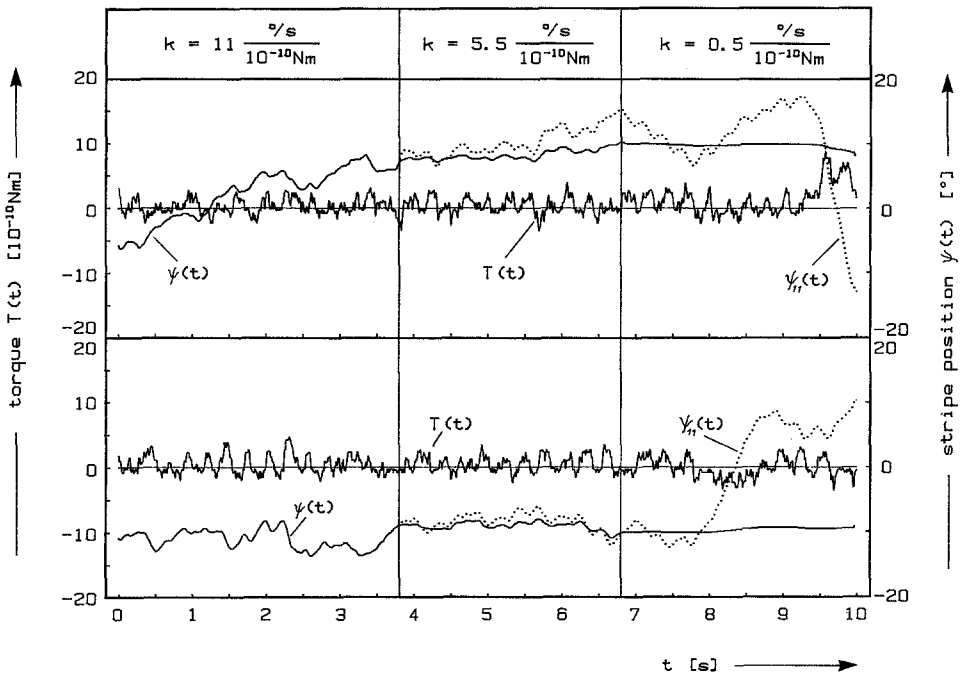

Fig. 9. Closed-loop condition with three different coupling coefficients. Yaw torque fluctuations are little affected by the amplitude of the reafferent motion. Only at the lowest coupling coefficient does the fly sometimes increase the amplitudes of low frequencies. To show the effect of increased fluctuations, position traces with $k = 11°/s/10^{-10}$ Nm are calculated from the torque (dotted curves; $\psi_{11}(t)$). Upper and lower traces are from different flies

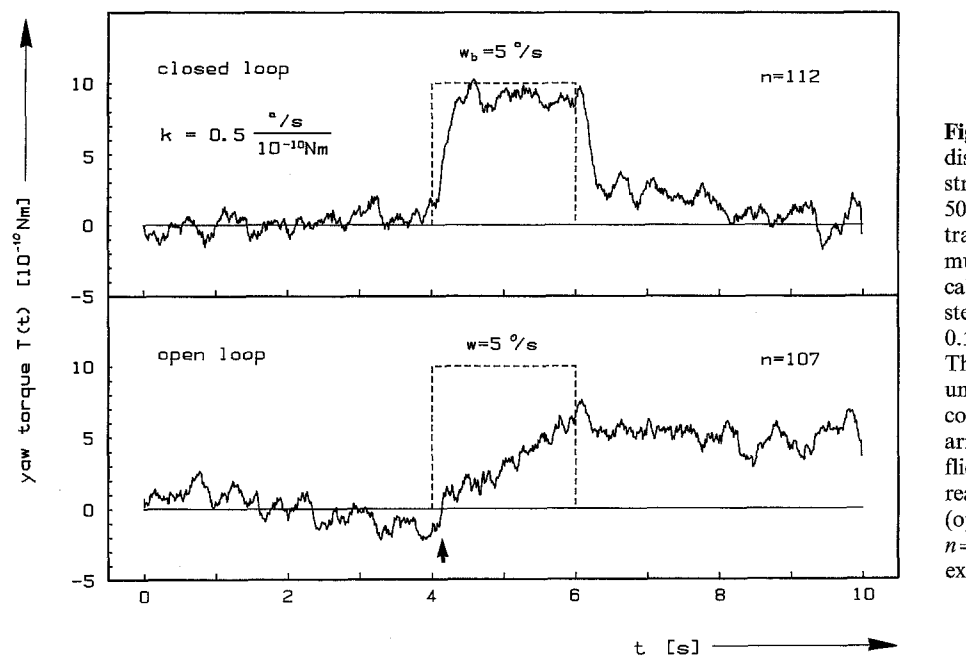

Fig. 10. Flies respond to the displacement of a single vertical stripe ($w = 5°/s$) with a latency of 50 ms. Taking into account a transmission time from eye to muscles in the order of 20 ms one calculates that the first or second step of the stepping motor ($\Delta\psi = 0.1°$–$0.2°$) triggered the response. The response had the same latency under open- and closed-loop conditions (for open loop see arrow). After another 30 ms the flies stopped responding if reafferent motion was missing (open loop). Traces are averages of $n = 112$ ($n = 107$) individual experiments

constant for the closed loop was again reduced in order to test how little exafferent motion the fly requires for generating a response. The shortest latency is around 50 ms, indicating that pattern displacements of only one to two steps of the stepping motor ($\Delta\psi = 0.1°$) are sufficient to elicit a response. After five steps the fly in open-loop conditions realizes that reafferent motion is missing and stops responding. This result may seem to contradict the one described in the preceding section. It was shown that the optomotor controller does not respond to the small-angle oscillations of the panorama since the size of these oscillations does not affect the fly's fast torque fluctuations (frequency > 1 Hz). How, then, can a fly respond so quickly to exafferent motion if it is insensitive to the degree of reafferent motion? The final visual stimulus is a superposition of the two. Thus, exafferent motion would first show as a reduction or enhancement of the reafference. This paradox can be

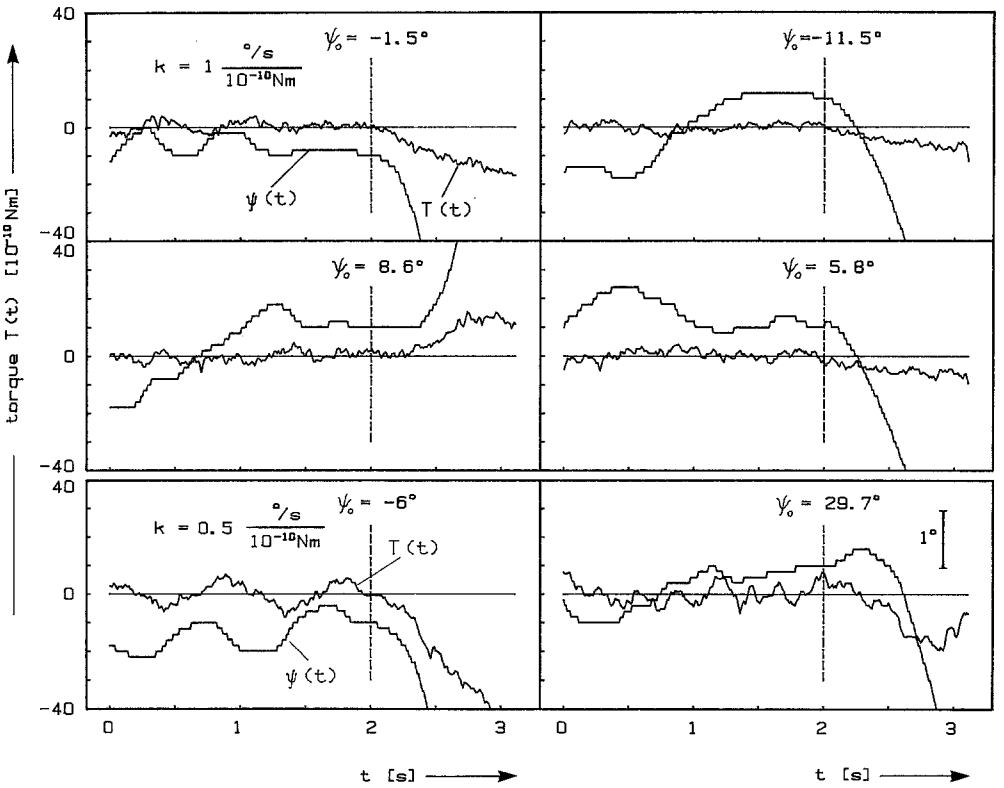

Fig. 11. Six examples of catastrophes due to inverted coupling during closed-loop conditions. Position traces are shown at high angular resolution. The coupling coefficient was set to a very low value in order to slow down the motion of the stripe ($\delta = 5°$). ψ_0 values indicate the position of the stripe at the moment when visual feedback was switched from negative to positive (vertical dashed lines). The catastrophe usually started with the first step of the stepping motor after the reversal. The rare exception is the last example where the stripe moved in one direction for three steps before its direction reversed and the catastrophe began

solved by assuming that the optomotor controller is unresponsive to reafferent motion only as long as this has the 'expected' direction. This proposal was tested in the following experiment.

At an arbitrary instant the sign of the feedback loop was inverted. Clockwise yaw now generated clockwise (instead of counterclockwise) rotation of the panorama. The purpose of the experiment was to observe how much the stripe is allowed to move into the 'unexpected' direction before the positive feedback starts to accelerate it. As can be seen from the examples of Fig. 11, the fly occasionally allows for a few steps in the 'unexpected' direction but in the great majority of cases the first step triggers the catastrophe. This result implies that the sensitivity of the optomotor controller is limited by the step size of the motor in the flight simulator and in free flight may even be better than that.

The high sensitivity of the optomotor controller should be well suited to reducing by a large amount any yaw torque oscillations in the frequency range between 1 and 8 Hz. The finding that they are not substantially reduced under closed-loop conditions suggests that the optomotor controller is indeed unresponsive to movement of the panorama in the expected direction of rotation but responsive to those in the opposite direction.

Visual course control without optomotor controller

So far it has been shown that under closed-loop conditions at the torque compensator visual course control is based on differential processing of exafferent and reafferent visual information. Evidence has been presented suggesting that the optomotor controller is insensitive to the direction of rotation caused by the fly's own yaw torque. This notion raises a new problem: how does the fly manage to fly straight under undisturbed closed-loop conditions if the optomotor controller is unresponsive to the motion induced by the endogenous torque fluctuations? In other words, how does *Drosophila* manage to fly straight?

Recently, a mutant strain of *Drosophila*, *reduced optic lobes*^{KS221} *small optic lobes*^{KS58}, (*rol sol*), has been described (Wolf and Heisenberg

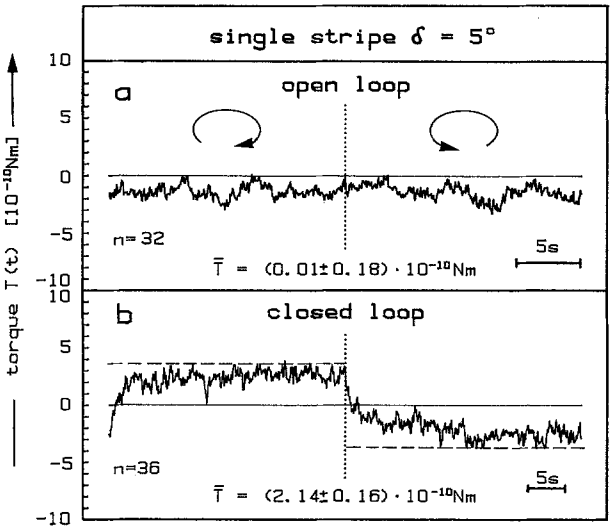

Fig. 12a, b. The mutant *rol sol* is directionally motion blind under open-loop conditions but nevertheless compensates a rotatory bias in the flight simulator (closed loop). **a** A single vertical stripe ($\delta = 5°$) rotated around the fly with a constant angular velocity $w = 20°/s$. It started behind the fly ($\psi = -180°$) rotating clockwise and inverted its direction of rotation after a full circle (dotted vertical line). The trace is the average of 32 experiments with eight male flies. **b** In the flight simulator (coupling coefficient $k = 11°/s/10^{-10}$ Nm the rotatory bias changed every 30 s between $w_b = +40°/s$ and $w_b = -40°/s$ (dotted vertical line). Under these conditions the bias was not fully compensated (but see Wolf and Heisenberg 1986). Trace is an average of 36 experiments with nine male flies

1986) which is directionally motion blind but still has some kind of nondirectional motion sensitivity when tested with isolated landmarks. Surprisingly, *rol sol* flies are able to compensate for a rotatory bias in closed-loop conditions (Fig. 12). It has been shown that neither position control nor directional motion responses are involved in this performance (Wolf and Heisenberg 1986). We describe the *rol sol* controller in this context since it is suited to complement the optomotor controller and, if implemented in the wild type, would enable the fly to fly straight.

The model is designed to accommodate the following properties of *rol sol* behavior. The mutant flies are directionally motion blind as tested by rotating patterns in open-loop conditions. The flies can compensate for a rotatory bias in closed-loop conditions. They do so irrespective of the sign of the feedback loop (i.e., even with positive feedback). The assumption that *rol sol* flies use a nonvectorial[1] motion function for course control is substantiated by their remarkable ability to compensate for rotatory bias in a special flight simulator in which the absolute value of angular velocity is proportional to yaw torque (Fig. 13).

The model (Fig. 14) envisages a flow of 'pretorque' which adds positively or negatively to the current pretorque level (integrator). The polarity of the flow of pretorque switches from time to time with a randomly varying interswitch interval (ISI). The newly introduced term pretorque indicates a neural entity the integral of which is proportional to the yaw torque the fly would generate with two identical wings. For course control a nonvectorial motion function controls the ISI. When motion slows down the next switch event is delayed; when the pattern accelerates the present ISI is shortened. Thus, course stabilization in *rol sol* flies is based on a special kind of random walk reminiscent of chemotaxis in bacteria.

Discussion

Reafference control

Exafferent and reafferent visual motion stimuli are processed differently in *Drosophila*. This was first discovered in the investigation of torque spikes, the equivalent of body saccades at the torque compensator (Heisenberg and Wolf 1979, 1984). Torque spikes have the same time course irrespective of whether the visual feedback loop is open or closed. This is remarkable since the angular motion of a stripe recorded during closed-loop conditions and subsequently displayed under open- or closed-loop conditions elicits a strong syndirectional torque response. Furthermore, during a torque spike the fly is particularly responsive to motion in the unexpected direction. Normally, responses to back-to-front displacements of a stripe or to fast displacements of a large texture are suppressed. Applied during a torque spike they lead to a response if they are directed against the expected motion (Heisenberg and Wolf 1979).

The data presented here show that the differential processing of exafferent and reafferent motion is not confined to the short moments of torque spikes but occurs continuously. This assertion is based on observations which are similar to those in the torque spike study. The size and shape of the small torque pulses which fill the periods between torque spikes do not change much with different settings of the coupling coefficient in closed-loop conditions. At the same time, however, the fly swiftly and sensitively responds to exafferent and reafferent motion in the unexpected direction.

The principle of reafference emphasizes that it is the activity of the animal which requires a dis-

[1] Only the rectified value of pattern velocity is taken into account. The fly has to be able to detect the minimum of pattern velocity independent of its rotational direction

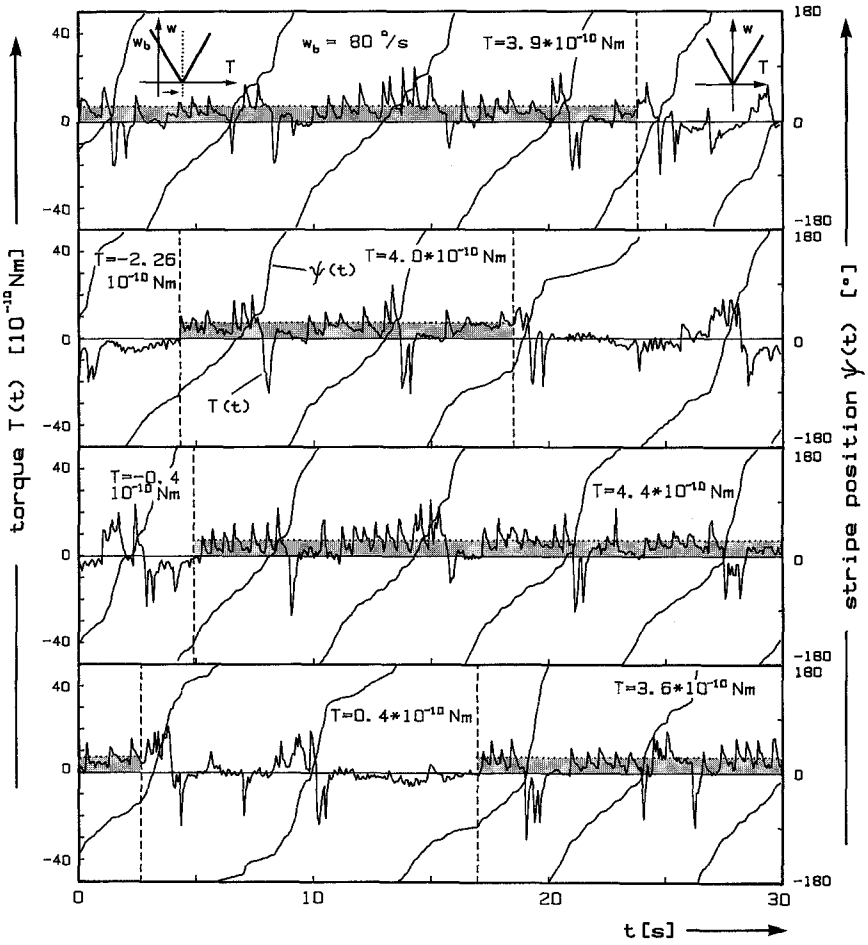

Fig. 13. Single trace of yaw torque of *rol sol* male under special closed-loop conditions where angular velocity of the stripe ($w=k|T|$; $k=11°/s/10^{-10}$ Nm) was proportional to the absolute value of the fly's yaw torque. During the periods marked by the shaded areas a rotatory bias of $w_b=80°/s$ was added into the loop. The fly responded to the bias by shifting its baseline of torque towards the new level of optomotor balance (upper boundary of shaded areas). Insets in the top row show the relation between the fly's torque and the resulting angular velocity of the stripe with and without injection of rotatory bias. Inset numbers give the mean torque during the respective periods (with and without bias). These numbers show that the fly invariably shifts its mean torque towards the value required for optomotor balance

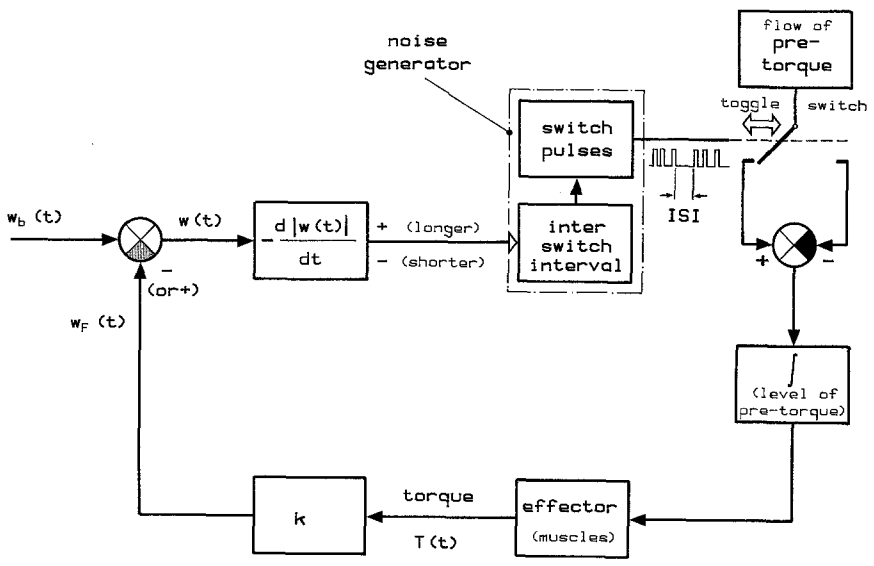

Fig. 14. Model of optomotor balance in the mutant *rol sol*. Flies perceive motion without direction $|w|$. Pretorque is distinguished from real torque in order to account for possible asymmetry in the efficiency of the wings. Pretorque in the model is represented by a reservoir (integrator), the level of which is modulated by the endogenous flow of pretorque of either polarity (toggle switch). In the visual feedback loop the interswitch intervals (ISIs), i.e., the periods between changes in polarity, are modulated by the nondirectional motion function. Acceleration increases and a deceleration decreases the probability of a switch in polarity

tinction between reafference and exafference. The special model proposed by von Holst and Mittelstaedt (1950) contains a subtraction of the efference copy (corollary discharge) of the yaw torque output from the afference, the visual motion input. However, this is not the only way in which the activity of the animal can lead to differential processing of exafferent and reafferent motion signals and today it seems questionable whether this scheme would actually work. In the present study

it is proposed that the generator of endogenous torque fluctuations produces a gating signal which blocks or opens the optomotor pathways for clockwise or counterclockwise rotation according to the turning commands it delivers to the motor system. A physiological and anatomical separation of the two directions of rotation in what presumably is the optomotor controller is found electrophysiologically in large flies (Hausen 1981). As another example of reafference control, K.G. Götz (personal communication) has proposed mutual inhibition between the antagonistic torque spike-generating muscles to be responsible for the fly's unresponsiveness to self-generated visual motion during body saccades. Still another example is provided here by the model describing the behavior of the mutant *rol sol* and, as pointed out on page 377, even the model of Fig. 3 generates a slight distinction between exafferent and reafferent stimuli as a consequence of boundary conditions.

Genetic elimination of the optomotor controller

If our proposal that the optomotor controller is not in operation during undisturbed closed-loop conditions is correct, an additional mechanism has to be postulated for generating straight flight under closed-loop conditions. In an accompanying paper (Mayer et al. 1988, this volume) this mechanism is investigated. In the wild type it is difficult to study since most tests would imply disturbances of the closed loop and thus exafferent motion stimuli which would be counteracted by the optomotor controller. Possibly, however, genetic dissection has provided a *Drosophila* strain by which this problem can be circumvented. In *rol sol* the optomotor controller has been eliminated genetically.

In the flies of this strain more than 85% of the neurons in the medulla, lobula, and lobula plate are missing. At the level of the light microscope the lobula plate in most flies is not detectable at all. This may well be the structural correlate of directional motion blindness. The remaining layers of neuropil in the optic lobes appear to be retinotopically organized and the eye projects normally through them. Thus, according to the structure, visual space should be represented in the *rol sol* nervous system at high resolution.

How stringent is the model of optomotor balance in rol sol*?*

A model based on position control is not supported by the data and, for instance, would not explain the fly's performance in the experiment of Fig. 13. A nonvectorial motion function must exist in the mutant. The time derivative of angular velocity reflects the comparison of a present state with a previous one. This seems to be an indispensable ingredient of any model of optomotor balance relying on a nonvectorial motion function.

The integrator of pretorque is required to account for the seeming absence of retinal slip (Heisenberg and Wolf 1984; Mayer et al. 1988, this volume). The biological significance of the integrator may lie in the fact that a fly cannot have a built-in knowledge of the actual efficiency of its wings. The wings may be damaged to varying extents. Thus, there is no *a priori* relation between the level of pretorque and real yaw torque which determines the direction and speed of turning. The endogenous *flow* of pretorque (of either polarity) and its integration yielding a *level* of pretorque are the core of the model and, at present, appear indispensable.

At first sight this arrangement is just a way of describing the drifting level of pretorque in the integrator. This drift is found in the wild type and mutants under open-loop conditions. However, the concept has profound consequences for the feedback control mechanism. While the control is a reactive process in the optomotor model (Fig. 3), it is an active process in the present model. Now, flight consists of a succession of pulses of pretorque each composed of agonistic and antagonistic actions. The so-called noise, which in part may reflect our ignorance of what is going on in the fly's brain, determines the size and polarity of the pulses. Their size seems to be independent of the level of the integrator. (Note, however, the efficacy factor in the transition from pretroque to torque in Mayer et al. 1988, this volume.)

Whether the visual feedback modifies the ISI as proposed in the model remains to be investigated. Alternatively, pulse size might be regulated by the flow rate of pretorque. Control of the ISI, however, would make the feedback loop much more resistant to changes in the coupling coefficient, as is actually found in the wild type. In summary, the model is not the only possible one but is the most parsimonious account of the data at present.

Does the wild type use the rol sol *controller for flying straight?*

It is important to note that without evidence to the contrary mutants like *rol sol* are considered to be lack-of-function mutants, i.e., some of the behavioral functions of the wild type are partially

or totally missing but what is found in the mutant exists in the wild type as well, even if it is not immediately visible there. Consequently, one would like to propose that the model of Fig. 14, although derived from observations on *rol sol*, also describes basic features of visual course control in the wild type.

Direct evidence for this conjecture comes from electrophysiological experiments on a pair of flight control muscles which, in biofeedback experiments, can be made to stabilize the panorama in a flight simulator irrespective of the sign of the feedback (Götz 1983).

As has been mentioned above, the model accounts well for several properties of yaw torque control in the wild type. In particular, the concept of yaw torque as a succession of active pulses of controlled duration (or amplitude) is not specific for the mutant. All the phenomena for which it accounts occur in the wild type as well. It is thus proposed that the torque fluctuations are also a functional part of the flight control process in the wild type.

In an accompanying paper (Mayer et al. 1988, this volume) optomotor balance of the wild type is investigated. The data presented there are in full accord with the idea that straight flight and constant bias compensation in the wild type are generated by the mechanism revealed by the *rol sol* mutant. The optomotor balance performance of the mutant for which the model is designed is far inferior to the performance of the wild type. Given the severe structural reduction of the optic lobes in the mutant it would not be surprising if the remaining perceptual subunits were functioning poorly. A computer implementation of the model shows that it is a very effective means for establishing and maintaining optomotor balance. Nevertheless, the results so far do not prove that the *rol sol* controller provides these functions in the wild type. The details of straight flight control in the wild type have still to be worked out.

General outlook on optomotor behavior

A salient feature of optomotor behavior, once instrumental noise is sufficiently reduced, is its probabilistic nature. A 'noise generator' is required to account for the random drift of torque in the open-loop situation. In the closed-loop situation under certain conditions a rotatory bias may be compensated very well for a while but then, for certain periods, may be ignored. After the onset of a rotatory bias the fly waits for a variable length of time before it generates a burst of syndirectional torque. The probabilistic occurrence of torque spikes has been emphasized before (Heisenberg and Wolf 1979, 1984). What looks like noise to the experimenter interested in yaw torque may, in a more natural context, be meaningful behavioral activity for the fly. It has been shown in this study that the classical optomotor response is the open-loop effect of an active behavior in which, under normal conditions, straight flight is maintained by a continuous series of torque pulses of alternating polarity. Thus, the organization of optomotor behavior conforms to the general description of visual behavior outlined in the Introduction.

There is a profound reason why optomotor behavior should be organized in this way: most situations are ambiguous. Therefore, for a response to a visual stimulus to be appropriate, the stimulus has to be 'interpreted' by the nervous system as to its causal origine. Is this UV-rich light source the sky? Is this dark dot a mate, this black stripe a branch? Such interpretations can be right or wrong. As actions the responses are experiments. The fly takes its chances. What this study has tried to show is that in optomotor behavior the situation is not any different. The fly has to ask: 'Is this exafferent motion self-rotation?' If the fly's answer was correct its action diminishes the disturbance and the success may induce a repetition of the same action; if it was wrong the fly's action at least changes the situation and the next guess may be an easier one. The open-loop optomotor response represents the *a priori* probability for a certain situation to be self-rotation. In other words, permanent rotation of a largefield pattern around the fly is such a strong cue for self-rotation that it elicits this hypothesis again and again although the response does not reduce the disturbance. This persistence is not surprizing if one takes into account that other hypotheses which the fly may try out intermittantly do not improve the situation either.

Acknowledgements. We thank B. Bausenwein, E. Buchner, K.G. Götz and M. Mayer for critically reading preliminary versions of the manuscript and for most productive discussions. We are particularly indepted to A. Apffel for secretarial help. The work was supported by Deutsche Forschungsgemeinschaft grant no. He968/5-6 and the Universitätsbund Würzburg.

References

Batschelet E (1981) Circular statistics in biology. In: Sibson R, Cohen JE (eds) Mathematics in biology. Academic, London

Bausenwein B, Wolf R, Heisenberg M (1986) Genetic dissection of optomotor behavior in *Drosophila melanogaster*. Studies on wildtype and the mutant *optomotor-blind*^{H31}. J Neurogen 3:87–109

Brun R (1914) Die Raumorientierung der Ameisen und das Orientierungsproblem im allgemeinen. Gustav Fischer, Jena

Buchner E (1976) Elementary movement detectors in an insect visual system. Biol Cybern 24:85–101

Götz KG (1964) Optomotorische Untersuchung des visuellen Systems einiger Augenmutanten der Fruchtfliege *Drosophila*. Kybernetik 2:77–92

Götz KG (1980) Visual guidance in *Drosophila*. In: Siddiqi O, Babu P, Hall LM, Hall JC (eds) Development and neurobiology of *Drosophila*. Plenum, New York, pp 391–407

Götz KG (1983) Genetik und Ontogenie des Verhaltens. Genetischer Abbau der visuellen Orientierung bei *Drosophila*. Verh Dtsch Zool Ges 1983:83–99

Götz KG, Buchner E (1978) Evidence for one-way movement detection in the visual system of *Drosophila*. Biol Cybern 31:243–248

Hausen K (1981) Monocular and binocular computation of motion in the lobula plate of the fly. Verh Dtsch Zool Ges 1981:49–70

Heisenberg M (1983) Initiale Aktivität und Willkürverhalten bei Tieren. Naturwissenschaften 70:70–78

Heisenberg M, Wolf R (1979) On the fine structure of yaw torque in visual flight orientation of *Drosophila melanogaster*. J Comp Physiol 130:113–130

Heisenberg M, Wolf R (1984) Vision in *Drosophila*. Genetics of micro-behavior. In: Braitenberg V (ed) Studies of brain function, vol. XII. Springer, Berlin Heidelberg New York

Holst E von, Mittelstaedt H (1950) Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. Naturwissenschaften 37:464–476

Kühn A (1919) Die Orientierung der Tiere im Raum. Fischer, Jena

Mayer M, Vogtmann K, Bausenwein B, Wolf R, Heisenberg M (1988) *Drosophila* flight control during 'free yaw turns'. J Comp Physiol A 163:389–399

Mittelstaedt H (1951) Zur Analyse physiologischer Regelungssysteme. Verh Dtsch Zool Ges, Zool Anz [Suppl]:150

Poggio T, Reichardt W (1973) A theory of the pattern induced flight orientation of the fly *Musca domestica*. Kybernetik 12:185–203

Rádl EM (1903) Untersuchungen über den Phototropismus der Tiere. Engelmann, Leipzig

Reichardt W (1970) The insect eye as a model for analysis of uptake, transduction and processing of optical data in the nervous system. In: Schmitt FO (ed) The neurosciences. Second study program. Rockefeller University Press, New York, pp 494–511

Reichardt W (1973) Musterinduzierte Flugorientierung der Fliege *Musca domestica*. Naturwissenschaften 60:122–138

Reichardt W, Poggio T (1976) Visual control of orientation behaviour in the fly. Part I. A quantitative analysis. Q Rev Biophys 9:311–375

Reichardt W, Wenking H (1969) Optical detection and fixation of objects by fixed flying flies. Naturwissenschaften 56:424–425

Sperry RW (1950) Neural basis of the spontaneous optokinetic response produced by visual inversion. J Comp Physiol Psychol 43:482–499

Wolf R, Heisenberg M (1986) Visual orientation in motion-blind flies is an operant behaviour. Nature 323:154–156

Note added in proof. In this paper directionally selective reafference control during small torque fluctuations has been deduced from the differences between open- and closed-loop conditions. In the meantime this property of flight control has been directly recorded.