Visual Motion and its Role in the Stabilization of Gaze
Eds. F.A. Miles and J. Wallman

CHAPTER 12

The sensory-motor link in motion-dependent flight control of flies

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1. Introduction

The role of sensory information in behavior is a seemingly simple but unresolved problem in the brain sciences. What happens between sensory input and motor output when, for instance, a dog notices another dog on the street and rushes out of the front yard? Some investigators (e.g., Hagenuk, 1990) have postulated a special dog-o-taxis, a reflex which varies in strength depending upon the other dog's distance, size and position in the visual field. This idea is simple and quantitative. Unfortunately, however, dogs are not willing to cooperate in our attempts to validate this hypothesis (unpublished results). Thus the sensory-motor link in dog-o-taxis cannot be investigated.

This is not so with the fly *Drosophila melanogaster*. Its optomotor response in tethered flight offers the unique opportunity to study the relation between motion input and yaw torque output in exquisite detail. This particularly reliable and robust behavior, which has been studied for many decades, is one of the best examples of a seemingly simple stimulus-response relation in orientation behavior. In this book Egelhaaf and Borst (Chapter 3) summarize our current knowledge about movement detection in arthropods, and in flies in particular. In the present chapter we build on this knowledge and discuss how the output of the movement detectors influences yaw torque. Is this relation a deterministic one? How are yaw torque and the information about motion used in the stabilization of the flight trajectory? Do the movement detectors and yaw torque operate as parts of a simple feedback loop? The answers to these questions teach us a general lesson about how sensory data influence behavior. Flight orientation in *Drosophila* is based on initiating activity which by definition has a probabilistic component. Initiating activity is distinguished from rhythmic activity and from induced behavioral activity elicited by a complex superposition of external and internal stimuli (Heisenberg and Wolf, 1984).

1.1. Open-loop, closed-loop

Freely walking or flying insects in a visually structured rotating drum have the tendency to turn with the direction of the movement. This behavior has been called the "optomotor response". It is thought to stabilize the animal in flight and, like the optokinetic response in vertebrates, it might also serve in the stabilization of gaze.

The optomotor response has been studied most intensively in flies. A turning point in this endeavour was the discovery that optomotor responses can be recorded in tethered flying flies. Tethered flies are hooked to a yaw torque meter which provides a D.C. voltage proportional to the fly's angular momentum around its vertical body axis. The fundamental advance in this technique lies in the fact that the optomotor response can now be tested in "open-loop": The tethered fly cannot turn and, hence, does not interfere with the visual stimulus applied. Much of what is known about visual motion detection in insects is derived from open-loop studies using the torque meter. In Chapter 11, Collett et al. relate these findings to the free-flight situation.

In a second step the feedback loop can be closed again (Reichardt and Wenking, 1969; Götz, 1975). For this type of experiment the output of the torque meter is used to drive a motor that moves the surrounding visual scene in the direction opposite to that in which the angular momentum would turn the fly in free flight. The assumption underlying this arrangement is that the fly's angular momentum should be roughly proportional to its angular velocity. Model calculations indicate that in turning, the fly's angular momentum is largely used up by air friction which, in turn, might roughly be proportional to angular velocity. This situation is called closed-loop. We refer to it also as "flight simulator" since the fly experiences the visual effects of its flight maneuvers without being able to turn. In this respect the closed-loop situation resembles the flight simulator used in the training of pilots. Of course, the simulation is limited to rotation in the horizontal plane since yaw torque is the only parameter of flight control recorded.

Investigation of the sensory-motor link in optomotor behavior is based to a large extent on a comparison of open- and closed-loop behavior. If yaw torque were a function of only the visual input and thus could be said to operate as part of a simple feedback loop reducing retinal slip, all relevant properties of this behavior could be deduced from open-loop experiments. (This has been claimed for *Musca domestica*. See, for instance, Reichardt and Poggio, 1976.) However, only an extensive comparison between open- and closed-loop can show whether this is the case. So far, *Drosophila melanogaster* is the only organism which has served in detailed flight simulator experiments (Heisenberg and Wolf, 1979, 1984, 1988; Mayer et al., 1988; Wolf and Heisenberg, 1980, 1986, 1990). A most telling comparison is one in which yaw torque is recorded under closed- and open-loop conditions with exactly the same visual input (master-replay experiments). In the master recording (closed-loop) the movement of the retinal image is an entirely reafferent stimulus whereas in the replay (open-loop) the same sequence of image motion is applied exafferently.

2. Open-loop behavior using the torque meter

2.1. Yaw torque, a single variable

Drosophila attached to the torque meter constitutes a bizarre behavioral preparation. The fly is immobilized except that it can beat its wings and can move its legs and abdomen. Of all the abolished behavioral options we can see only what is manifested in yaw torque. This single variable, however, is recorded at high resolution and in real time. A technical point should be emphasized here. The torque meter has no zero torque setting. All we can measure is relative torque, its temporal modulation, range and dynamics.

2.2. Endogenous behavioral activity

Even when the tethered fly is flying in a bright featureless panorama its yaw torque reveals a surprising degree of behavioral activity. The fly continuously modulates its yaw torque, not keeping a preferred value which might be considered an internal zero. Three components can be distinguished: a slow drift superimposed upon small, fast fluctuations and on less frequently occurring large bursts of torque called torque spikes. These spontaneous modulations cover most of the torque range of the fly as recorded in optomotor experiments. Torque spikes have been identified as intended body saccades (see Collett et al., Chapter 11, this volume). They are observed as isolated events of either polarity (right; left) but also occur in volleys of the same polarity as the underlying slow modulations, suggesting an intended search behavior for visual cues (Heisenberg and Wolf, 1979, 1984). Body saccades are fixed action patterns in the sense that the burst of yaw torque is coordinated with turning of the head and abdomen as well as a lateral deflection of the hindlegs (Götz et al., 1979; Heisenberg and Wolf, 1984). (In tethered flight routinely the head is glued to the thorax in order to avoid interference of head movements with the visual input.) Body saccades are generated spontaneously but in frequency and polarity are influenced by visual stimuli.

2.3. Yaw torque elicited by horizontal motion

Nothing much changes when fixed contours are introduced into the arena. However, systematic measurements reveal that flies show a mean turning tendency towards a stationary black landmark (Bausenwein, 1984). Moving patterns, however, elicit immediate yaw torque in the same direction (Götz, 1964, 1975, 1983) superimposed on spontaneous torque modulations similar to those found in a stationary panorama. Apparently the fly interprets the pattern motion as self-rotation in the opposite direction and tries to regain a stable orientation by counteracting the disturbance.

2.4. Yaw torque is the time integral of the motion signal

A feedback loop working against self-rotation with movement detectors as sensors can only partially stabilize the fly unless their signal is integrated in time before transmission to the effectors (Mittelstaedt, 1971). Indeed, a careful examination of small yaw torque responses to optomotor stimuli directly reveals an extremely efficient integration of the movement detector signal (Fig. 1). A large volume of more indirect evidence supports this notion (Wolf and Heisenberg, 1990; Mayer et al., 1988; Zimmermann, 1973 cited in Götz, 1975). A perfect integrator in the optomotor pathway would cause the optomotor response to eventually rise to its maximum torque level whenever a rotatory stimulus is apparent for the fly. The only differential response to stimulation with different contrast frequencies and pattern contrast should be the steepness of the torque trace during its rising phase after the onset of the stimulus. Yet, different levels of the steady-state torque are observed at different stimulus strengths (Götz, 1983). We interpret this phenomenon as the fly's ability to try out other behavioral options if the salience of the stimulus is low and if no correlation is detected between visual input and yaw torque output (see Section 3.2.2.6 below). With a perfect (nonleaky) integrator, the torque-generating effector system always stays at the level to which the movement detectors or any other signals push it. One can assess the input to the integrator simply by calculating the first time derivative of yaw torque. We have called this neural entity "pretorque". The relevance of pretorque will become obvious when we discuss closed-loop behavior.

2.5. Transfer properties of the optomotor system

If the whole optomotor system were a simple transducer using linear operations to generate yaw torque from motion, its transfer properties could be derived from a comparison of input and output in open-loop experiments. In fact, the response to an oscillating panorama of black and white vertical stripes is an oscillation of the same basic frequency as the stimulus. As would be expected the response shows some of the properties of the movement detector array discussed by Egelhaaf and Borst (Chapter 3, this volume). With increasing pattern speed, for instance, the response shows higher harmonics (Fig. 2a) which are in accordance with model calculations of an array of elementary movement detectors by Egelhaaf and Reichardt (1987). Other aspects of the transfer properties cannot easily be accounted for by the movement detectors. The response latency of 40–50 ms (see for instance Fig. 10) and the amplitude and phase relations between input and

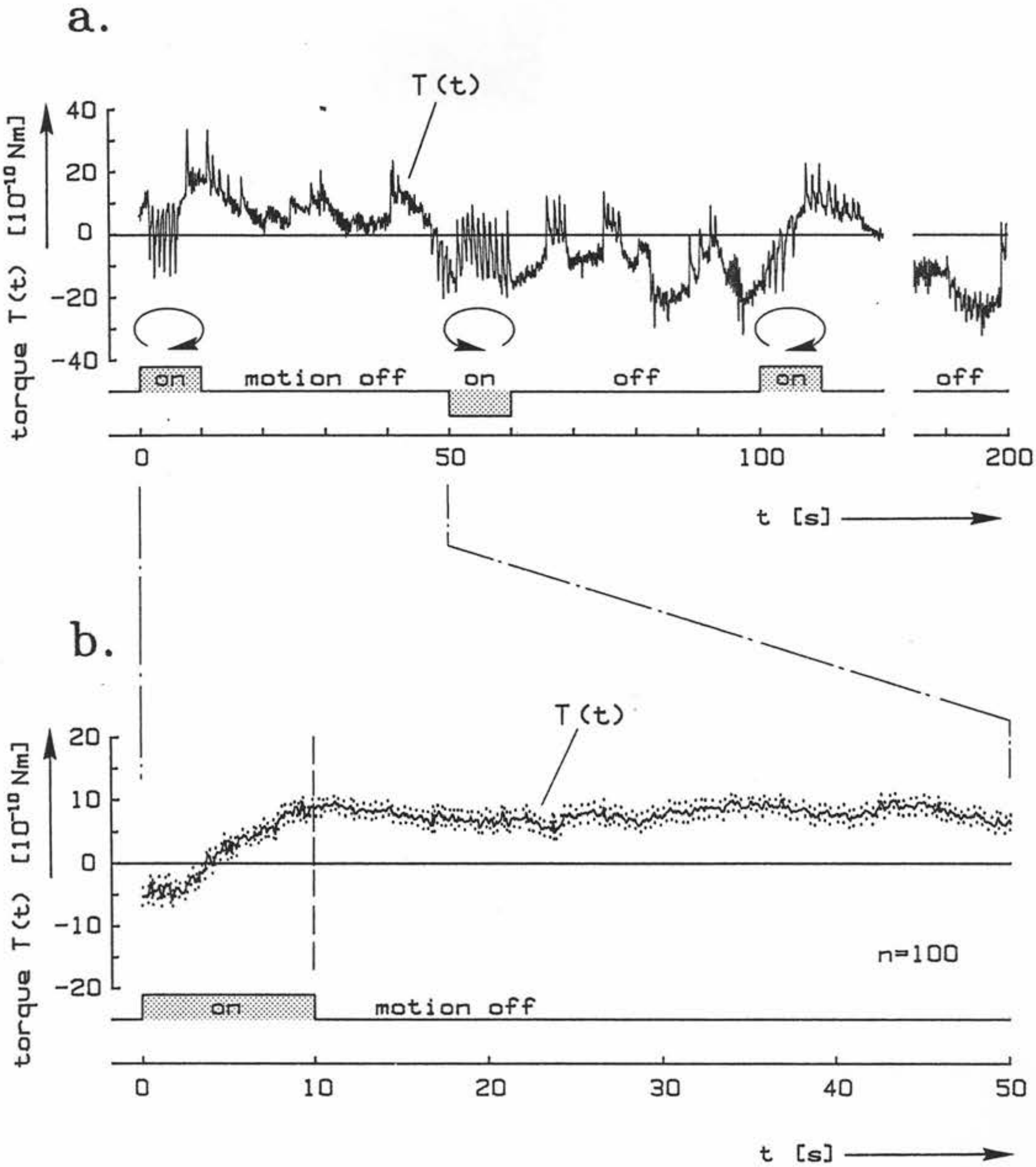
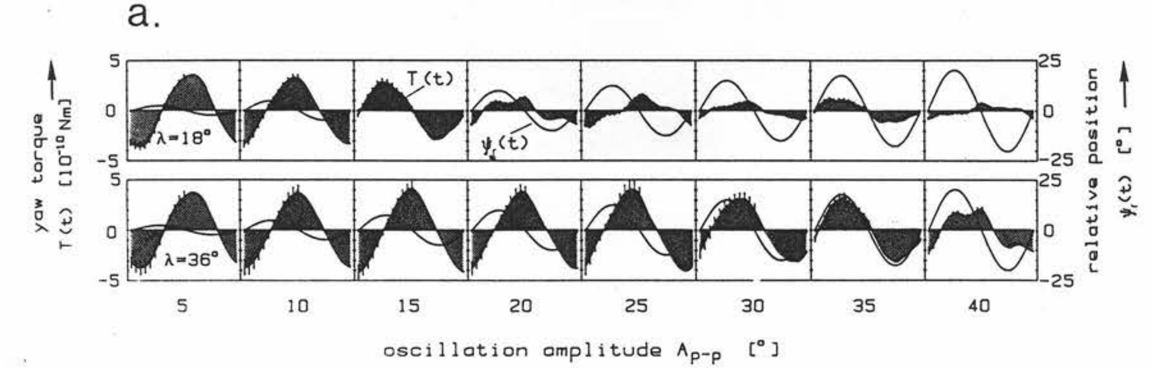


Fig. 1. Integration of movement detector signals is apparent in optomotor responses to weak motion stimuli. Average yaw torque $T(t)$ stays at the level to which it is driven by the stimulus (**b**). Striped drum; pattern wavelength $\lambda = 45$ deg; pattern contrast $m = 0.3$; angular velocity $w = 0.9$ deg/s (or zero). In (**a**) an unaveraged torque trace $T(t)$ is shown. Responses to pattern motion can hardly be distinguished from endogenous torque modulation typical for open-loop situation. Dotted envelopes in (**b**) are SEMs of the $n = 100$ sweeps. (From Wolf and Heisenberg, 1990, modified.)

output (Fig. 2b) suggest a complex sensory-motor interface (Mayer, 1989).

Input-output analysis of the optomotor system may be complicated by the torque spikes (body saccades). Although these are not triggered by any known stimuli their frequency and polarity are influenced by visual stimuli in a probabilistic manner. Motion of a striped drum increases the



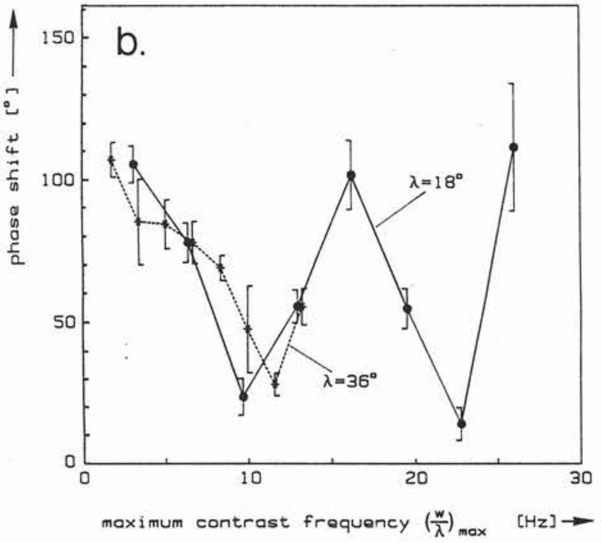


Fig. 2. Yaw torque responses to oscillating striped drum. (**a**) Response amplitude $T(t)$ decreases with increasing oscillation amplitude $\psi_r(t)$ of stimulus. Note higher harmonics in the response with increasing oscillation amplitude. Pattern wavelengths $\lambda = 18$ deg and $\lambda = 36$ deg; oscillation frequency $f = 3.75$ Hz. Responses are averages of 95 cycles from each of six flies (WT Berlin); traces in addition are averaged *modulo* π and data plotted twice for full cycle. (**b**) Dependence of phase shift between yaw torque and relative position of drum (equivalent to phase shift between pretorque and angular velocity) on contrast frequency. Data suggest that contrast frequency is the relevant independent variable. (Therefore contrast frequency at the relative pattern position $\psi_r = 0$ deg is indicated on abscissa.) Phase shift and maximum contrast frequency are derived from the data in (**a**). For evaluation of phase shift sine functions are fitted to averaged torque traces by least-squares method. Error bars in (**a**) and (**b**) are SEMs for number of flies. (Data from Mayer, 1989.)

probability of torque spikes directed against the motion (see for instance Fig. 1). This tendency is particularly evident immediately after the onset of motion or its reversal in direction. This biased torque spike activity is superimposed upon any optomotor response including the one in Fig. 2a (Heisenberg and Wolf, 1984).

2.6. Genetic dissection

Dissection of the optomotor system by genetic variants has shown that responses are mediated by at least two partially redundant subsystems, one called the large-field response, the other the object response. In both subsystems movement of visual patterns leads to yaw torque in the same direction. The large-field response is elicited preferentially by visual patterns subtending large fractions of the visual field. In the absence of such stimuli even small patches of contours or single landmarks are effective. The large-field response is thought to be about equally sensitive in all parts of the visual field and to movement in either direction (front-to-back vs. back-to-front).

The object response, in contrast, is preferentially stimulated by an isolated landmark such as a single vertical dark stripe. It is a response to front-to-back motion and is observed only in the frontal half of the visual field (Heisenberg and Wolf, 1984; Bausenwein et al., 1986).

These findings have been corroborated and extended by elegant ablation studies in large flies (Geiger and Nässel, 1981, 1982; Hausen and Wehrhahn, 1983, 1990). Strong evidence from large flies as well as *Drosophila* supports the hypothesis that the large-field response, but not the object response, is mediated by the three so-called Horizontal-System (HS-)neurons in the lobula plate. Another type of neuron in the lobula plate, the Figure-Detection (FD-) neuron identified by Egelhaaf (1985), is a good candidate to be involved in the object response.

Behavioral experiments with *Drosophila* in which the spatial resolution of the two optomotor subsystems was tested suggest that the two use somewhat different sets of elementary movement detectors (EMDs) (Bausenwein et al., 1986). The two subsystems may even have different dynamic properties. Egelhaaf (1987) tested *Musca domestica* with oscillating patterns and observed the decline of the yaw torque response with increasing oscillation frequency. Using an extended grating the response declined sooner than when a single stripe was used.

2.7. *Gain control by flicker frequency*

Input-output analysis of the open-loop optomotor response is further complicated by observations indicating that the time constant of the movement detectors (de Ruyter van Steveninck et al., 1986; Borst and Egelhaaf, 1987) and possibly also the internal gain of the optomotor response (Kirschfeld, 1989) adapt to the local flicker frequency of the stimulus (Chapter 3, this volume).

3. Optomotor behavior in closed-loop

3.1. *The flight simulator*

Although in flight simulator experiments the temporal structure of the visual stimuli is not controlled, these experiments being closed-loop, may shed some light on the role of the fly's spontaneous torque modulations in visual flight control.

Two problems arise in setting up a closed-loop experiment that links angular velocity of the scene to yaw torque. For one, it is not known at which reading of the torque meter the fly actually has zero angular momentum. Secondly, a proportionality constant for the relation between angular velocity of the panorama and yaw torque has to be found which lies within the range of free flight conditions.

With respect to the first problem we briefly record the whole range of yaw torque in open-loop by rotating the pattern clockwise and counterclockwise and then take the mean value of these torque responses as zero. As will be discussed below, the zero setting in the flight simulator is not very critical since *Drosophila* has an efficient zero control mechanism.

3.1.1. *Neural versus physical torque*

Let us define a new variable to be called "neural torque". This is the neural signal the fly sends to its effector system generating the torque. What normally is called "yaw torque" is the actual angular momentum of the fly; we will call it here "physical torque". The relation between neural and physical torque depends upon the efficacy of the two flight motors. For a healthy, intact fly this relation may be constant most of the time but even a tiny droplet of nectar on one of the wings may severely alter its aerodynamic properties. Hence, the fly may all of a sudden have to apply large neural torque in order to achieve zero physical torque and vice versa (Fig. 3).

A bias in the zero setting of the flight simulator is equivalent to an imbalance of the flight motors. In other words, considering that all our closed-loop experiments work without a good knowledge of the fly's zero physical torque, we always inadvertantly test the fly's ability to compensate for a differential effectiveness of the two flight motors. The astounding proficiency of *Drosophila* in this compensation will be discussed below.

3.1.2. *Finding the right coupling coefficient*

Fortunately, the second problem of finding the right coupling coefficient between angular velocity of the panorama and yaw torque could be solved experimentally. Mayer et al. (1988) de-

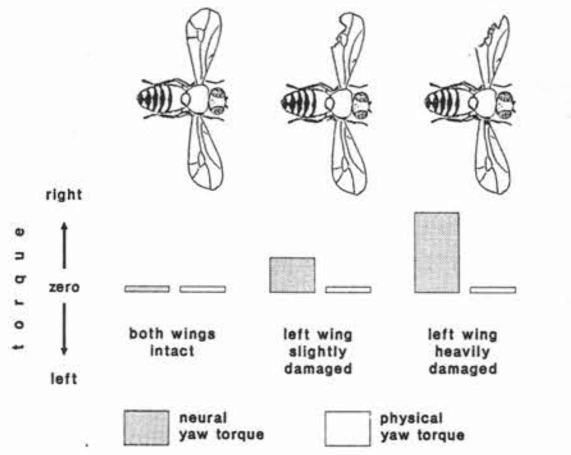


Fig. 3. Physical and neural yaw torque may differ from each other if, for instance, one wing is damaged. (Physical yaw torque is the actual yaw torque which in free flight would turn the fly. Neural yaw torque is the output of the neuromuscular flight machinery.)

signed an apparatus which allows to determine the size of body saccades. In this setup a tethered fly is flying stationarily and free to rotate around its vertical axis. It is suspended from an ultrathin polyamide thread and carries a little metal pin on its back which keeps the fly in the center of a strong radial magnetic field. There, the longitudinal body axis of the fly is recorded optoelectronically. To guarantee unrestrained rotation of the fly a servo motor turns the thread in register with the fly. In this apparatus flies show essentially the same behavior as in the flight simulator (see below). Periods of fairly straight flight are interrupted by body saccades.

Assuming that the size distribution of body saccades in the thread apparatus is similar to that in free flight (in fact, the few saccades recorded in high-speed motion pictures of freely flying *Drosophila* (Bülthoff et al., 1980) fall into this range), one can now adjust the coupling coefficient in the flight simulator such as to make the angular displacements of the panorama during torque spikes equal to the angular displacements of the flies during body saccades in free flight.

Unfortunately, with this experimentally determined coupling coefficient angular velocities of the panorama in the flight simulator are about ten times lower than those of the flies in free flight. The reason for this surprising result is that the dynamics of body saccades in the flight simulator differ from those in free flight (or the thread apparatus). An angular displacement that is achieved in about 250 ms in the flight simulator is generated within 50 ms in the thread apparatus. When rotating freely, flies sense their angular acceleration and use this proprioceptive signal to cut the torque spikes short (Heisenberg and Wolf, 1979). The low coupling coefficient simulates a low efficacy of neural torque which might occur in free flight because of injury to one or both wings.

In summary, the inadequacies of the flight simulator are equivalent to wing injury. Impairment of the wings changes the scaling factor between neural and physical torque and, secondly, may displace the two scales with respect to each other. In free flight moderate wing injury does not dramatically interfere with flight control (our own unpublished observations).

3.2. Behavior in the flight simulator

Two behavioral processes can be distinguished in the flight simulator: turning and flying straight. This is shown in Fig. 4b which is a computer reconstruction of the flight path from the data in Fig. 4a. In most instances turns are performed by body saccades; in the intervals between saccades the flight path appears straight (Fig. 4b) although, at a higher resolution it consists of a continuous series of small, fast turns of alternating polarity. As in open-loop the fly actively modulates its yaw torque (Wolf and Heisenberg, 1990; Heisenberg and Wolf, 1984). Despite the small turns we will call this behavior "straight flight" according to its overall appearance.

3.2.1. Body saccades

A fly generates saccades in order to change, choose and obtain certain orientations. The vol-

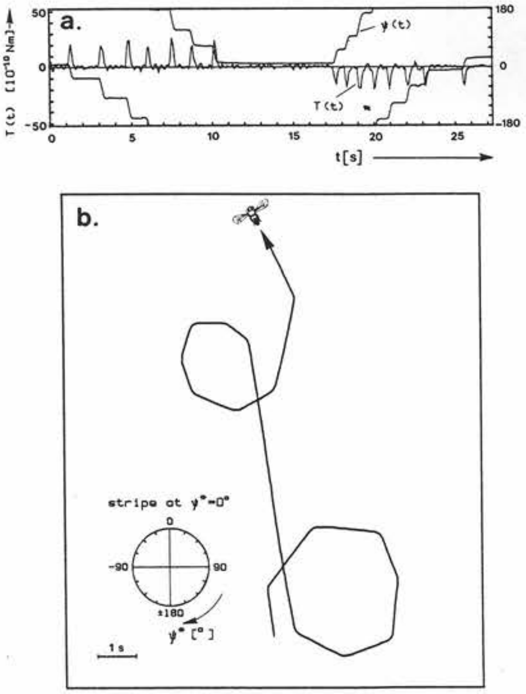


Fig. 4. Straight flight trajectories and abrupt turns characterize the behavior of *Drosophila* in the flight simulator. In this case the visual pattern is a single vertical black stripe. (**a**) Yaw torque and pattern position traces showing torque spikes and, in between, small torque modulations. (**b**) Computer reconstruction of flight trajectory assuming constant flight velocity. In this graph the stripe is at position $\psi^* = 0$ deg at infinite distance. (Modified from Heisenberg and Wolf, 1984.)

leys of torque spikes observed in open-loop also occur in the flight simulator. Now it becomes apparent that they form patrol loops since in many cases the flies keep adding saccades until they have turned the panorama by a total of 360 deg (Fig. 4).

The function of the saccades can be nicely documented in a flight simulator equipped with two concentric platforms, one carrying on its periphery a single vertical stripe as landmark and beneath it a second, slightly larger one, carrying a drum textured all around. Both platforms are in closed loop with the fly's yaw torque. We now add a constant rotatory bias into the closed loop with one of the platforms only. This gives the stripe and the background texture, relative to each other, a fixed angular velocity which the fly cannot change. In this situation the fly will keep a straight course with respect to the textured drum (optomotor balance) and will, for long periods of time, generate body saccades towards the stripe in order to keep it in the frontal visual field (Fig. 5; Heisenberg and Wolf, 1984). This behavior corresponds to saccadic tracking in the free-flight condition. It is well known from other arthropods (Sandemann et al., 1975; Rossel, 1980).

It has been suggested repeatedly (e.g., Chapter 11) that the body saccades of flying insects serve to prevent the optomotor system from interfering with voluntary turns. Pattern velocities during body saccades might be too high to stimulate the optomotor system significantly. For *Drosophila* this issue can be addressed directly in the flight simulator if the dynamics of torque spikes in open- and closed-loop are compared (Heisenberg and Wolf, 1979, 1984). The results reveal a complex interaction of the torque spike motor program with the optomotor system. In the following the results are briefly summarized (Fig. 6):

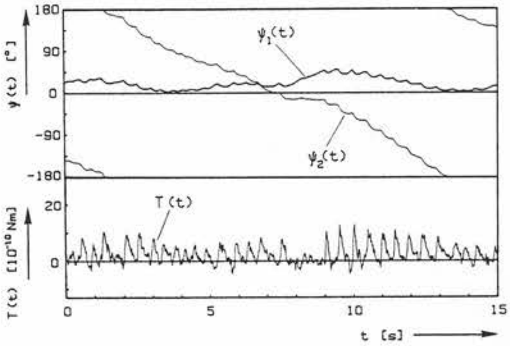


Fig. 5. Saccadic tracking in the flight simulator. The fly is suspended in the center of a double-arena. The inner one carries a single dark vertical stripe on its periphery, the wall of the outer one is covered with a random-dot texture. Both patterns (stripe and background texture) are in closed-loop with yaw torque. The feedback loop with the stripe in addition is "disturbed" by a rotatory bias $w_b = 30$ deg/s. $\psi_1(t)$: position trace of stripe; $\psi_2(t)$: position trace of outer cylinder. The baseline of torque ($T = 0$) corresponds to zero net rotation of the large-field texture; torque spikes (corresponding to body saccades) keep the stripe in the frontal visual field.

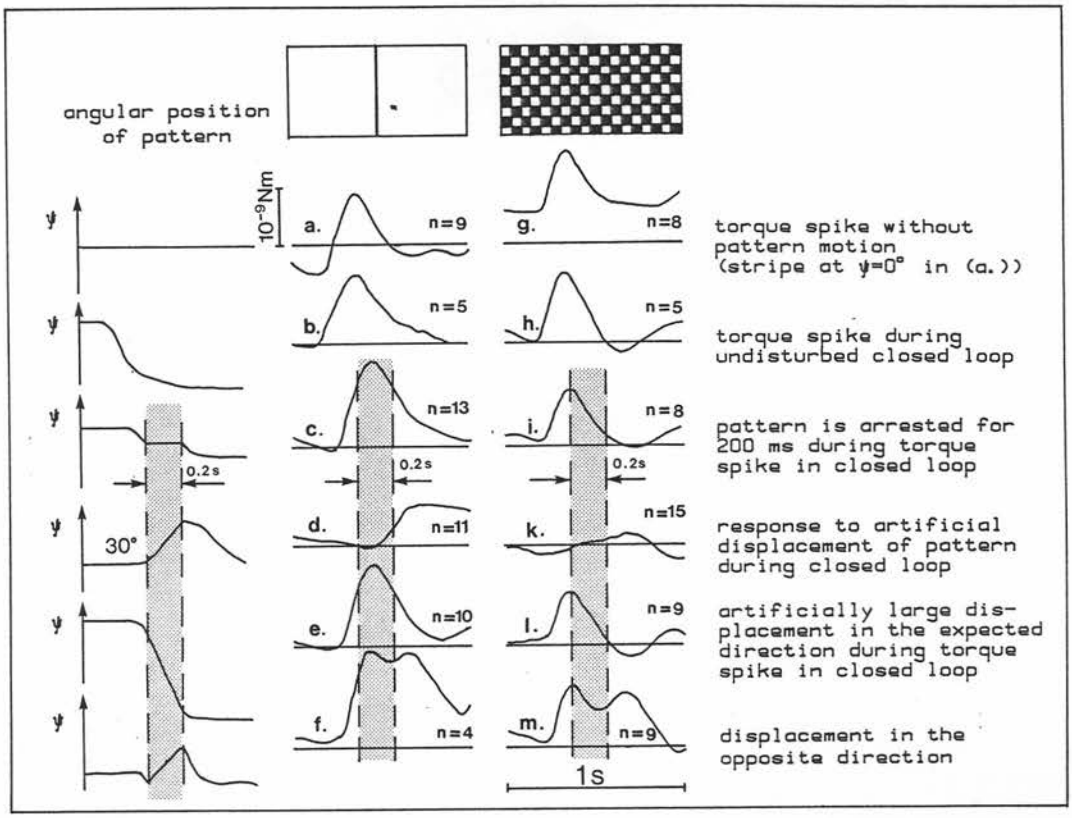


Fig. 6. Directionally selective saccadic suppression and sensitization. In the flight simulator during torque spikes flies are unresponsive to motion in the direction which would be caused by the turning maneuver but are fully responsive to motion in opposite direction. For further details see text. (Modified from Heisenberg and Wolf, 1984.)

(a) Visual feedback over a wide range of angular velocities has no significant effect upon the time course of torque spikes. During torque spikes the optomotor system, indeed, is insensitive to the concomitant pattern motion. (b) Pattern motion induced by torque spikes in closed-loop can be recorded and later displayed to the same or another fly in open- or closed-loop. In open-loop flies respond quite regularly to these motion stimuli. In closed-loop responses depend upon the pattern, direction of motion and position in the visual field. Motion of a single stripe from front to back in the frontal visual half-field has an 85% chance of eliciting a response as long as the pattern displacement does not coincide with a torque spike. As mentioned above, during torque spikes the response frequency falls to 0% if the direction of motion corresponds to that induced by the torque. If, however, motion is in the opposite direction the response frequency goes up to near 100%. Furthermore, closed-loop responses to the sudden displacement of a striped drum during straight flight are rare but if the displacement occurs during a torque spike and is in the "wrong" direction their frequency also goes up to near 100%. In summary, the optomotor system is selectively suppressed for certain visual stimuli and is sensitized for others by the torque spike motor program.

3.2.2. *How can flies fly straight?*

3.2.2.1. Orientation should not be determined by landmarks. Since the zero values of neural and physical torque often are not identical the fly needs visual feedback to compensate for the asymmetries of its motor output and to steer through air turbulences. As has been mentioned above, an array of movement detectors in a simple feedback loop would only partially stabilize the fly. Therefore, a second control loop using the position of landmarks as desired values (position servo) has been discussed (Reichardt and Poggio, 1976). A position servo may be useful during very turbulent flight as a last resort. Under most other circumstances it would be fatal if the objects in the visual field were to force the fly into a certain direction. During normal flight conditions an insect needs to choose an appropriate direction of propagation on the basis of many other determinants besides visual cues. The critical question of where to go should be thoroughly uncoupled from the problem of course stabilization. In fact, we have been unable to show the involvement of a position servo in the stabilization of straight flight. In the flight simulator *Drosophila* has no difficulty in flying straight with respect to an evenly textured panorama without any distinct landmarks and, furthermore, it can stabilize a single landmark at any position in the visual field. Very special position control systems would have to be postulated to accommodate these properties. At present we will disregard this type of course control mechanism. The powerful integrator in the optomotor system of *Drosophila* (Fig. 1) offers a much better solution.

3.2.2.2. The integrator in closed-loop (flight simulator). The effect of the integrator is very prominent in the flight simulator. Over a wide range of zero settings of the electronics, the fly will arrest the movement of the panorama and keep a stable baseline of torque (optomotor balance). However, already with a moderate rotatory bias and a striped drum as panorama one observes a 5% retinal slip which also is present in the thread apparatus (Mayer et al., 1988). On the other hand, the extremely long time constant of the integrator as shown under open-loop conditions in Fig. 1 suggests a better stabilization. High resolution analysis of the flight traces, in fact, reveals that this slip is not due to a leaky integrator but rather to the uneven efficacy of the turning commands under bias conditions. Straight flight is a succession of small right and left turns irrespective of whether maintenance of optomotor balance requires high or low neural torque. When neural torque is high torque pulses that reduce neural torque have a greater effect than torque pulses that increase neural torque. The asymmetry may just reflect some limitations of the effector organ. The relevance of the small torque pulses for straight flight will be discussed below.

3.2.2.3. Closed-loop responses are larger than open-loop responses. If the optomotor system equipped with the above-mentioned integrator operated in a "passive" feedback loop as depicted in Fig. 7a the steady-state properties of the system could be described by the equations shown in Fig. 7a below, indicating that the torque responses to a rotatory bias (w_b) would be larger in open- than in closed-loop. Yet, the behavior in the flight simulator is at odds with this simple model. One of the first observations in the flight simulator was that by the application of an increasing rotatory bias yaw torque could be driven to considerably larger values than had ever been observed in open-loop experiments with optimal stimuli (Heisenberg and Wolf, 1984). In the lower trace of Fig. 7b a striped drum with high pattern contrast covering a large part of the fly's visual field is rotated at optimal angular velocity (w = 20 deg/s). In the closed-loop experiment (upper trace of Fig. 7b) the same pattern is used and the rotatory bias had been increased to a level at which it is not fully zeroed any more. The fly happens to leave a retinal slip of w_b = 20 deg/s.

3.2.2.4. Flies compare motor output and motion input. The crucial argument against a simple feedback loop model comes from experiments in which open- and closed-loop responses to the same stimuli are compared. In these so-called master-replay experiments we first record yaw torque generated by the fly in response to a sinusoidally modulated rotatory bias in the closed-loop situation (flight simulator, master trace). We also recorded the temporal pattern of retinal slip motion and subsequently played it back in open-loop to the same fly (replay). Since in the first and second parts of the experiment the visual stimuli were the same one would also expect to measure the same yaw torque responses. Again, however, responses in closed-loop were considerably larger and more consistent than in open-loop (Fig. 8).

This experiment is particularly interesting because the only feature present in the closed-loop case and lacking in open-loop is the coincidence between the patterns of motor output and visual motion input. We have shown that the fly continuously makes this distinction and that it needs only about 50 ms for it (Heisenberg and Wolf, 1984; Wolf and Heisenberg, 1990).

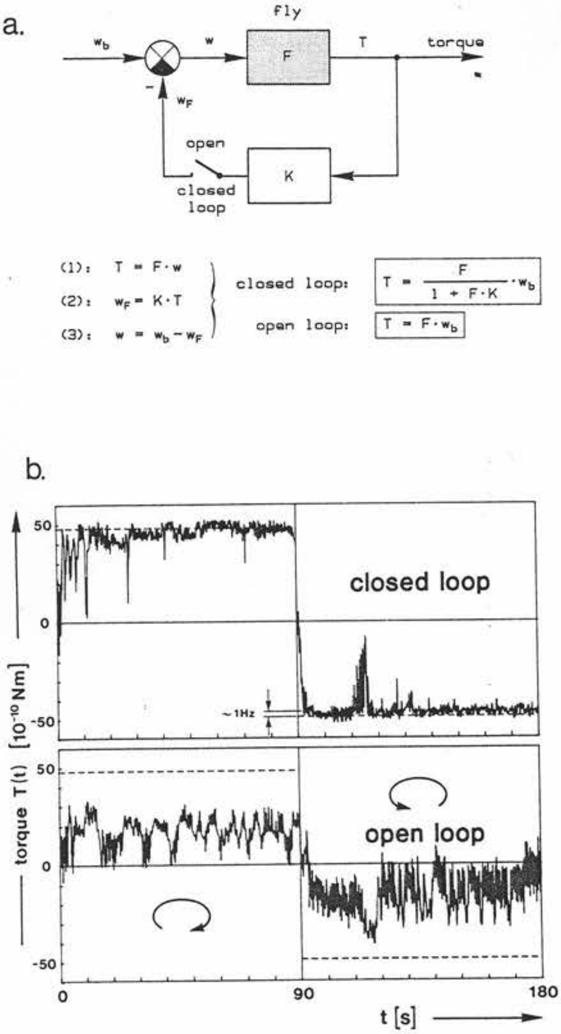


Fig. 7. The fly as a transducer of visual motion signals into yaw torque. In this model the steady state responses to a constant stimulus w_b under open- and closed-loop conditions can be calculated if F and K refer to linear transfer functions which characterize dynamic properties and amplification factors of the transducer (F) and the coupling conditions (K). For any K and F open-loop responses are larger than closed-loop responses. (From Wolf and Heisenberg, 1990.) (**b**) In the *Drosophila* optomotor system the opposite is found. The upper trace shows the response of a fly in the flight simulator (closed-loop) to a rotatory bias of $w_b = 530$ deg/s. The fly happens to leave a slight retinal slip of about $w = 20$ deg/s corresponding to a mean contrast frequency of $w/\lambda = 1$ Hz. In the lower trace the same fly is stimulated in open-loop in the same striped drum at a constant contrast frequency of $w/\lambda = 1$ Hz. (Modified from Heisenberg and Wolf, 1984.)

3.2.2.5. Which variables are compared?. If an efference copy of the motor output and some processed result of the visual input are compared, what are the actual variables and what is the mode of comparison? Could it be angular velocity and proprioceptively recorded physical yaw torque? The dipteran flight apparatus is poorly suited for a proprioceptive evaluation of physical yaw torque. Wing beat amplitude would be more closely related to neural torque than to physical torque. Deformation of the wing during the stroke would be influenced in an unpredictable manner by wing injury. We interpret the drifting baseline of torque in open-loop as an indication that the tethered fly without visual feedback has no reliable measure of zero physical torque.

Could the variables be angular velocity and neural torque? The answer clearly is no. Angular velocity is not unambiguously related to neural torque (Fig. 3). As discussed above the relation between neural and physical torque (and therefore angular velocity) depends upon the states of the two flight motors.

For these reasons we were led to consider

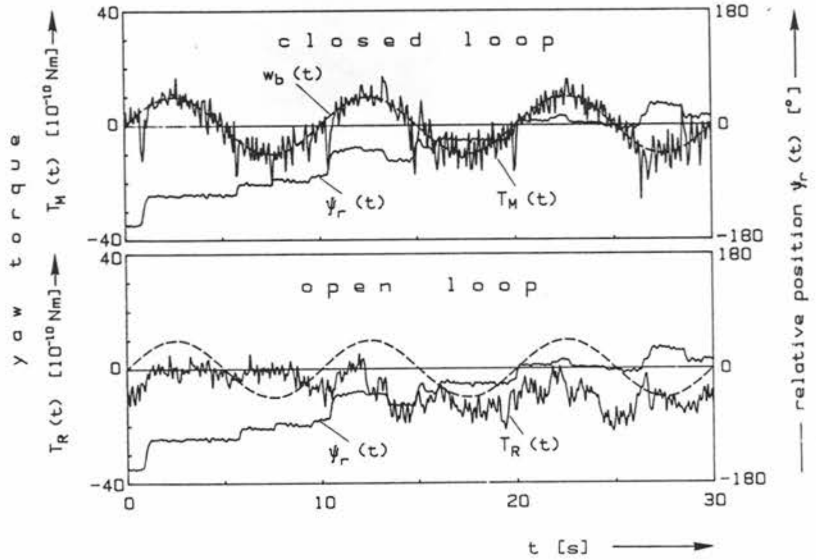


Fig. 8. Yaw torque responses in closed- and open-loop to identical temporal sequence of motion stimuli. If the fly's yaw torque responses depended solely upon the visual input they should always be the same if the stimuli were the same, irrespective of whether these were presented in open- or closed-loop. In the upper trace the fly's response to a sinusoidally modulated rotatory bias leads to a near to perfect compensation of the disturbance. The time course of pattern motion is digitally recorded, stored and subsequently displayed again to the same fly but now in open-loop (lower trace). Striped drum; pattern wavelength $\lambda = 18$ deg. (Data from Heisenberg and Wolf, 1988.)

pretorque and angular acceleration as the important variables. A change in neural torque (pretorque) of one polarity always causes a change in angular velocity (angular acceleration) in the same direction irrespective of the actual levels of neural and physical torque.

The two variables so far have not been measured directly. Pretorque being the input to the integrator can easily be calculated from yaw torque as the first derivative in time. Neurons specifically sensitive to changes in angular velocity may well exist in the visual system of insects. In *Calliphora* the HS-neurons of the lobula plate, for instance, have complex transient responses to the onset of visual motion (Egelhaaf and Reichardt, 1987; Egelhaaf and Borst, 1989). Adaptation of motion sensitive cells to constant angular velocity would make them "acceleration detectors". In any event, we do not have an alternative to assuming that pretorque and angular acceleration are compared.

3.2.2.6. What is the mode of comparison? We have proposed that pretorque and angular acceleration are cross-correlated (Wolf and Heisenberg, 1990). Model calculations show that this type of computation yields a significant mean signal for closed-loop-ness within 50 ms using the *Drosophila* torque modulations as motor output and a correlation type movement detector array as the corresponding input transducer (data not shown). We have not found any other satisfying computational model. Subtraction, as originally proposed for a general "Principle of Reafference" (von Holst and Mittelstaedt, 1950), does not work in this system.

Recently, Kirschfeld (1989) suggested that the master-replay experiment might be explained by an optomotor gain control mechanism. He argued that an efference copy of the motor output might exert a frequency-dependent influence on the optomotor gain. Since the frequency composition of yaw torque is necessarily different in open- and closed-loop this might affect the response component in the output. The difficulty with this explanation is that the Fourier-spectra of yaw torque in open- and closed-loop are very similar and differ primarily in the low frequency range. Such a gain control mechanism would, therefore, depend upon the low frequency components of the torque-modulations and changes between the open-loop and the closed-loop gain would be correspondingly slow. Also, a dependency of the optomotor gain upon the level of neural torque (frequency $f = 0$) has not been observed.

3.2.3. *Why should output and input be compared?*

3.2.3.1. Re- and exafferent stimuli must be distinguished. Most sensory stimuli of animals and man are self-generated. Obviously, these have entirely different possible consequences than externally generated ones. The two classes should be thoroughly distinguished. In the present context the master-replay experiments demonstrate this ability. Formally speaking, the distinction consists of a larger internal gain of the optomotor response under closed-loop conditions than in open-loop. One would like to speculate that without visual feedback the fly might shift its attention to behavioral options other than yaw torque and would therefore respond only part of the time.

3.2.3.2. Switching between yaw torque and thrust control. Observations supporting this hypothesis come from a recording device which simultaneously monitors yaw torque and foreward thrust. We discovered that as with yaw torque also with thrust the fly is able to stabilize a single horizontally moving landmark in the lateral visual field (flight simulator for thrust). Similar observations had independently been made by K.G. Götz, Tübingen (personal communication). With the apparatus measuring both yaw torque and thrust we can now switch back and forth between the two control modes (Fig. 9). Interestingly, the fly immediately locks in with the effective behavior indicating that it is constantly trying to find the appropriate options for control.

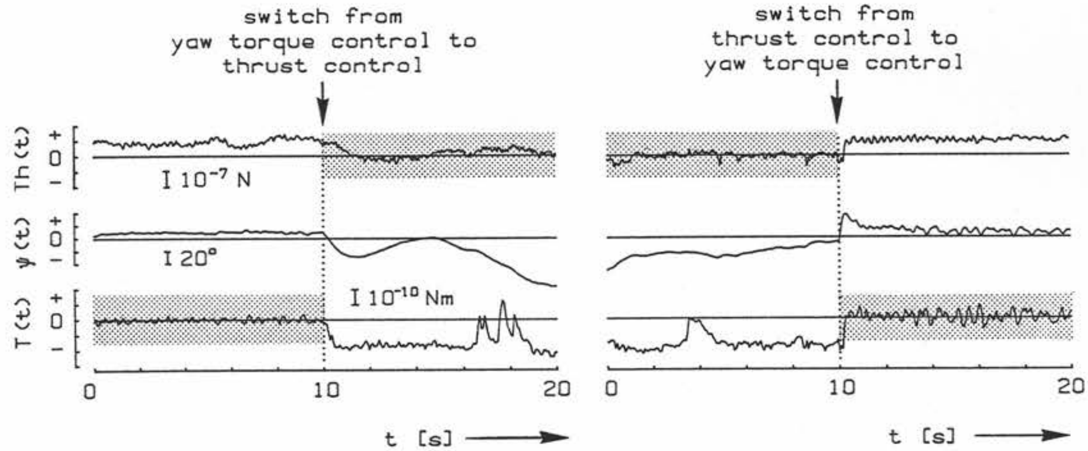


Fig. 9. Yaw torque and forward thrust are recorded simultaneously and can be alternatively used to drive the panorama, a single vertical dark stripe. On the left side an episode is shown where feedback was switched from yaw torque control to thrust control. The flight episode on the right shows the inverse switch. While the flight simulator operates on thrust control the fly keeps its thrust $\mathrm{Th}(t)$ in a narrow range which avoids fast rotation of the stripe (stripe position $\psi(t)$). At the same time yaw torque $T(t)$ drifts randomly as is typical of an open-loop situation. After switching to yaw torque control the fly in a fraction of a second shifts its baseline of torque to the corresponding level of "zero" net angular rotation of the panorama and thrust immediately starts drifting. When the switch is from yaw torque to thrust control it takes the fly more than a second to adjust its thrust to the level of zero net rotation. Shading marks periods of closed loop. Coupling coefficient for thrust control $k_{\mathrm{Th}} = 5.86$ deg/s/10^{-7}N; for torque control $k = 11$ deg/s/10^{-10}Nm.

3.2.3.3. The fly measures steering efficiency. This "trying-out" is a basic property of orientation behavior. It is the ultimate reason why the fly actively stimulates itself by angular motion. A further benefit of this self-stimulation is found in an experiment with yaw torque alone in which both the efficacy of the turning commands and the zero setting of yaw torque are varied. This can be achieved in the flight simulator if at different coupling coefficients a rotatory bias is injected into the loop. The result shows that irrespective of the coupling coefficient the fly is able to compensate for 80% of the disturbance within 250 ms (Fig. 10; Wolf and Heisenberg, 1990). Thus the comparison of output and input provides for the system a measure of the efficacy of the steering command rendering it much more flexible than it would be in a simple feedback loop.

3.2.4. A model for flying straight

In the old feedback control model the fly features as a "black" box surrounded by the world (Figs. 7a and 11a). In the new flight steering model the world is a white box inside the fly (Fig. 11b). It should be kept in mind that in such models depicting the various computations and their interactions the layout of the components is irrelevant as long as their connectivity is correct. It therefore does not matter whether one draws the world inside and the fly around it or vice versa. We prefer the new presentation since it reminds us of the fact that the fly is not dealing with an *a priori* world but with its own needs and concerns, in the present context the effectiveness of its steering commands and the balance of the flight motors. In addition this scheme makes it easy to accommodate, in future editions, further complexity in the processing of sensory information and in the structure of motor programs yet to be discovered.

The new model contains the three features discussed so far: (1) the integrator, (2) the cross-correlation between angular acceleration and pretorque and finally (3) the calculation of the

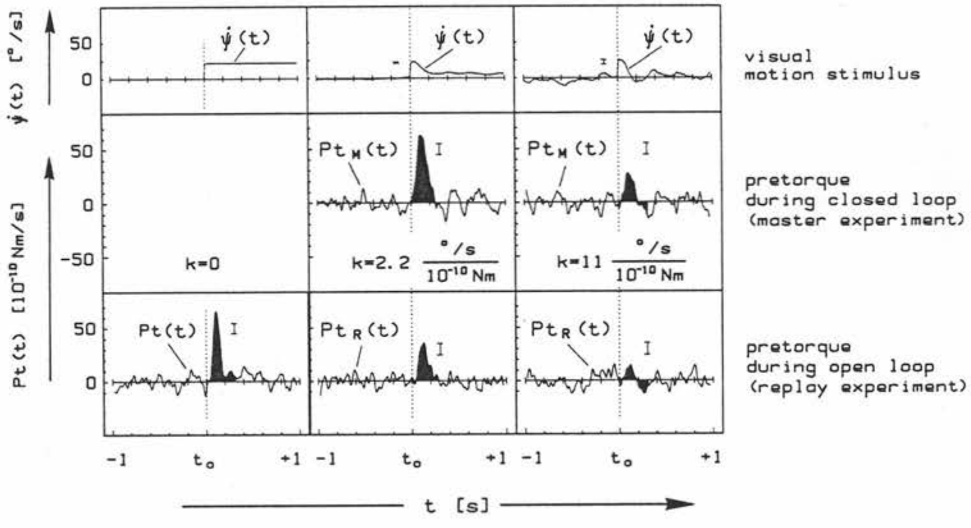


Fig. 10. Pretorque (Pt) responses to the same onset of angular velocity at different coupling coefficients K (i.e., different steering efficiency) and in open-loop (left). The fly partially compensates for the low coupling coefficient by an increased pretorque response (Pt_M; middle row, middle column). Note reduced responses in the replay experiments (Pt_R; bottom row). In open-loop the pretorque response is large but particularly brief. Striped drum; pattern wavelength $\lambda = 18$ deg. Most of the pretorque response is confined to the first 300 ms (black areas). Traces are averages of 250 records from 63 flies. Vertical bars are SEMs. Detailed description of this experiment in Wolf and Heisenberg, 1990.

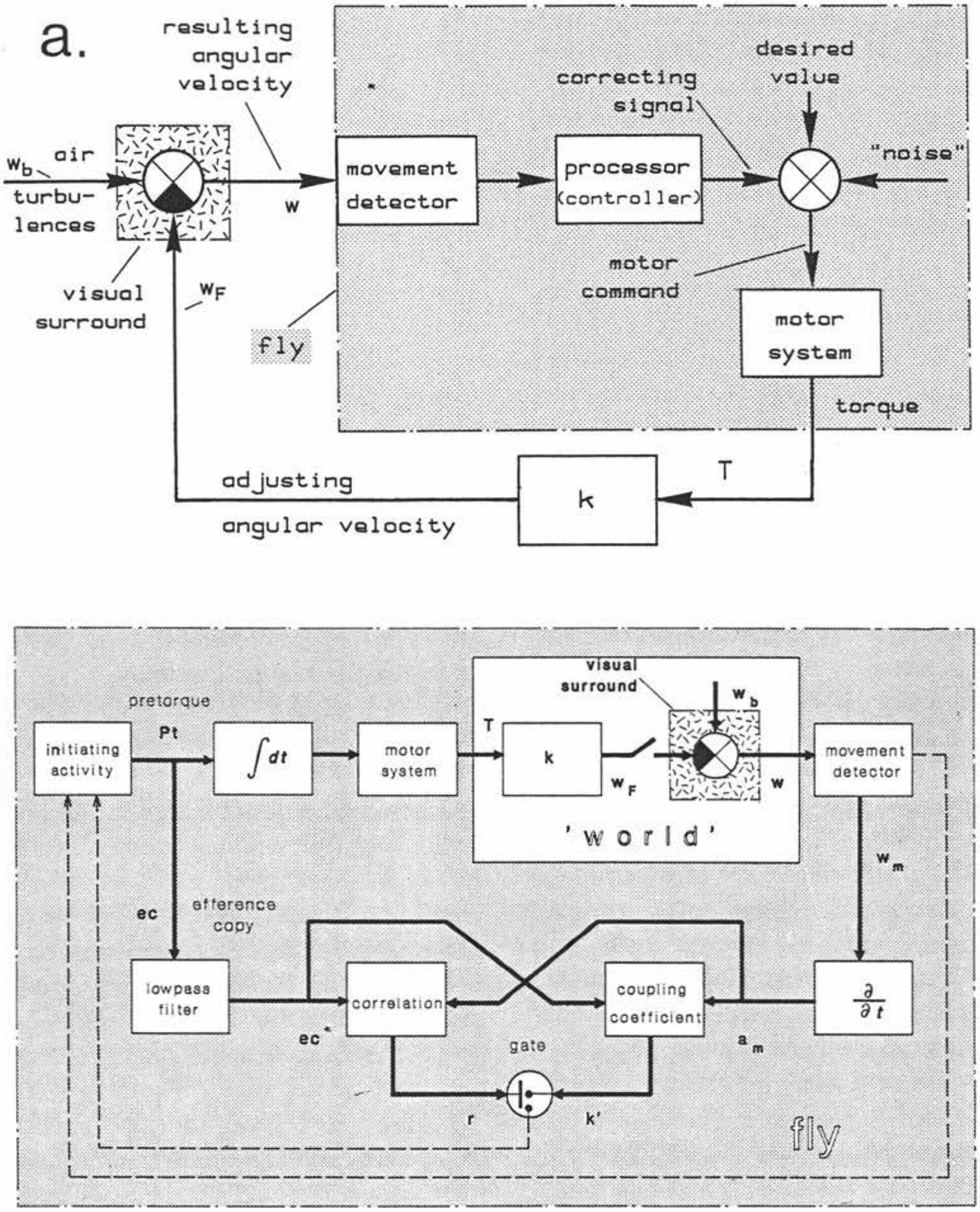


Fig. 11. Old (**a**) and new (**b**) model of optomotor yaw torque control. In both models visual motion as caused for instance by self-rotation is recorded by the movement detector array. In (**a**) its output signal is converted by the processor into a motor output (yaw torque). In (**b**) the system endogenously generates pretorque pulses which after integration are observed as yaw torque. Open-loop stimulation of the movement detectors with angular motion of constant velocity may increase the probability of the source of initiating activity to produce pretorque of the same polarity (outer dashed line with arrowhead). In closed-loop the endogenous yaw torque leads to additional angular motion of the panorama. The output signal of the movement detectors is differentiated and as angular acceleration signal (a_m) is compared in two ways with a (low-pass- filtered) efference copy of the pretorque pulses (ec*). One mode of comparison is a crosscorrelation (*r*) which decides whether the system is in closed- or open-loop. The other is a calculation of the coupling coefficient (*k*') which has an effect on yaw torque only if the system is in closed-loop. The effects of these calculations on initiating pretorque activity (inner dashed line with arrowhead) are only partially known (see also text and Fig. 12).

coupling coefficient. These properties immediately follow from our experimental results. There is one additional feature in the model, however, which we have deliberately chosen as the more reasonable of two options. In the model shown here the result of the comparison of output and input influences the size, polarity, frequency and/or duration of the pretorque pulses (initiating activity). Alternatively, the output might modulate the gain of a conventional feedback loop circuit modulating pretorque independently from the initiating activity. The drawback of the latter scheme is that it would spoil the comparison of output and input even without external disturbances of the flight track. If open- and closed-loop stimulation would simply lead to different levels of optomotor gain, master and replay torque traces in the experiment of Fig. 8 should differ in response amplitude but not in phase. In contrast, the corresponding average traces in this experiment show a pronounced phase shift (data not shown; Heisenberg and Wolf, 1988). Therefore we propose a direct influence of the above computations upon the initiating activity although this leaves open the question of how the activity is affected. The open-loop response to a steady-state motion stimulus, hence, has to be considered the movement detector's directional influence upon the initiating activity.

3.2.5. Reorganizing the sensory-motor link

The first indication of some sort of "trying-out" in optomotor behavior came from a flight simulator experiment with two concentric platforms as described in the experiment of Fig. 5. We have mentioned above that with a vertical dark stripe in an evenly textured panorama the fly has the tendency to orient towards the stripe. In the set-up of Fig. 5 the stripe and the texture are independently driven by two motors and two control units but as long as the fly is in undisturbed closed-loop with both patterns they move in perfect synchrony. If one now inverts the sign of the feedback for the stripe one can observe a fascinating process: As in the experiment of Fig. 5 the fly still maintains a straight course with respect to the textured drum. It also tries to turn towards the stripe by body saccades but now these have the opposite of their normal effect: A body saccade for a clockwise turn now causes the stripe also to move clockwise instead of counterclockwise. Thus, the stripe "jumps" to the rear and is moved from one side to the other by the fly's attempts to turn towards it. However, in the course of the next 45 min most flies learn to adjust the polarity of their torque spikes with respect to the direction of motion of the stripe. The rotatory bias experiment of Fig. 5 can now be repeated with inverted coupling for the stripe and the fly still keeps the stripe in a frontal position against the rotatory bias. This learning process requires that the fly "tries out" how to generate the desired visual effect (Heisenberg et al., 1984; Heisenberg and Wolf, 1984). The experiment unambiguously shows that optomotor behavior is not a deterministic stimulus-response system.

3.2.6. Steering without directional movement response

The dominant role of "trying-out" in visual orientation behavior was revealed in a study of the *Drosophila* double mutant *reduced optic lobes, small optic lobes (rol sol)*. When hooked to the torque meter flies of this strain show no directional response to motion of a grating or a single stripe. Nevertheless, in closed-loop with a single stripe, they are able to fly straight and to compensate for a rotatory bias. So far the only model accounting for this performance is shown in Fig. 12. It requires that the flies measure nonvectorial angular acceleration and on the output side generate pulses of pretorque which are either positive or negative. The rule for flying straight states that they should maintain the polarity of their pretorque pulses as long as angular acceleration is negative. When it gets positive they should switch to the opposite polarity.

3.2.7. "Trying-out" in leg positioning

A basically similar type of "trying-out" has been

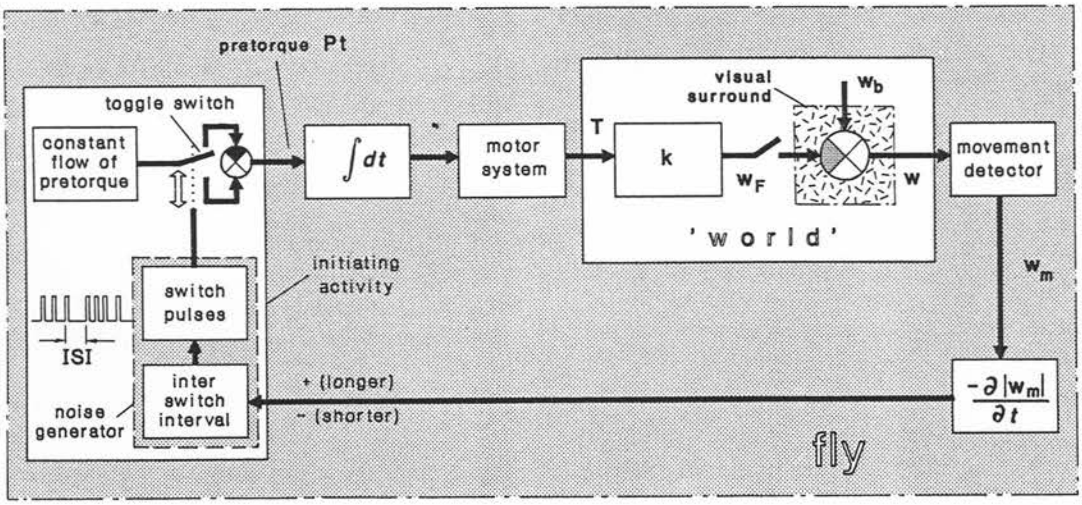


Fig. 12. Model of optomotor yaw torque control in the double mutant *rol sol.* These flies respond only to the amount but not the direction of motion $(|w|)$. The nondirectional motion signal influences the initiating pretorque activity. If the amount of motion increases (decreases) the probability for the polarity of pretorque to change, also increases (decreases). (Redrawn from Heisenberg and Wolf, 1988.)

investigated by H. Mariath (1985) in an entirely different behavioral context. A tethered fly was positioned over a small platform which it could move right and left with its feet. In the actual experiment a heat source was switched on whenever the fly moved the platform to the left (right). The fly immediately shifted the platform to the right (left), and kept it there with recurrent short excursions into the heating zone, to test, whether this position still had the dangerous effect.

What these examples have in common is that the fly establishes a contingency between a certain behavioral output (pretorque, thrust, positioning of legs) and a particular sensory input (angular acceleration, heat). We believe that in all these cases cross-correlation between an efference copy of the motor output and the sensory input is an adequate formal description for the underlying neural mechanisms. Establishing contingencies between different sensory inputs or between a motor output and a sensory input presumably is the most basic task of a brain. However, except in the special context of associative conditioning (e.g., Kandel et al., 1987), no example of it has been worked out so far in detail at the neuronal (or synaptic) level.

4. Conclusions

The sensory-motor link in *Drosophila* optomotor behavior is not a causal stimulus-response relation. The famous hiatus ultimately separating our actions from all the deterministic influences guiding them, this fundamental pause in the stream of behavioral causations (e.g., Bergson, 1896), is already found in the visual orientation behavior of a little fly.

Of all the well-studied behaviors of invertebrates, the optomotor response of flies had been considered the most reflex-like. It now turns out that flying straight, in contrast, is an active steering process. The fly generates a continuous flow of alternating pretorque pulses which cause a slightly undulating flight trajectory. The comparison of motor output and motion input gives the fly the continuous information that its motor commands are effective (closed-loop). Furthermore, the fly can instantaneously calculate the appropriate action compensating for a sudden turbulence. What at a macroscopic level is called a response, at the micro-level looks like a modification of the probabilities for one or the other polarity of pretorque pulses, their frequency and possibly size distribution. The above-mentioned hiatus has its biological realization in the basically probabilistic nature of behavioral actions (see Heisenberg, 1983; Heisenberg and Wolf, 1984). The sensory-motor link in optomotor behavior is an example of this general organization.

Flight orientation determines the direction of propagation and, hence, the places an organism will reach. The underlying mechanism refers to the ambiguity of an open future. Head or eye control are different matters in that these organs are attached to the body. They are forced to go where the body goes and, therefore, always have the body as one frame of reference. Even in walking visual orientation may be organized differently since the organism is attached to the ground and may obtain reliable information about self-motion by proprioception. It will be a fascinating task to compare at the micro-level visual eye and head control to all-animal control during walking and flight.

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