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On the Fine Structure of Yaw Torque in Visual Flight Orientation of *Drosophila melanogaster*

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Summary. Yaw torque fluctuations of *Drosophila* in stationary flight at the torque meter in many cases represent meaningful behavior patterns (e.g., Figs. 4, 9a). In the closed loop situation for rotations around the fly's vertical axis *Drosophila* stabilizes any panorama by adjusting its "optomotor balance" (e.g., Figs. 2, 3, 8, 11) – a presumably integrative directionally movement sensitive flight control mechanism.

In this state of "harmony" with the environment *Drosophila* often performs active turns by means of body-saccades (Fig. 2). In this study these are recorded as "torque spikes" – an elementary motor pattern of typical size and time course (Fig. 3). Their polarity and frequency are dependent upon visual stimulation (Figs. 4, 5, 6).

During a torque spike the fly does not respond to the visual stimulation caused by the relative displacement of the environment (Fig. 13); an artificial displacement in the opposite direction, however, causes a fast vigorous turning response. This is attributed to a directionally selective *efference copy* of the torque spike motor pattern which suppresses the reafferent visual input (Fig. 13a–f). The efference copy also relieves the visual system from certain inhibitory interactions which, in larger flies, have been shown to provide "figure-ground" discrimination (Fig. 13g–l). In addition the asymmetry in the fly's response to progressive and to regressive movement of small patterns is eliminated by the efference copy. Such information processing steps may be of minor importance during body-saccades.

Optomotor balance in *Drosophila* is the basis of oriented flight. In closed loop experiments with one vertical black stripe the fly spends only part of its time keeping the stripe in its direction of flight (fixation). More often it stabilizes the stripe in other positions (non-fixation) (Fig. 8). Torque responses to the position of objects in *Drosophila* appear to be centrally controlled. Various situations in which the fly favors fixation (anti-fixation) or non-fixation are described.

Introduction

Visual guidance of insect flight is currently being studied from two points of view: as a combination of "passive" visual responses (e.g., Reichardt and Poggio, 1976; Götz, 1975a) and, complementary to this approach, as a series of "active" behavioral patterns (e.g., Land, 1977). These are not just two terminologies of the same subject; they refer to processes at different levels of complexity (see also Poggio, 1977).

In the last 20 years studies of "passive" visual flight control have reached a high degree of sophistication experimentally and theoretically. They are mostly performed on tethered flies under controlled visual stimulation and have provided satisfactory models of directional movement detection (Götz, 1968; Poggio and Reichardt, 1973) and basic orientation behavior (Reichardt and Poggio, 1976). These models quantitatively account for important aspects of visual behavior also in free flight. Studies of flight *activities* on the other hand have relied so far mainly on the evaluation of high speed motion pictures of freely flying flies. With the rich behavioral repertoire in particular of hoverflies these studies have much to offer. They reveal an abundance of flight control systems amongst which a fly seems to choose freely (Collett and Land, 1975a, b).

Our paper is an effort to combine the two approaches: We describe several "active" flight patterns of *Drosophila melanogaster* flying at a torque meter (Götz, 1964) under controlled experimental conditions (Reichardt, 1973). This allows us to study the visual stimuli which influence these behavior patterns

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and it provides the opportunity to interfere with the visual feedback during flight maneuvers.

First attempts to record behavior patterns of flies in stationary flight came from Land (1973) who took high speed motion pictures of *Calliphora erythrocephala* suspended on a pivot in a glass tube allowing the fly to rotate around its vertical axis. Under these partially restrained conditions *Calliphora* performed so called "head-saccades", sporadic fast turning movements of the head relative to the body. Subsequently Geiger and Poggio (1977) showed that these "saccades" were apparently due to the large inertia of the pivot which had to be turned by the fly. Thus, while a neural program for "head-saccades" still may exist in *Calliphora* its use in free flight remains to be demonstrated.

In *Drosophila* no gross head movements relative to the body are seen in flight. However, similarly to the hoverfly *Syritta pipiens* (Collett and Land, 1975a), *Drosophila* performs "body-saccades". The stationary flight situation in our experiments allows a closer examination of this element in the various behavior patterns which we observe. Three topics have attracted our particular attention: a) the relation of body saccades to visual stimulation; b) the control of reafferent stimulation and c) visual flight orientation.

a) The first part describes the fine structure of flight torque at the torque meter and alludes to the differences between "actions" and "responses".

b) Reafference control is a special aspect of "actions". The problem of how an organism distinguishes between sensory stimuli from the environment which are due to its own actions and those which have other causes has been discussed for over a century. One of the most debated examples is the perceptual stability of the world during our saccadic eye movements. In their historic paper von Holst and Mittelstaedt (1950) introduced the formulation of the reafference principle by describing the behavior of the fly *Eristalis* walking inside a cylinder of vertical black and white stripes. They had observed that the fly very closely followed the rotational movements of the cylinder; but if the cylinder was at rest the fly had no difficulty making turning movements itself. It took 25 years (Götz, 1975a) to fully appreciate the complexity of the visual stimuli the freely walking fly encounters even in "simple" environments. Unaware of these complications von Holst and Mittelstaedt intuitively interpreted the seeming difference in the degree of coupling between the fly and the visual environment as an indication for the control of reafferent stimulation. The alternative of total blindness during the fly's turn was eliminated since twisting the fly's head by 180° caused perpetual rotations of the fly as was to be expected for a closed loop in which the sign of the feedback was inverted. Originally von Holst and Mittelstaedt (loc. cit.) proposed a model for the control of reafference which required either a copy of the motor command (efference copy[1]) or proprioception from the effector organs to be compared with the total afference. A year later Mittelstaedt (1951) pointed out that neither of the two was necessary. The observed behavior of *Eristalis* could be understood as an endogenous turning activity superimposed on the optomotor control system. Once the theoretical problem was solved the question of how *Eristalis* controls reafferent stimulation was abandoned since at that time optomotor "responses" of stationary animals could not be quantitatively measured and the necessity to define "actions" or "commands" was not yet obvious.

The body saccades of *Drosophila* seem to reflect very constant endogenous motor patterns. Thus our experimental situation provides the opportunity to reinvestigate the possibility of reafference control phenomena in flies.

c) The last part of the paper is devoted to pattern induced flight orientation. Mechanisms similar to the fixation and tracking system in *Musca domestica* which is described by a theory of Reichardt and Poggio (1976) seem to be used by chasing males of *Fannia cannicularis* (Land and Collett, 1974), in the "smooth angular tracking" of *Syritta pipiens* (Collett and Land, 1975a) and to some extent also by *Drosophila* (Heisenberg, 1972). In this theory torque is decomposed into a visually induced component and spontaneous torque "noise". In the torque recordings obtained from *Drosophila* much of the fluctuations appears to be non-random. In particular, if torque spikes, as we will argue, are "actions" rather than "responses" their part in visual flight control may elucidate the nature of orientation behavior in *Drosophila*. We hope to show, that in *Drosophila* the theory of Reichardt and Poggio (loc. cit.) may fit very well into a more general concept of visually controlled orientation (see for instance Poggio, 1977) in which the fixation paradigm reflects only special situations of free flight behavior.

Material and Methods

Flies. Wildtypes *Canton S* and *Berlin* and the non-fixation mutant S100 derived from wildtype *Berlin* are used. 4–10 days old females are narcotized with ether or nitrogen and are prepared as described by Götz (1964).

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[1] A neural correlate of the "efference copy", the "corrolary discharge" was independently postulated by Sperry (1950) on the basis of eye inversion experiments in fish

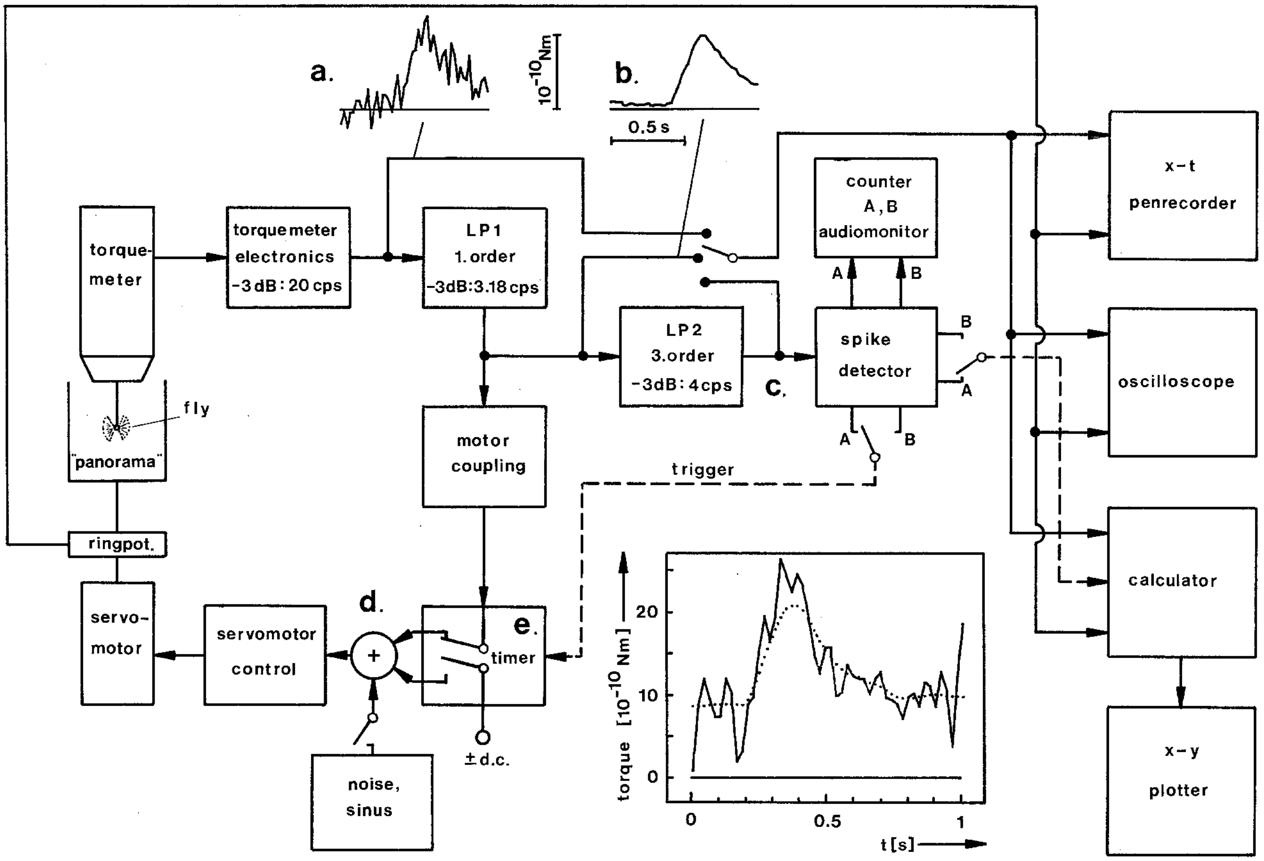

Fig. 1. Simplified diagram of the experimental set up used in all experiments except that of Fig. 2. The signal from the torque meter is passed through a low pass filter (LP1) and an amplifier which adjusts the torque signal to the mechanical properties of the flying fly (motor coupling). The voltage signal is used to drive a servomotor which turns the panorama surrounding the fly. The angular position ψ of the panorama is monitored by a ring potentiometer. The visual feedback loop can be opened at "e" and can be "disturbed" by the addition of d.c. or a.c. voltage or voltage noise at "d". The right side of the diagram shows the data output. For pen recorder tracings of torque the loop is normally tapped at "b" while for computer averages the torque signal in most cases is recorded at "c". The traces at "a" and "b" show an average of 90 "torque spikes" (see Fig. 3) before and after LP1. In the closed loop this filter is equivalent to an unnaturally large moment of inertia of the fly causing a delay of 48 ms at 1 cps. Inset shows computer average of 8 torque spikes shown also in Fig. 3a, b (dotted curve; recorded at "c") and calculated trace of this average before the two low pass filters at "a". (Only Fourier-components up to 17 cps were included.) Here torque spikes are masked by "torque meter noise"

Apparatus. The torque compensator (Götz, 1964) as well as the motor control unit were generously provided for these studies by the Max-Planck-Institut für biologische Kybernetik, Tübingen. The experimental set-up (Fig. 1) is similar to that of Reichardt (1973) except that a 20 V. d.c. servomotor (Nr. 35.57/220-3307/505-60, Faulhaber, Schönaich, Germany) without gear is used to drive the panorama. Care is taken to avoid any vibrations reaching the torque compensator; since the compensator has a strong resonance at 11 cps we empirically chose a low pass filter (LP1, 1. order) with a cut-off frequency (−3 dB) at 3.18 cps to suppress high frequencies in the signal from the torque compensator. This introduces a phase shift of 48 ms at 1 cps which corresponds to an unreasonably large inertia of the fly. The use of this filter can only be justified by the closed loop results and may represent the minimum of all possible disturbances for the fly in this apparatus. The gain (which corresponds to the aerodynamic friction of the fly) is adjusted to 9.9×10^{-10} Nms (see Results (2)).[2]

If necessary d.c. potentials or voltage noise (upper cut-off frequency 1.5 cps (−3 dB)) from a Hewlett-Packard noise-generator (Model: 3722A), which was also kindly provided by the Max-Planck-Institut für biologische Kybernetik, Tübingen, is added (at "d" in Fig. 1) to the torque signal before the motor control unit.

For averaging torque spikes and for controlling the movement of the panorama during the torque spike a spike detector was designed which consists of an active band pass filter adjusted to the main frequency component of the spike (resonance frequency: 2.15 cps; −3 dB: 1.26/3.75 cps) and a gate which makes the "pointedness" of the spike a criterion for its detection.

Torque spikes and phasic responses in Figs. 1, 3b and 13 are averaged using the spike detector and a pre-trigger analysis program with a HP 9825A calculator. For this analysis the torque signal is smoothed further by an active low pass filter (LP2, 3. order, −3 dB at 4 cps).

The torque traces of Figs. 3c and 4 to 12 are from a Servogor 2 S pen recorder which functions as an additional low pass filter.

For filming *Drosophila* body-saccades (Fig. 2) flies carry a mu-metal pin (2 mm long; ∅ 0.3 mm) suspended on a polystyrene fibre (35 cm long; ∅ 10 µm). A pointed magnet underneath the fly

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[2] 1 mdyn · cm $\triangleq 10^{-10}$ Nm

keeps it in place. The torsion spring tension of the polystyrene fibre increases by 1.76×10^{-11} Nm per revolution of the fly. The pin increases the fly's moment of inertia by about 5%. (This arrangement was originally proposed by E. Buchner, Max-Planck-Institut für biologische Kybernetik, Tübingen). Flies were filmed at 18 frames/s.

Results

1. Free Flight Behavior

Drosophila in the vicinity of its natural habitat often assumes a posture similar to that of a bee approaching a flower (Wehner, 1972): the long axis of the body is tilted rear down at about 60° to the horizontal and the wings beat in a nearly horizontal plane[3]. In this position the forward component of the force of flight is close to zero; the fly can move in all directions and (at least if there is a slight, constant breeze) it can even stand still over ground[4]. In this respect *Drosophila* resembles a hoverfly although the latter has a quite different posture while hovering and presumably excels the former in maneuverability. It is this flight mode in which *Drosophila* is readily observable; in other modes it easily escapes our observation. Hovering flight in *Drosophila* has one other property in common with that of hoverflies: turning maneuvers are often executed not smoothly but in series of abrupt, small turns separated by periods of straight flight. Such flight patterns have been called body-saccades (Collett and Land, 1975a; Land and Collett, 1974) in analogy to fast eye movements in mammals. Figure 2 shows such body-saccades of a *Drosophila* fly which is free to rotate around its vertical axis (see "Methods", last paragraph) but otherwise is kept stationary. (Here the fly is fixed in horizontal position. From our preliminary observations on free hovering flight it seems that under natural conditions saccades are somewhat smaller).

2. The Torque Spike

In all following experiments *Drosophila* is not able to turn. It is glued in horizontal position to the torque meter and has its head fixed to the thorax. Thus most sensory feedback of free flight is eliminated.

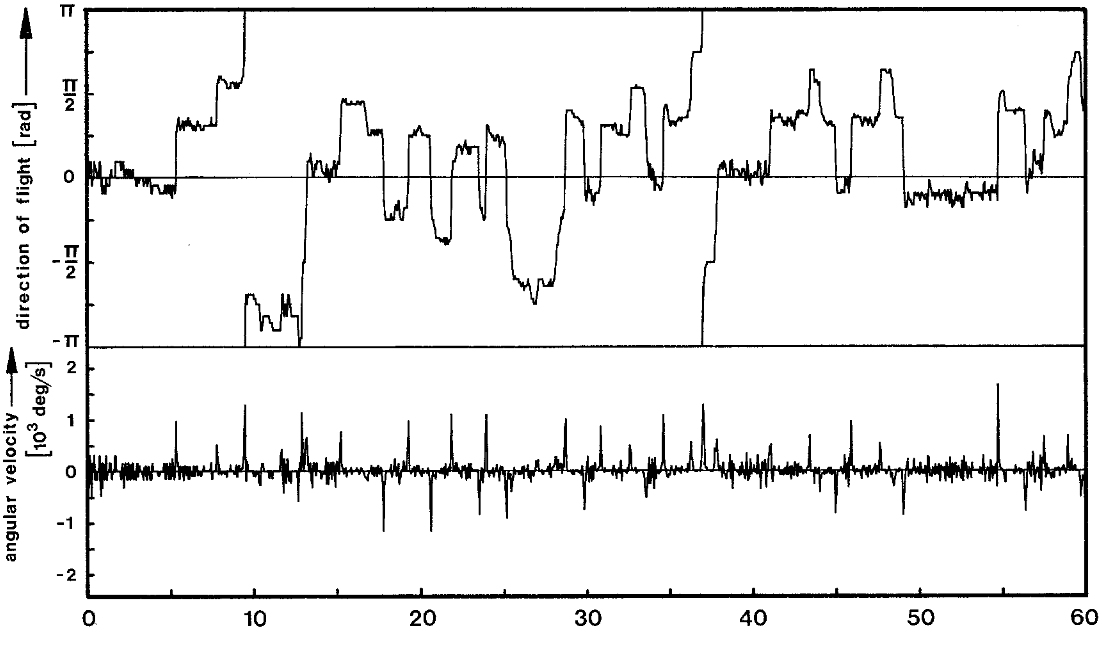

Fig. 2. a) Orientation of flying *Drosophila* (non-fixation mutant *S100*) free to rotate around its vertical axis in the center of a brightly illuminated stationary panorama with a single vertical black stripe (width 10°). For experimental details see "Methods". Left hand scale: direction of flight with position of stripe at 0 rad. b) Lower trace shows approximate angular velocity ω (computed from directional change between successive measurements divided by the sampling time (56 ms)). As shown by Reichardt (1973) flight torque is roughly proportional to angular velocity

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[3] Götz (1968) measured the direction of the force of flight in *Drosophila* at the torque meter to be +24° to the fly's long axis. The force vector seems to be invariant to various visual stimuli

[4] While this manuscript was revised a report on free-flight postures of *Drosophila* was published (David, 1978)

Only for the fly's rotations around its vertical axis in some experiments visual feedback is artificially provided (closed loop). Surprisingly under these conditions *Drosophila* often performs torque fluctuations which correspond fairly well to the type of turning maneuvers described above. The basic element in this behavior is the *torque spike* (Fig. 3a, b), a small package of torque delivered in about 0.5 s with a typical time course, a short rising time of about 0.15 s and a somewhat slower decay time. It is preceded by a beat of the antenna on the side opposite to the direction of the intended turn followed by "steering" movements of the abdomen and the hind legs towards the side of the turn. These latter transient changes of posture seem to occur in synchrony with the torque spike.

It is suggestive to equate torque spikes with body-saccades; their abundance during non-fixation (see below (6b)) hardly allows a different interpretation. However, the time course of this motor pattern in the two experiments is quite distinct. At the torque meter it takes 3 to 4 times as long as it does when the fly is free to turn. This is not a measuring artefact: The torque meter operates linearly up to about 20 cps and already before the low pass filter in the recording chain torque spikes have about the same duration as shown in Figs. 1 and 3a, b (although the real rising phase will be somewhat steeper than shown). (Recently Dr. J. Blondeau (unpublished) designed a new type of *Drosophila* torque meter which allows to record linearly up to 200 cps. With this instrument the long duration of torque spikes of non-rotating flies has been confirmed.)

We have to conclude that the motor patterns leading to saccades differ significantly in the two experimental situations. This is supported by the observation that at the polystyrene fibre the fly does not noticably twist the abdomen and the hind legs during or after the saccade as it does at the torque meter. Since the shape of the torque spikes at the torque meter is largely independent of visual feedback (see below (7c)) we assume that during real turns proprioceptive feedback from angular acceleration or reafferent stimuli from air currents abruptly terminate the burst of torque which, on the other hand, can fully develop when the fly is kept stationary. The shape of torque spikes as shown in this paper is thus an artefact of tethered flight; it represents a motor pattern devoid of most of its sensory control.

The size of the torque spikes is variable; however, torque spikes of one animal have a typical size for each polarity (turns to the right or left). Averaging many spikes from many flies, one spike causes roughly a 30° turn of the panorama under our "standard" closed loop conditions. Comparing this figure with the saccades shown in Fig. 2 one worries whether the gain in these "standard" closed loop experiments is too small. Doubling the gain leads to instability in the system – most likely as a consequence of the low pass filter in the visual feedback loop (see Methods). However, at our coupling conditions the flies themselves seem to adjust their gain between stimulus and torque response (see below (6a)). Also, the size of a saccade in response to a torque spike depends upon body posture and air flow. Thus, the low gain factor in our artificial closed-loop situation

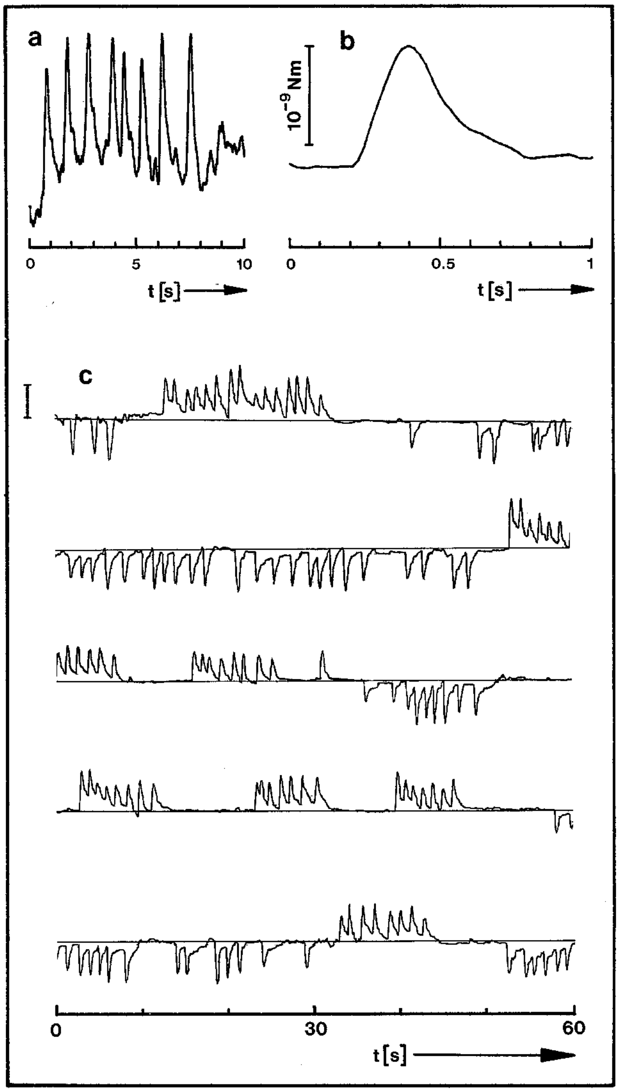

Fig. 3a–c. An irregular sequence of 8 torque spikes (**a**) from an open-loop experiment. The same torque spikes are detected by the spike detector and superimposed at the trigger point to show their typical shape (**b**). **c** A 5 min period of flight in a closed-loop experiment in a panorama consisting of a single black stripe. Note the regular clusters of spikes of one polarity and the consistent return to the base line which represents optomotor balance (straight flight). (Wildtype *Berlin*)

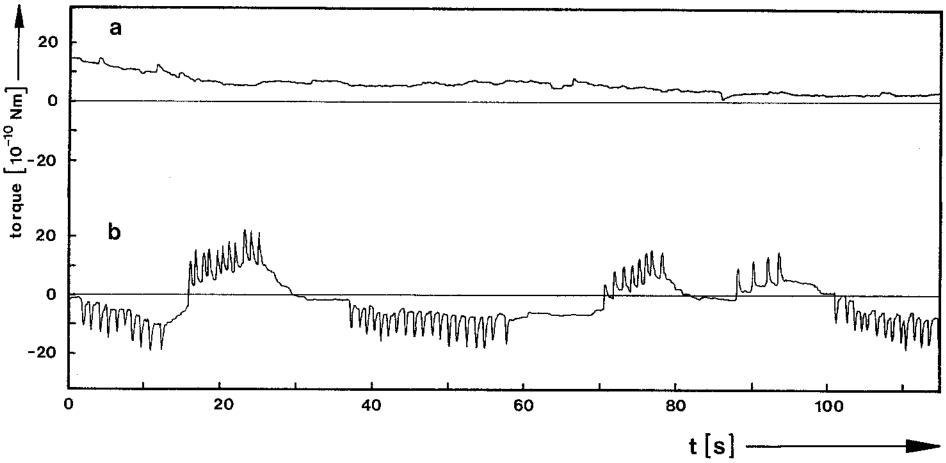

Fig. 4. a Torque fluctuations in darkness; the fly generates no torque spikes; torque fluctuates irregularly, often more than in this recording. **b** Torque fluctuations in the light: the panorama contains a stationary black stripe at $\psi = 0°$. The fly performs turns to the right and to the left, the turns are supported by sequences of torque spikes in the same direction. (Wildtype *Canton S*)

may still "satisfy" the fly. At least it seems not to be critical for most of the experiments described below.

On the torque meter the fly keeps the torque mostly at zero if it has visual feedback and if this feedback is not disturbed. This corresponds to periods of straight flight when the fly is free. Torque spikes are often delivered in fairly regular sequences with 0.5–1 spikes/s interrupted by short periods of zero torque (Fig. 3c).

In the following we first describe the influence of visual stimuli on the frequency and polarity of torque spikes. In the second part we turn to the interaction between torque spikes and other visual functions.

Although torque spikes obviously reflect an endogenous, fixed pattern of neural activity they are under visual control. Certain conditions of illumination favor their occurrence and others suppress it; certain visual stimuli evoke spikes of one or the other polarity etc. But so far we have found no way to trigger a torque spike with a high probability at a predictable moment (see below (5)). All our statements about the relation between visual stimuli and torque spikes are therefore only statistically valid. In this first part we confine our description to phenomena which are immediately obvious and which, therefore, in the context of this study do not require statistical quantification.

3. Flight Patterns in Light and Darkness

Stationarily flying *Drosophila* keep flying in complete darkness. The torque they produce consists of small, apparently random fluctuations. Only rarely are torque spikes observed. If the *stationary* surround (irrespective of the patterns presented) is illuminated with light intensities in the physiological range the flies immediately start to produce large torque fluctuations. One large component of these is very *slow*. The flies vigorously try to turn for many seconds to one side and then for a similar length of time to the other. Flights in the light without visual feedback may be full of quite regular sequences of torque spikes. Their polarity is the same as that of the slow torque fluctuations; they accentuate them (Fig. 4). We interpret this torque pattern under physiological illumination as a searching maneuver for visual cues.

Aside from light and darkness there is a third situation which globally affects the visual system: the prolonged depolarizing afterpotential (PDA) (Cosens and Briscoe, 1972). Intense blue irradiation of the eyes of the eyecolor mutant *white* induces full depolarization of photoreceptors R1-6 which lasts for over an hour after this treatment. We were curious whether *Drosophila* regards this state as darkness or light. Few torque spikes and no pronounced slow fluctuations are produced during the PDA. It seems that in this unnatural situation searching maneuvers are not initiated although the photoreceptors R7/8 are not fully depolarized.

4. Torque Patterns in the Striped Drum

In the classic optomotor experiment in which the fly is surrounded by a vertically striped black and white cylinder which rotates at a constant speed the fly tries to follow the rotation by tonic modulation of

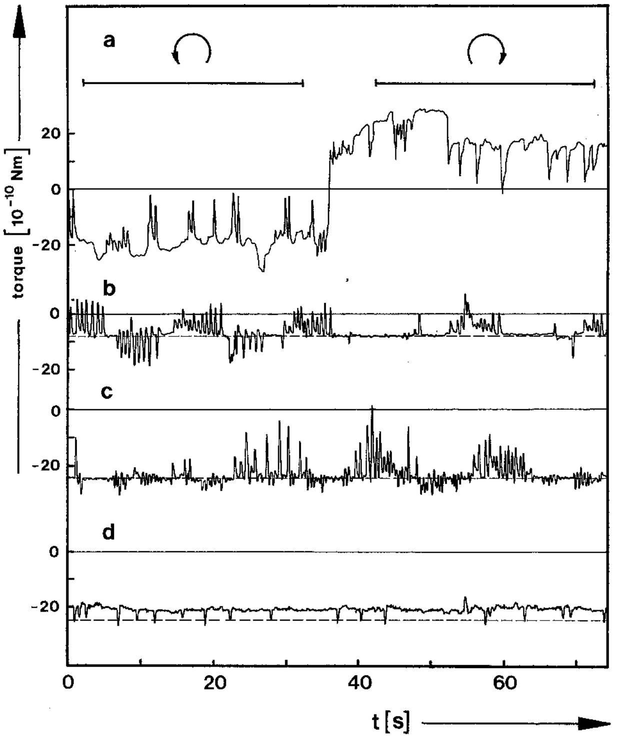

Fig. 5. **a** Classical optomotor experiment with a vertically striped drum of pattern wavelength $\lambda = 18°$; angular speed: 0.36°/s. Between the two periods of pattern motion the drum is stopped for 10 s (wildtype *Berlin*). **b–d** Stationary tracking with striped drum ($\lambda = 18°$) during a closed loop experiment. The drum would rotate with an angular speed of 50°/s (**b**) and 150°/s (**c**) if the fly would not apply an average torque of precisely the same magnitude in the same direction. Apparent slip is quantal and results from torque spikes of opposite polarity. **d** Conditions as in **c** but this time the fly does not quite stabilize the stripe except for brief moments during torque spikes of the same polarity as the tonic torque component. (Wildtype *Canton S*)

its flight torque (Götz, 1964). In this situation the fly frequently produces series of torque spikes superimposed upon the tonic torque modulation but with *opposite* polarity (Fig. 5a).

This result is reminiscent of experiments with *Syritta pipiens* (Collett and Land, 1975a) tracking a rotating striped drum and of optokinetic nystagmus in mammals. In the present case, however, the fly receives no visual feedback. Under partial closed-loop conditions (a d.c. potential is added at "d" of Fig. 1 causing by itself a rotation of 50°/s) *Drosophila* may perform torque spikes of either polarity with roughly the same frequency (Fig. 5b). Under extreme tracking conditions (150–250°/s) a series of torque spikes of opposite polarity to that of the steady torque may be observed (Fig. 5c). But occasionally the fly does not quite stabilize the drum. In this case it produces trains of small spikes with the same polarity as the tonic torque component (Fig. 5d). If one compares the open loop result in the drum with the torque spike patterns during search (Fig. 4), one notices that tonic torque modulations and torque spikes are quite independent of one another at the output side. During a smooth turn to the right a fly is able to perform a saccade to the right and to the left. Of cause, this independence must have natural limitations imposed by the performance of the flight system.

5. *One Stripe, Open Loop Experiments*

In the basic experiment a single vertical stripe is rotated with a constant angular speed around the fly. The fly does not receive any visual feedback from its torque. Poggio and Reichardt (1976) used this stimulation to decompose the torque response into a component sensitive to the position of the stripe but not to the direction of motion ($D(\psi)$) and a component sensitive to the direction of motion of the stripe ($r(\psi)$). The pattern of torque spikes the fly generates in this experiment is quite regular: while the stripe moves around the fly one can observe the smooth $D(\psi)$ function and the normal $r(\psi)$ function without averaging (Fig. 6a). While the stripe moves back-to-front the smooth torque response is superimposed by very pronounced torque spikes of the same polarity as the $D(\psi)$ function. During front-to-back movement of the stripe torque spikes are absent or very small and again of the same polarity as the $D(\psi)$ function. Occasionally (data not shown) the fly resumes the torque spike pattern of back-to-front motion already before the stripe has reached the back side ($\psi = \pm 180°$). It seems to anticipate the next round of rotation. The position and not the direction of motion of the stripe seems to determine the polarity (and size) of the torque spikes in this experiment. That this statement is an over-simplification can be shown by two further experiments.

a) The $D(\psi)$ function can be inverted by inverting the contrast of the pattern. In the closed loop experiment (see below (6)) a bright stripe on a black background is kept in the back of the visual field (antifixation). In this situation also the torque spike pattern is inverted: large torque spikes are elicited only by front-to-back motion of the stripe and again with the polarity of the (inverted) $D(\psi)$ function (Fig. 6b).

b) Oscillating a black stripe on one side of the animal (Pick, 1976) with an amplitude small enough not to produce directional movement stimuli elicits spikes of either polarity (Fig. 6c). Thus a special interaction between motion and position of the stripe is responsible for the particular torque spike pattern which is found in response to the rotating stripe.

One further point may be of interest in this context. Even in the above experiment in which torque

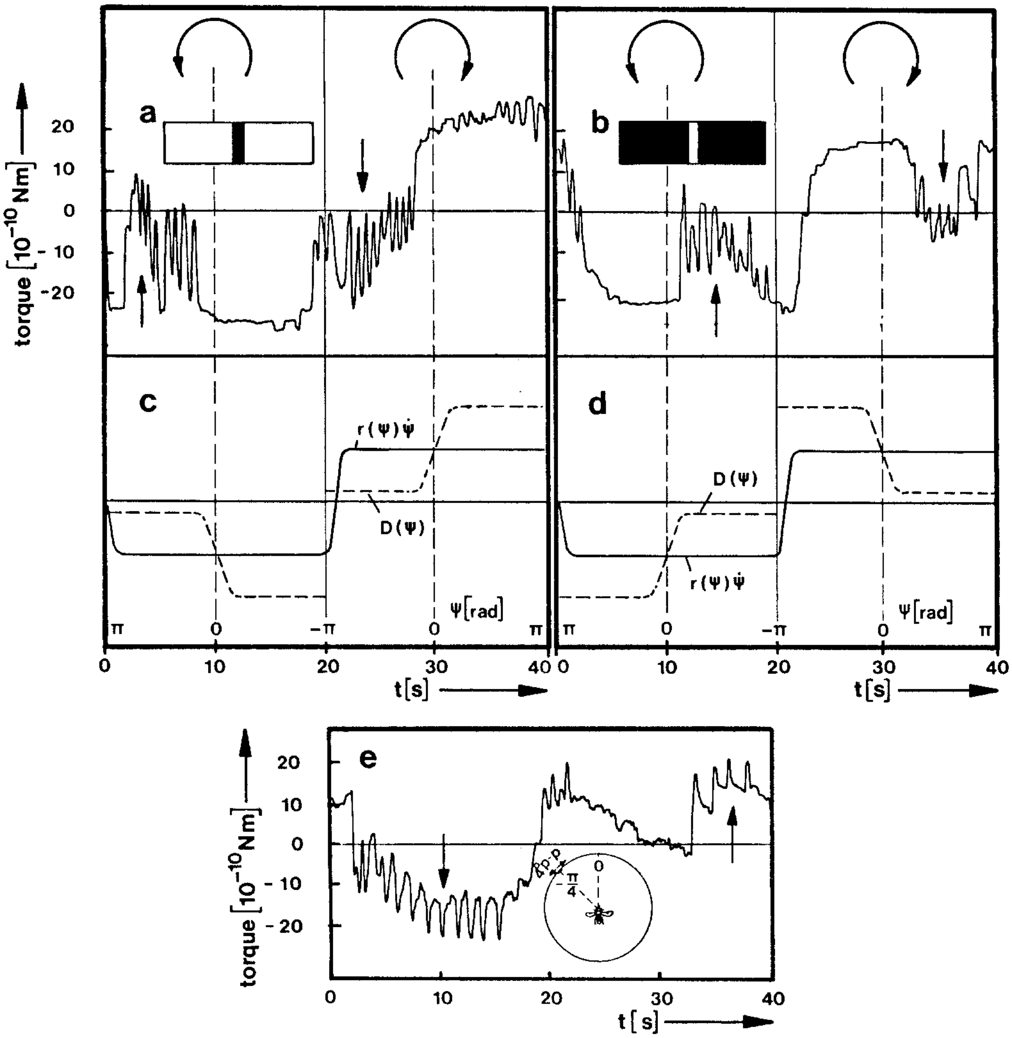

Fig. 6. a A black stripe (width 3°, pattern contrast $\Delta I/\bar{I}>0.9$) is rotated around the fly first clockwise, then counterclockwise. During back-to-front (regressive) movement ($\psi=\pm\pi\rightarrow\psi=0°$) the fly responds with torque spikes of opposite polarity to that of the steady optomotor response. During front-to-back (progressive) movement ($\psi=0°\rightarrow\psi=\pm\pi$) in this experiment the fly does not produce torque spikes. **b** If the pattern contrast is inverted (bright stripe on black background, width 10°) polarity of torque spikes again is opposite to that of the optomotor response but now they occur during front-to-back movement. **c** and **d** Schematic decomposition of torque response into response to motion $r(\psi)\dot{\psi}$ and to position $D(\psi)$ of stripe. An experiment as shown in (**a**) had been reported by Heisenberg et al. (1978), however, data were averages from many recordings of several flies. Averaged traces do not reveal any torque spikes. Note in **a** and **b** large size and somewhat irregular shape of torque spikes. With other flies more typical torque spikes are found. (These traces were selected since they clearly indicate $D(\psi)$ and $r(\psi)\dot{\psi}$ components even without averaging.) Occasionally also torque spikes during front-to-back movement are observed in experiments as the one shown in **a** which have the polarity of the optomotor response. **e** A black stripe (width 3°) is sinusoidally oscillated with 3 cps at a fixed lateral position ($\psi=-\pi/4$; peak-to-peak amplitude for the midline of the stripe is a $=\pi/45$); torque spikes of either polarity (arrows) are observed. For further explanations see text. (Wildtype *Berlin*)

spikes are elicited very consistently by back-to-front motion of the black stripe no such spikes are detected in averages from many identical experiments (as shown in Fig. 6a) with the same fly. Apparently there is no well defined delay between the onset of motion and the generation of the first torque spike. This may be one of the reasons why in previous experiments (Zimmermann, 1973) torque spikes have not been detected.

6. *Pattern Induced Flight Orientation*

a) Fixation. Under the conditions of Reichardt's (1973) basic flight orientation experiment in which the torque is roughly proportional to the negative angular speed of the panorama which consists of one vertical black stripe a variety of torque patterns are found in *Drosophila*. Let us first consider those experiments in which the flies keep the stripe very well

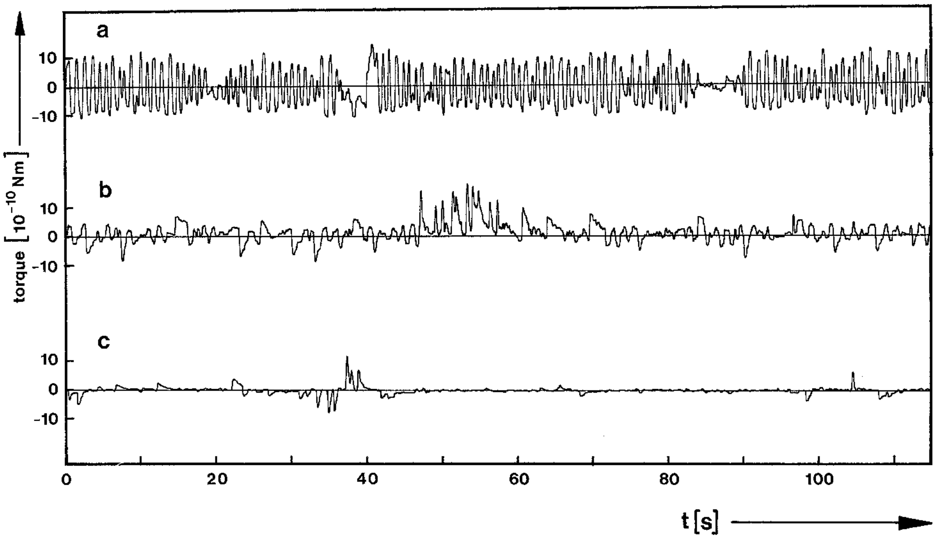

Fig. 7a–c. Three typical flight modes occurring in *fixation* behavior. **a** Sinusoidal torque fluctuations; **b** apparently "random" torque fluctuations; the fly fixates well for 47 s then performs a 360°-loop followed by another min of fixation. **c** Quiet flight mode; except for a short escapade between the 33rd and 40th s the fly keeps its torque very precisely at a value which causes the panorama to remain stationary. Position traces or histograms not shown (see e.g., Heisenberg et al., 1978). (Wildtype *Canton S*)

in the frontal position (fixation). Here three modes of flight can be distinguished. The first is a sinusoidal modulation of the torque causing an oscillation of the stripe with a frequency of 1–2 cps and an average peak to peak amplitude of about 20° (Fig. 7a). Flies can maintain this type of flight for several minutes. The oscillations are much too slow to be caused directly by the low pass filter in the visual feedback loop. But a combination of the filter and the low gain could possibly cause such a behavior in an indirect manner. The second mode corresponds best to the "Gaussian coloured torque noise" observed for *Musca* by Poggio and Reichardt (1973). Occasionally torque spikes of either polarity are observed in this mode of flight (Fig. 7b). The third torque pattern is very quiet without large fluctuations at all, except for occasional torque spikes in either direction (Fig. 7c). (This description is certainly a simplification since each *Drosophila* strain and even each fly has its individual torque pattern in the fixation paradigm. Torque traces of *Canton-S*-flies as compared to those of wildtype *Berlin* are often more "regular" and contain less torque "noise".)

The meaning of these patterns under artificial closed loop conditions is not clear. One has to keep in mind that the aerodynamic properties of the flies are simulated electronically in order to provide the visual feedback of rotation around the fly's vertical axis. These "coupling conditions" are not adjusted individually. Thus possibly large and strong flies might produce the oscillatory behavior since for them the torque might produce too fast a speed of the panorama (over-coupling) while small (and correspondingly weak) flies might show the quiet, straight flight because of undercoupling in the closed loop. We can not exclude this interpretation with certainty. In particular, the oscillatory flight mode may be an instrumental artefact. However, during an experiment a fly may go through different torque patterns which, if the above interpretation is correct, would call at least for the ability of the fly to adjust its gain factor between stimulus and torque response. Whether *Drosophila* uses these torque patterns for different purposes in free flight remains an open question and should be studied with flies which are free to rotate (see Discussion (3), and Pfau, 1973).

b) Non-Fixation. Initially most flies keep the stripe in the frontal position. With some flies this behavior may last for most of the experiment with others, however, this period is quite short (i.e., 0.5 min). Particularly in the quiet mode of flight, (as shown in Fig. 7c) the stripe may suddenly start to be shifted to any position and may be kept there quietly for some time (Fig. 8). We will call this behavior "non-fixation". Non-fixation is generally associated with torque spikes (Figs. 3c and 8) which may occur singly or in clusters. (The same torque pattern is observed with a striped drum ($\lambda = 18°$) or a checkerboard pattern with 9° × 9° squares).

Several years ago one of us (M.H., unpublished) isolated *Drosophila* mutants disturbed in pattern induced orientation behavior. One of them carrying the laboratory name *S 100* (Heisenberg et al., 1978)

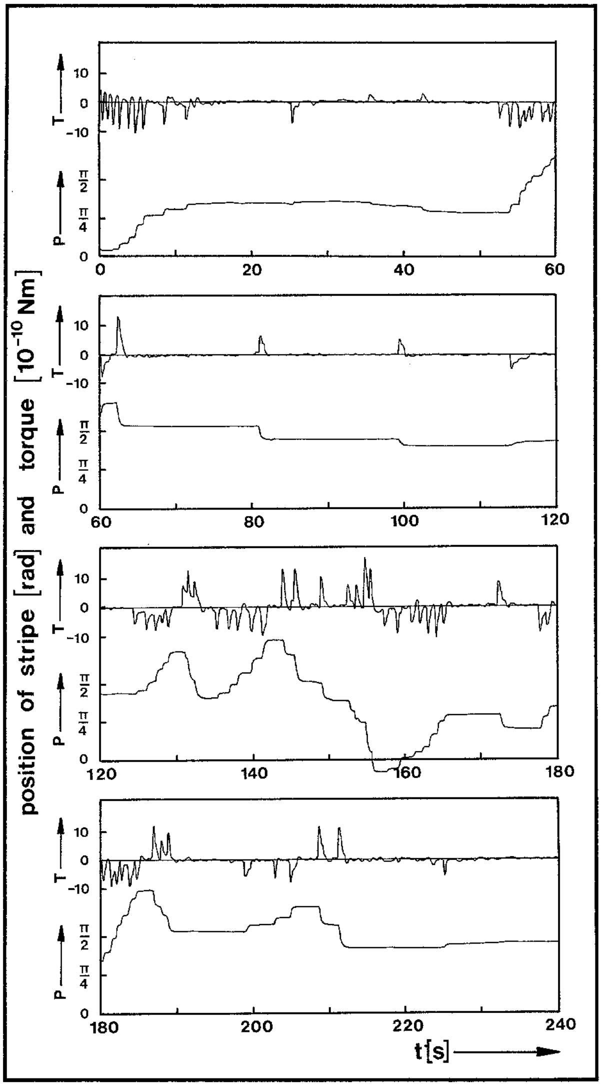

Fig. 8. A 4 min period of *non-fixation* behavior during which the fly keeps the stripe between $\psi=\pi/4$ and $\psi=\pi/2$ except for short escapades into both directions. Note that this is not a tracking experiment (see also Fig. 3c). As in all fixation experiments "zero torque" (which causes no angular velocity of the panorama) is adjusted such that the fly has to produce the same amount of torque in order to stabilize the pattern during clockwise and counterclockwise tracking of the same angular speed of the panorama. (Wildtype *Canton S*)

shows typical non-fixation behavior much more frequently than wildtype. It is again associated with an abundance of torque spikes. Both wildtype and the mutant can be prompted to switch back from non-fixation to fixation immediately if random small-angle motion of the stripe is added to the closed loop. Torque spikes are no longer generated and the flies try to stabilize the stripe in the frontal position (dynamic tracking). Fixation and increased torque "noise" persist for a while even after switching off the additional motion of the stripe.

7. Conceptual Analysis of Non-Fixation

Drosophila often fly 360° turns (Fig. 2). At the torque meter in the quiet flight mode (Fig. 7c) they often do this by a fairly regular sequence of torque spikes (Fig. 9a). This observation led us to investigate the interaction between torque spikes and visual responses. How does this behavior relate to the model by which Reichardt and Poggio (1976) describe the pattern induced flight orientation behavior of *Musca*? From many closed loop experiments (Heisenberg, 1972; Heisenberg and Buchner, 1977; Heisenberg et al., 1978, and Fig. 6a in this paper) it is obvious that fixation behavior in *Drosophila* is quite similar to that in *Musca*. The main response which stabilizes the stripe in the frontal position, the $D(\psi)$ function, is a torque response dependent upon – and reducing – the angular deviation of a target from the forward direction. If in a 360° turn the torque spikes and the $D(\psi)$ function were completely independent of one another the torque recording should show the sequence of torque spikes superimposed on the $D(\psi)$ function (schematically shown in Fig. 9b) as it was indeed found in the open loop experiment (Fig. 6a). For the front-to-back motion of the stripe either the torque spikes should be larger than for the back-to-front motion or alternatively more torque spikes of the same size would be needed. Neither is the case. The same number of torque spikes of equal size are needed to bring the stripe from the frontal position to the back as for moving it back-to-front (Fig. 9a and Table 1). The $D(\psi)$ function seems to be "suppressed" during the loop. This observation raises two questions: What type of mechanism stabilizes the stripe in lateral positions and, what happens to the $D(\psi)$ function during non-fixation? These questions can not be easily tested since interference with the closed-loop situation of non-fixation often prompts the fly to fall back into fixation behavior.

a) Stability of Orientation During Non-Fixation

A detailed treatment of this problem is beyond the scope of this article. But we describe some properties of this stability:

– Torque patterns very much like those of non-fixation in the one-stripe panorama are found in closed-loop experiments with the striped drum or the 9° x 9° checkerboard panorama.

– Flies perform stationary tracking with all three patterns. At moderate tracking speeds (up to 100°/s) no slip of the pattern is observed at the resolution of our pen recorder; i.e., the flies generate an average torque which reduces the net movement of the pano-

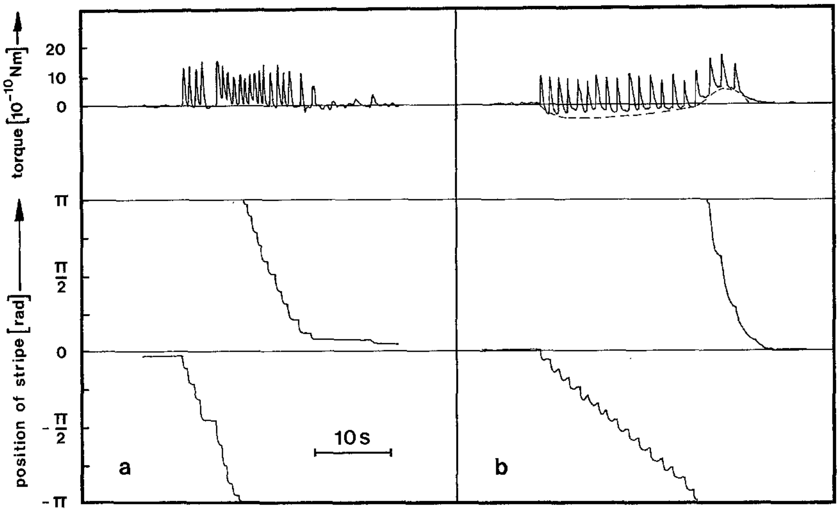

Fig. 9. a A typical 360°-loop which is performed by a train of 20 torque spikes (wildtype *Canton S*). **b** One of several hypothetical torque patterns which would be expected on the basis of an additive superposition of torque spikes and the $D(\psi)$ function during a 360°-loop (see also text and Table 1)

Table 1. No. of torque spikes in eleven 360°-loops of wildtype Berlin and Canton S. No. of spikes during regressive motion of the stripe is the same as during progressive motion

	No. of spikes	
	Regr.	Progr.
WT Berlin	3	3
	8	7
	6	6
	4	5
	7	7
	6	7
	5	5
Canton S:	6	6
	10	10
	9	9
	11	9
	6.8±0.8	6.7±0.6

rama to near zero. Flies track a stripe without obvious slip at any lateral position. No special regions of the visual field are required for tracking.

– If in a tracking experiment with a striped drum of a checkerboard panorama the artificial rotation of the drum is suddenly stopped or inverted the fly needs many seconds to adjust to the new situation.

– During non-fixation the fly may keep the stripe at a certain position for several minutes. Often only the frequency of torque spikes seems to determine the duration of such a state.

These and other observations suggest that patterns are stabilized by a movement-dependent mechanism, which attains a closed loop gain of nearly one (by means of an integrator with a long time constant). For the present context we will call it the "optomotor balance" (see Discussion).

b) The $D(\psi)$ Function

Let us now turn to the second question. What happens to the $D(\psi)$-function? One might argue that during non-fixation the stripe is stabilized so well that it becomes invisible for the fly like a stabilized image. This idea is rejected as soon as one compares the torque trace of non-fixation with that which is produced by the fly if the loop is opened and thus the image (stripe) is truely stabilized (Fig. 10): in the latter case the fly immediately starts its "search" maneuvers whereas in the former situation it keeps its torque very steadily at the value which is necessary to compensate any steady motion of the panorama. Also one occasionally observes flies holding the stripe at a lateral position to return to that orientation after a 360°-loop or a short escapade to a different orientation (Fig. 11). Finally the non-fixation experiment at the polystyrene fibre (Fig. 2) unambiguously shows that the small torque fluctuations (±5°) lead to continuous stimulation from the panorama. The stripe is permanently perceived as "motion" and "position" but the fly does not produce a torque response towards $\psi = 0$. Not only the small torque fluctuations produced by the fly are inefficient in stimulating this response, it can also be shown that artificial perturbations of the visual feedback loop of similar amplitude and time course elicit no significant tracking response.

However, if a black stripe is artificially displaced

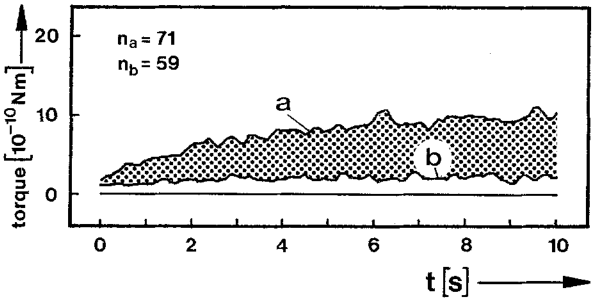

Fig. 10. Is optomotor balance due to the lack of motion of the stripe in respect to the fly? At arbitrary times during non-fixation torque is recorded for 10 s (*a*, *b*). For averaging many torque traces negative deviations from zero are multiplied by −1. In *a*) the visual feedback loop is opened for the 10 s period, in *b*) the fly is left undisturbed. The starting points of the traces represent the first 0.1 s. Trace *b*) is not at zero since flies occasionally produce torque spikes. Torque in the averaged trace increases during the experiment since it is started when torque is close to zero. n gives the number of sweeps averaged for each trace. The same 5 flies contributed to both traces. Occasionally flies would not take any notice of the artificial stabilization of the stripe during the 10 s interval

by about 30° (as a torque spike would do it) while the fly holds the stripe at a lateral position the fly nearly always immediately corrects the displacement when it is from front to back. Thus the stripe stays about where it had been previously. An artificial forward displacement often (but not always) goes uncorrected; the stripe stays further in front of the animal (Fig. 12). This asymmetry probably reflects the fixation mechanism. In summary, at lateral positions the stripe seems to be *stabile* against slow disturbances (optomotor balance). Fast disturbances are ignored if small ($<2\Delta\varphi$) but generate a torque response if they are large ($>2\Delta\varphi$) and from front to back.

c) Reafference Control

The above finding poses the question of how the fly avoids responding to the visual feedback during its own torque spikes as though they were phasic disturbances. Is the fly just blind while producing the spike or does it compensate the visual feedback by an "efference copy"? Some preliminary answers are given in Fig. 13a–f. Opening the loop (and, thus, stabilizing the stripe) for 200 ms during the torque spike does not change its shape. Adding a similar artificial displacement with the same polarity, thus displacing the stripe about twice the angle the fly alone would produce, does not change the shape of the torque spike either. But displacing the stripe into the *opposite* direction in most cases produces a strong response just like the response to an artificial displacement in straight flight. The fly turns the stripe back to about the previous (but not the "expected") position. It seems that an efference copy (corrolary discharge) of the torque spike suppresses the response to pattern displacement in that direction which is caused by the spike.

These experiments do not distinguish between an efference copy as a gating signal specific for the direction of motion of the stimulus and an efference copy

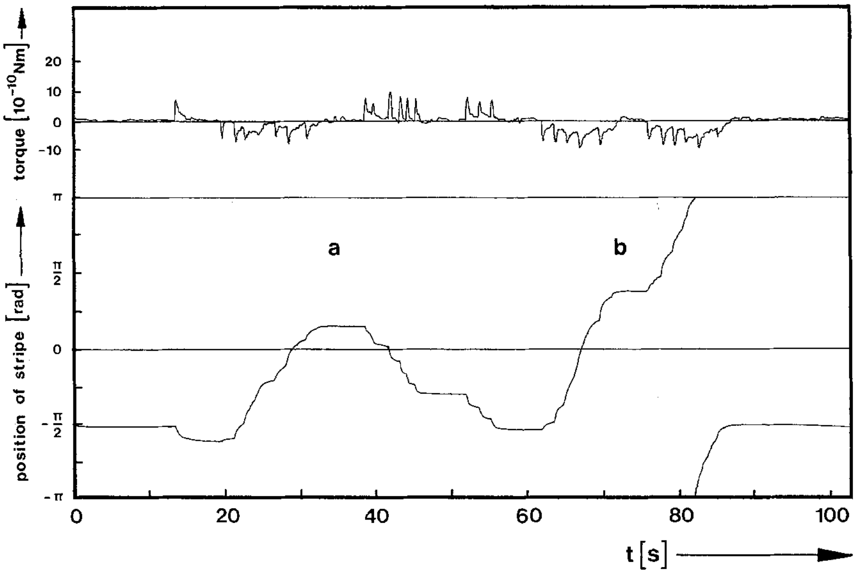

Fig. 11a and b. The fly returns to the same "lateral" orientation after **a** a short escapade, **b** a 360° loop. The fly seems to remember the previous position of the object. 360° loops are very rarely observed with periodic patterns ($\lambda = 18°$-cylinder or checkerboard panorama) and may, then, occur by chance. (Wildtype *Berlin*)

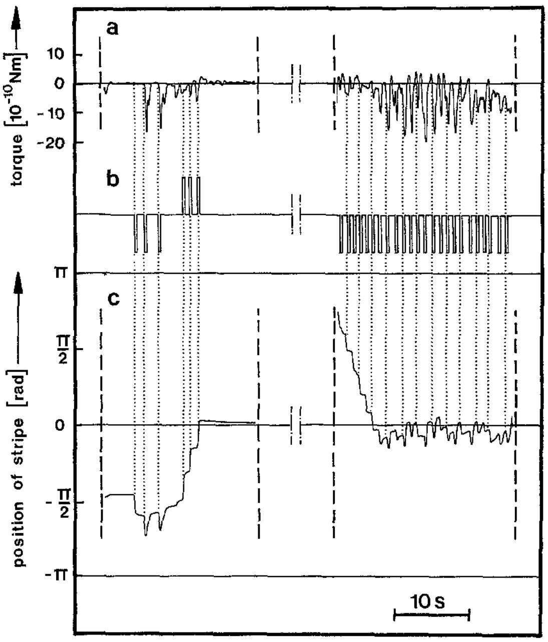

Fig. 12a–c. Artificial displacements of the stripe during straight flight in a closed loop situation. 200 ms pulses of a d.c. potential are added at "d" in Fig. 1 to the closed loop. Displacements are similar to those caused by torque spikes. The fly does not respond to displacements from back to front but does respond vigorously to displacements from front to back. **a** Torque signal of the fly; **b** artificial "torque" (d.c. potential pulses); **c** angular position (ψ) of the stripe. Note that the first artificial displacement is not corrected although it is from front to back. Similarly, back-to-front displacements may occasionally be corrected. These are exceptions to the rule (left: wildtype *Canton S*; right: wildtype *Berlin*)

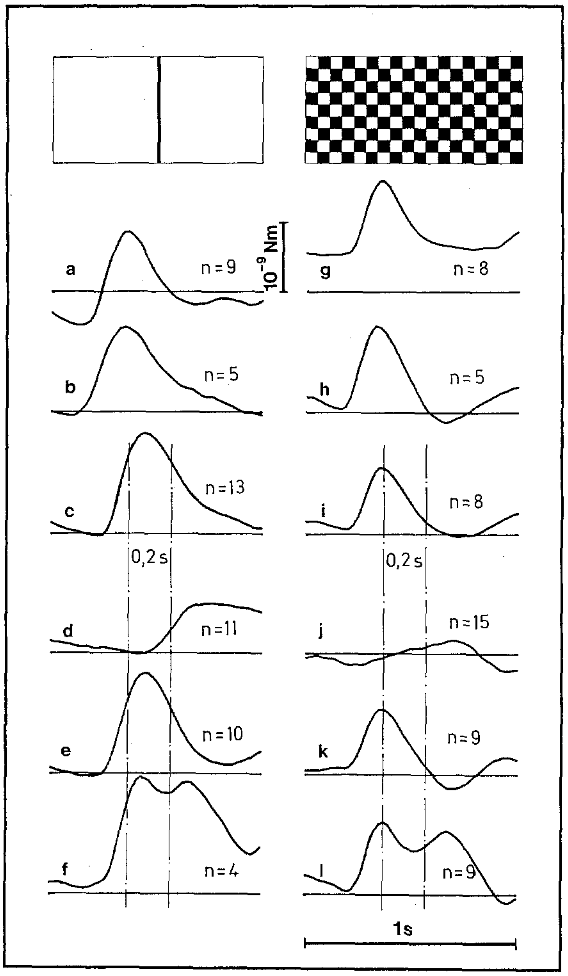

Fig. 13a–l. Artificial displacements of patterns during torque spikes. **a–f** Experiment with a single black stripe (with 3°) and one wildtype *Berlin* fly. **a** Stripe is stationary at $\psi = 0°$; **b** normal closed loop conditions; **c** the stripe is stopped for 200 ms during the torque spike; **d** the stripe is displaced artificially by 30° in 200 ms during straight flight; note the long delay of about 100 ms which in part ($\sim$50 ms) is due to phase shift caused by the low pass filter in the closed loop; **e** the stripe is displaced twice as much and in the same direction as it would have been by the torque spike alone; **f** the stripe is displaced by 30° in the direction opposite to that into which the torque spike would have displaced it. **g–l** Experiment with a checkerboard panorama (9° × 9° squares) and a *Canton S* wildtype fly. Otherwise stimulus conditions are the same as in the recordings to the left. Note the overshoots in **h** and **k**. No overshoot is observed with a stationary checkerboard panorama (**g**). While flies obviously react differently to the two patterns (compare **b** to **h**, and **e** to **k**) the overshoot may still be a consequence of the low pass filter in the closed loop set up. *n* indicates number of torque spikes averaged for each trace shown

in the sense of von Holst and Mittelstaedt (loc. cit.) of which the size matters. In our case the size of the efference copy may be proportional to the size of the torque spike but it can hardly match precisely the size of the potential visual response to the saccade. Thus one might expect to find some visual response of the fly to its own saccades in closed loop experiments with patterns other than the single stripe. Such an experiment is shown in Fig. 13g–l. A checkerboard pattern with black and white squares of 9° × 9° surrounds the fly in a closed loop situation. The fly's torque pattern is very similar to that during non-fixation. The fly produces torque spikes of both polarities. An artificial displacement of the panorama during a torque spike is corrected if it is in the opposite direction to that into which the torque spike would have displaced it. But with this visual surround also a slight response to the "normal" direction of displacement occurring in the undisturbed closed loop situation is found. The shape of the torque spike with the loop closed differs somewhat from the normal shape: the decay time is shorter and a slight overshoot after the spike is observed. The "efference copy" obviously is not quite strong enough to cancel the effect of the unnaturally strong visual stimulus[5]. While this interpretation seems very plausible it does not include all the complications of the experimental situation: In the closed loop experiment with the checkerboard pattern the fly normally does not respond to an artificial displacement of the panorama during *straight* flight. In *Musca* lateral inhibitory interactions largely suppress the torque response to the position of wide field stimuli (summarized in Reichardt, 1977). Likewise the torque response to the displacement of the checkerboard panorama seems to be suppressed in *Drosophila* since this inhibition is annihilated by the efference copy of the torque spike motor pattern. Normally during saccades no movement stimuli in the direction of the turns are to be expected from the stationary surround. Thus such movements are visually unnatural irrespective of whether they result from a small object or from a large field stimulus.

Still another effect of the efference copy is observed in the case of torque spikes. As stated above the artificial displacement of the stripe during nonfixation is corrected very consistently if it is from front to back but only rarely if it is in the opposite direction. This asymmetry does not hold for artificial displacements during torque spikes. The unexpected motion of the single stripe is corrected when it is from back to front or from front to back.

Discussion

Body saccades in the flight of *Drosophila* would not be of exceptional interest if it were not in stationary flight at the torque meter where the flies perform them. It is indeed a remarkable fact that much of the torque fluctuations the fly produces in this pathetic situation of sensory and motor deprivation obviously reflects well organized behavior patterns. Comparing this experimental situation with that in the cinematographic study of Collett and Land (1975a) on flight patterns in *Syritta* the high price we have to pay for completely stabilizing the fly becomes immediately apparent. The behavioral repertoire to be discovered at the torque meter must be very limited. First of all we only record one out of the six degrees of freedom the fly has for moving its body and we ignore movements of its body appendages. Secondly we prevent most behavioral sequences requiring sensory feedback to develop properly and finally many moods through which a fly goes in normal life probably will never occur at the torque meter. On the other hand the behavioral sequences one does find are open to the same kind of rigorous analysis as for instance the optomotor response has been in the last 25 years. This brief look into the fine structure of flight torque has provided starting points for analysis in three directions.

1. Torque Patterns as Actions

The striking phenomenon of a fly switching from one behavior pattern to an other without an obvious external cause inspired Collett and Land (1975a) to invoke the "free will" of the fly as an explanation, – unfortunately without an experimental proof. The lack of an external cause is difficult to demonstrate with freely flying flies (see Götz, 1975a; Reichardt and Poggio, 1976). "Free will" may be a challenge to conscious beings; but we find it useful along with Collett and Land (1975a) to distinguish in the behavior of a fly *actions* and *responses*. Some criteria for an action will be given in this and the following section. It is obvious that actions should depend upon a variety of sensory stimuli while a one to one relationship between a stimulus and the motor pattern should not be the prevailing characteristic. An "action" may occur "spontaneously" at least for the partially ignorant observer.

Torque spikes are actions in this respect. They occur in various visual situations and, although this has not yet been shown, we would like to assume that they depend upon other sensory modalities as well. The relation between stimulus and motor pattern is less direct than for instance in the optomotor response. Most visual situations tested just modify the probability of the occurrence of spikes and there seems to be no fixed delay between stimulus and action.

The interplay between different visual stimuli in their effect on the polarity and frequency of torque spikes may be complex. This is shown in the two open loop experiments with the striped drum and the single stripe. With the striped drum only the direction of motion determines the polarity of the spikes. The position of a single stripe oscillating at a certain position in the visual field has no obvious effect on the polarity. Both, movement and position information together (a rotating single stripe) influence the polarity of torque spikes in a manner which could not be predicted from the two isolated stimulus components. Reichardt's (1973) original notion of regressive and progressive motion may in this case be appropriate.

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[5] This argument is valid only for the comparison of the two patterns in our experimental situation. The artificial phase shift in our apparatus must reduce the effectiveness of the efference copy. Thus in free flight the reafferent stimulus from a checkerboard panorama may also be completely suppressed

Torque spikes are an element of longer torque sequences like "search" and 360°-loops. These too seem to represent centrally generated behavior patterns. The 360°-loops are of particular interest: *Drosophila* can use different torque patterns performing them. If one briefly stops the panorama during a loop which is performed by a series of torque spikes the fly may just add more torque spikes or may switch to a different torque pattern. But it seems to be determined to finish its loop. The fly obviously uses visual feedback to arrive at the previous orientation. The intricate cooperation between response and action in such behavioral sequences may be the origin of central brain functions.

2. Reafference Control

Although the theoretical concept of reafference control today is firmly established, neither in the case of saccadic eye movements in primates nor in the case of visual behavior of flies have the mechanisms which enable the organism to distinguish between exafferent and reafferent stimulation been worked out. In fact, it is only very recently that the first electrophysiological data from the monkey have been obtained indicating that certain sensory cells in the superior colliculus indeed receive an efference copy of the motor signals generating saccadic eye movements. The cells seem to be sensitive to visual movement in any direction (thus they are likely to be flicker sensitive) and also their activity is suppressed during saccades in any direction (Robinson and Wurtz, 1976; Richmond and Wurtz, 1977). The rôle of these cells in visual perception is just beginning to be understood.

The mechanism which suppresses reafferent stimulation during body- (and thus also eye-) saccades of *Drosophila* is directionally selective. An "efference copy" of the motor pattern generating a saccade is passed to the visual system where it suppresses the response to that direction of movement which is induced by the execution of this saccade. Since in flies directionally selective movement-sensitive centers for clockwise and counterclockwise rotation around the fly's vertical axis are known (see Hausen, 1976) it is not surprising that the efference copy may leave the fly fully responsive to movements in the direction opposite to that induced by the saccade.

Obviously partial blindness is better than total blindness during a saccade. This leads to the very general problem raised by the reafference principle of how specific an efference copy may be. Except for certain laboratory situations only some properties of the reafferent stimulus can be predicted from the subject's own action. During a saccade to the right the environment will certainly be shifted to the left but precisely how strong this reafferent movement stimulus will be depends on the actual environment. The crudeness of the efference copy may be the explanation for our observation that in the checkerboard arena reafferent stimulation during the torque spike seems not to be fully suppressed. The reafference control system obviously is not independent of the visual patterns in the periphery. But the present observations show that this question about the specificity of the efference copy may be misleading. It may be more appropriate to consider the relevance of the visual information for the fly during fixation (or moving straight) and for the fly during a body saccade. We observed that the inhibitory activity of a network, which – if the analogy to *Musca* holds (Poggio and Reichardt, 1976b) – may normally provide "figure-ground" discrimination, is suppressed during the torque spike. During the chase of another fly the visual background may be irrelevant, but if during a body-saccade the background moves in the "wrong" direction this may be an important information.

The two systems in the monkey and in the fly which obviously serve similar purposes may be built similarly; but the few details which have been worked out so far do not allow a critical comparison.

For von Holst and Mittelstaedt (1950) "actions" and "commands" of animals at that time were self-evident and seemed not to require experimental validation. In more artificial experiments, however, purely functional criteria for *active* behavior would be very valuable. Partial unpredictability as a property of actions has been mentioned above. Reafference control is another one.

3. Why Black Stripes are Poor Fly Traps

A further area in which torque spikes may become a focus for further investigations is flight orientation. To one who over years has been accustomed to the very clear-cut, stereotypic fixation behavior of *Musca* (Reichardt and Poggio, 1976; Poggio and Reichardt, 1976b) non-fixation behavior in *Drosophila* comes as a surprise. However, from a more general point of view a fly should be able to keep a straight course irrespective of the visual patterns in its surround. It is of interest here that Reichardt (pers. comm.) very carefully looked for torque spikes and for episodes of non-fixation in the orientation behavior of *Musca* at the torque meter but did not find any. We suggest that non-fixation in *Drosophila* may correspond to hovering flight when the forward component of flight is small, when the fly is undisturbed and the environment at rest.

Each Dipteran may have its own life style. However, our observations indicate that in other flight modes, too, the actual behavior of the free fly may be dictated much more by endogenous motor patterns than by visual reflexes. Our preliminary observations on smooth 360°-loops show that these are also performed under control of reafference.

Drosophila wildtype and particularly the mutant *S100* spend large parts of their flight time at the torque meter with non-fixation behavior. Thus one would like to describe orientation in terms which comprise fixation *and* non-fixation. Our experiments show that during non-fixation the fly reduces tonic motion of the panorama (stationary tracking) to such an extent that within the resolution of our recording technique the pattern seems to be stabilized. This state of "optomotor balance" is achieved with single stripes as well as *periodic* patterns which are held without any preferred orientation. If one interrupts the closed loop in such an experiment the fly keeps its torque of the tracking situation for a while superimposed on the searching behavior which it initiates. This and similar observations suggest an integrative optomotor control system.

Stationary tracking corresponds to a free flight situation in which for instance one wing is partially clipped. Thus optomotor-balance can be understood as a zero control device for yaw torque. Such a device must be essential for an insect like *Drosophila* since its flight apparatus is constantly threatened by accidents which may asymmetrically change the efficiency of the wing beat. If such accidents would abolish the ability to fly straight they would be fatal. On the other hand a zero control device for torque should impose the least possible restrictions on other torque control systems. Indeed, in *Drosophila* slow and medium tracking speeds seem to have no obvious influence on the fine structure of torque during non-fixation. Optomotor balance is less pronounced in walking flies. They do not need it as much as in flight; they have tarsal contact to the substrate. The mechanism of optomotor balance has yet to be worked out. In this context it is sufficient to note that an additional mechanism (as for instance in menotaxis (i.e., Jander, 1957)) for keeping the single stripe at a certain position (for flying straight) is not necessary.

It might be argued that the fly stabilizes periodic patterns by its optomotor balance but that it uses a different mechanism to stabilize small patterns. Alternative models of stabilization would imply that the fly shifts its $D(\psi)$-function to the position where to hold the stripe. Such a shift is not observed; in fact, the artificial disturbances during non-fixation (Fig. 12) show that the zero crossing of the $D(\psi)$ function stays at $\psi = 0$.

If one acknowledges the existence of "optomotor balance" as the stabilizing principle during non-fixation and thus as the basis of oriented flight one is left with the conclusion that the fly does not all the time express the behavior recorded as fixation or $D(\psi)$ function. We will discuss three interpretations of this result; the first one, which has been mentioned already in the "Results" section can be easily dismissed on the basis of our experiments; the second one is designed to keep fixation as much a reflex-like behavior as possible. The third interpretation to us seems the most plausible one but has the draw-back that it does not lend itself to a simple model.

In one of his early experiments on fixation in *Musca* Reichardt (1973) showed that a laterally stabilized stripe does not elicit a significant torque response towards it. One might be inclined to regard non-fixation in *Drosophila* as a similar situation. Several experiments clearly exclude this as a possibility. During non-fixation *Drosophila* in most instances produces a continuous flow of apparently random small torque fluctuations. The resulting small angle displacements of the surround are sufficient to be perceived by the fly (Fig. 2). The baseline of torque is kept firmly at zero during non-fixation. If one interrupts the closed loop the fly immediately realizes the lack of visual feedback (Fig. 10). Thus non-fixation can not be regarded as a pseudo-open-loop situation.

The second interpretation maintains that the $D(\psi)$ function is permanently present but that it is a response only to large front-to-back displacements of small objects. This concept seems to be in agreement with most of our observations. The fly does not respond to small angle fluctuations of objects. This is demonstrated in a variety of experiments. At the polystyrene thread (Fig. 2) the fly's own turning movements during non-fixation are of that size. Dynamic tracking of a small object is very poor if the object oszillates randomly in a narrow range around a certain position (in preparation). Also small discrete displacements of objects are ineffective in eliciting turning responses. The $D(\psi)$ function seems to be present also during non-fixation (Fig. 12) as an asymmetry in the response to large discrete displacements.

This interpretation implies that the fly could in principle choose between fixation and non-fixation by increasing or decreasing its torque fluctuations. Whether this is a realistic assumption remains to be demonstrated. But the $D(\psi)$ function would have various implications in free flight. While flying forward in the vicinity of objects the fly would be led to a landing site. Far above ground large air turbulences would cause the fly to head for shelter and if in an escape maneuver *Drosophila* would produce large random torque fluctuations without reafference control it would "automatically" arrive at the nearest hiding place. It seems essential for the fly not to respond to small angle displacements during flight since small fluctuations in the fly's orientation during non-fixation are necessary for maintaining optomotor balance and would, under most circumstances, be caused by air turbulences anyway.

This interpretation has the virtue of making the fewest additional assumptions to the concept of fixation in *Musca*. However, it does not easily account for two aspects of our results which when incorporated lead to the third interpretation. One is the existence of the third flight mode of fixation behavior (Results, 6a). *Drosophila* can (and does occasionally) keep the stripe in the forward position for long periods of time without producing large torque fluctuations. It is obviously able to extend its $D(\psi)$ response also to *small* front-to-back displacements of objects. The other point is – and this should be made very explicit here – that the $D(\psi)$ response of *Drosophila* by no means is a simple visual *reflex*. As pointed out above (Fig. 12) the fly "spontaneously" chooses to respond or not to respond to a standard stimulus. In an ambiguous situation as to fixation and antifixation the fly is not unresponsive; it does one *or* the other switching back and forth. The $D(\psi)$ function is highly variable. Already Götz (1975b) found that the relative strength of the torque response to progressive and to regressive motion significantly changes during the course of a one hour experiment. The shape of the $D(\psi)$ function depends very much upon the procedure by which it is recorded. Size and shape of the patterns, contrast, color (K.-F. Fischbach, unpublished), motor activity of the fly (see above) and even such involved matters as the phase relation between foreground and background (Poggio and Reichardt, 1976a) seem to be parameters of importance.

In this concept one might assume to find a torque response towards (or away from) the position of an object, whenever the fly chooses to generate it, without any relation to the fine structure of its torque and the artificial disturbances applied. However, this would be an extreme position which would not be true even for decisions of humans. Obviously under some circumstances the fly more often chooses to respond than under others. For instance, large artificial random disturbances of stripe position in a closed loop experiment in our experience nearly always prompt the fly to perform fixation behavior; large endogenous torque fluctuations generally coincide with fixation, etc. In any stimulus situations fixation (or antifixation) has a certain probability to occur, in some it occurs nearly as regularly as a reflex in others occasionally and in still others hardly ever. Like the 360° loops mentioned above fixation seems to be an example for the interaction between responses and more complex behavioral functions – in this case the fly's choice to respond or not to respond. We consider it a challenge to define this interaction more closely.

The present interpretation assumes that the asymmetrical responses to disturbances during non-fixation (Fig. 12) are in themselves not necessarily the basis of fixation; they only indicate the fly's disposition to perform fixation (or anti-fixation) but may possibly be generated by a different mechanism. A detailed investigation of these response properties may give an experimental basis to distinguish between the second and third interpretation.

It is evident that in the latter concept the position response can not be regarded as the output of a simple network somewhere in the optic lobes but rather as a complicated set of rules based on large parts of these networks governing the fixation-antifixation dichotomy. The position response appears to be the result of *orientedness*. It is of central importance for the fly: by approaching or receding from an object the fly takes its chances.

This account does not intend to give a thorough description of visual flight orientation in *Drosophila*. The work was initiated by our puzzling observations on flight orientation behavior of the non-fixation mutant *S100*. We now try to give a first synopsis of this behavior in *Drosophila*. A variety of phenomena with wild type and several mutants can be accounted for by this concept. Evidently, some of the problems have to wait for a more quantitative analysis. In this paper we want to show that the torque fluctuations *Drosophila* produces in the deprived situation at the torque meter may still correspond to meaningful behavior patterns which are worth analyzing if one is trying to understand visual behavior of flies.

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