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Flight control during 'free yaw turns' in *Drosophila melanogaster*

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

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Summary. 1. A new method for studying flight control in flies is introduced. In this set-up (thread paradigm) the fly is free to rotate around its vertical body axis but is otherwise kept stationary. The fly's orientation is continuously monitored opto-electronically. For statistical evaluation flight traces are divided into 'turns' (summed successive angular displacements until the direction of turning changes).

2. In the thread paradigm flies perform quick turning maneuvers corresponding to torque spikes at the torque compensator and to body saccades in free flight. In between, flies maintain a rather straight course. This obvious observation is reflected in bimodal velocity and turn histograms, both of which are composed approximately of a Gaussian and an exponential distribution.

3. The frequency of body saccades declines exponentially (decline constant 0.026/°), angular peak velocities increase linearly (12.5(°/s)/° = 12.5/s), and the duration of saccades saturates (at about 250 ms) with increasing size of saccade. After a quick rising phase (40–60 ms) body saccades show, as a mean, an exponential drop of angular velocity with a time constant of about 40 ms.

4. The pattern dependency of the turning behavior resembles that measured using the torque compensator. The size of body saccades is influenced by the visual pattern wavelength. The direction of a body saccade may depend on that of the preceding one thus revealing its special status as part of a larger behavioral sequence.

5. Experiments with constant torque bias reveal an internal reference of zero torque. Corresponding measurements using the torque compensator suggest an efficacy model to be applicable in characterizing torque traces with constant rotatory bias. This new model allows simulation of constant-bias torque traces by applying a single efficacy factor to no-bias torque traces.

Introduction

Flight behavior in flies has predominantly been studied in two ways: by recording flight forces of tethered animals, e.g., using the torque compensator (e.g., Götz 1968; Reichardt and Poggio 1976; Poggio and Reichardt 1976; Heisenberg and Wolf 1979), and by taking high-speed motion pictures of freely flying flies (e.g., Collett and Land 1975; Bülthoff et al. 1980; Wehrhahn et al. 1982; Zeil 1983; Wagner 1986; for other methods see for instance Vogel 1966; David 1978; Blondeau 1981; Nachtigall and Roth 1983; Götz 1983).

Recording of free flight may catch the behavior in its natural context and provide cues about the motivation of the animal, but the sensory stimuli reaching the animal are complex due to the animal's own behavior. Thus their significance for the behavior is difficult to assess. Tethering the fly is a drastic solution to this problem. Yet, the strong interference with behavior (flies are prevented from performing any rotatory or translatory body movements) may well suppress the motivation for most of it. Recording yaw torque (torque with reference to the vertical body axis) under conditions of controlled visual stimulation has nevertheless revealed some basic principles of visual flight control. In particular, using the fly's yaw torque to control the angular velocity of the panorama (in a flight simulator) shows this special feedback loop to be one of the essential components of the course control system (Heisenberg and Wolf 1984, 1988; Wolf and Heisenberg 1986).

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* To whom offprint requests should be sent

As an alternative to the torque compensator we explore in this study a new apparatus using the so-called thread paradigm. In contrast to flight simulation using the torque compensator, in this case the fly's yaw torque results in real rotations of the fly. The first attempts to record the orientation behavior of flies that were able to rotate around their vertical body axis were made by Land (1973) who took high-speed motion pictures of *Calliphora* suspended on a pivot in a glass tube. A preliminary version of the thread paradigm has been described before (Heisenberg and Wolf 1979). In the present apparatus the orientation of the fly is continuously monitored optoelectronically. As the fly can only perform yaw turnings its visual input is known to a much higher degree of precision than in freely flying flies. Due to the real rotations of the fly in the thread paradigm it provides the opportunity of investigating additional components of the course control system. The fly's air friction in the thread paradigm closely matches that in free-flight conditions, allowing the study of the dynamics of flight behavior.

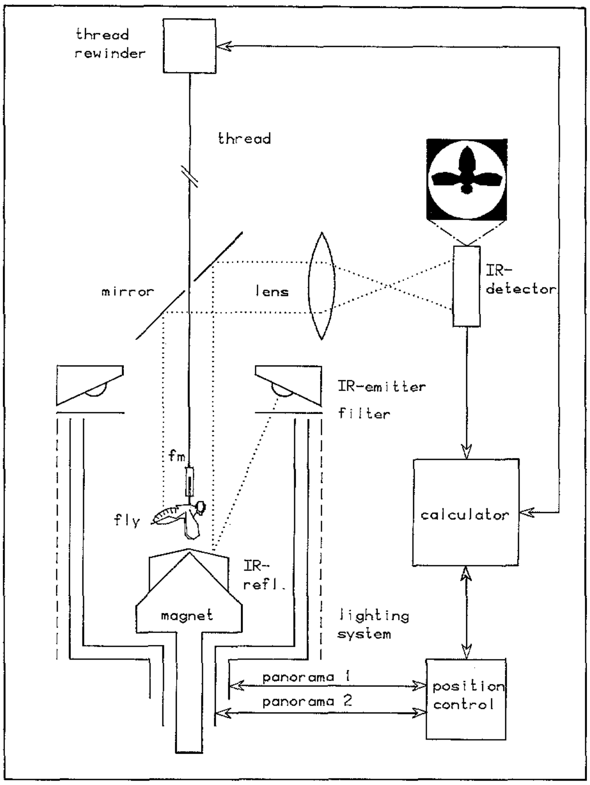

Fig. 1. Thread paradigm. The fly is glued by its thorax to a ferromagnetic microtube (*fm*) suspended from a polyamide thread. It is free to rotate around its vertical body axis but otherwise is kept stationary by a cone-shaped magnet. The fly's image above the IR-reflecting surface of the magnet is projected onto an IR-sensitive two-dimensional position detecting photodiode by a mirror and a lens. Processing of light flux results in a continuously monitored light vector (center of light intensity) the direction of which corresponds well to the fly's flight orientation. To avoid excessive twisting the suspended end of the thread is turned by a servomotor (thread rewinder) as much as the fly turns. The set-up allows for continuous recording of *Drosophila* flight orientation with respect to stationary or moving visual patterns. Double arrows indicate flow of information in both directions (for further details see Material and methods)

Material and methods

Thread paradigm. The fly is glued by its thorax to a ferromagnetic microtube (2 mm long, diameter 0.3 mm) suspended from a polyamide thread (30 cm long, diameter 12×10^{-3} mm). A cone-shaped magnet (VM170, Vacuumschmelze, Hanau) 2 mm underneath the fly keeps it in place. Thus the fly is free (see mechanical properties) to rotate around its vertical body axis (yaw) but cannot perform roll, pitch, or translatory body movements (Fig. 1). For continuous recording of the fly's orientation an infrared (IR) sensitive two-dimensional position detecting photodiode is used (UDT-PIN SC/10 4276, TS-Optoelectronic, Munich). A diffusely IR-reflecting surface underneath the fly is illuminated from above by 16 IR-emitting diodes (maximum wavelength 960 nm) which are shielded from direct sight by a circular IR-transparent filter. The fly's image is projected onto the detector surface by a mirror and a lens (Fig. 1). The processing of light flux results in a continuously monitored light vector (center of light intensity), the direction of which corresponds well with the fly's direction of flight (see 'Accuracy of measurements'). To avoid excessive twisting the suspended end of the polyamide thread is turned by a servomotor as much as the fly turns. The maximal remaining twist (one revolution) exerts less than 1% of the flies' mean maximal torque (4×10^{-9} Nm). For visual stimulation the fly is kept in the center of one or two concentric acrylglass cylinders homogeneously illuminated from behind. Different visual patterns such as gratings or single vertical black stripes can be attached to the walls of the cylinders, which can be rotated separately by two servomotors. In this study only stationary patterns (one cylinder) were used.

For suspending the flies on the thread they are cooled to 4 °C and are placed on a porous aluminum plate perfused by cold air (4 °C). A fly is held horizontally while a thin plastic pin (2 mm long, diameter 0.13 mm) is glued onto the center of its thorax using an adhesive which polymerizes within seconds during irradiation with UV light. With an additional drop of this glue the head is fixed to the thorax. Although flies perform well within 1 min after the cooling procedure they are not tested before the next day. The plastic pin fits into the ferromagnetic microtube.

Accuracy of measurement. The X and Y signals of the photodiode are digitized (8-bit converter; calculator: Apple II plus with Z80+ card) and the values used to calculate the fly's orientation. The accuracy by which the relative orientation of the fly can be determined is limited by the signal-to-noise ratio of the detector system and, in our case, amounts to about 1.4°. The inaccuracy due to digitizing the X and Y signals amounts only to about 0.7°. The accuracy of the absolute orientation also depends on the precision with which the plastic pin is fixed to the center of the thorax (since this aligns the direction of the light vector with the fly's longitudinal axis) and on how closely parallel to the longitudinal axis the head is fixed to the thorax. These manipulations add an inaccuracy of 5° to the assignment of visual pattern locations to positions in the fly's visual field. In addition, the fixed fly can misalign the direction of the light vector and the flight direction by bending its abdomen sideways. This may add a further inaccuracy to the measurement. Torsion experiments show that this situation does arise: static bending of the abdomen can be observed when the fly has to compensate a torque bias of more than 2×10^{-9} Nm. With a constant torque bias of 10^{-9} Nm, bias-dependent bending of the abdomen can be ignored (see Results). However, during quick turns dynamic abdomen bending may modify the velocity time course of the maneuvers.

Mechanical properties. By means of torsion oscillations with objects of known rotational moment of inertia the torsion spring tension of the thread can be determined to be 3.3×10^{-11} Nm per revolution. The rotational moment of inertia of the fly can be measured in the same way as 9×10^{-13} Nm s^2. The ferromagnetic microtube increases the fly's moment of inertia by less than 5%. The magnetic reset force gradient experienced by the ferromagnetic microtube under experimental conditions is 3×10^{-4} N/mm in the center. (The fly's maximal forward thrust force is 4×10^{-5} N). An estimate of the fly's air friction during rotation can be obtained by comparing its maximal torque with the maximal angular velocity. On average flies compensate 4×10^{-9} Nm torque disturbance generated by twisting the thread; the maximal torque of single flies can be up to 8×10^{-9} Nm, both using the torque compensator and the thread. Flies which do not respond to any visual stimulus (structural brain mutant *disco*) and in addition have their halteres removed generate a maximal angular velocity of 8×10^3 °/s. Assuming the fly's air friction f to be proportional to its angular velocity v ($f = kv$; Reichardt and Poggio 1976), an upper limit of the fly's air friction constant k_{tp} in the thread paradigm can be calculated as 5.7×10^{-11} Nms. Decline of angular peak velocities during body saccades gives a lower limit of $k_{tp} = 2.3 \times 10^{-11}$ Nms, assuming the torque to be zero when peak velocity is reached and the decline to be due to air friction (Fig. 7). The corresponding air friction constant $k_{tc} = 5.2 \times 10^{-10}$ Nms using the torque compensator simulates unnaturally high air friction under closed-loop conditions. Adjusting k_{tc} according to k_{tp} is not feasible for reasons of stability and because of the time course of the torque spikes (Heisenberg and Wolf 1984).

Experiments and evaluation. Female flies, 2–3 days old, of the wild type Berlin were tested in three groups with the following visual patterns: vertically striped drums (pattern wavelengths 120° and 90°; pattern contrast $m = (I_{\max} - I_{\min})/(I_{\max} + I_{\min}) = 0.29$ where $I_{\min}$ and $I_{\max}$ are minimum and maximum luminance, respectively; average luminance in arena $\bar{I} = 130$ cd/m^2; 44 flies) and a single vertical black stripe (width 5°; $m = 1$; $\bar{I} = 180$ cd/m^2; 10 flies). Each fly was tested at least twice, once under 'normal' conditions and once with a constant torque bias of 10^{-9} Nm caused by a twist of 30 revolutions in the thread. Half of the flies were first tested with the torque bias, and the other half under normal conditions. Every test consisted of a 3-min flight period. During that time flight direction was recorded every 20 ms. For statistical evaluation flight traces were divided into 'turns' (summed successive angular displacements until the direction of turning is changed). The thread paradigm evaluations (Figs. 3–13) are based on a total of 6.5 h of flight in 54 flies. In the curves of Figs. 5, 6, 8, 9, and 12 all points are averaged twice with their adjacent neighbors. Error bars are not shown for all data points.

Torque compensator. A description of the torque compensator is given elsewhere (Heisenberg and Wolf 1988). The experiments using the torque compensator corresponded to those using the thread paradigm (visual pattern: striped drum, pattern wavelength 18°; $m = 1$; sampling rate 70 ms; 8 flies, each tested for 2 min with a rotatory bias of 110°/s, 2 min with a rotatory bias of -110°/s, and 4 min without a bias). A rotatory bias of 110°/s corresponds to a zero-torque shift of 10^{-9} Nm in the feedback loop of the flight simulation. As with the thread, flies had to generate a torque of 10^{-9} Nm to stabilize the panorama during a bias experiment.

Results

Bimodal distribution of turn size

Watching freely flying *Drosophila* one notices that flies change the flight direction in the horizontal plane abruptly by body saccades. In between, flies maintain a rather straight course. This flight behavior can also be studied with the thread paradigm. Figure 2 shows two flight periods of single flies using the thread paradigm. Histograms of angular velocity (Fig. 3) and turn size (Fig. 4) are consistent with the existence of two processes. Both histograms show a bimodal distribution composed approximately of a Gaussian and an exponential distribution.

Dynamic properties of turns

Angular peak velocities increase linearly with turn size (Fig. 5, increasing constant = 12.5/s) whereas the duration of turns saturates at about 250 ms (Fig. 6). The velocity profile of turns (Fig. 7) shows that angular peak velocities are reached early during the maneuvers, after about 40–60 ms. Larger turns are primarily caused by increasing maximal torque (which can be calculated from angular peak velocities) and keeping the duration constant rather than maintaining the same torque for a longer time. After the rising phase angular peak velocities show an exponential drop with a time constant τ of about 40 ms (Fig. 7). This is in accordance with the measured value of the fly's moment of inertia ($\theta = 9 \times 10^{-13}$ Nms^2) and an estimated upper limit of $k_{tp} = 5.7 \times 10^{-11}$ Nms (fly's air friction constant), resulting in $\tau = \theta / k_{tp}$ of 16 ms; the time constant τ of 40 ms allows one to calculate the lower limit of k_{tp} to be in the range of 2.3×10^{-11} Nms, assuming the torque to be zero when peak velocity is reached and the decline to be due to air friction. If torque becomes negative during the decline the air friction constant k_{tp} may be even smaller.

Pattern dependency of turning behavior

Turning behavior of flies differs with different visual patterns. With a single stripe as the visual pat-

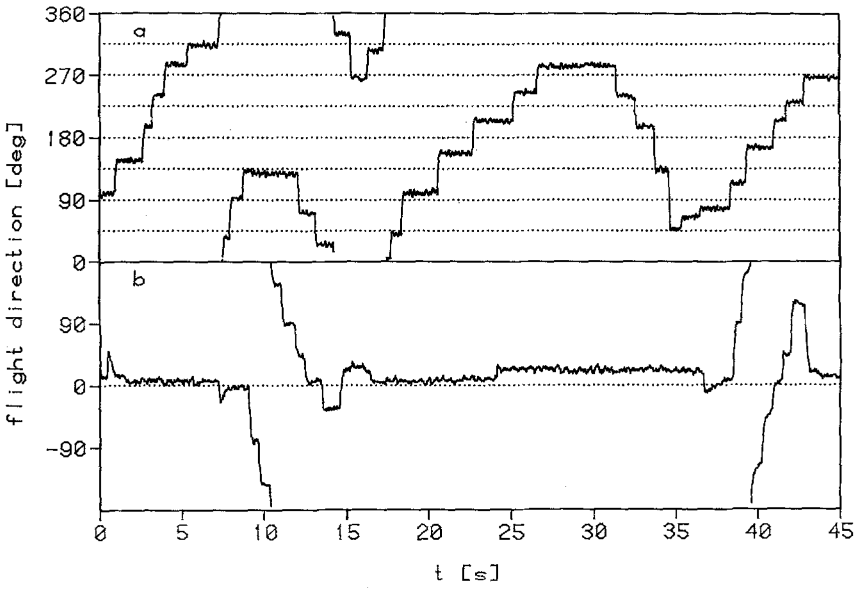

Fig. 2a, b. Flight traces from single flies in the thread paradigm with different stationary visual patterns. **a** Striped drum; pattern wavelength 90°, pattern contrast $m = 0.29$; horizontal lines indicate stripe boundaries. **b** Single black stripe placed at position 0°. Flight direction is changed abruptly by body saccades. In between, flies maintain a rather straight course

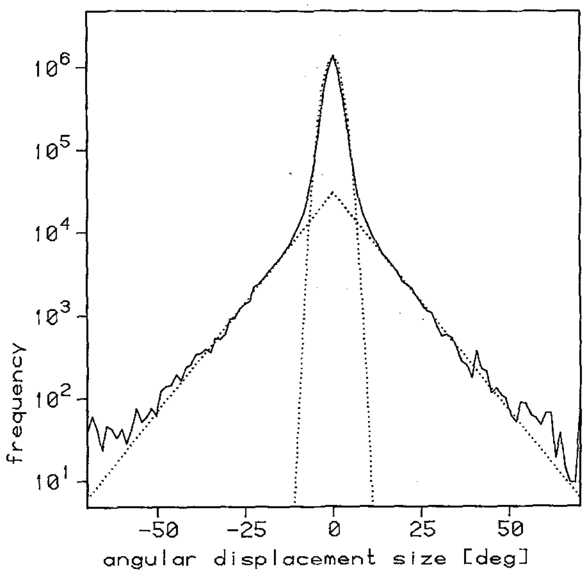

Fig. 3. Histogram of angular velocity (angular displacements between successive measurements; sampling rate 20 ms) reveals the distribution to be approximately composed of a Gaussian distribution ($\sigma = 3.3°$) and an exponential distribution

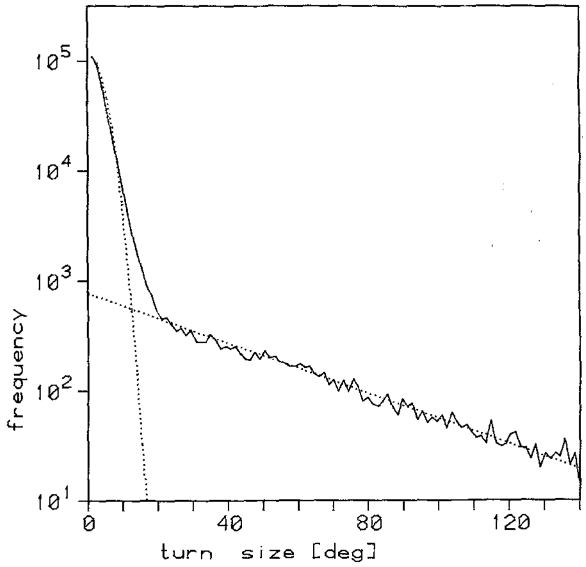

Fig. 4. Histogram of turn size (turns are summed successive angular displacements for which the direction of turning does not change) is approximately composed of a Gaussian distribution ($\sigma = 3.6°$) and an exponential distribution (decline constant 0.026/°)

tern a fly in the thread paradigm shows a pronounced orientation preference towards the stripe. Figure 8a shows the mean frequency of orientation in relation to a single stripe placed at position 0°. The mean angle of orientation from 21 tests with 10 flies amounts to 1.5±10° (circular statistics, Batschelet 1981). While flies most of the time stabilize the stripe in the frontal region of the visual field there are also episodes of stabilizing the stripe laterally; even in the frontal region the fly keeps different stable orientations (see Fig. 2b). Due to this menotaxis ability (Heisenberg and Wolf 1984) mean angles of orientation in successive tests of a single fly can differ considerably. This is the explanation for the comparatively large mean angular deviation.

In the striped drum (pattern wavelength = 120° or 90°) flies have no significant orientation preference with respect to the basic unit of the visual pattern (one stripe and one interstripe interval; data not shown). Nevertheless, the size distribution of the turns is influenced differently by the two pattern wavelengths. Figure 9 shows for each turn size the ratio of the mean frequency of turns mea-

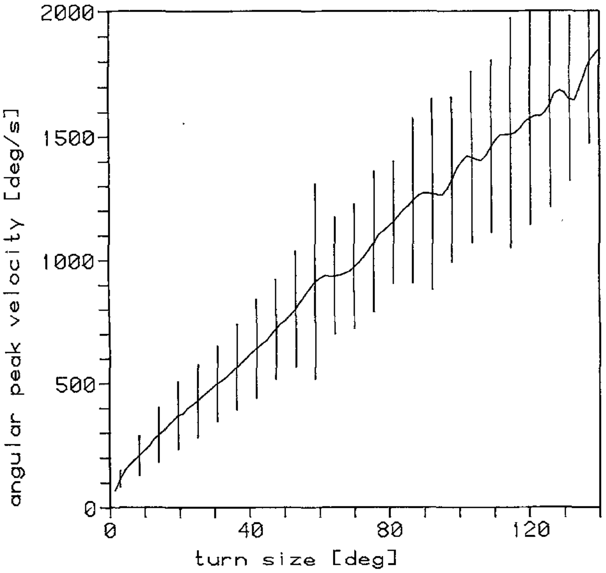

Fig. 5. Angular peak velocities of turns (mean values and standard deviation) increase linearly with turn size by 12.5/s

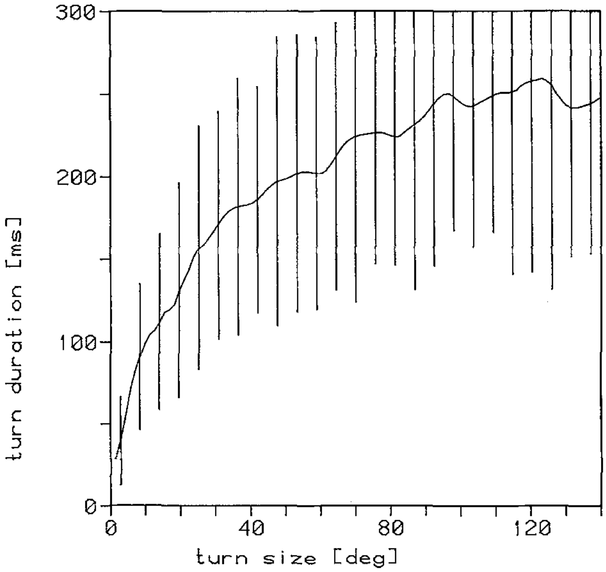

Fig. 6. The duration of turns (mean values and SD) saturates at about 250 ms with increasing turn size

sured with the 90° pattern wavelength and the sum of turns measured during both tests. The results suggest a correlation of turn size with pattern wavelength but further measurements are necessary to reveal the underlying mechanism.

Figure 10 shows the mean duration of flight periods containing only turns up to a particular limit. Data are split in two groups according to the visual patterns used. The single stripe and striped drums differ significantly (SEM). This indicates smoother flight behavior and fewer turn oscillations with the single stripe. This is in accor-

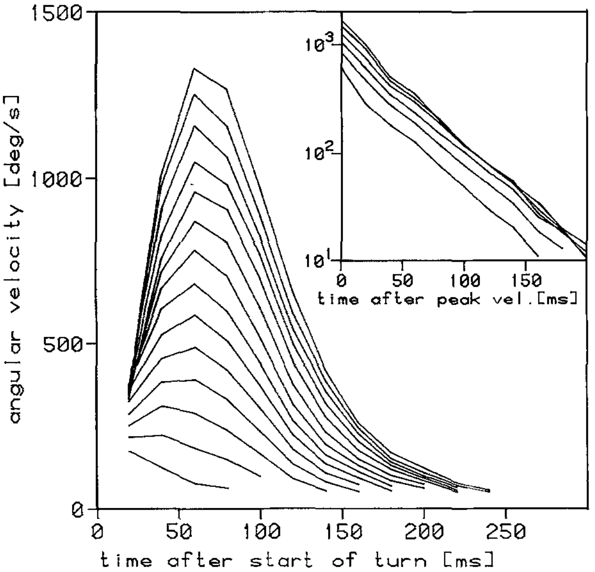

Fig. 7. The velocity profile of turns (only 14 turn classes are shown, from 10° to 140° in steps of 10°) shows that angular peak velocities are reached early during the maneuver (after about 40–60 ms). Larger turns are primarily caused by increasing maximal torque (which can be calculated from the angular velocities) and keeping the duration constant rather than by maintaining the same torque for a longer time. Inset shows the exponential drop of angular velocity (turns are rearranged according to peak velocity) with a time constant of about 40 ms. Only six turn classes are shown with peak velocities in the range of 600°–1700°/s, corresponding to turn sizes of 40°–140°

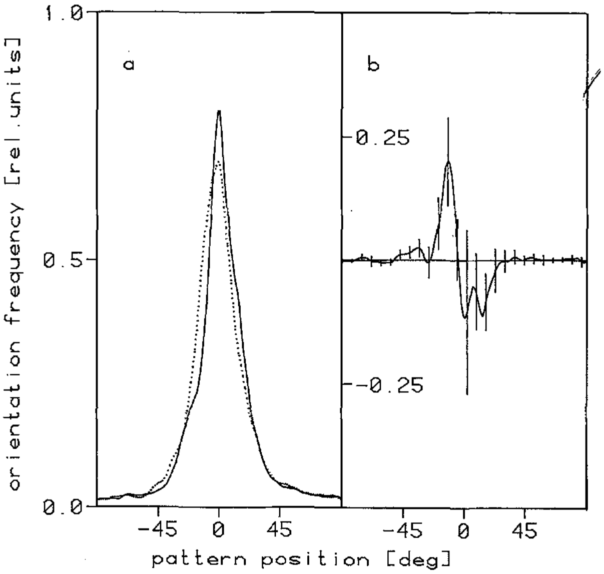

Fig. 8. **a** Frequency histogram of orientation in relation to a single black stripe (width 5°) placed at position 0° during no-bias (continuous line) and bias conditions (dotted line; torque-bias was directed towards negative angles). Mean difference of mean orientation angles (bias minus no-bias) amounts to $-2.5 \pm 1.5°$ (SEM; 21 pairs of measurements from 10 flies). **b** Calculating for each fly a difference function of orientation (bias minus no-bias) results in a significant mean difference function (SEM)

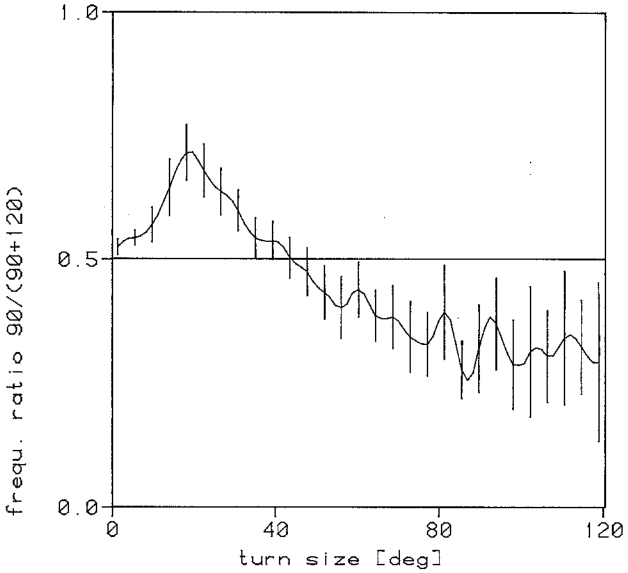

Fig. 9. Pattern dependency of turn size. The ratio of the mean frequency of turns measured with the 90° pattern wavelength compared to the sum of turns measured during both tests (90° and 120° pattern wavelength) is shown as a function of turn size. Data suggest a correlation of turn size with pattern wavelength (SEM; 44 measurements with both the 90° and 120° pattern wavelengths)

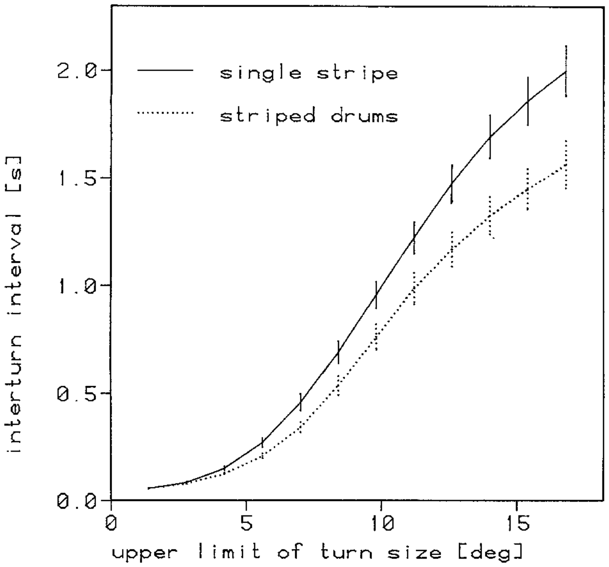

Fig. 10. Mean interturn interval as a function of the upper limit of turn size. For a given upper limit of turn size the function represents the mean time by which two turns equal to or bigger than the limit are seperated. Data are presented in two groups according to the visual patterns used. Single stripe and striped drum data differ significantly (SEM) indicating smoother flight behavior with the single stripe

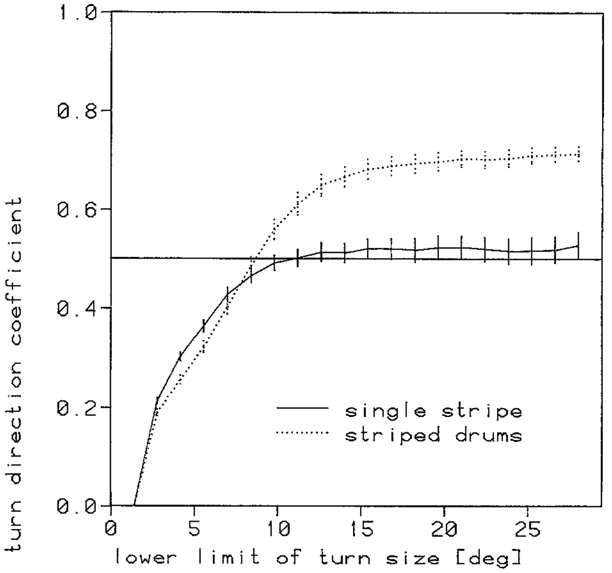

Fig. 11. Probability of a turn having the same direction as the 'preceding' one (turn direction coefficient) is shown as a function of a lower limit of turn size. For a given turn size limit all turns smaller than the limit are ignored. Thus the size of the preceding turn must be equal to or bigger than the respective turn size limit. With striped drums larger turns (body saccades) depend on the preceding one so that the direction is maintained more often than changed

dance with Fourier spectra evaluated by Heisenberg and Wolf (1988, this vol.) from corresponding measurements using the torque compensator. This difference in flight behavior can also be shown by referring to the overall turn angle (sum of all angular displacements irrespective of their direction). Single stripe flight traces result in a significant (SEM) lower overall turning angle (single stripe, 85.3±5.2°/s; striped drums, 106±9.4°/s and 116±22.5°/s).

Figure 11 shows a further pattern-dependent difference in flight behavior. The probability of a turn having the same direction as the 'preceding' one (turn direction coefficient) is shown as a function of a limiting turn size. For a given limit all turns smaller than the limit are ignored. Thus the size of the 'preceding' turn must be equal to or larger than that limit. Larger turns (body saccades) depend on the preceding one in such a way that the direction is more often maintained, resulting in an accumulation of turns in the same direction. As there is a strong orientation preference with the single stripe (Fig. 8a) this presumed searching behavior (Heisenberg and Wolf 1984) is rare in the case of the single stripe but can readily be observed with striped drums.

Influence of a constant torque bias

For studying the capabilities of the course control system, flies were exposed to a constant torque bias of 10^{-9} Nm. This torque bias corresponds to about 25% of the flies' mean maximal torque and would produce a constant final angular velocity

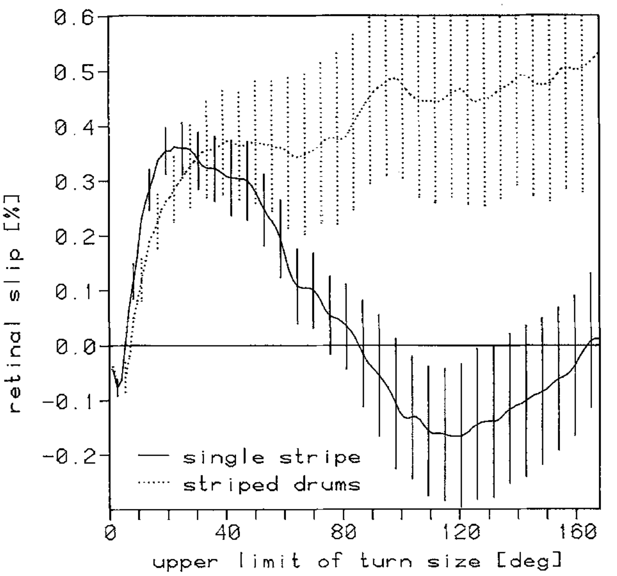

Fig. 12. Slip during bias conditions as a function of upper limit of turn size. For a particular limit all turns smaller than this limit are summed according to their size and direction to give a net turn angle. The slip function approaches the final residual retinal slip. Torque bias of 10^{-9} Nm corresponds to a constant angular velocity of 1000°/s (100% retinal slip). Single stripe data reveal an additional slip compensation process by larger turns (body saccades)

of 1000°/s (assuming an air friction coefficient of $k_{tp} = 5.7 \times 10^{-11}$ Nms). Flies very effectively compensate for this bias. There is only a small shift detectable in the orientation histogram with a single stripe comparing bias with no-bias situations (Fig. 8a). The difference between the mean angles of orientation (bias minus no-bias) amounts to $-2.5 \pm 1.5°$ (SEM; 21 measurements; bias was directed to negative angles). Calculating a difference histogram (bias minus no-bias) for each fly results in a significant (SEM) mean difference function (Fig. 8b). One might argue that the slight position shift could perhaps be caused by static bending of the flies' abdomens during the torque bias. However, the following analysis also reveals dynamic influences. The histogram of turn size (like Fig. 4 but split according to clockwise and counterclockwise turns) during constant bias can be used to investigate how much the different size classes contribute to retinal slip. For this purpose the slip as a function of the 'upper limit of turn size' is calculated by summing all turns smaller than this limit according to their size and direction to give the net turn angle. With increasing limits the slip function approaches the final residual retinal slip (Fig. 12).

Flies compensate for the constant torque bias to a high degree. With striped drums as visual patterns a residual retinal slip of 0.5% is found. The single stripe experiments show that small turns (<20°) generate about as much slip as in the experiment with striped drums, but flies compensate the slip with larger turns (body saccades). These have about a 3:2 tendency to be directed against the bias. Thus, for the single stripe an additional position control mechanism must be invoked by which the polarity of larger turns is influenced. Nevertheless, the bias dependency demonstrates an internal representation of zero torque.

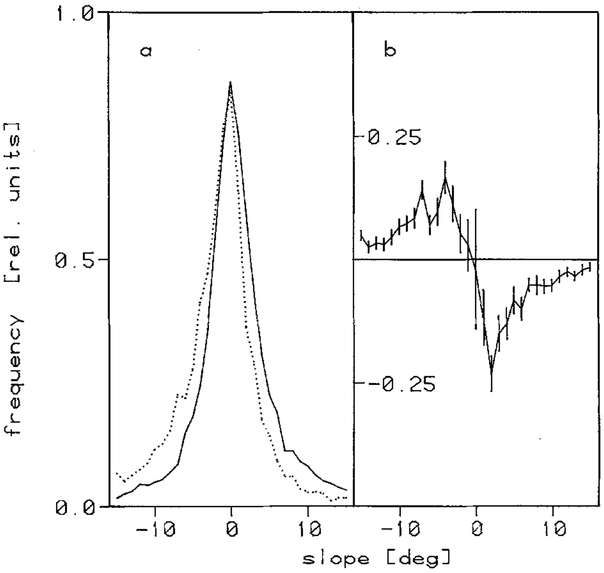

Fig. 13. **a** Mean slope distributions of flight periods during bias (dotted line; bias was directed towards negative angles) and no-bias conditions (continuous line). Analysis is confined to flight periods containing only turns smaller than 15° in size and last for 1 s; such periods account for more than 50% of total flight time. The slope of each flight period was evaluated by linear regression. Mean difference of mean slopes (bias minus no-bias) amounts to $-3.6 \pm 3.1°$/s (SD). **b** Calculating for each fly a difference function of slope distributions (bias minus no-bias) results in a significant mean difference function (SD). Bias slope distributions evaluated during the first half of the flight trace (0–1.5 min) closely resemble those measured during the second half (1.5–3 min; data not shown)

Simulations of constant-bias conditions

Assuming a simple velocity control mechanism (retinal slip speed model) to underlie the process of constant-bias compensation, one has to postulate that during bias conditions a mean slip is superimposed on the orientation trace. The slope distribution of bias flight traces should be shifted in parallel by a corresponding amount compared to no-bias slope distributions. To test this assumption flight periods during both bias and no-bias conditions were analyzed by evaluating their slope using linear regression analysis (slope distribution, Fig. 13). The bias slope distribution is not shifted

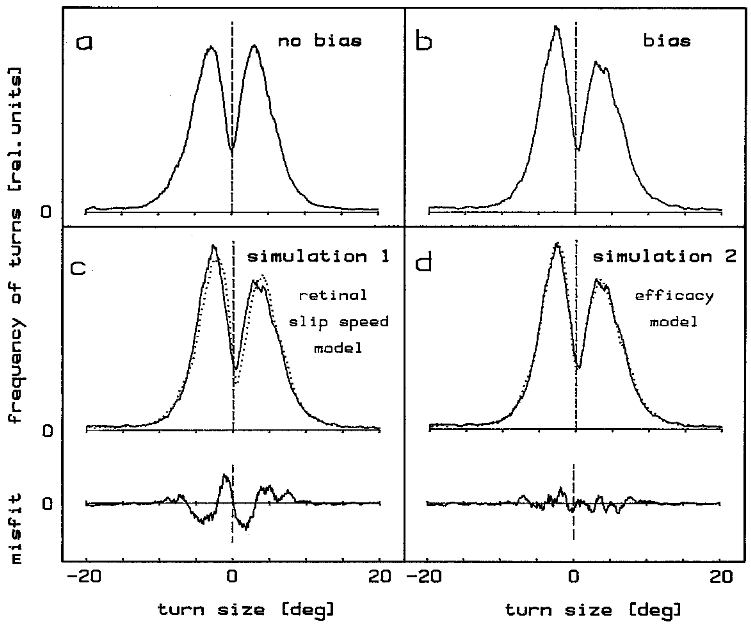

Fig. 14a–d. Torque compensator experiments. **a, b** Turn histograms of bias and no-bias torque traces. **c, d** No-bias torque traces are used in two simulations (dotted lines) to match the turn histogram of bias torque traces (continuous lines). Simulation 1 (retinal slip speed model) which assumes a constant mean retinal slip (6.0°/s) is not as satisfactory as simulation 2 (efficacy model) where an efficacy factor $e = 1.12$ is used. Each no-bias torque value $T(t) > 0$ ($T(t) < 0$) is multiplied (divided) by the factor. The misfit function shows the difference of the bias turn histogram and the respective simulation. (Running average range ±0.5°. Data are based on eight flies each tested for 4 min with and without rotatory bias)

in parallel but is tilted with respect to the no-bias condition. Thus, the data do not support the retinal slip speed model.

Corresponding investigations with the torque compensator strengthen this view (Fig. 14; note that a constant torque bias in the thread paradigm is equivalent to a rotatory bias, i.e., a constant angular velocity added into the closed loop, with the torque compensator). The histogram of turn size evaluated during bias situations (Fig. 14b) suggests that turns in (against) the direction of the bias tend to be enlarged (reduced) in size. However, shifting the zero-torque level of no-bias torque traces according to a retinal slip speed model does not give a satisfactory simulation of the results obtained under bias conditions (simulation 1; Fig. 14c). On the other hand, treating no-bias torque traces so that each torque value measured in (against) the direction of a hypothetical bias is reduced (enlarged) by division (multiplication) with an efficacy factor ($e = 1.12$; efficacy model; simulation 2; Fig. 14d), one can closely match bias torque traces and the corresponding turn size histograms.

In order to compare the data to those obtained in the thread paradigm a slip function (see also Fig. 12) was calculated for the bias torque traces and for the simulation (efficacy model) from no-bias traces (Fig. 15). For small turns (<15°) the match is nearly perfect; for larger ones the simulation deviates from the data. However, since the slip function is based on an integrative procedure deviations accumulate. A further evaluation of the bias torque traces and their simulation shows that even for large turns the efficacy model provides a good approximation to bias conditions (Fig. 16). Figure 16a shows turn histograms arranged according to the maximal torque measured during the respective turn. Figure 16b gives the difference function for the occurrence of turns in and against the direction of the bias. In this plot, again, the

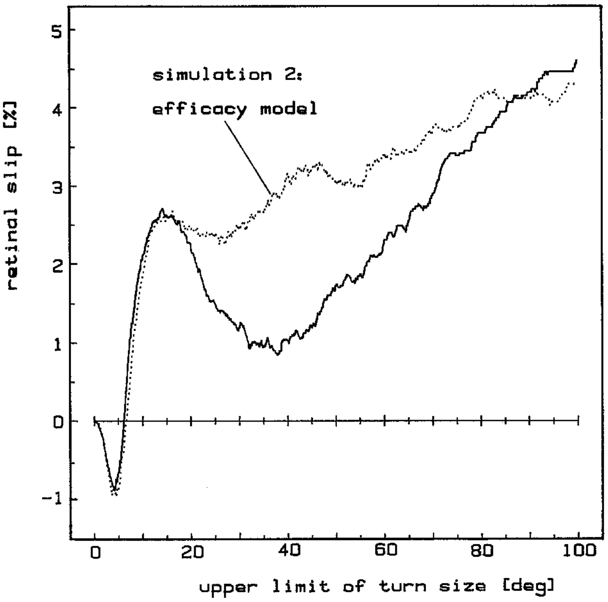

Fig. 15. Torque compensator experiments: slip function (see Fig. 12) of bias torque traces (continuous line) and no-bias torque traces treated according to the efficacy model. 100% retinal slip corresponds to 110°/s (equivalent to a torque of 10^{-9} Nm)

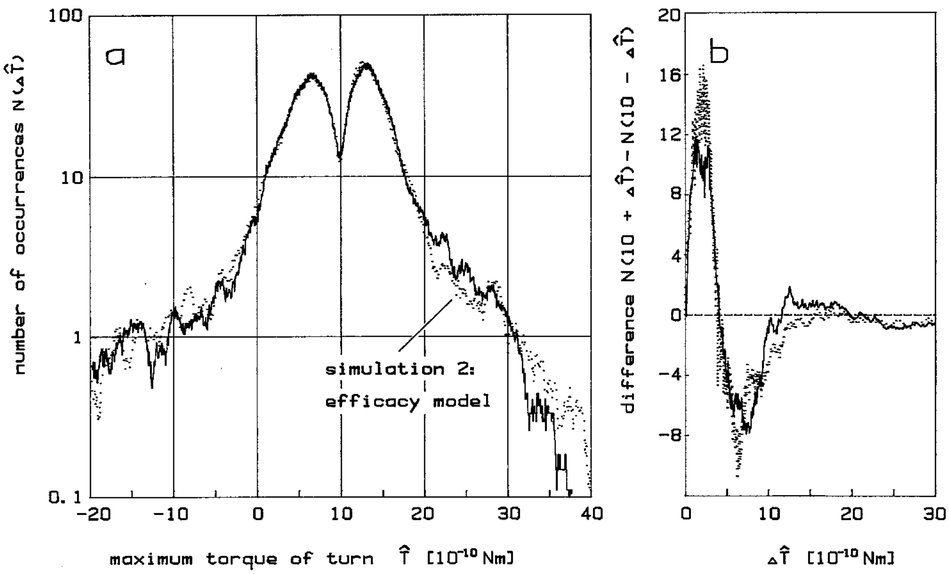

Fig. 16a, b. Torque compensator experiments. **a** Turn histograms (note the logarithmic scale) of bias torque traces (continuous line) and simulation 2 (efficacy model; dotted line) arranged according to the maximal torque measured during the turn (running average range $\pm 0.5 \times 10^{-10}$ Nm). **b** Differences of turn histograms with respect to the compensation level 10×10^{-10} Nm

simulation closely matches the bias data. As turn size depends on both duration and torque amplitude we can now conclude that torque amplitude is the most important parameter for successful simulation. Turn duration seems to be of minor importance. Comparing no-bias with bias torque traces, the fraction of time for which torque is below the theoretical level of compensation changes from 0.505 to 0.526. This difference is not accounted for in the present form of the efficacy model. It may indicate that turn duration does play a role as well. The total numbers of turns during bias (14731) and no-bias conditions (14752) are surprisingly similar.

Discussion

Comparison of torque compensator and thread paradigm experiments

Visual orientation behavior as recorded using the thread paradigm in many aspects resembles that measured with the flight simulator (torque compensator). The low coupling coefficient in the torque compensator simulating unnaturally high air friction seems to have no major effect on the fly's performance except that, in percentage terms, the net retinal slip during bias conditions is about 10 times as large as in the thread paradigm. This general result corroborates our original assumption that meaningful behavior can be observed at the torque compensator.

Body saccades

Our statistical turn analysis disregards the temporal context of flight traces. Nevertheless, it distinguishes two types of turns according to their size-dependent frequency distribution. This is in accordance with a distinction between a mechanism for stabilizing (optomotor balance) and a mechanism for changing the direction of flight (body saccades) proposed by Heisenberg and Wolf (1979, 1984)[1]. Similar results have recently been described for *Musca* (Wagner 1986). The frequency histogram of turn sizes evaluated from free flight episodes of *Musca* (Wagner 1986) corresponds qualitatively to those measured with *Drosophila* in this study.

Body saccades on the thread seem to have a larger time constant for the decline of angular velocity than body saccades in free flight (Bülthoff et al. 1980). If this difference is significant it might be explained by taking into account that in free flight body posture can be changed and, hence, the moment of inertia may be smaller than in our experiments. In the thread paradigm we have measured the moment of inertia and also an upper limit for the air friction constant k_{tp}. Torque compensator measurements show that torque spikes under most conditions have no undershoot below baseline. If this applies to the torque during body

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[1] Our turn histograms, indicating the frequency of body saccades from many flies to decrease exponentially with increasing size, do not contradict the statement of Heisenberg and Wolf that body saccades of single flies have a typical fly-specific size

saccades in the thread paradigm as well, the velocity decline also provides a lower limit for the air friction constant.

Influence of visual patterns

The most conspicuous influence of the visual patterns on behavior in the thread paradigm is the pronounced orientation preference towards the single stripe and the lack of orientation preference in the case of the three (or four) stripes in the striped drums. With the periodic gratings of low contrast as panorama, flies seem to have no tendency to keep the individual stripes in a frontal position. In addition, flight traces recorded in the single stripe arena are smoother than those measured in the striped drums (Fig. 10). Bausenwein et al. (1986) have shown in open-loop studies that yaw torque responses to single stripes and to periodic gratings are mediated by different perceptual subunits. In the present study the difference in the performance in the striped drum and the single stripe arena may in part reflect the properties of these subunits (for perceptual subunits in *Musca* see Geiger and Nässel 1982; Hausen and Wehrhahn 1983; Wagner 1986; Egelhaaf 1985).

Previously no influence of visual patterns on the size of torque spikes had been detected in the flight simulator (R. Wolf and M. Heisenberg, unpublished). Turn analysis now shows that in the thread paradigm the pattern wavelength in the striped drum does affect body saccade size. This is remarkable considering that no orientation preference with respect to the edges of the stripes is observed and that body saccades of the same size as (or of half the size of) the pattern wavelength seem not to be particularly favored.

In the thread paradigm with the single stripe the torque bias causes a slight shift of the peak of the orientation histogram (Fig. 8). This shift alone might be interpreted as proof of a position control mechanism. Turn analysis, however, reveals that with the single stripe the fly allows for as much retinal slip as with the striped drums if only small turns are considered. Position control in the single-stripe arena is provided by the tendency of body saccades to be directed against the bias. Thus the shift of the peak in the orientation histogram seems to reflect higher-order position control.

Zero-torque reference and efficacy factor

The results obtained during constant-bias situations demonstrate an internal zero-torque reference. Data are in agreement with the assumption that deviations of torque from the compensation level are condensed (stretched) if they are directed against (towards) the zero reference. The successful simulation of an arbitrary bias with an efficacy factor suggests that this factor is a function of the bias applied. This function is not yet known. Pilot experiments under different conditions indicate that the efficacy factor may depend, in addition to on the bias, on other variables such as visual pattern and coupling conditions – compare for instance slip functions obtained in the thread paradigm (Fig. 12) and with the torque compensator (Fig. 15).

Efficacy model for constant bias compensation

Our data do not support the retinal slip speed model and the successful simulation of the bias conditions using the efficacy factor suggests a different model. This model is based on two important features:

1. The application of the efficacy factor requires the setting of a 'baseline of torque' above (below) which torque is divided (multiplied) by the factor. This baseline of torque coincides with the bias applied.

2. Bias torque traces can be predicted from no-bias torque traces, thus flies generate the same flight maneuvers during bias and no-bias situations. However, these turning maneuvers are increased in one direction and reduced in the other. The retinal slip measured during a bias situation is caused by this asymmetry.

One of the reasons why this slip is not compensated by the fly with striped drums as visual patterns might be that body saccades are under directionally selective reafferent control (Heisenberg and Wolf 1979). During a torque spike (body saccade) in closed-loop conditions the fly does not respond to additional visual stimulation in the same direction, but a displacement in the opposite direction causes a fast vigorous turning response. The main effect of constant bias in our model is nothing but an enlargement of turning maneuvers in one direction and a reduction in the other. Thus, at least for the retinal slip caused by larger turns, it is a reasonable assumption that the fly does not compensate because these maneuvers are under reafferent control. It is now possible to propose a similar directionally selective reafference control mechanism for small turns. This view is supported by independent studies (Heisenberg and Wolf 1988, this vol.). The results presented here are, so far, applicable only to constant-bias conditions. The dynamic characteristics of the bias compensating system remain to be investigated.

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