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FLIGHT PERFORMANCE AND VISUAL CONTROL OF FLIGHT OF THE FREE-FLYING HOUSEFLY (*MUSCA DOMESTICA* L.)

III. INTERACTIONS BETWEEN ANGULAR MOVEMENT INDUCED BY WIDE- AND SMALLFIELD STIMULI

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CONTENTS

The flights of free-flying houseflies are analysed in different behavioural and environmental situations. The angular movements about the vertical body axis are characterized by a cascade of steplike changes of long axis orientation ('turns'). Most of these turns are separated by periods of little or no rotation. Turns about the vertical axis are short (under 120 ms). They are performed at angular velocities of up to about 4000 deg s^{-1}. These characteristics are found (i) when a single fly cruises in a stationary environment; (ii) if the visual input is eliminated; (iii) if a textured surround (optomotor stimulus) is moved around the fly; (iv) during visually guided pursuit of small targets in stationary as well as in moving environments.

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Optomotor stimulation increases the number of turns in the direction of pattern motion relative to those against it. This leads to a correlation between the average angular velocity of the fly and the stimulus velocity. However, optomotor stimulation does not interfere with chasing and tracking. A model is proposed that qualitatively accounts for the observed behaviour in free flight of houseflies.

1. Introduction

Researchers in the field of insect behaviour have for long been interested in the visual control of angular movement (for example, Stellwag 1916; Gaffron 1934; Tonner 1938; Mittelstaedt 1949; Hassenstein 1951; Reichardt 1961; Fermi & Reichardt 1963; Varju 1975; Collett & Land 1975; Reichardt & Poggio 1976). While most of the previous quantitative investigations have concentrated on either walking or tethered flying animals, the turning behaviour of free-flying houseflies (*Musca domestica* L.) is analysed in this paper.

During flight an insect has six degrees of freedom to move its body. It may rotate about the three body axes and may translate along these axes. Internal asymmetries as well as external disturbances would cause deviations from an intended course, if control systems did not act as correcting mechanisms. The optomotor response is such a control system (for a review see Wehner 1981). If, for example, external forces cause a fly to drift from its course, a shift of the image of the environment on the eyes takes place. This signal (slip speed) is fed into a negative feedback loop. The resulting turn is supposed to lead to a stabilization of the flight course. During flight, however, the course is not only controlled with respect to the stationary environment: houseflies, in addition, perform visually guided aerial pursuits of small targets (Wehrhahn 1979). Thus, object motion as well as self-motion induces retinal signal flow.

In principle, self-motion and object motion can be distinguished by the retinal flow they create (Gibson 1966); self-motion leads to a flow in the entire visual field, whereas object motion is usually confined to a restricted area of the eye. Based on observations in humans and insects von Holst & Mittelstaedt (1950) proposed a feedback loop that provides a separation of 'voluntary' rotations from those caused by external disturbances or internal asymmetries (reafferent control): only during a 'voluntary' turn a copy of the command transmitted to the flight motor centres (efference copy) is supposed to cancel the expected input signals. Although the discussion about this scheme is not finished (MacKay 1973), the physiological correlate, 'corollary discharge' (Sperry 1950), has been reported in some species since then (locust (Zaretsky & Rowell 1979); monkey (Richmond & Wurtz 1980)). In the fruitfly *Drosophila*, Heisenberg & Wolf (1979) have shown that visual input is processed during self-motion. However, the fly reacts differently to additional visual stimulation, if it is (i) in the direction of self-motion or (ii) against it. This behavioural difference was interpreted as showing the action of a kind of (direction-selective) reafferent mechanism. On the other hand, the experiments performed with tethered flying houseflies are fully in accordance with the hypothesis that only the retinal displacements control the behavioural responses (Reichardt & Poggio 1976). During tracking the torque signals induced by both the retinal motion of the target and the surrounding pattern are added. This leads to a second type of interaction, the 'additive model' (Virsik & Reichardt 1976). Tracking performance is impaired by widefield stimuli in this model.

For the purpose of this study flies have been filmed in different situations: when they fly in low as well as in high contrast environments. Flight sequences in which no obvious destination can be detected (cruising flights) as well as visually guided pursuits of targets are analysed. From these data a hypothesis of the interaction of the different control systems is derived which incorporates the ideas of optomotor control, tracking, figure-ground discrimination by relative movement (Reichardt *et al.* 1983; Egelhaaf 1985), and the role of non-visual sensory inputs to the flight motor.

2. Methods and definitions

The flies were simultaneously filmed from two sides with a camera and the aid of a mirror at 100 frames per second (paper I). The two sides of the cage used for filming were made of normal glass. Four sides of the cage (three vertical and the upper side) were covered with beige linen (low contrast environment). To create a high contrast environment, the linen of the three vertical walls was painted with statistically distributed 4 cm × 4 cm orange elements (Julesz 1971). The films were projected frame by frame onto a digitizing table and the position as well as the orientation of the fly's body axes were recorded as is described in paper I. From these data the angular velocities and accelerations were derived.

Although in the examples evaluated in this paper, the inclination and direction of the transverse axis (connecting the two wing bases) could not be reconstructed, this did not critically influence the conclusions. It was shown in paper I that there is a strong linear correlation between the angular velocity values measured under the conditions here and the 'true' values of the angular velocity.

This study is confined to the changes of long axis orientation. The term 'angular velocity' used for reasons of simplicity here does, strictly speaking, refer to angular velocity about the vertical axis.

3. Characteristics of turning

3.1. *Cruising flights in a stationary environment*

Figure 1*a* shows an example of a cruising flight of a female in a low contrast stationary environment as seen from above. The flight path is almost circular, as is indicated by the nearly linear dependence of the horizontal flight direction on time (figure 1*b*, broken line). This is, of course, not a typical flight path. It helps, however, to outline the difference between the changes of flight direction and body rotations. Although flight direction changes smoothly, the fly turns its long axis not at constant velocity, but in a cascadic manner leading to intermittent changes of body orientation with time (figure 1*b*, solid line, figure 3*a*). The time course of the angular velocity is characterized by steep increases as well as decreases without an indication of a plateau in between (figure 3*a*). During such a change of body orientation, termed 'turn' in this study, the angular velocity does not change its sign. Start and end of a turn is defined by either a zero crossing of the angular velocity or by the minimum absolute value of it in between two subsequent velocity peaks. This definition helps to subdivide the turning behaviour into single events. A turn may be characterized by the time it lasts (turning time), the change of orientation it leads to (turning amplitude) and the angular velocity and acceleration reached during it.

By this definition of a turn, events due to imprecise recording (digitizing errors) are not excluded. In the following a quantitative analysis of the turns of cruising females will be

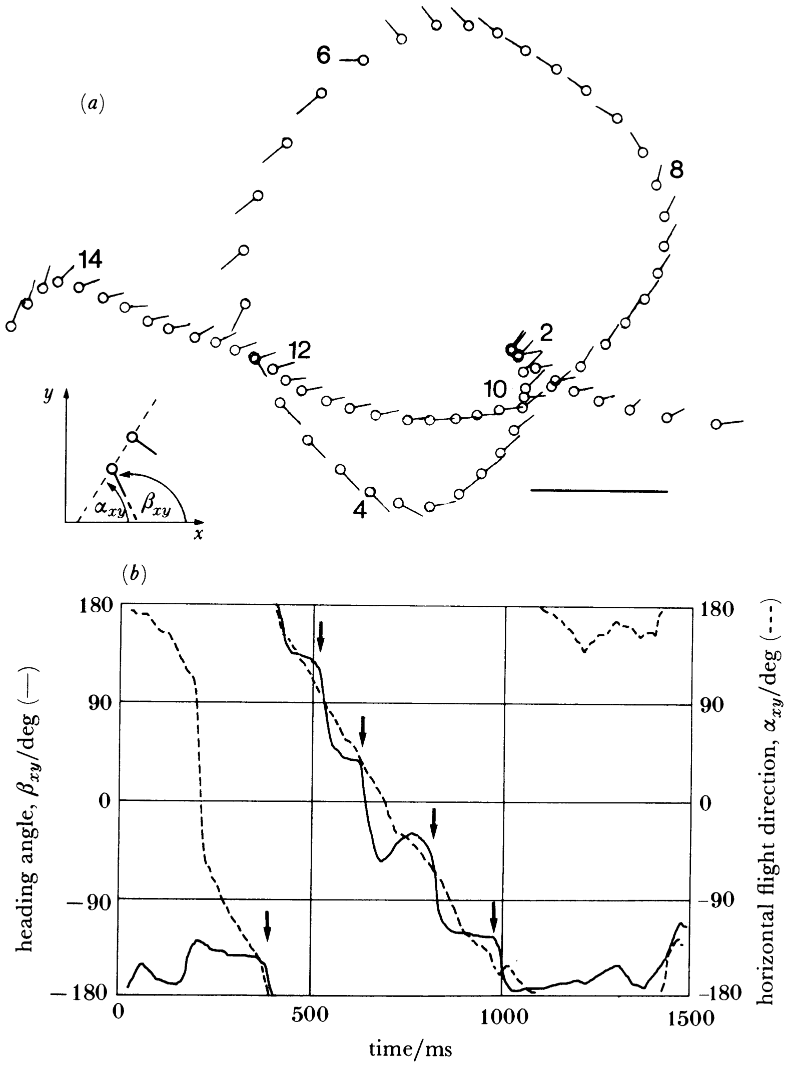

FIGURE 1. Cruising flight of a female fly in a low contrast environment. (*a*) Trajectory: the head of the fly is represented by the circle, the direction of the long axis by the line connected to the head; the time interval between two positions is 20 ms; numbers represent time in 0.1 s; the bar denotes 5 cm; the scene is viewed from above. (*b*) Time course of the horizontal flight direction (broken line) and the orientation of the long axis (solid line); horizontal flight direction is defined as the angle covered by the connection of two successive head positions with an external reference coordinate system (inset); orientation of the long axis is given by the inclination of the fly's long axis to the x-axis of the external coordinate system (inset, paper I). Although the course is circular, the changes of the orientation of the long axis are steplike (arrows).

performed. The aim is to discriminate between 'real' turns and those that can be accounted for by digitizing errors. The source of these errors is twofold; long axis orientation may not be exactly recorded in any frame (amplitude characteristics). In addition, it may happen that an increasing digitizing error in the same direction occurs in consecutive frames. This simulates a change of axis orientation lasting some time (temporal characteristics). To estimate these errors one frame was digitized 128 times (control). In this situation all recorded angular displacements represent digitizing errors. The error distribution is calculated, normalized and compared with the corresponding distribution obtained by the evaluation of cruising flights in females (sample, 1663 frames at a time interval of 10 ms stemming from 20 sequences). Thus, it becomes obvious that all 'angular displacements' of an amplitude of less than 5° can be accounted for with a high probability by digitizing errors. Most of the 'orientation changes' lasting 10–30 ms of an amplitude between 5 and 10° are probably digitizing errors too. The distribution that results from the subtraction of the control values from the sample, represents those events that are probably real turns. This distribution, consisting of 255 turns, is shown in figure 2. It can be seen that the upper value of the turning time is 110 ms in this sample.

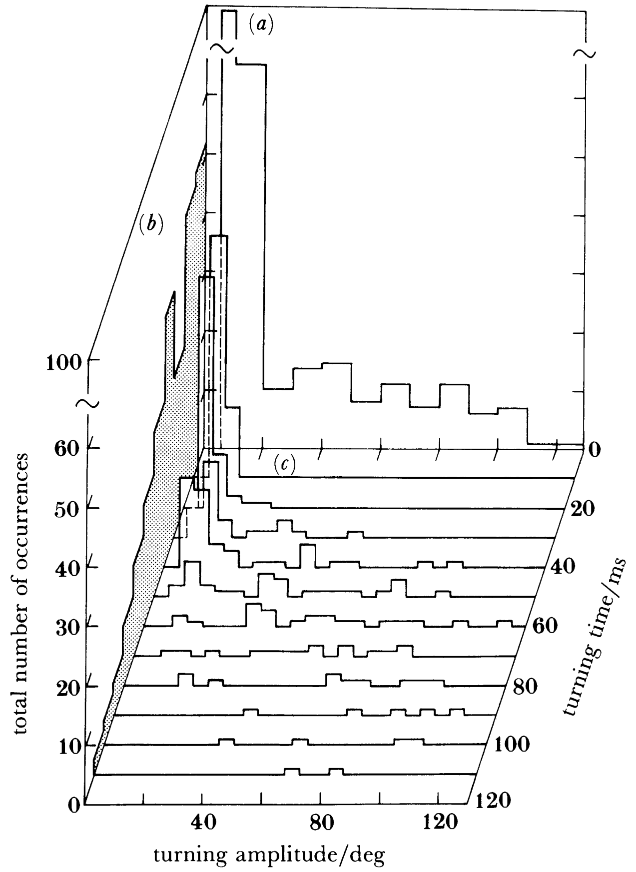

Figure 2. Distribution of turning amplitude (α_v) and turning time (t). (a) Histogram of α_v; (b) histogram of t; (c) distribution of α_v with respect to a particular t. Sample size, 255. The distribution shown here is a difference distribution: at each time interval (step of 10 ms ≡ sampling time) the distribution of sample and control were separately calculated and normalized. Then the percentage difference was derived. The total number denoted here is the product of the percentage difference and the sample size at this particular value of time. Negative values were set to zero. The histogram of α_v shows a nearly equal distribution between 20 and 110°. The maximal t value is 110 ms, its mean value about 40 ms.

The histogram of the turning time (left side) shows a bimodal distribution with maxima at 10 (sampling interval) and 40–50 ms. The mean value is 40 ms. Turning amplitudes of 5–20° are most frequent (posterior surface). Maximum turning amplitude is 125°. The values between 20 and 110° are nearly equally distributed. Peak velocities of up to 1000–4000 deg s^{-1} are usually reached during the turns (figure 3). Angular accelerations of more than 100000 deg s^{-2} can be measured. The turning amplitude is significantly correlated with both turning time and the peak velocity reached during a turn.

In summary, the main characteristics of body rotations about the vertical axis are cascades of quick turns at peak velocities of several thousand degrees per second separated from each other by periods of little or no turning. These temporal characteristics differ considerably from those observed in tethered flight. If tethered *Muscae* fly in a stationary surround and their angular movements have no influence on the motion of the environment ('open-loop experiment'), they spontaneously produce torque fluctuations. In particular a torque in one direction lasting for several seconds can often be observed (time traces see Wehrhahn 1981). In free flight, this would correspond to the generation of an angular velocity in one direction for seconds. In the present investigation such a behaviour has not been observed. The differences might be due to the absent feedback from the visual and other sensory systems (halteres, wind sensitive hairs, antennae) in those open loop experiments. In free flight these feedback loops are closed (that is, angular movements lead to counterrotations of the image of the environment on the retina and may also be registered by the other sensory systems).

One hypothesis, therefore, could be that the time course of the turns in free flight is an effect of the optomotor control circuit being closed during turning. In fact, if the optomotor loop is closed in tethered flight, changes in the sign of the torque response are more frequent than in the situation when the loop is open (Wehrhahn 1980; Reichardt & Poggio 1981). Thus, the angular velocity would change its sign more often in the closed than in the open loop experiments. A change of angular orientation initiated by an internal signal will not be totally cancelled by the counteracting optomotor response, because the delay of this control reaction is not zero, but some 20–30 ms (Reichardt 1979; Wehrhahn 1981). Therefore, during a turn the optomotor reflex could, in principle, lead to a reduction of the angular velocity and terminate a turn. Indeed, peak velocity is reached about 20–30 ms after the beginning of the turn in many cases. However, in contrast to a reafferent scheme, the optomotor system would have to be active during turning.

3.2. *The flight of blinded flies*

The hypothesis sketched above has been tested in an experiment in which both compound eyes and ocelli of the flies have been occluded with black paint to eliminate the visual input. Controls have demonstrated that the flies do not react to visual stimulation. Although the flight activity is reduced, the animals are still able to fly in a manner not obviously different from normal cruising animals. No significant differences are found in the time course of the spontaneous turns in normal and blinded flies (figure 3*b*).

In conclusion, the visual input is not the main source of setting the time course of the spontaneous changes of the long axis orientation in free flight. Since, in tethered flight, long lasting torque fluctuations are seen, other non-visual sensory inputs, which are active during free but not during fixed flight, must be responsible for the difference in the time structure of the turns in tethered and free flight. Possible candidates are the halteres (Sandeman & Markl 1980; Sandeman 1980), which act as high velocity detectors (Hengstenberg 1984).

3.3. *Cruising flights in a moving environment*

To unravel the role of the visual input during free flight, a further type of experiment has been performed. Female flies have been filmed within the contrasted pattern, which has been horizontally moved at 2.5 Hz oscillation frequency (optomotor stimulus). This frequency has been chosen to allow a comparison with behavioural data in tethered flight and electro-

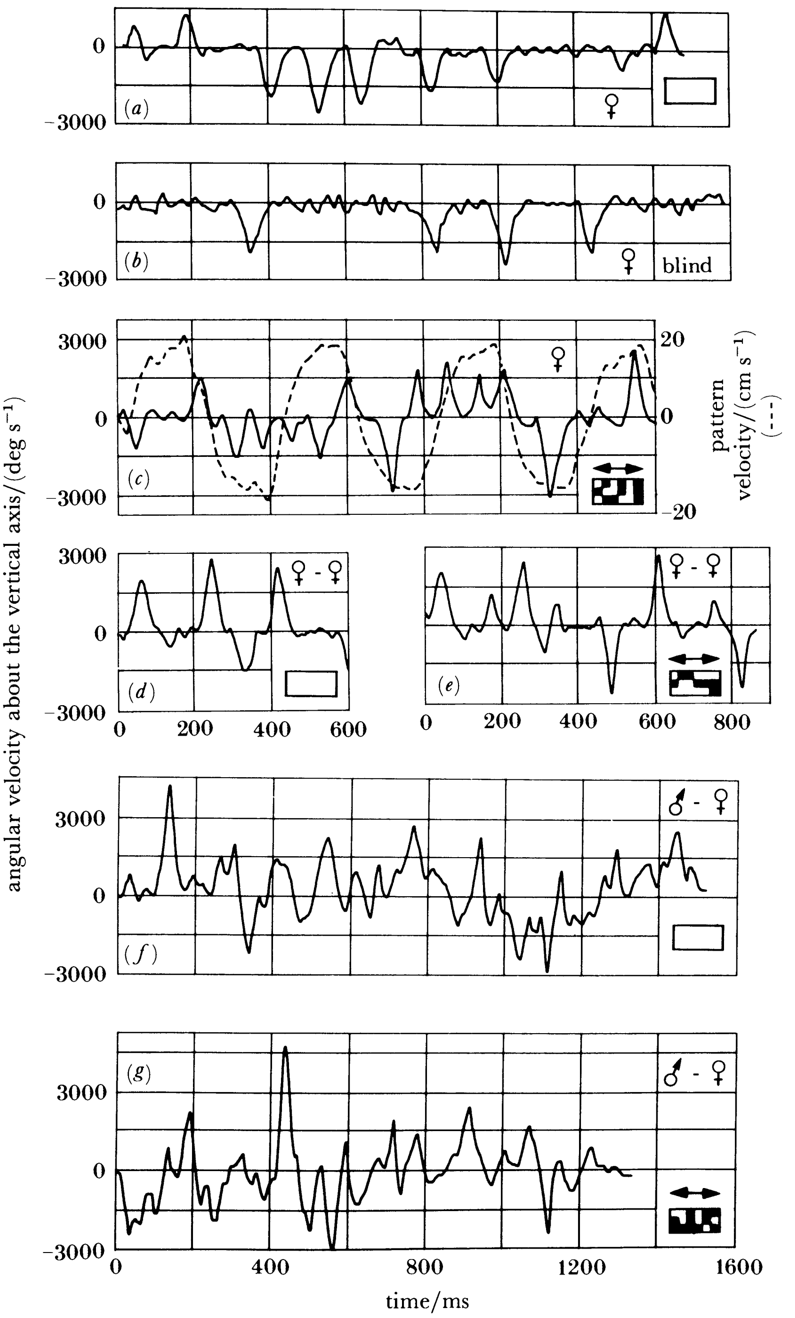

FIGURE 3. Time course of the angular velocity about the vertical axis in different situations; angular velocity is measured in a fly-centred coordinate system as the change of orientation of the long axis from one position to the next (see paper I); the values were smoothed with a binomial filter of order three: (*a*) cruising flight of an intact female; (*b*) cruising female with occluded complex eyes and ocelli; (*c*) cruising female flying in a cage, three vertical walls of which were covered with a contrasted pattern. The pattern moved horizontally at 2.5 Hz oscillation frequency; pattern velocity is shown by the broken line: (*d*) tracking of a female in a low contrast environment; (*e*) tracking female in the situation described in (*c*); (*f*) chasing male in a low contrast surround; (*g*) chasing male in the situation described in (*c*). Although the angular velocity is measured in quite different situations, its main characteristics, cascades of peaks and short duration of the turns, remain constant.

physiological recordings (Reichardt *et al.* 1983; Egelhaaf 1985). From optomotor measurements in tethered flight one would expect the flies to follow closely the movements of the pattern by corresponding angular movements. Peak velocity of the pattern is about 20 cm s^{-1}. The motion of the widefield stimulus induces retinal image velocities of up to 700 deg s^{-1}. It causes optomotor reactions in tethered flight. The influence of pattern motion on the fly's translatory movements will not be investigated here. In figure 3*c* the angular velocity of a fly is shown together with the velocity of the pattern. It is obvious that the time course of the turns is not qualitatively changed if compared with the situations in figure 3*a*, *b*. Especially, no component of the angular velocity that might reflect the pattern velocity can be detected. The rate of turning is slightly increased compared with the situation of figure 3*a* (from 15 turns per second to 19 turns per second) and more turns in the direction of the moving pattern are induced than against it. The mean ratio is about 2.5:1 ($p < 0.001$, χ^2 test). Smooth rotations at low angular velocity are very rarely found. The fluctuations of the angular velocity in figure 3*c* between 60–160 and 1200–1300 ms are such examples. No preference to the direction of the moving pattern is observed during these 'rotations' (χ^2 test). Thus, very surprisingly, the turns seem to be the only indication of an optomotor response.

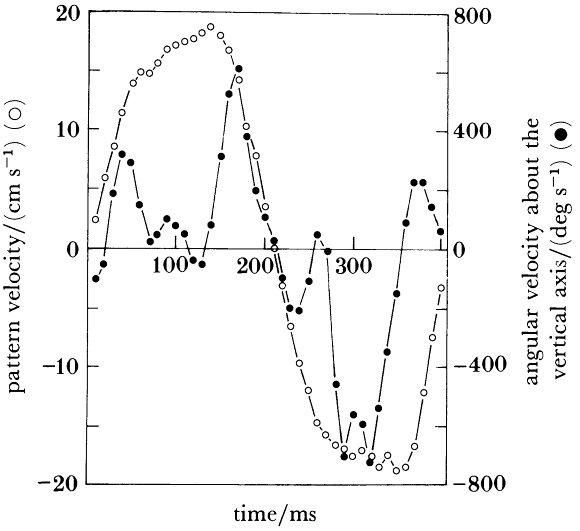

FIGURE 4. Average of eight cycles of pattern movement (○) and angular velocity about the long axis (●) in the situation described in figure 3*c*; a dependence of the mean angular velocity of the fly on pattern movement can be seen. This is because turns are more frequent in the direction of pattern movement than against it.

If, however, several cycles are averaged, a closer dependence of the fly's angular velocity on pattern velocity appears (figure 4) indicating that the turns are not positioned at certain phases of the stimulus cycles. It seems feasible that averaging over much more than the eight cycles of stimulus motion averaged in figure 4 could lead to such a satisfactory correspondence of the time courses of the mean angular and the stimulus velocity that an 'ordinary' optomotor response is pretended. The behaviour of the flies is not qualitatively changed at different oscillation frequencies (1 Hz) or different peak velocities of the pattern (100 cm s^{-1}). In conclusion, visual stimulation cannot be responsible for the time course of the single turns.

3.4. *The time course of the angular velocity during tracking and chasing*

Males and females perform visually guided reactions to targets passing by. Since there are remarkable sex-specific differences in the pursuit behaviour, these sequences are called 'tracks', if a female pursues the target and 'chases', if a male is the pursuer. Figure 3*d*–*g* shows examples of the time course of the angular velocities in four different situations. The angular velocity of the pursuing fly is determined during tracking (*d*, *e*) and chasing (*f*, *g*) in front of a moving high contrast pattern (*e*, *g*) as well as in a low contrast stationary environment (*d*, *f*). In all four situations the temporal characteristics of the single turns are similar to those of female cruising flight. Body rotations are again characterized by a series of peaks in the angular velocity.

For example, even during the curved path of chasing shown in figure 5*a*, the pursuing male does not turn its long axis at constant velocity, but in a cascadic way (figure 5*b*) similar to the sequence in the example of figure 1. Most obvious the range of the angular velocity does not change. However, the rate of turning is raised at least in male chasing.

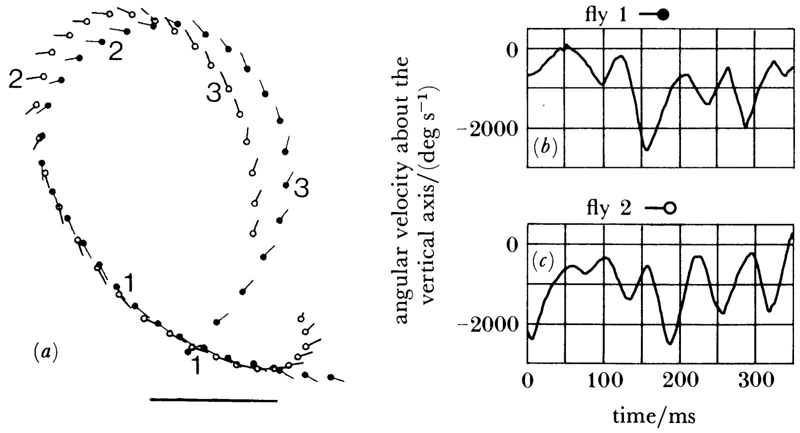

FIGURE 5. Episode of a chase between two males; symbols as in figure 1; the time interval between two positions is 10 ms; the bar denotes 5 cm; the leading male (●) flies a nearly circular curve; the chasing fly (○) closely matches the path, but the orientation of the long axis of both animals does not change at constant velocity (*b*, *c*). Values of angular velocity are evaluated as described in the legend to figure 3.

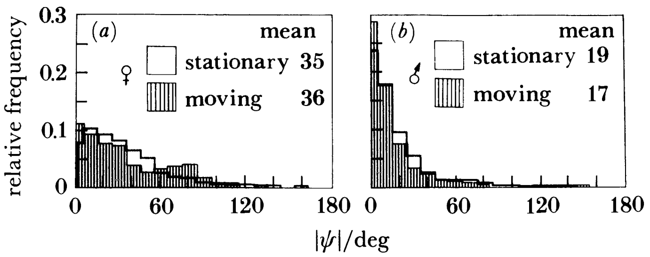

FIGURE 6. Distribution of the horizontal error angle. This angle is defined as the azimuthal deviation of the target from the midsagittal plane of the pursuer and ranges from −180 to +180° (paper II). Absolute values are plotted, because the midsagittal plane is a symmetry plane and the target is fixated frontally. (*a*) Female tracking in a stationary low-contrast environment (□, total number of points, $N = 1203$) and in a moving high-contrast environment (▥, $N = 217$); (*b*) male chasing in the same environments indicated by the same symbols as in (*a*); total number of points 1432 and 305, respectively. The mean deviation from zero error angle is denoted in the plots. No difference in the distributions in moving and stationary surroundings is indicated.

Marked deviations of the target from the frontal part of the pursuer's eye (error angles) occur in all four situations. The retinal target velocities (defined as the differences of two successive values of the error angle divided by the sampling time) are in the range of the measured angular velocities of the flies (for a description of the control systems see paper II). The distributions of the error angles and retinal target velocities might be used as a criterion for the precision of the pursuit. If optomotor stimulation would interfere with tracking and chasing, the mean value should be greater than in the pursuit sequences in a low contrast environment. However, the distributions are very similar, if chasing in a low contrast environment is compared with that in a high contrast moving surround (figure 6*b*). The same seems to hold for tracking (figure 6*a*).

Especially, the mean deviations of the target from the frontal eye part of the pursuer are nearly identical (figure 6*a*, *b*). The distributions of the retinal horizontal target velocities which are not shown here are also very similar. Thus, the pursuits seem not to be disturbed by a moving environment.

4. Discussion

In free flight the turns of houseflies are short and are performed at high angular velocities (figures 1–3). Turning amplitudes of 20–110° are almost equally distributed (figure 2). Long-lasting angular movements at constant velocity are found neither spontaneously nor in response to external stimulation. An optomotor stimulus (widefield motion) influences the turning behaviour so that more turns are performed in the direction of the stimulus motion than against it (figure 4). However, tracking and chasing of small targets in stationary and moving environments do not seem to be different (figure 6). Thus, the effect of widefield stimulation is much weaker than the reaction to the smallfield stimulus (target). Since optomotor stimuli cause only weak reactions in free flight (see also figures 3*c*, 4), all free flight data are consistent with each other. Nevertheless, the influence of widefield stimulation on the rotations is surprising, because it differs from results found in tethered flying houseflies (Virsik & Reichardt 1976) and free flying hoverflies (*Syritta pipiens*) rotating at low angular velocity (less than 100 deg s^{-1}) (Collett 1980*b*). In those experiments the reaction of the flies has been proportional to the velocity of the widefield pattern (control of slip speed) and a strong influence of widefield motion on tracking has been observed.

Questions that demand an answer are: why are no long lasting turns at moderate angular velocities induced during free flight? Why is tracking and chasing not influenced by widefield stimulation? What is the source of the observed difference in tethered and free flight? These questions are tackled in the following sections and the block diagram of figure 7 is a summary of the considerations.

4.1. *The time course of the turns*

Turns in free flight may be induced, for example, by internal signals and visual or other external stimulations (figure 7). In the different situations examined here, the time course of the angular velocity has been similar. In this study the widefield pattern has been regularly moved, thus providing a defined stimulus. Therefore, the considerations of this section are explained along this stimulation.

Widefield motion induces an optomotor turning reaction in free-flying *Musca* that may be characterized by quick turns of variable amplitude in the direction of the moving stimulus (figure 3*c*). This is phenomenologically similar to the saccades in the direction of the moving pattern found in *Syritta* sometimes interspersed with the smooth changes in angular velocity (figure 5 in Collett 1980*a*). Contrary to the expectations the angular velocity of *Musca* is not proportional to the stimulus velocity. A control of slip speed has not been found. How can these pecularities be explained?

The motion-sensitive cells that are supposed to be the main output elements of the neuronal network underlying the optomotor response are the horizontal cells of the lobula plate (HS-cells) (Hausen 1982*a*, *b*; Hausen & Wehrhahn 1983). The main response of these cells to ipsilateral stimulus motion from front to back is a graded depolarizing potential. This response quickly reaches a plateau which is maintained throughout the duration of the stimulation (Hausen 1982*a*). Thus, the HS-cells could induce the turns, but do not seem to be responsible for the time course of them.

It is assumed here that the action of the halteres is responsible for this characteristic (figure 7). The halteres are gyroscopic organs (Fraenkel & Pringle 1938) that are able to detect high angular velocities (over 200 deg s^{-1} Hengstenberg 1984). Their output is fed into the flight motor (Sandeman & Markl 1980). Thus, their signal could be adequate to terminate a turn. The haltere signal can reach the flight motor in 2–3 ms (Sandeman & Markl 1980). In free flight the angular velocity increases for 10–40 ms. Only after this delay can a haltere action be seen.

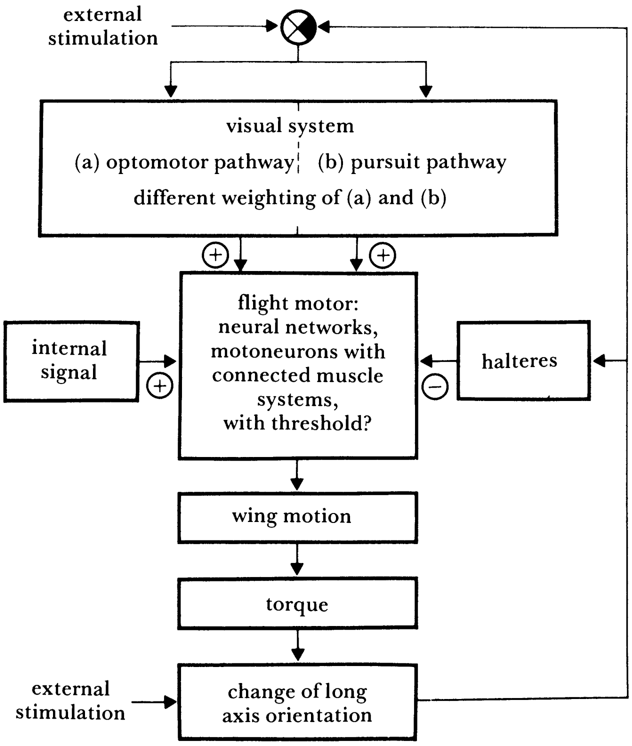

FIGURE 7. Speculative block diagram for the control of angular movement in flies; three different components (visual system, haltere system and an internal signal) feed their signals into the torque-generating unit of the flight motor. The output of this unit is transmitted to the steering muscles by motoneurons. Whether a threshold mechanism is active is not quite clear. The torque generated in this way leads to a change in the orientation of the long axis which is signalled by the sensory systems. The weight of the two visual subcircuits is different to explain the results. Possible mechanisms are discussed in the text. This model produces short time angular movements because the visually induced response is supposed to stimulate the halteres in any case. These terminate body turning after a short time interval. For further explanations see text.

It seems feasible, however, to attribute this delay to (i) the dependence of the gain of the haltere signal on the angular velocity (Hengstenberg 1984); (ii) summation effects in the muscle system (Sandeman 1980) and (iii) the fly's moment of inertia. In the natural environment image flow over the whole eye occurs normally only in cases of self-motion. Therefore, it is understandable that the feedback loop of the halteres reduces the angular velocity to zero and does not leave a visually induced slow component (figure 3*c*). On the other hand, the observations can be hardly explained with a simply visually driven reafferent mechanism or the additive model. However, the fly must cope in some way with its self-generated image motion, otherwise it could not fly straight along a wall which has contrast.

Periods of little or no turning are observed although the stimulus motion is not interrupted. One possibility that could create the sequence of turns and pauses is a threshold mechanism. Such a mechanism must not prevent the generation of different turning amplitudes (figure 2). In addition, turning amplitude is related to the retinal position and velocity during pursuit (paper II). A physiological correlate for this threshold is not yet known.

The difference between the 'smooth' torque output during tracking and figure-ground discrimination experiments in tethered flight (Virsik & Reichardt 1976; Reichardt *et al.* 1983) and the turns at a much higher angular velocity than the stimulus velocity observed in free flight cannot be explained at present. Perhaps the result of figure 4 is the key that will resolve this problem. The recordings in tethered flight have been obtained from averages. In this context, it should be remembered that McCann & Fender (1964) have observed that averaging may alter the time course of the visually induced yaw-torque response. It seems to be worthwhile to investigate optomotor reactions in tethered flight, without averaging, with stimuli equal to those in free flight, use the same conditions to recordings from the HS-cells and compare the results with each other and with the free flight data.

4.2. *Pursuit of targets and the optomotor stimulus*

The influence of the target and the widefield stimulus on the generation of yaw-torque must be differently weighted during pursuit, because tracking and chasing seem to be not significantly influenced by the optomotor stimulus used here. The data can be explained if two pathways, one for the processing of the widefield stimulus (optomotor pathway) and the other for the smallfield stimulus (pursuit pathway) are assumed (figure 7), because a different weighting can be easily accomplished in separated networks. In fact, two pathways for the control of yaw-torque in *Musca* females have been postulated from quite different experimental approaches (Geiger & Nässel 1982; Hausen & Wehrhahn 1983; Egelhaaf 1985). Although there is a marked difference in the pursuit behaviour in males and females, the model shown in figure 7 does not distinguish these peculiarities. The notion 'pursuit pathway' is simply used. The sex-specific differences are discussed in paper II.

Several mechanisms could achieve the different weighting. First, the gain (conversion factor of input to output) in the pursuit pathway might be so high that the output of this system masks the optomotor response during pursuit. This could be achieved by an inhibition of the optomotor pathway by the pursuit pathway or by a selective enhancement of the signal of the pursuit pathway. The turns of *Musca* often lead to a quite precise fixation, especially in males (paper II). Therefore, the gain of the pursuit systems seems to be quite well adapted to the task of fixation. On the other hand, the optomotor reaction, when the flies do not pursue targets, is much weaker than the reaction to the target during pursuit. Thus one may doubt that an active inhibition takes place. Such a phenomenon has also not been observed in tethered flight

(Virsik & Reichardt 1976). The following hypotheses, considering the dynamic aspects of flight behaviour, might explain why the optomotor gain is low in the free-flight experiments reported here.

Land (1975) argued that the head saccades of *Calliphora* might be so fast that they lie outside the operating range of the optomotor system. The turns of *Musca* are performed at even higher peak velocities that the head movements of *Calliphora*. If, now, the pursuit system were more sensitive in the high velocity range, a separation of widefield and smallfield motion could be achieved. This proposal is, however, highly speculative, because (i) all neural networks probably obtain the same motion detector input; and (ii) electrophysiological recordings have not yet been performed with stimuli moving so fast as in free flight.

In the last hypothesis to be discussed here it is also assumed that the optomotor and pursuit pathway have different dynamic properties. It is proposed that the gain of both neuronal networks depends on the turning frequency of the flies (the changes of the sign of the angular velocity). If the gain of the optomotor system will decrease at lower turning frequencies than that of the pursuit system, the interference of widefield stimulation with tracking and chasing would be strongly reduced at high turning frequencies. Indeed, Collett (1980*b*) found a different dynamic tuning for the optomotor reflex and the pursuit system in the hoverfly *Syritta*. When he oscillated a widefield pattern around the males the gain of the optomotor system remarkably decreased if the frequency was higher than 1 Hz. In contrast, the gain of the pursuit system seemed to be independent of the oscillation frequency up to 6–10 Hz. It is interesting to find a similar behaviour in *Musca*, too. Preliminary experiments of Egelhaaf (1985) indicate that the torque response to a moving widefield pattern measured during tethered flight is maximal if the pattern is oscillated at 0.5 Hz. In contrast, the torque reaction to a stimulus consisting of a small figure moving relative to the surrounding pattern shows a characteristic peak at higher oscillation frequencies. The amplitude of the peak is maximal at about 4–8 Hz oscillation frequency. The response of the widefield optomotor and smallfield selective cells of the lobula plate did not reveal these differences (Egelhaaf 1985). Therefore, the tuning must result from the neural processing of the signal after the lobula plate output.

In free flight up to 5–10 changes of the sign of the angular velocity occur per second (figure 3*d*–*f*). Commonly the turning frequency during cruising as well as during pursuit is well beyond one change of sign per second. Thus, most examples could easily be explained with this hypothesis. One feels, however, a little bit uncertain when inspecting figures 3*a*–*c* and 5. Figure 3*a* represents a seldom case and in both Figure 3*c* and 5 the turning frequency is greater than 1 (in figure 5 only the last part of the chase is shown).

At present it is an open question which mechanism is actually implemented in the neuronal networks of *Musca*. Therefore, the block diagram of figure 7 remains very unspecific with respect to this point. It should be mentioned here, that similar diagrams have been proposed by Land (1975) and by Hengstenberg (1984). These authors, however, emphasized the control of head movements, which is not specified in figure 7, and not the different visual pathways underlying smallfield and widefield stimulation.

Finally an interesting feature of the last hypothesis will be mentioned. If the different dynamic tuning of the two pathways is taken into account, the efference copy model and the additive model, mentioned in the Introduction, become equally effective at high turning frequencies, because the gain of the optomotor system is low then and the disadvantage of the additive model vanishes.

4.3. *Turns of Musca and similar observations in other fly species*

Part of the turning characteristics of flies have been interpreted as body saccades (Collett & Land 1975) or torque spikes (Heisenberg & Wolf 1979) from their apparent similarity with the human saccadic system. Torque spikes of *Drosophila* occur during visually guided behaviour only if the stimulus moves horizontally from back to front (regressive motion). They have a distinct amplitude. In contrast, the turning amplitudes of *Musca* are almost equally distributed between 20 and 110° (figure 2). In addition, turns of *Musca* during pursuit are not confined to regressive motion, but are elicited in a complex manner. Retinal target position, retinal target velocity and further cues influence the turning amplitude (paper II).

Collett & Land (1975) divided the angular movements of the hoverfly *Syritta pipiens* into fast saccadic and slow continuous ones. Similarly, two modes of angular tracking have been observed. In *Musca* no evidence for two different turning behaviours is found. The turns of *Musca*, however, are similar to the body saccades of *Syritta*. Perhaps also in *Syritta* only one system is present, because in both modes of tracking the retinal target position is related to the angular velocity or saccade amplitude in a similar manner (see also Collett & Land 1975, p. 29).

Flight provides the possibility for quite different manoeuvres. To stabilize body and course, precise sensory systems are required. The contributions of these systems must be integrated at the latest at the level of the flight motor. Widefield motion is, in principle, an important cue for a stabilization of course by an optomotor system. On the other hand, such a control hinders 'voluntary' angular movements and pursuit of targets. As has been mentioned, several mechanisms could serve to cope with this problem. A different dynamic tuning in the two pathways processing widefield and smallfield motion would be a very elegant solution.

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