Biol. Cybern. 45, 123–130 (1982)

Biological
Cybernetics

Tracking and Chasing in Houseflies (*Musca*)

An Analysis of 3-D Flight Trajectories

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Abstract. The flight trajectories of free flying female and male houseflies have been analyzed in 3 dimensions. Both female and male flies track other flies. The turning velocity $\dot{\alpha}$ (around the vertical axis) is linearly dependent upon the horizontal angle ψ_F (that is the angle between the trajectory of the tracking fly and the target) for small values of ψ_F in females and for the whole range of ψ_F in males. The 3-dimensional velocity v_{xyz} of the chasing fly is linearly dependent upon the distance between leading and chasing fly in males but not in females. Male chasing thus appears to be more efficient than female tracking. It is shown that earlier assumptions on visual control of flight in female flies derived from experiments on fixed flying flies are justified.

1. Introduction

Houseflies will often fly towards objects in the surroundings. Depending on the particular object, different control systems are activated (Land and Collett, 1974; Wehrhahn, 1979; Reichardt and Poggio, 1981; Wagner, 1980). Fixed flying male and female flies fixate and track moving targets in an almost identical manner (Reichardt and Poggio, 1976; Brede, in preparation). Also in free flight male and female flies were found to track other flies. Female chases, however, are brief and poorly controlled compared to male chases. In addition female flies use the lower frontal part of their field of view for tracking other flies and landing on an object whereas male flies use the upper frontal part for chasing and the lower frontal part of their field of view for landing on an object (Wehrhahn, 1979; Wagner, 1982a).

In this paper the free flight tracking in female and male flies is analyzed and compared with quantitative results on fixed flying flies. Some aspects of male and female tracking are also compared. A similar analysis was used to study the 3-D flight behaviour of *Drosophila* (Bülthoff et al., 1980).

2. Methods

Between 50 and 100 flies *Musca domestica* of either sex from the laboratory stock were kept in a cage (50 × 50 × 50 cm). Four sides of the cage were covered with white linen and illuminated by four 1000 W halogen lamps positioned outside. The upper and one frontal side of the cage were made of nonreflecting glass. A mirror inclined by 45° was positioned at the glass side of the cage allowing simultaneous observation of the flies' motions from above and from the side, Fig. 1. A 16 mm highspeed movie camera (Redlake Locam, 80 fps) was positioned 400 cm above the ground of the glass cage. Its optical axis coincided with the vertical midline of the glass side of the cage. Hence, the xy-plane and the xz-plane (via the mirror) of the cage could be seen on each frame. The coordinates x, y, z of the flies and two reference points of the cage were determined for each frame by means of a digitizing tablet (HIPAD) connected to a digital computer (PDP 11/34). After corrections for perspective errors the flight trajectories were reconstructed from successive frames with a computer program. Other programs compute additional variables like angular velocity or forward velocity of each fly and angles (with respect to another fly) or relative distance to this fly (see Fig. 2). Time plots of these functions as well as histograms or scatter diagrams and stereoplots of the trajectories were calculated by further programs. The main variables used may be subdivided into two groups:

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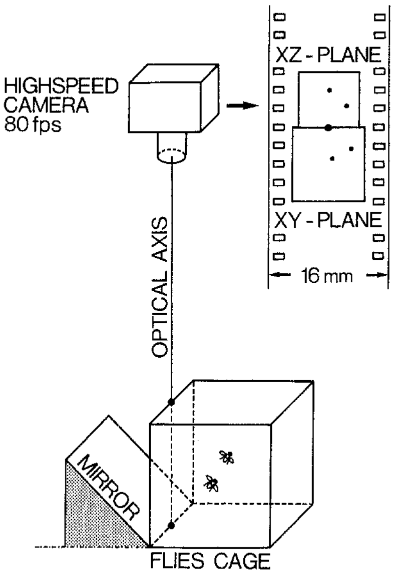

Fig. 1. Schematic drawing of the experimental set up used for the films. The flies cage was illuminated by 4 × 1000 W movie lamps. The highspeed camera was fixed about 4 m above the cage

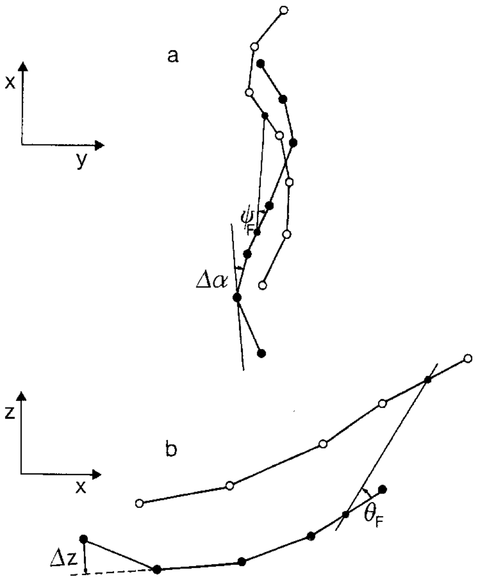

Fig. 2a and b. Plots of the two dimensional quantities used through the paper. **a** The horizontal angle ψ_F and the angle $\Delta\alpha$ by which the tracking fly turns at a certain instant. When the direction of the body axis coincides with the direction of flight and the head is fixed relative to the body the variable ψ_F represents the retinal error angle under which the following fly "sees" the targets image. The angular velocity $\dot{\alpha}$ (turning response) of the tracking fly is given by the ratio $\Delta\alpha/\Delta t$. **b** The vertical error angle ϑ_F defined according to 1a but in the vertical (z, a) plane and the vertical displacement Δz at a certain instant. The vertical velocity (lift response) of the tracking fly is given by $\Delta z/\Delta t$

1. The stimulus (input) variables: horizontal angle ψ_F between the path of the leading fly and that of the chasing fly, vertical angle ϑ_F and distance ϱ between leading and tracking fly.
2. The response (output) variables: horizontal angular velocity $\dot{\alpha}$ (corresponding to the torque around the vertical axis) and the vertical velocity v_z (corresponding to the lift force generated by the fly) and the 3-dimensional velocity v_{xyz} (corresponding to the resultant thrust). Other variables were also examined but will not be discussed in the present study.

Stimulus response relations may be obtained by plotting scatter diagrams between a variable of the first group and a corresponding one of the second group. The fly requires a certain time to compute and generate a response from a given stimulus. Hence, the two sets of data have to be shifted in time relative to each other to account for the delay. The maximum of the linear correlation coefficient may be used as a criterion for the "best" time shift (Land and Collett, 1974, Fig. 8, p. 342). It is important to note that all quantities used in this paper are calculated from the flight trajectories since the orientation of the body axis of the fly (not to speak of head orientation) is unknown in the data presented here. Recent data (Wagner, 1982b) showed that the body orientation of a flying fly may deviate significantly from the orientation of the flight path. A first order description of the control systems involved in free flight tracking and chasing in flies and a comparison with experiments in fixed flight seems however possible with the method described here.

3. Results

3.1. Female Tracking

A tracking episode between two female flies is shown in Fig. 3. The brief duration as well as the relatively straight course of leading and tracking animal are typical properties of female tracking. It is in principle possible that events like that shown in Fig. 3 are the result of chance rather than of female tracking. To decide between these two possibilities, the angle ψ_F is correlated with the turning response $\dot{\alpha}$ of the tracking fly. This can be done for different time shifts of the two functions. The correlation coefficient has a maximum for a time shift of 30 ms of $\dot{\alpha}$ against ψ_F as shown in Fig. 4 (inset). Thus the turning response of the tracking fly seems to be driven by the leading fly represented by the angle ψ_F. The response delay is about 30 ms. Figure 4 shows a scatter diagram for the two functions ψ_F and $\dot{\alpha}$ delayed by 30 ms. For $-20° < \psi_F < 20°$ there is a roughly linear relationship between ψ_F and $\dot{\alpha}$. This is in accordance with the results of experiments on fixed flying flies fixating and tracking a vertical black stripe on a bright background (Reichardt, 1973; Virsik, 1976). The slope of the regression line is about $24.5\ \mathrm{s}^{-1}$. It is important

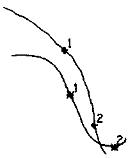

Fig. 3. 3-dimensional reconstruction of a flight episode where a female fly is tracking another fly. The data points were taken at an interval of 12.5 ms. Flight duration is 225 ms

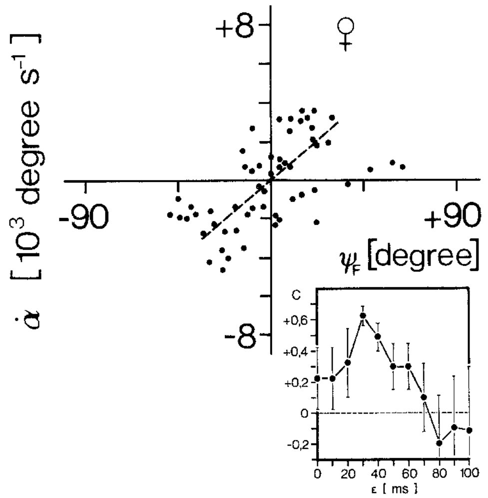

Fig. 4. Scatter diagram showing the relationship between horizontal angle ψ_F and turning velocity $\dot{\alpha}$ for all points measured on Fig. 3 and for 4 other tracks. In all cases the delay has been taken at 30 ms, i.e. the ordinate of each point corresponds to an instant 30 ms later than that of its abscissa value. The dashed line indicates the linear regression. Inset: The correlation coefficient between the two functions ψ_F and $\dot{\alpha}$ for different time delays ε for the track shown in Fig. 3 and for all data shown in the figure. Bars indicate standard deviation of the mean

to note here that ψ_F corresponds to the position of the target's image on the retina of the chasing fly only when the body head axis coincides with the direction of flight.

Earlier experiments on fixed flying female flies had revealed that the torque generated by a fly flying in a contrastless bright surround can be characterized as a gaussian random process (Poggio and Reichardt, 1973). Figure 5 shows an amplitude histogram of the angular velocity $\dot{\alpha}$ (roughly proportional to the torque around the vertical axis) of cruising female flies in free flight. A χ^2-test ($p=0.001$) shows that the shape of the histogram differs from that of a normal distribution at a highly significant level. Figure 6 shows the amplitude histogram of $\dot{\alpha}$ of 5 tracking female flies. The shape of the distribution is not distinguishable from that of a gaussian, but the number of data points in the histogram is only $N=85$. An analysis with more data points including the body axis of the flies is presently underway (Wagner, in preparation).

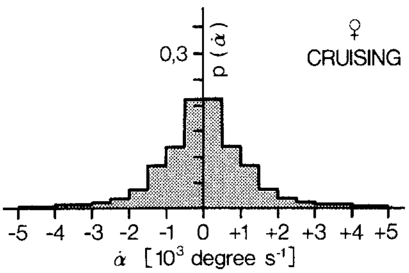

Fig. 5. Amplitude histogram of the angular velocity $\dot{\alpha}$ (turning response around the vertical axis) of 3 cruising female flies. The difference to a normal distribution in highly significant (χ^2-test)

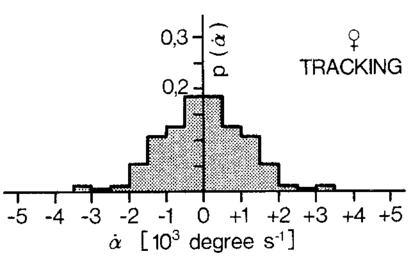

Fig. 6. Amplitude histogram of the turning velocity $\dot{\alpha}$ of 5 tracking female flies taken from the same episodes as the data in Fig. 4. Not separable from a normal distribution at the 2.5% level (χ^2-test)

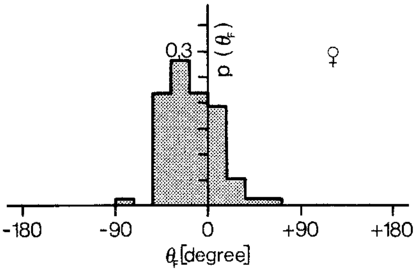

Fig. 7. Amplitude histogram of the vertical angle ϑ_F of the 5 female tracks used for Fig. 4. The mean value is situated at $\vartheta_F = -15.5°$ that is below the plane of the flight trajectory. Hence, these results are in agreement with the earlier finding that female flies use the frontal or lower frontal part of their field of view for tracking objects

Figure 7 shows an amplitude histogram of the vertical angle ϑ_F of the five female tracks from Fig. 4. The mean value of the distribution is situated at $\vartheta_F = -15.5°$, that is below the plane of the flight trajectory. This is in accordance with the earlier finding that the functional fovea where a target is fixated during tracking is situated in the frontal lower part of the field of view as shown by earlier experiments in fixed flying female houseflies, *Musca* (Reichardt, 1973; Wehrhahn and Reichardt, 1975).

3.2. Male Chasing

Much higher performance is achieved by the male chasing system than by the female tracking system. An example of this is shown in Fig. 8. We can see directly

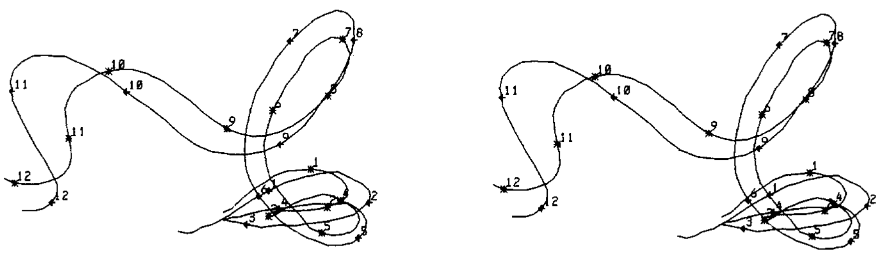

Fig. 8. 3-dimensional reconstruction of the longest recorded chase between two male flies. The numbers correspond to 100 ms intervals. The plot should be observed with standard stereoglasses. Note the elaborate flight path the chasing fly is able to keep and the length of the chase and compare it to Fig. 3

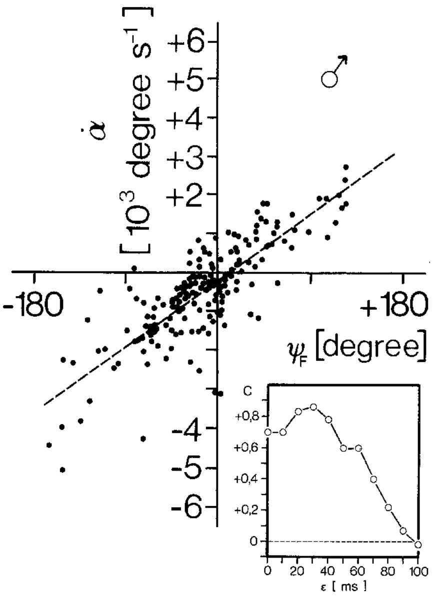

Fig. 9. Plot of ψ_F and $\dot{\alpha}$ for the chase shown in Fig. 8 and two shorter chases. $\dot{\alpha}$ has been delayed by 30 ms with respect to ψ_F. Inset: The correlation coefficient for the two functions $\dot{\alpha}$ and ψ_F for different delays ε

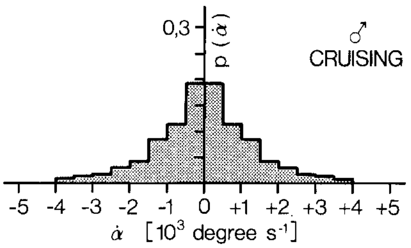

Fig. 10. Amplitude histogram of turning velocity $\dot{\alpha}$ of the cruising flights of 3 male flies. Differs significantly from a normal distribution (χ^2-test)

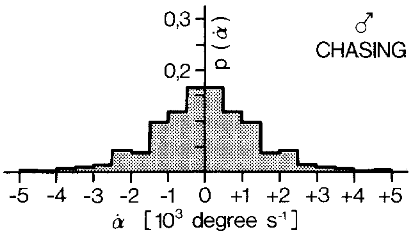

Fig. 11. Amplitude histogram of the turning velocity $\dot{\alpha}$ of 3 chasing flies of Fig. 9. With high significance different from a normal distribution (χ^2-test)

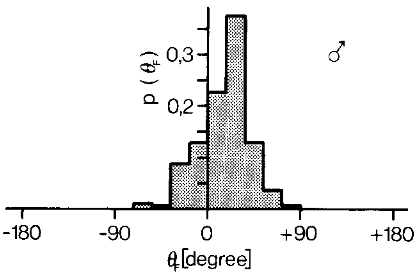

Fig. 12. Amplitude histogram of the vertical angle ϑ_F of 3 chasing flies from Fig. 9. The mean value of the distribution is at about $\vartheta_F = 16.5°$. This is in accordance with the assumption that male flies use the upper frontal part of their field of view for the fixation of other flies

from this episode that the chasing fly is keeping track of the leading one for a much longer time than that of Fig. 3. In addition the tracking path is quite tortuous.

The scatter diagram of the horizontal angle ψ_F against the turning response (delayed by 30 ms) has a range of almost the whole scale of ψ_F as shown in Fig. 9. The slope of around $19.6\,s^{-1}$ is very near to the value of the female tracking in 3.1. The delay of the turning response $\dot{\alpha}$ is around 30 ms corresponding to the value found for female tracking.

The histogram of the angular velocity $\dot{\alpha}$ of a cruising male fly is shown in Fig. 10. Its approximation to a gaussian is not good as in cruising females. The amplitude histogram for chasing males (Fig. 11) shows larger amplitudes especially when compared to the amplitude histogram for tracking females (Fig. 6). Also here the approximation to a gaussian distribution is not satisfactory.

Figure 12 shows an amplitude histogram of the vertical angle ϑ_F. The mean value of the distribution is around $\vartheta_F = 16.5°$, that is above the plane of the flight trajectory of the chasing fly. This is in accordance with the earlier observation that male flies use the upper frontal part of their field of view for fixating other flies during chasing (Wehrhahn, 1979).

The distance ϱ to the leading fly depends on the 3-dimensional velocity v_{xyz} (which corresponds to the resultant 3-dimensional thrust) as shown in the scatter diagramm of Fig. 13. In this plot v_{xyz} was delayed with respect to ϱ by 70 ms. The inset shows the dependence of the correlation coefficient from the delay time ε.

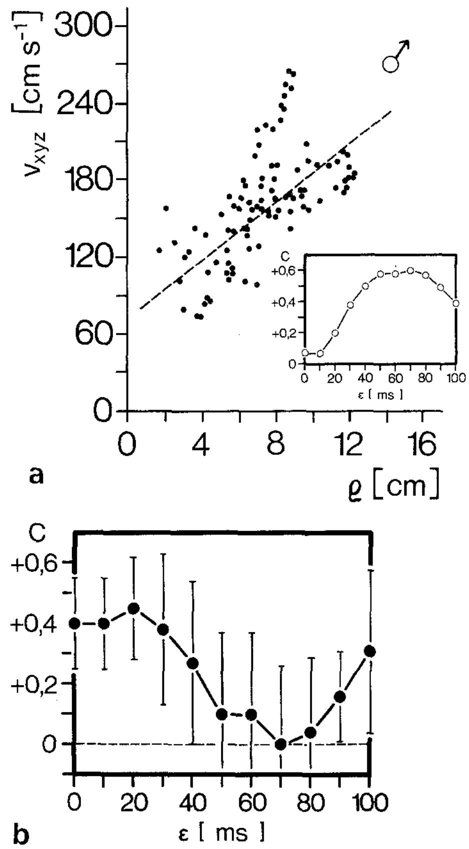

Fig. 13. **a** Scatter diagram of the distance ϱ between the leading and the chasing fly and the 3-dimensional (linear) velocity v_{xyz} of the chasing fly of Fig. 8. Inset: The correlation coefficient of the two functions ϱ and v_{xyz} for different time delays ε for the data given in the figure. **b** The correlation coefficient of the two functions ϱ and v_{xyz} for different time delays ε for the five female tracks used in Fig. 5

The slope of the regression line amounts to around 10.1 s^{-1}. Thus the larger the distance to the target the higher is the velocity of the chasing fly. A similar behaviour has not been found in free flying female flies in the films taken for this and other free flight studies. A quantitative test was carried out and the correlation coefficient for the two functions ϱ and v_{xyz} for the five tracks used for Fig. 5 at different time delays ε was computed. The results are shown in Fig. 13b. No significant linear correlation between ϱ and v_{xyz} exists for the delays shown.

4. Discussion

The data evaluated in this paper are flight trajectories of free flying female and male houseflies. The orientation of the body axis as well as head orientation could not be extracted with sufficient accuracy from the films. Hence only a rough description of the tracking and chasing behaviour can be achieved since the exact location of the stimulus on the retina as well as the exact mode of execution of the response in terms of forces exerted by the motor system are unknown. The meaning of the trajectories is that they are the result of a correct translocation of the chasing or tracking fly with respect to the moving target. A more precise description of the flight behaviour of free flying houseflies including body axes will be given in subsequent papers (e.g. Wagner, 1982b).

Visually guided behaviour in free flying Dipterans has been analyzed earlier, in two dimensions (Land and Collett, 1974; Okubo and Chiang, 1974; Okubo et al., 1977; Collett and Land, 1975a, b; 1978; Collett, 1980a, b) and in three dimensions (Wehrhahn, 1979; Okubo et al., 1981). However, the 3-dimensional data were either incoherent in two planes or only approximative in the vertical plane (but see Zeil, 1981). The analysis performed on free flying *Drosophila* corresponds to the present one concerning the techniques used (Bülthoff et al., 1980; Poggio and Reichardt, 1981).

4.1. Female Tracking

Female tracking of other flies appears to be weak and poorly controlled already from a casual observation of the flight trajectory (Fig. 3). This impression is confirmed by the examination of the quantitative data presented here. In Fig. 4 the turning response $\dot{\alpha}$ around the vertical axis of tracking female flies is plotted as a function of the horizontal angle ψ_F. Maximal correlation between $\dot{\alpha}$ and ψ_F is found if $\dot{\alpha}$ is delayed by 30 ms with respect to ψ_F. This value agrees with earlier findings in free flying male houseflies *Fannia c.* (Land and Collet, 1975) and in free flying female *Drosophila* (Bülthoff et al., 1980). The linear range of the turning response $\dot{\alpha}$ in Fig. 4 is linearly dependent upon ψ_F for values $-20° < \psi_F < 20°$. This agrees with findings on fixed flying female houseflies (Reichardt, 1973, Fig. 6a) although the ψ_F values are restricted in Fig. 4 to a rather small range. The reason for this is the mostly straight course of female tracks.

The distribution of the vertical angle ϑ_F during female tracking has a mean value of about $\vartheta_F = -15°$. This means that the region of fixation is around or below the equatorial plane of the compound eyes. This result can only be considered as a rough indication of the real situation since the inclination of the body axis and the position of the head are unknown in the data presented. It is, however, consistent with the more recent data of Wagner (1982b), which show that the vertical inclination of the body axis with respect to the flight trajectory varies as a function of forward velocity. The height orientation in free flying female houseflies is thus consistent with experimental findings on fixed flying female houseflies (Wehrhahn and Reichardt, 1975).

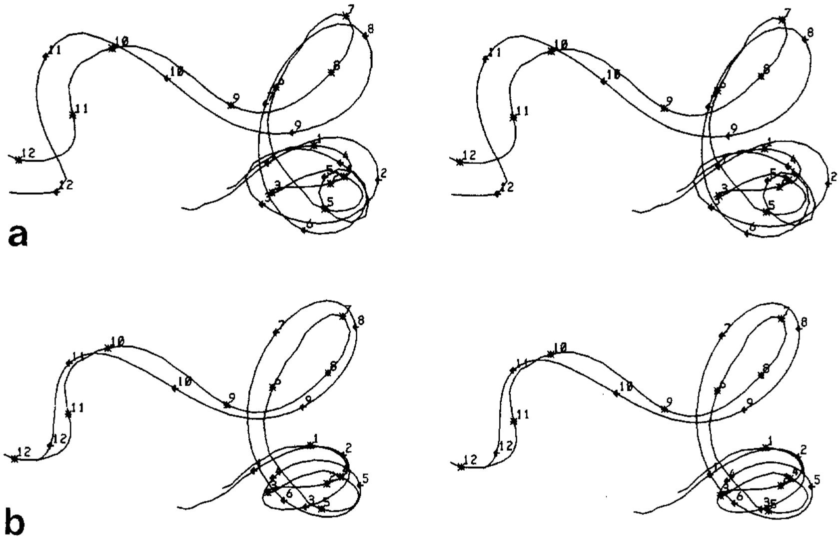

Fig. 14. a Simulations of the flight path of the chasing fly in the chase of Fig. 8a. The forward velocity of the chasing fly is kept constant according to the average value measured in the real chase. **b** The forward velocity of the chasing fly is controlled by $v_{xyz}(t+\varepsilon)=\chi\cdot\varrho(t)$; $\chi=10.1\,\mathrm{s}^{-1}$; $\varepsilon=70\,\mathrm{ms}$

4.2. Male Chasing

4.2.1. A Simulation. The first attempt to simulate a chase in the horizontal plane was made by using only the angular control system (Land and Collet, 1974). The forward velocity was varied for reasons of flight dynamics, since flies reduce their forward velocity when turning. However, male flies regulate their forward velocity as a function of the distance to their target (see Fig. 13). It has been shown that this additional system can account for the control of the forward velocity of a chasing fly (Wehrhahn, 1980; Poggio and Reichardt, 1981). The following simulations indicate that the control of forward velocity in flies indeed represents an optimization strategy as argued by Reichardt and Poggio (1981; see also the 3-D simulations in Poggio and Reichardt, 1981). Figure 14a shows the simulation of the chase of Fig. 8. In this simulation the forward velocity is kept constant throughout the whole chase. Figure 15a shows a histogram of the horizontal angle ψ_F determined from the simulation in Fig. 14a. It can be seen that the distribution is quite wide (standard deviation ~55°). In strong contrast to this is the behaviour of the simulated chasing fly in Fig. 14b. Here the parameters of the angular tracking system are the same as in Fig. 14a but in addition the forward velocity of the chasing fly is controlled as a function of its distance to the first fly. The chasing performance is remarkably accurate although the delay of the velocity control is 70 ms. This impression is supported by inspecting the histogram of the horizontal angle ψ_F for this simulation in Fig. 15b. The distribution is narrower compared to that of Fig. 15a (standard deviation ~37°). Thus by controlling their forward velocity as a function of distance male flies optimize angular tracking. Distance tracking is also observed in flying *Syritta* during hovering behaviour and throughout tracking (Collett and Land, 1975), and in walking *Drosophila* during courtship tracking (Cook, 1980, 1981).

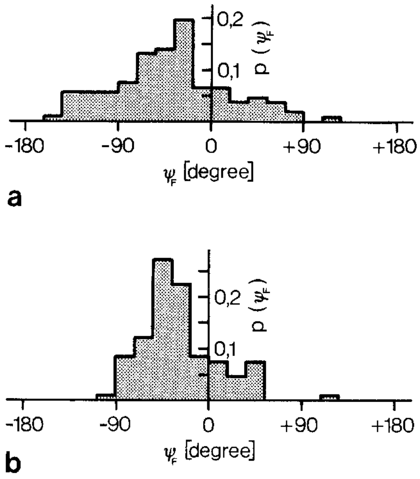

Fig. 15. a Histogram of the horizontal angle ψ_F of the chasing fly in the simulation of Fig. 14a. **b** Histogram of the horizontal angle ψ_F of the chasing fly in the simulation of Fig. 14b

4.2.2. Comparison with Fixed Flight Experiments. A theoretical description of tracking behaviour on a phenomenological level and some mechanisms possibly underlying fixation (Reichardt, 1973; Reichardt and Poggio, 1976; Poggio and Reichardt, 1974, 1981; Wehrhahn and Hausen, 1980; Wehrhahn, 1981) and distance control (Collet and Land, 1975) have been discussed. The phenomenological theory may be applied to describe female angular tracking as well as male angular chasing. This has been shown in detail by Poggio and Reichardt (1981). The analysis carried out in this paper represents a purely phenomenological description of the flight behaviour of free flying houseflies. In particular the head movements of the flies were not restricted as in most experiments in fixed flight. Hence no decisive evidence in favour of possible mechanisms may be expected here. It is important to note that in fixed flight experiments male and female flies behave almost identically. Thus the "female" system exists also in males and is used by them to fixate and track large objects and to land on them (Brede, in preparation). Recently Wagner (1982b) observed that the target's position on the retina of the following fly often deviates from the angle ψ_F between the two flight paths.

The overall delay for the turning response was found in this study to be around 30 ms ($\pm$12.5 ms) for both male and female systems. This is in accordance with earlier findings in free flight on *Fannia* (Land and Collett, 1974). The value of 30 ms is also consistent with results of fixed flight experiments, the results of which vary between 31 and 40 ms (depending on absolute brightness) for real motion of a vertical black stripe (Wehrhahn, 1981; Brede, 1982) and between 22.5 and 28 ms (also depending on absolute brightness) for a vertical stripe jumping very fast into another position (Reichardt, 1980; Wehrhahn, 1981). A possible difference between males and females with respect to the response delay cannot be discussed on the basis of the present data.

The delay involved in the control of forward velocity as a function of the distance to the leading fly during male chasing is around 70 ms. Hence the motor system generating thrust appears to be somewhat slower than that generating torque. This is also consistent with earlier findings on fixed flying houseflies (Wehrhahn and Reichardt, 1975).

Comparison of Fig. 4 and 9 shows that the turning response is a linear function of the horizontal error angle ψ_F between $-20° < \psi_F < 20°$ in female flies. This is in quantitative agreement with experiments on fixed flying female houseflies (Reichardt, 1973). The angular velocity corresponding to the maximal value in Fig. 4 is in the order of 500 [degree s^{-1}]. The corresponding torque value given by Reichardt (1973) for fixed flying flies is about 1 [dyn cm]. In Reichardt's artificial closed loop experiments the "physiological" values of angular velocity corresponding to 1 [dyn cm] were estimated to lie between 150 and 600 [degree s^{-1}]. Hence the quantitative values used in the artifical closed loop experiments of Reichardt (1973) and Virsik and Reichardt (1976) agree with our free flight data. Hence to a first order approximation the findings of this free flight study confirm that the phenomenological theory of Poggio and Reichardt (1973) with the additional control of foward flight can be applied to describe flight trajectories of free flying female and male houseflies respectively. Both models which Poggio and Reichardt (1981) discuss will serve as a first order approximation (see also Wehrhahn and Hausen, 1980; Wehrhahn, 1981). The different region of fixation in female and male flies, however, suggests that different physiological systems are responsible for the behavioural differences observed in free flying females and males (Wehrhahn, 1979; von Praagh et al., 1981; Zeil, 1981). The male chasing system appears to be inoperative during experiments in fixed flying male houseflies (Brede, in preparation).

In the films shot for this study attempted male chases of 200 ms or even shorter ones have been observed. Hence it is possible that the initiation of the chasing behaviour may be observable in fixed flight, although transient recordings of the flight torque and flight thrust responses of fixed flying male houseflies revealed no evidence for this (Wehrhahn, unpublished). It is possible that important conditions for the maintenance of chasing in male flies are not only a certain object size, at the same time serving as an input stimulus for velocity control, but also other not necessarily visual parameters of the chased fly. If one of these conditions is lacking the chasing mode of male flies is disrupted and replaced by other types of behaviour.

Acknowledgements. We would like to thank V. Braitenberg for the loan of the Highspeed Camera, H. Hadam for drawing the figures and I. Geiss for typing the manuscript. J. Brede, T.S. Collet, R. Cook, M. Egelhaaf, K.G. Götz, K. Hausen, M.F. Land, W. Reichardt, and H. Wagner, read various versions of the manuscript. We thank them all.

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Received: May 20, 1982

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