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Flight Performance and Visual Control of Flight of the Free-Flying Housefly (Musca Domestica L.) II. Pursuit of Targets

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

II. PURSUIT OF TARGETS

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The pursuit behaviour of houseflies has been analysed by the evaluation of movie films. On the floor, males, but not females, turn towards passing targets. Males as well as females pursue targets in the air. Male chasing seems to be functionally different from female tracking. Males attack targets in the air from below. They sometimes retract from the target fly after an approach. Thus, a chase may be divided into attacks, periods of pursuit and retreats. Males catch females, but not other males. The pursuer is therefore able to discriminate between the sexes. Close approach or contact with the target fly seems to be necessary to obtain the information. During pursuit both sexes increase the rate of turning. The male but not the female target fly performs evasive translatory reactions to the attacks (figure 4). Females do not catch other flies. They often react with a single turn in the direction of a passing object. They seldom follow the target, which is then normally positioned below the tracking fly.

The rotations about the vertical and transverse axis (yaw and pitch) are visually controlled in both sexes. The horizontal and vertical error angle, as well as the horizontal and vertical retinal target velocity, influence the turning behaviour. At least in males, further, hitherto unknown, cues seem to be additionally involved in the control of the rotatory movements. The male control systems operate more precisely than those of the females. Rotations are characterized by steplike changes in angular orientation ('turns') at high angular velocity. Smooth rotations at angular velocities less than about 200 deg s^{-1} seem not to play any role either in males or in females. 'Sideways' tracking, most probably mediated by rolling about the long axis, occurred in a single sequence only. A correlation between the translation velocity and the distance between pursuer and target is observed in the pursuit sequences of both sexes. This correlation is interpreted as a by-product of the organization of the flight motor. Therefore, neither males nor females control the translation velocity by the distance to the target.

The discussion concentrates on the problems in characterizing the control systems and a comparison with data from optical and electrophysiological measurements. The behavioural differences between hoverflies and houseflies are attributed to the different flight motors.

1. INTRODUCTION

The aerobatic flights of insects have always fascinated amateurs as well as scientists. Gruhl (1924) was among the first to describe the variety of the flight behaviours of the dipterans. These ethograms demonstrated an important role of the aerial displays in pre-mating behaviour. In some species the behaviour might be described as an aerial pursuit. During the sequences, one fly (pursuer) closely follows the movement of a second one (leading fly, target). The fast movements can best be recorded on films shot at a high frame rate and this method is applied in this study. By using the same technique Collett & Land (1975), Wehrhahn *et al.* (1982) and Zeil (1983*b*) have quantitatively analysed the pursuit behaviour of hoverflies, houseflies and marchflies, respectively. Obviously the pursuits are visually guided. The authors describe sex-specific differences in the behaviour. A great variety of targets is pursued by the male, which has specialized regions of the eyes and the brain (Collett & Land 1975; Hausen & Strausfeld 1980; Hardie *et al.* 1981; Zeil 1983*a*, *c*). For a long time females were not observed to pursue targets. However, female houseflies not only follow the movement of a small stripe in tethered flight (Virsik & Reichardt 1976), they also 'track' small targets in free flight (Wehrhahn 1979). I shall distinguish male 'chases' from female 'tracks' in this study.

The resolution of the animals on the moving films has previously been so poor that the three-dimensional movements of houseflies could only be derived from the motion of the centre of gravity. The orientation and the movement of the body axes of the flies (long, transverse and vertical axes) could not be read from the films. Two-dimensional analyses of flight sequences of hoverflies have demonstrated an astonishing capability of these animals to control sideways, forward and angular movements independently of each other. Significant differences between body orientation and flight direction have been observed (Collett & Land 1975). The first clear demonstration of sideways movements in *Musca* came from the analysis of landing trajectories (Wagner 1982). Subsequent analysis of flight sequences, in which no visual reaction could be detected ('cruising flights'), showed that the flight motor of *Musca* independently generates torques about the three body axes in free flight. The angular movements of the flies are characterized by a cascade of large-amplitude turns that are separated by periods of no or only little turning. The direction of the force vector is found to be inclined upwards in the midsagittal plane of the fly at about 20° on average. It can only be slightly varied around this mean value by the fly, therefore the animals cannot actively move backwards. Sideways movements are not due to an actively generated force in the direction of the transverse axis. They occur (i) during rotations about the vertical axis in curved flight and result then from inertial (ballistic) forces and (ii) during roll movements in straight flight (papers I and III).

The pursuer controls its movements with reference to the target. The neural networks mediating this control are referred to as 'control systems' here. Land & Collett (1974) have pointed out that the variables giving information about the target can be regarded as input variables to the control systems underlying chasing and tracking, whereas the movements of the pursuer represent the corresponding output. These authors proposed the methods of linear correlation for the analysis of the sequences. Input and output variables are correlated frame by frame at different delays. The position of the maximum of the cross-correlation coefficient of a certain sample gives the delay of the control system. The point at which the regression line crosses the abscissa represents the stability point (that is, the point at which the pursuer 'tries' to fixate the target) and the slope of the regression line the corresponding gain (the conversion factor from input to output). This method has been used in most previous studies of free-flight behaviour for the characterization of the control systems. Since the rotational output of houseflies (angular velocity) is characterized by quick and steplike turns at high angular velocity which are often separated by periods of little or no turning, the angular velocity is probably not uniformly related to the input signals. Therefore, the method of the continuous linear correlation could lead to misinterpretations and should not be used. Many of these aspects could not be examined previously. Therefore, it seemed necessary to reinvestigate aerial pursuit.

2. METHODS

2.1. *Filming and basic principles of the analysis*

The flies were simultaneously filmed from two sides with a movie camera and the aid of a mirror (paper I). Films were projected onto a digitizing table (Summagraphics-ID) with a film projector (Vanguard M 16C-1200 CW-MW). The position of the fly's head and abdomen were read from the films together with a reference coordinate system and stored in a computer (PDP 11/34). Three-dimensional coordinates of any point in space were computed (for a detailed description see paper I). The orientation of the fly's body axes in this coordinate system is given by three angles ('Euler angles'), denoted as heading angle β_{xy}, pitch (body) angle β_{xz} and roll angle β_{yz} here (for definition see table 1). In the films evaluated for this study the direction of the fly's transverse axis could not be reliably recorded. Therefore, the roll angle was not measurable. It was assumed to be zero. This means that the fly's transverse axis always remains horizontal. Although in free flight houseflies perform roll movements during straight as well as during curved flight, the impossibility of recording these movements does not detract from the interpretations of the flight manoeuvres. It was shown that roll movements cause certain changes in variables that are measurable under the conditions of this study (angle of sideslip, sideways velocity) (paper I).

2.2. *Variables used for the evaluation*

In table 1 a list of the variables is presented. Velocities and accelerations are the kinematically relevant variables to analyse the flight behaviour.

Three-dimensional translation as well as angular velocity is a vector that is decomposed with respect to the fly's body axes. The turning amplitudes denote the change of axis orientation belonging to a single turn. If not stated otherwise, the values are smoothed with a standard digital filter of order three.

Table 1. List of variables

The time derivatives represent the difference quotients and not differentials; all rotations and angles are positive in the mathematical sense of rotation; coordinate systems are cartesian and righthanded.

Δt	sampling time (10 ms)
V_{3D}	three-dimensional translation velocity; the distance travelled between two successive frames divided by Δt
x_b	long axis of the fly; the connection of a point on the abdomen with one on the head
y_b	transverse axis; the connection of the two wing bases; positive to the right if seen from the head
z_b	vertical axis; positive dorsal
β_{xy}	heading angle; the direction of the fly's long axis in the horizontal plane; defined from -180 to $+180°$
β_{xz}	pitch (body) angle; the inclination of the long axis to the horizontal plane; defined from -90 to $+90°$; positive head up; it is the negative value of the corresponding Euler angle
β_{yz}	roll angle; inclination of the fly's transverse axis to the plane formed by the long axis and the direction of the transverse axis at zero roll angle; defined from -180 to $+180°$
v_f	forward velocity; distance travelled in the direction of x_b-axis; equal to x_b-value at time $t+\Delta t$ divided by Δt
v_s	sideways velocity; measured according to v_f in the direction of the transverse axis
v_u	upward velocity; measured in accordance with v_f in the direction of the vertical axis
$\dot{\alpha}_t$	angular velocity about the transverse axis; the pitch (body) angle of the fly at $t+\Delta t$ divided by Δt
$\dot{\alpha}_v$	angular velocity about the vertical axis; the heading angle of the fly at time $t+\Delta t$ divided by Δt
α_v, α_t	turning amplitudes about vertical or transverse axis respectively; the integral of the values of the corresponding angular velocity from one zero crossing to the next; if zero velocity is not reached before the next turn starts, the minimum absolute value of the angular velocity between two peaks is taken as the end value of the first turn
ψ	horizontal error angle, the azimuthal deviation of the target from the midsagittal plane of the pursuer, defined from -180 to $+180°$; zero directly in front of pursuer
θ	vertical error angle, the elevational deviation of the target from the horizontal plane of the pursuer, defined from -90 to $+90°$, positive upwards
ρ	distance between target and pursuer, $\rho = \surd(x_t^2+y_t^2+z_t^2)$, with x_t, y_t, z_t coordinates of the target in a fly centred coordinate system
$\dot{\psi}$	horizontal retinal target image velocity, the difference of two successive horizontal error angles divided by Δt
$\dot{\theta}$	vertical retinal target image velocity, the difference of two successive vertical error angles divided by Δt
1 or ta	target fly
2 or tr	tracking fly

2.3. *The geometry of the pursuit situation*

The movement of the tracking fly can be described by the translations in the direction of the three orthogonal body axes and the rotations about these axes (see table 1, figure 1). Since the target is regarded here as a point it has three degrees of freedom to move. I use spherical coordinates for the evaluation of the target's position, because they are the best approximation to the eye geometry that is available so far. As is shown in figure 1, these coordinates are the horizontal error angle ψ, the vertical error angle θ and the distance between tracking fly and target ρ (for definition see table 1). The two angles can, in principle, be directly determined by the fly. However, it cannot easily compute the distance to the target because stereopsis does not play a role in houseflies at most of the distances found during pursuit. If the flies were to use this information, they have to derive it indirectly.

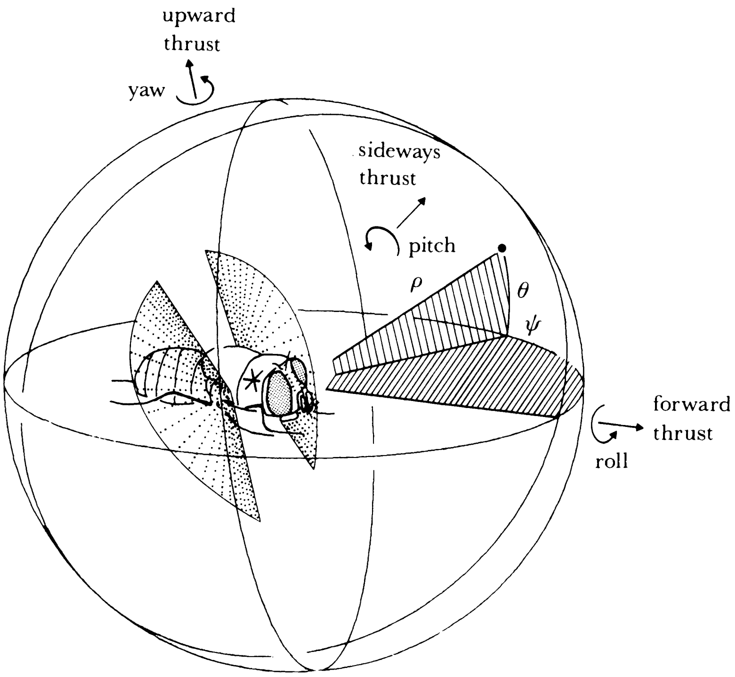

Figure 1. Geometry of the pursuit situation. The fly's head is in the centre of a sphere of radius ρ (distance to the pointlike target). ψ and θ are the horizontal and vertical error angles, respectively. The output variables (forces and torques), decomposed with respect to body-centred cartesian coordinates, are also shown. Note that the centre of the output coordinate system is not in the centre of the sphere, since the thorax is slightly displaced with respect to the head.

In a spherical coordinate system the position of the target on the eye of the tracking fly is given by

$$\psi = \arctan\,(y_t/x_t) \text{defined from } -180 \text{ to } +180°, \tag{1}$$

$$\theta = \arctan\,(z_t/\sqrt{(x_t^2+y_t^2)}) \tag{2}$$

and

$$\rho = \sqrt{(x_t^2+y_t^2+z_t^2)}, \tag{3}$$

where x_t, y_t, z_t are the coordinates of the target in a fly-centred cartesian coordinate system.

The time derivatives of these equations give the relative movement of target and pursuer in spherical coordinates. Details of the derivation are explained in the Appendix. If one follows Rieger (1983) the equations denote in component form

$$\dot{\psi} = \frac{1}{\rho \cos(\theta)}((v_f(\text{tr})+v_f(\text{ta}))\sin(\psi)-(v_s(\text{tr})+v_s(\text{ta}))\cos(\psi)) + \tan(\theta)\,\dot{\alpha}_t \sin(\psi) - \dot{\alpha}_v, \tag{4}$$

$$\dot{\theta} = 1/\rho(-(v_f(\text{tr})+v_f(\text{ta}))\sin(\theta)\cos(\psi)-(v_s(\text{tr})+v_s(\text{ta}))\sin(\theta)\sin(\psi) + (v_u(\text{tr})+v_u(\text{ta}))\cos(\theta)) - \dot{\alpha}_t\cos(\psi), \tag{5}$$

$$\dot{\rho} = -((v_f(\text{tr})+v_f(\text{ta}))\cos(\psi)\cos(\theta)+(v_s(\text{tr})+v_s(\text{ta}))\sin(\psi)\cos(\theta) + (v_u(\text{tr})+v_u(\text{ta}))\sin(\theta)). \tag{6}$$

Equations (4)–(6) have already been reduced to the situation in this study, where no roll movements can be measured. As previously pointed out, the variables that provide information about the target may be regarded as input variables to sensory control systems, whereas the movements of the pursuer are the corresponding output. Equations (4)–(6) give the adequate geometrical situation, which may be used to investigate which output variables may be driven by an input variable. Only those outputs that lead to a change of retinal target position have to be considered. Despite these restrictions, a variety of ways to accomplish fixation remains. However, it is easily seen that a main component in the control of the horizontal error angle ψ might be the angular velocity about the vertical axis $\dot{\alpha}_v$. The forward v_f and sideways v_s velocities influence the change of ψ in a distance-dependent manner. The influence of the angular velocity about the transverse axis $\dot{\alpha}_t$ is dependent on ψ itself and also on θ. The upward velocity v_u does not influence the horizontal error angle. Similar considerations can be made for the vertical error angle (5) and the distance to the target (6).

2.4. *Flies and reconstructed sequences*

Houseflies aged 5–20 days, from the institute stock, were used for the experiments. In some cases 50–100 flies, in others only two were filmed and 25 tracks (female–female) at a frame interval of 10 ms have been evaluated. In the same manner 9 sequences, in which the male chased another male, and 12 chases, in which the male pursued a female, were reconstructed. In all these sequences the head of the pursuing fly was free to move. As a control, 10 chases were recorded in which the head of the chasing male was fixed to the thorax so that the horizontal plane of head and body coincided. In these sequences the behaviour was not significantly changed. Many more chases have only been qualitatively evaluated (table 2).

3. RESULTS

3.1. *General features of chasing and tracking*

Aerial chases of male houseflies may last for several seconds. The very long chase shown in figure 2 reveals most of the types of interactions of the flies. The chase is subdivided into two successive temporal parts and is plotted in top view on the left and in side view on the right side. The time course of important variables is shown in figures 4, 6, 8 and 10. The animals are indicated by the head (circle) and the direction of the long axis (line). The time interval between two successive positions is 10 ms. Numbers denote the time in 0.1 s.

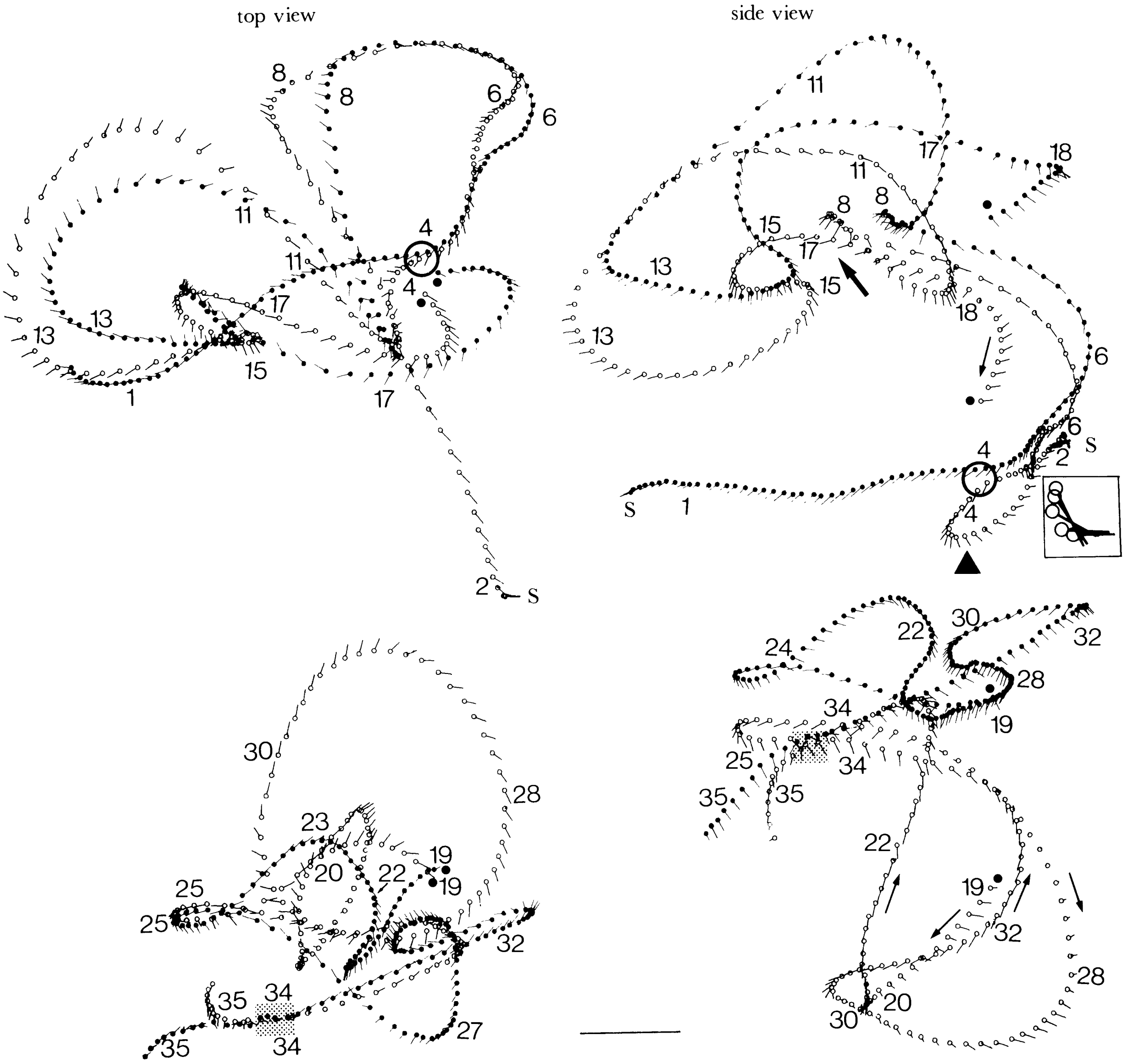

Figure 2. Example of a male chase. The sequence with two males is presented in top view on the left and in side view on the right hand side. Upper drawings show the beginning (0–18), lower the continuation and end of the chase (19–35) in which the start is indicated by S. The end point of the upper and start point of the lower part are marked by large points. The flies are indicated by the position of the head (circle) and the direction of the long axis (line). The target is characterized by the filled circle. The numbers denote the positions of the flies in 0.1 s. The interval between two successive positions is 10 ms and the bar denotes 5 cm. For description and symbols see text. Inset in the centre right shows in enlargement the turn on the wall before the start.

The temporal sequence of the interactions will be described here. Important topics are analysed in §§3.2–3.7.

Initially the pursuer (open circle) is sitting on the wall, where it turns in the direction of the target (a second male, filled circle) (0–0.1 s in figure 2; inset). After taking off, the chasing fly fixates the leading fly dorsofrontally with a precise turn and approaches it (0.2–0.4 s; top view in figure 2). The side view shows that the pursuer flies in a position underneath the target. At about 0.35 s the chasing fly turns about the transverse axis (triangle, side view). This change of long axis orientation has two effects: it leads to a change of ascent so that the fly starts to move upward and prevents a fast dorsal displacement of the target. The pursuer comes close to the leading fly at about 0.4 s for the first time (encircled area). However, it does not manage to contact the target fly which begins to climb, accelerates and starts curved flight (0.4–1.1 s, side view, see also figure 4). The chasing fly closely follows the movements of the leading fly from below (0.4–1.1 s, top and side view). At 0.8 and 1.15 s the pursuer is above the target (side view). At once it starts to move down and soon reaches a position underneath the target again. Between 1.75 and 2 s the chasing fly no longer maintains course with the target (thick arrow, the thin arrows indicate the direction of the vertical movement). Although no specific external stimulus can be detected, the male turns away from the target and flies downward. The leading fly does not lose height during this period, whereas the chasing fly almost reaches the floor of the cage before it again fixates the target dorsomedially (about 2.0 s, see figures 6*a*, 8*c*), starts to move up in a steep path and chases the target from below (2.0–2.5 s, side view). Probably as a reaction to the approach, the other fly also moves upward and starts curved flight (2.1–2.7 s, side and top view). At 2.6 s the pursuer begins to move down again (compare 2.5 with 2.8 s in side view and follow thin arrows). It starts a new approach and hits the target from below (3.4 s, side and top view, hatched area). The contact lasts about 10–20 ms. Afterwards the chasing male flies away and sits down on the floor (not shown). Thus, it looks as if the goal of the chase was to contact the target in the air. I call these approaches 'attacks' for this reason and the observation that the pursuer often reaches the target at a high translation velocity.

In contrast to males, females mostly just turn towards a target passing by. Sometimes, the females may also follow the target's translational movements and react with a few successive turns to a target.

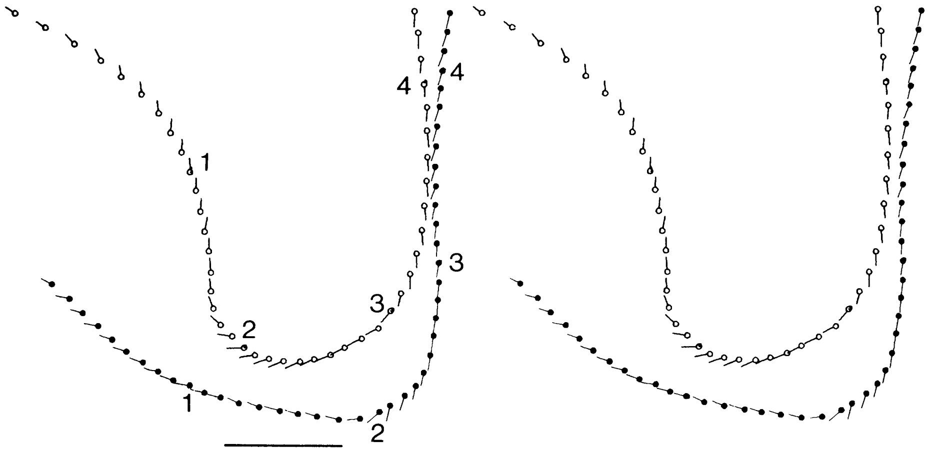

FIGURE 3. Stereopair of a female fly tracking another female. The scene is viewed from above. If normal stereoglasses are used, the excursions in the third (vertical) dimension become visible; further symbols as in figure 2; description in the text.

In figure 3 such an example is plotted as a stereopair viewed from above. In this example the tracking fly turns towards the target and approaches it (0–0.2 s). The target's image on the eye crosses the midline of the fly during the second turn (0.2 s). In the beginning of the sequence the tracking fly rises. With a certain delay it follows the descent of the leading fly.

The target is located in the lower part of the tracking fly's eyes during the whole sequence. The track stops without contact in the air, even without an attempt to contact the target.

3.2. *The behaviour before the start*

Male houseflies may perform a turn towards the flying target before taking off (inset in figure 2). This behaviour has not been observed in females. In contrast to the turns in flight (figures 6 and 7), the turns on the ground seldom compensate for the target's deviation from the midsagittal plane. The duration of the turns is in a range of 10–40 ms. The time course is similar to that for the turns in free flight. The maximum change of long axis orientation observed on the floor is about 80°.

In addition to these single turns towards flying targets, interactions of the pursuer and the target can be found on the ground before the take-off (such interactions have been mentioned earlier in other contexts too: see, for example, Vogel 1957). In these cases one fly starts to approach another fly in a typical manner: after some fast steps in the direction of the target (duration about 50–70 ms), the fly remains quiet for a while (about 150–250 ms). The same sequence may be repeated several times so that these approaches may last for seconds. The other fly may react in a similar manner. At the end, the pursuer jumps onto the target fly or the latter flies away, closely followed with a delay of about 30–50 ms by the second fly.

3.3. *The strategy of the male during the chases*

The chasing male in figure 2 repeatedly attacks and retreats from the target: first attack (0.2–0.4 s); afterwards pursuit of the target including an attack at 1.5 s (0.4–1.7 s); first retreat (1.75–2.1 s); third attack and a short period of pursuit (2.1–2.6 s); second retreat (2.6–3.1 s); fourth attack, at the end of which the target is hit (3.1–3.4 s). Thus, male houseflies do not continuously attempt to follow the leading fly ('shadowing', Collett & Land 1975). In table 2 the attacks during male–female (162 in 105 chases) and male–male chases (105 in 74 chases) are evaluated. Males pursue other males and females in a similar manner. However, one striking difference appears. Whereas females are caught in the air in about 20% of the chases, males are caught in about 3% only (table 2). In addition, after the first attack the male ceases to

TABLE 2. ANALYSIS OF MALE CHASES: THE INFLUENCE OF THE SEX OF THE TARGET FLY ON THE PURSUING FLY'S BEHAVIOUR

	1st attack		2nd attack		3rd attack		4th attack	
	♂–♂	♂–♀	♂–♂	♂–♀	♂–♂	♂–♀	♂–♂	♂–♀
total number of chases	74	105	22	46	8	10	1	1
contact	29	56*	7	34**	7	9	1	1
no contact	45	49	15	12	1	1	0	0
caught target in the air	0	16	0	6	2	1	0	0
stop after contact	28	44*	5	30†	7	9	1	1
continue after contact	1	12	2	4	0	0	0	0
stop without contact	24	15*	9	5†	0	0	0	0
continue without contact	21	34	6	7	1	1	0	0

* With probability > 0.95 difference between male–male and male–female chases: increased rate of stops or decreased rate of contact in the male–male sample (χ^2 test for 2 × 2 tables).

** Probability > 0.99.

† Not significant; others not tested.

chase a leading male more often than a leading female (table 2). In fact, the male stops chasing the male target in almost all cases, if (i) it contacted the male target (41 of 44, table 2) or (ii) after a close approach. Thus, the pursuer is able to distinguish females from 'non-females'. The conditions mentioned above seem to be a prerequisite for obtaining this information. The pursuer often continues to chase the female target after it hit the target, but did not manage to catch it. Since the fly cage was relatively small, it sometimes happened that one or both flies crashed into the glass wall of the cage. However, even then the chase often continued after less than 100 ms. If the male has caught the female target, both animals fall to the floor, where the male tries to copulate in the typical sequence described by Vogel (1957). A further aspect arises from table 2: chases, which are composed of more than two attacks, eventually lead to contact with the target.

3.4. *The reactions of the leading fly*

The start of a chase between two males may often be observed by eye because both animals accelerate and start curved flight.

Figure 4 shows the translation velocity and the angular velocity about the vertical axis of the leading fly of the chase in figure 2. The target accelerates after the first attack (0.2–0.4 s). A similar, but less pronounced, behaviour is found during and after the third attack too (2.1–2.6 s). After the pursuer has turned away, the leading fly slows down again (not shown). In 8 of 12 male–male interactions the translation velocity of the target was significantly

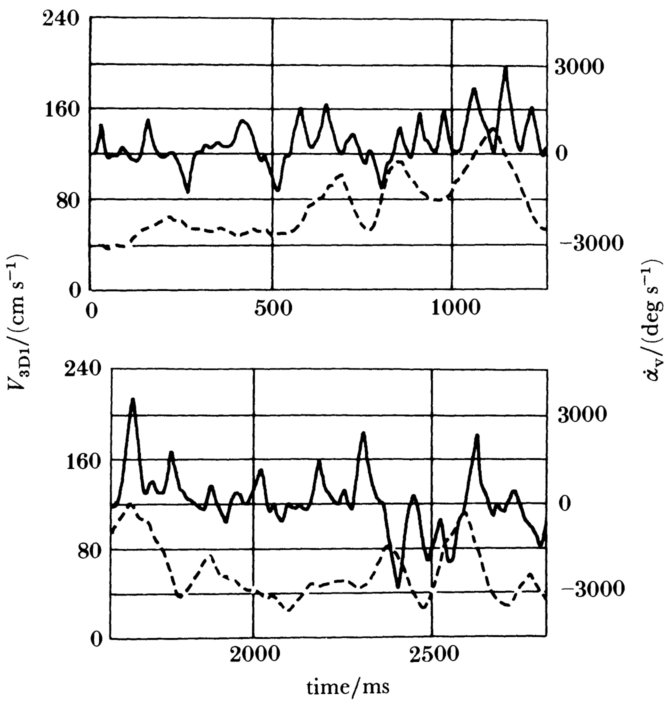

FIGURE 4. Evasive movements of the target fly in part of the chase of figure 2 (0–1.25 s and 1.6–2.8 s); ----, three-dimensional translational velocity V_{3D1}; ——, angular velocity about the vertical axis $\dot{\alpha}_V$. After the first attack (0.2–0.4 s) the target accelerates and increases its rate of turning; it decelerates during the first retreat (1.7–2.1 s) and accelerates during the third attack again (2.3–2.6 s).

increased during the periods of chasing compared with the time before or after the chase. In none was the velocity decreased (test of Dixon and Monod). Similarly, the rate of turns about the vertical axis seems to be increased during the period of pursuit (25 turns per second compared with 17 turns per second; see figure 4). The female target does not significantly raise its translation velocity during the chases. However, females perform more turns when being chased (21 per second) than during cruising flight (11 per second) or during female tracking (14 per second). These evasive reactions of the target are probably visually guided. They are astonishing in so far as the pursuer's image is located in the most caudal part of the target's eyes for most of the time. As has been mentioned above, the male target is hit less often than the female target at the end of the first attack. This indicates that the sexes behave differently even shortly after the beginning of a chase.

3.5. *Input variables*

From the distributions of the positions of the target on the pursuer's eye and the distance between pursuer and target, first indications can be obtained whether a control during pursuit takes place or not. How this control is achieved can not be derived from the distributions, however. Houseflies fixate their targets in a distinct part of the eyes. This proves that they control the object positions on the eye. As can be seen from figure 5*a*, *b*, females hold the targets

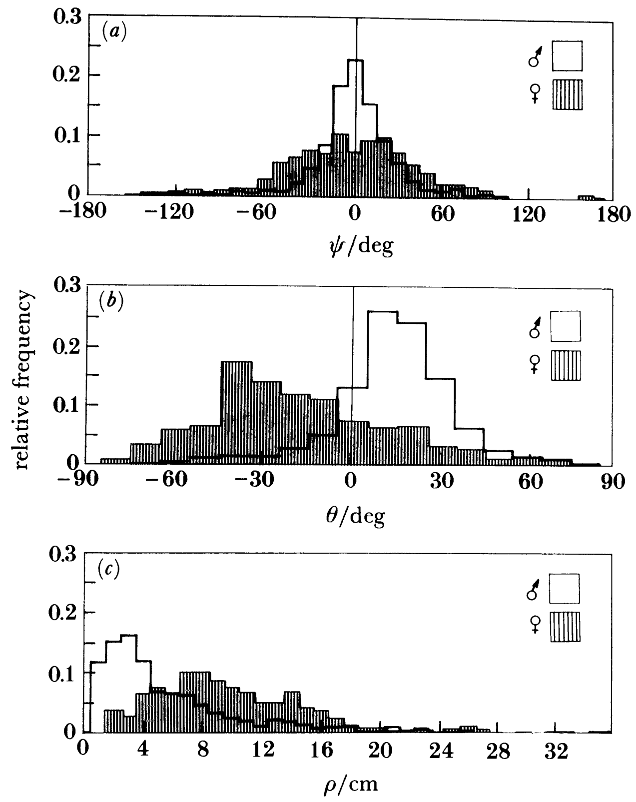

Figure 5. Distribution of the horizontal error angle ψ (*a*), the vertical error angle θ (*b*) and the distance between pursuer and target ρ (*c*) for female tracking (striped histogram) and male chasing (blank histogram). Values during retreats are omitted. Total number of points: females, 1203; males, 1423; binwidth, 10° (*a*, *b*) 1 cm (*c*). Notice the differences between males and females. Mean deviation from 0 (in degrees) is 19 for males and 35 for females (*a*); mean (in degrees) is 14 ± 20 for males and -18 ± 31 for females (*b*).

in the lower-frontal part of the eyes and males fixate them in the upper-frontal part (see also Wehrhahn 1979). The deviation of the target from these 'desired' regions may be used as a criterion for the accuracy of fixation. In males the target deviates less from the frontal region of the eyes than in females (figure 5*a*), indicating more precise control mechanisms in the former. The considerable scatter in the distribution of the vertical error angle in the male sample (figure 5*b*) is at least in part due to 'overshooting' the target in the close vicinity (see also figure 8*c*). The distances found during tracking and chasing range between 0 and about 30 cm. The maximum of the distribution of the male sample is shifted to smaller values compared to that of the females. This is probably a consequence of the male strategy of attacking.

3.6. *The control of angular movements*

3.6.1. *Defining input and output to the control systems*

As stated before, the method of continuous linear correlation should not be used for the quantitative characterization of the rotational control systems. The time course of the angular velocities (output of a possible control system) may be characterized by a cascade of peaks related to single turns and separated by periods of little or no turning (figure 6*a*, *b*). The basic properties of these turns and their existence in different behavioural situations are analysed in paper III (see also paper I). Here it is important that during a turn successive values of the angular velocity are most probably not independent of each other (that is, the increase and decrease of the angular velocity lasts each for some 10–30 ms). Therefore, the angular velocity (and also torque) seems not to be uniformly and continuously related to the input signals. As a consequence, misleading results are obtained if a continuous linear correlation analysis is performed. Some will be mentioned here to substantiate further the above statements. Since turns and periods of no turning alternate, a hysteresis is often found when the angular velocity is plotted versus the error angle (input to the control system), even at the delay where the correlation coefficient is maximal. Thus, the slope of the regression line, being a measure of the gain of the control system, is reduced. Similarly a stronger gain for regressive (from back to front) than for progressive (from front to back) motion would then result. But this is in contradiction to all known results from tethered flight (Reichardt 1973; Wehrhahn & Hausen 1980). If there is no continuous relation between input and output, a continuous linear correlation may nevertheless be used as a first order indicator for a control.

The change of long axis orientation related to a single turn is regarded as a criterion for the output of the control systems in this study. The method of evaluation used in this part (see table 1) does not exclude digitizing errors. It turns out that all amplitudes of an absolute value of less than 5° and many of a value between 5 and 10° are with a high probability digitizing errors (paper III). The rest may be regarded as 'real' turns.

While the turning amplitude is the output of the control system, the corresponding input has to be defined too. A good method seems to be to consider the values of the input variables some time before the beginning of the turn. However, it is not clear whether an integration of the input values over some time (over 10 ms which is the sampling time) should be used or only the value at the discrete point of time obtained by the evaluation of a single frame. I found that in a range of time between 10 and 50 ms before the beginning of the turn in females and 10–30 ms before the turn in males the linear correlation between the input variables (see below) and the turning amplitude is high. Thus, averaging of the input signals in this range does not markedly change the basic results. At greater delays the cross-correlation coefficient decreases. Thus, I decided to use the values of the input variables at 25 ms delay. Previous delay measurements in tethered flight revealed similar values (Reichardt 1979; Wehrhahn 1981; Strebel 1982).

3.6.2. *Turns about the vertical axis*

From figure 5*a* it has been concluded that males and females control the target deviations from the midsagittal plane. How they could accomplish that may be read from (4), §2.3.

In figure 6 the time course of the angular velocity about the vertical axis (solid line) and the horizontal error angle (broken line) is plotted for parts of the chase shown in figure 2*a* and

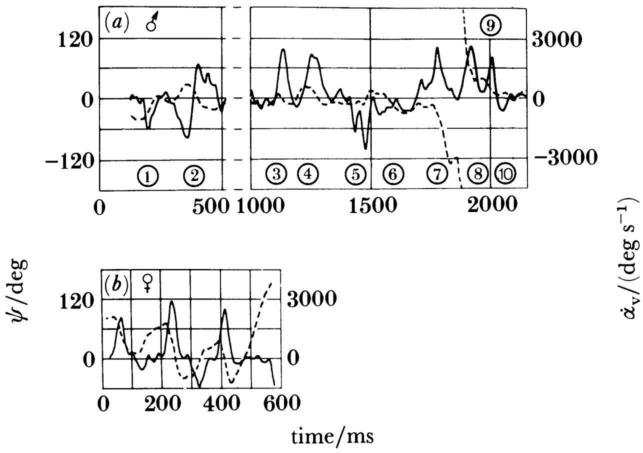

FIGURE 6. The time course of the angular velocity about the vertical axis $\dot{\alpha}_V$ (solid line) and the horizontal error angle (broken line) of the pursuer. (*a*) Parts of the chase of figure 2; numbers refer to manoeuvres described in the text; (*b*) the same variables of a female track (not illustrated); notice the much greater error angles in the female track.

of a female track that is not illustrated (*b*). In both examples the time profile of the angular velocity is characterized by consecutive peaks. Every peak can be attributed to a turn and is correlated to a certain change of the orientation of the long axis (turning amplitude α_V). Pursuit at constant, moderate angular velocity seems to play no role. Some of the turns in figure 6*a* are marked by numbers: 1 is the turn shortly after the start, which brings the target to the front of the pursuer; 2–6 are turns during the period of pursuit including the second attack (5 includes in fact two turns); 7 marks the turn that initiates the first retreat, whereas with turns 8 and 9 the image of the target is again shifted to the front and 10 belongs to the subsequent period of pursuit.

These turns serve to fixate the target in the frontal eye region. The simplest hypothesis to be tested might be to ask how the amplitude is statistically related to the horizontal error angle at which it is initiated. The resulting distributions are plotted in figure 7*a*, *c*, *e*. The broken lines in this figure indicate where the turning amplitude would be equal to the corresponding error angle. The turning amplitude depends on the error angle. This holds for both sexes. Although there is a considerable scatter in the data, further specific statements are possible.

Firstly, there is a profound difference between male and female turning. About 65% of the female 'turns' are probably due to digitizing errors, whereas only 35% of the male 'turns' are so small. Only 52 (out of 423) female turns have an absolute value of more than 20°, whereas

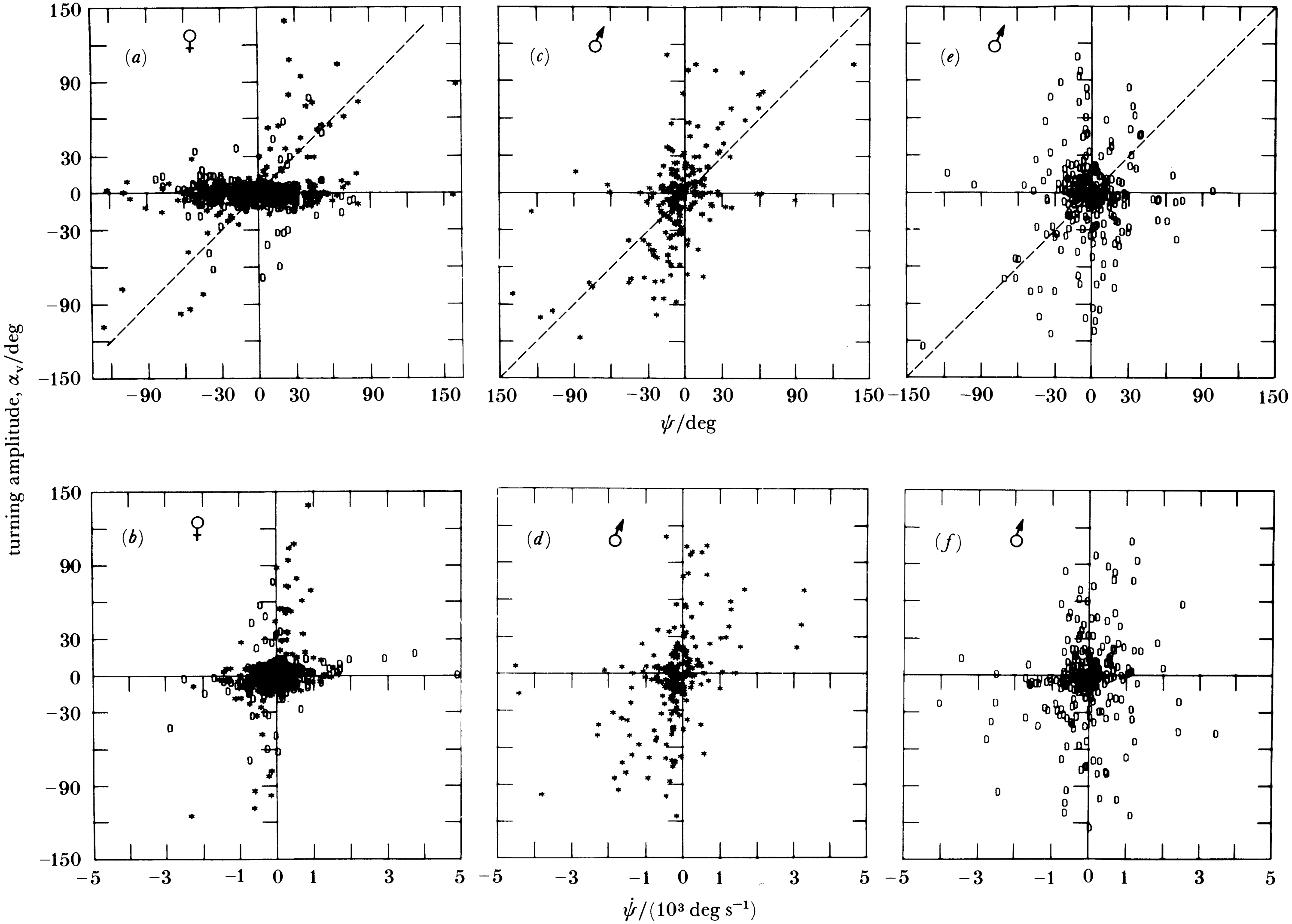

FIGURE 7. Distribution of the turning amplitudes about the vertical axis (α_v) with the horizontal error angle ψ (*a*, *c*, *e*) and its time derivative $\dot{\psi}$ (*b*, *d*, *f*). Values of the variables on the abscissa are taken 25 ms before the start of the turn; inaccuracy of delay determination ±5 ms due to discrete sampling; pro, progressive motion (*); re, regressive motion (0). The broken line in (*a*), (*c*) and (*e*) denotes the 45° angle. If values for α_v were closely related to the error angle, their values should scatter around this line. Turns induced by progressive motion are more closely related to ψ and $\dot{\psi}$ than those induced by regressive motion. Total number of points: females, 423; males, 454.

190 (out of 456) male turns belong to this range. There are almost equal numbers of 'real' turns with an amplitude of less than 20° (98 in females and 107 in males). However, these female turns are distributed over the whole range of the error angle, whereas in males they seem to be initiated mainly frontally. Thus, low-amplitude turns of females seem not to be related to the error angle. In contrast, turns of an absolute amplitude of more than 20° depend on the horizontal error angle in both sexes (figure 7*a*, *c*, *e*).

Secondly, direction-dependent effects are characteristic for both sexes. Turns initiated during progressive (front to back) target motion (*) are more closely related to the horizontal error angle than those initiated during regressive (back to front) target motion (0). To see these differences better the male sample is split up according to this criterion. The linear cross-correlation coefficients for turns found during progressive motion are highly significant for both the male (correlation coefficient, $r = 0.69$; total number, $N = 90$) and female samples ($r = 0.80$, $N = 34$), if only amplitudes greater than 20° are considered. The corresponding correlation coefficients for the turns observed during regressive target motion are smaller, but significant in the male ($r = 0.37$, $N = 100$, $p < 0.05$) and not significant in the female sample ($r = 0.23$, $N = 18$). It should be mentioned that turns generated while the target's image is located in the binocular eye region (about $\pm 10°$) cannot be related to progressive and regressive motion. Many turns of a considerable amplitude are elicited in this region.

Thirdly, most turns are greater than the corresponding error angle. Turns initiated during regressive motion may often have a different sign from ψ. The precision of the control system, which generates the turns, may be estimated from the error angle at the end of the turn compared with the error angle at which the turn is initiated. Although most turning amplitudes of a size of more than 20° are more than 10° greater or even have different signs from the error angle (56% in females, 84% in males), they often compensate the target deviation within a range of $\pm 10°$ (17% in females, 41% in males) or undershoot by more than the 10° (48% in females, 46% in males). In males few turns overshoot by more than 10° (13%) whereas in females this happens more often (35%). This again indicates that the male control system is more elaborate than that of the female. At first glance $\pm 10°$ seem to be rather imprecise. However, one has to take into account that with a turn of an amplitude of 50 or 120°, initiated at an error angle between $\pm 10°$, the target may be stabilized frontally (figures 6 and 7). This may happen because marked relative motion between target and pursuer occurs during the turns. The comparison demonstrates clearly that the fixation is better than indicated in figure 7*a*, *c*, *e*. This improvement results from the influence of further cues.

Turning amplitude is also correlated to the retinal azimuthal target velocity $\dot{\psi}$ in females (figure 7*b*) and males (figure 7*d*, *f*). Again the linear cross-correlation coefficients for turns initiated by progressive target motion ($r = 0.55$, $N = 90$ in males and $r = 0.74$, $N = 34$ in females) are much greater than those for the turns elicited during regressive target motion ($r = 0.17$, $N = 100$ in males and $r = 0.18$, $N = 18$ in females). Only the correlation coefficient of the sample composed of the female regressive turns is not significant. It would now be feasible that the components of target position (ψ) and velocity ($\dot{\psi}$) are the only variables influencing the generation of the yaw-turns. Neither by parametrizing nor by a multiplication of these variables could a consistent result be obtained. Therefore, these two variables are most probably not sufficient to explain the data. In addition, further influences on the turning behaviour are indicated, at least in males. This may be seen from a comparison of the values of the turning amplitudes with the two input variables just considered and is exemplified by the turns of figure 6*a*. (i) Turns 1, 3, 5 and 9 have similar amplitudes. They all occur at low retinal target velocities, but the error angles differ considerably. Turns 1 and 9 are initiated at more than ±30°, but 3 and 5 at less than ±10° horizontal error angle. (ii) Turns of different amplitudes are found at similar ψ and $\dot{\psi}$ (compare turns 3, 5–6 and 10). (iii) The turns with numbers 4 and 5 occur at similar error angles, but different $\dot{\psi}$. Nevertheless, they have similar amplitudes. Despite these complexities, most turns seem to be 'appropriate', because they serve to fixate the target in the front part of the eyes. This is also the main reason why the different turning amplitudes do most probably not reflect a simple scatter.

The additional influences demonstrated in the last paragraph are probably related to the translational movement of the flies. As can be seen from (4), translation influences the retinal target velocity, especially at small distances. These geometrical effects should be counteracted by a visual control system to improve fixation. Therefore, it was tested whether distance, the forward velocity of the pursuer or the relative retinal expansion velocity (RREV, Wagner 1982), being a measure for time-to-contact, play a role. Although at moderate forward velocities and RREVs (time-to-contact over 200 ms), a better linear correlation between the turning amplitude and the horizontal error angle results, a consistent relation was not found.

If only turning amplitudes occurring at error angles between ±30° are considered, there seems to be an enhancement of the gain (figure 7*a*, *c*), because the slope of the regression line found by a linear correlation between turning amplitude and horizontal error angle becomes steeper (from 1.1 to 1.9 in males). However, a constant increase of the gain in this region cannot explain why different turning amplitudes occur at similar error angles and retinal target velocities. Thus, one may doubt that an increase of the gain in the frontal part of the eyes is a main component of the unknown influences. Since not all cues used for fixation could be uncovered a meaningful equation that characterized the control of yaw torque cannot be presented. It could be shown, however, that the horizontal error angle and its time derivative are input variables to this control system, which allows the flies to perform very appropriate turns irrespective of the complexity of the situation.

3.6.3. *Turns about the transverse axis*

During the pursuit sequences the target is located in a certain region of the eye relative to the horizontal plane of the pursuer's body (figure 5*b*). This fixation seems to be even more difficult to achieve than that just described. Firstly, gravity influences the vertical movement of the fly. Secondly, the direction of the force vector generated by the flight motor is relatively fixed with respect to the body axes (paper I). Thus, a torque about the transverse axis (pitch) will normally change the angle of ascent. If pitch were also controlled by the vertical error angle or its time derivative, a quite precise adjustment is necessary if the target should be stabilized in a certain eye region. Thirdly, approach and especially vertical movements have an influence on the target's retinal position. Continuous linear correlation analysis reveals positive correlations between the angular velocity about the transverse axis and the vertical error angle as well as its time derivative. This indicates that pitch is controlled by these input variables. Since the time course of the angular velocity about the transverse axis resembles that of the vertical axis (figure 8), the control system cannot be characterized with a continuous correlation.

In figure 8 the time courses of the angular velocity about the transverse axis $\dot{\alpha}_t$, the vertical retinal target velocity $\dot{\theta}$ and the vertical error angle θ are shown for parts of the male chase

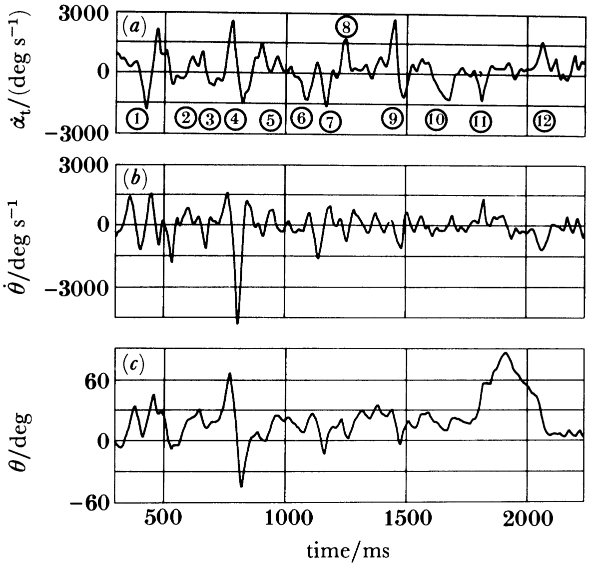

FIGURE 8. Time course of the angular velocity about the transverse axis $\dot{\alpha}_t$ (*a*); the vertical error angle θ (*c*) and its time derivative $\dot{\theta}$ (*b*) for parts of the chase of figure 2. Numbers in (*a*) refer to manoeuvres addressed in the text.

of figure 2. The target is fixated in the upper eye region at an angle of about 10–30° during most of the time (figure 8*c*). Oscillations of the vertical error angle occur and there are indications of a pitch control. During the approach of the target, shortly before overshooting it, the target's retinal image moves to the dorsal margin of the pursuer's eye (about 0.7 s). Similarly the target's own movement may displace its image on the pursuer's eye (1.1–1.3 s). The pursuer reacts with turns that serve to correct the deviations (turn 4 and turns 6, 7 in figure 8*a*, respectively). These turns are most probably induced by the vertical retinal target velocity (figure 8*b*), because at similar error angles, but different target velocities, the sign of the turn follows that of the retinal target velocity. An example, in which mainly the target's position seems to induce the turn, occurs during the refixation after the first retreat (turn 12 in figure 8*a*). Turns numbered 2, 3 and 10 refer to movements of the pursuer below the target that change the path of ascent and may also be part of a control. Further influences on the vertical error angle that probably do not underlie a visual control are observed. Firstly, during the retreats the pursuer may actively turn away from the target (turn 11 in figure 8*a*). Secondly, turns 5 and 8 correspond to manoeuvres that allow the male to rise again after it has reached a position below the target after an overshoot (0.9 and 1.2 s, respectively). Thirdly, turns that are most probably banked are numbers 1, 4, 7, 8, 9 and 10. During a banked turn angular movements about the vertical and transverse axis occur simultaneously. The angular velocity about the transverse axis often increases steeply and may change sign, whereas the angular velocity about the vertical axis normally does not change sign (see also paper I). At least some of the movements about the transverse axis during these turns are due to aerodynamic constraints and not under visual control.

As would be expected from these considerations, the statistical analysis provides a rather confusing picture (figure 9*c*, *d*). However, a relation between the turning amplitude and the retinal elevational target velocity is obvious in chasing (figure 9*d* , linear cross-correlation coefficient $r = 0.4$, total number $N = 540$, $p < 0.05$). At first glance there seems to be no dependence of the turning amplitude (α_t) on the vertical error angle. However, the pursuer sometimes performs turns towards the target after the start or at the beginning of a new approach (see number 12 in figure 8). Such turns are marked by the circles in figure 9*c*. They seem to be related to the vertical error angle.

Females approach their targets neither as fast nor as closely as males. Thus, in female tracks pitch control may be better studied independently of translational influences. As in the control of yaw-torque, turning amplitudes smaller than a certain absolute value are not related to the error angle. For figure 9*a*, *b* turns have been selected that are not related to a banked turn and are greater than ±10°. A correlation between the vertical error angle and α_t is found ($r = 0.66$, $N = 41$, $p < 0.05$; figure 9*a*). The regression line crosses the abscissa at about -25 to $-10°$ of the error angle. Thus, as was indicated by the error angle distribution

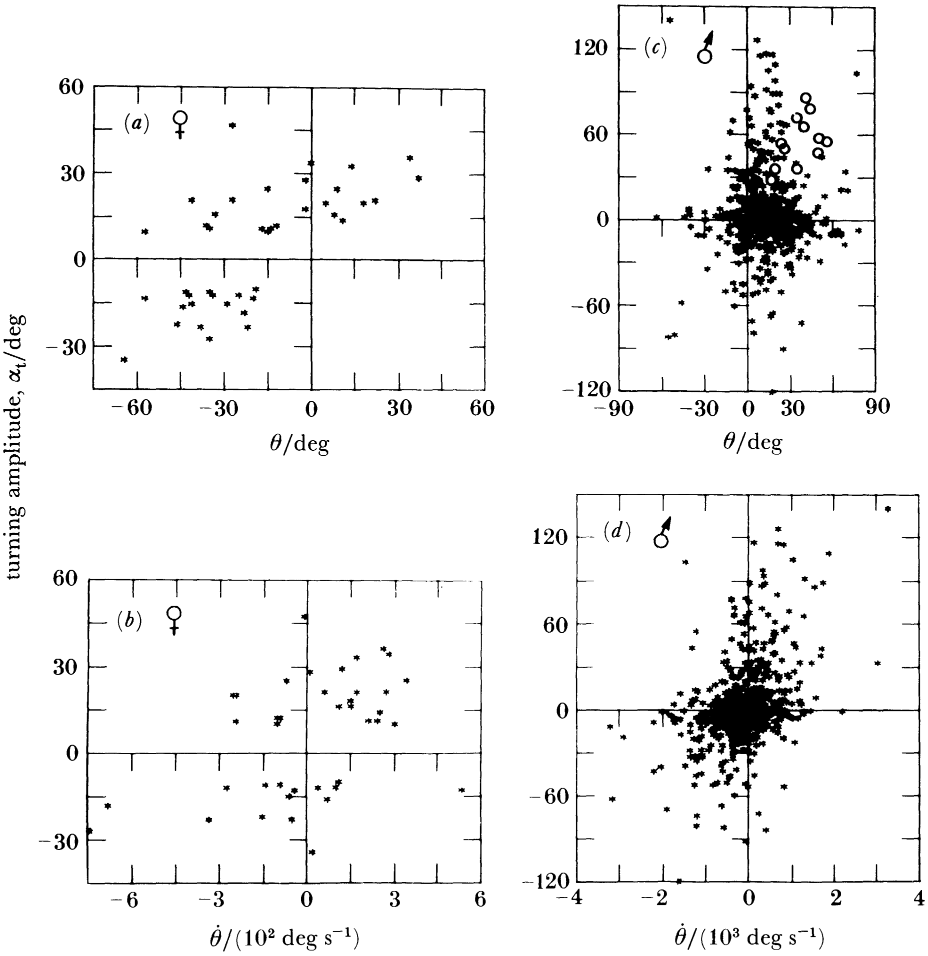

FIGURE 9. Distribution of the turning amplitudes about the transverse axis (α_t) with the vertical error angle θ (*a*, *c*) and its time derivative $\dot{\theta}$ (*b*, *d*). The values of θ and $\dot{\theta}$ are taken 25 ms before the start of the turns. Only those turns of the females with an absolute amplitude of more than 10° and that are not related to a banked turn are included (*a*, *b*; total number of points, 41). The turning amplitudes depend on both, the vertical error angle and its time derivative (*a*, *b*). In the male sample (*c*, *d*; total number of points, 540) a correlation is indicated between $\dot{\theta}$ and the α_t only. The circles in (*c*) mark the turns performed shortly after take-off or after a retreat (where translational movement was not dominant). These values seem also to be related to the vertical error angle.

(figure 5*b*), the turns serve to fixate the targets in the lower part of the eyes. An additional influence of the time derivative of the vertical error angle is indicated by the scatter diagram of figure 9*b* ($r = 0.42$, $N = 41$, $p < 0.05$). The data base is not large enough to unravel possible interrelations between the vertical error angle and its time derivative. However, females seem to control pitch in a similar manner as yaw.

3.7. *Translational movements*

In many of the tracks and chases a correlation between the three-dimensional translation velocity or also forward velocity of the pursuer and the distance to the target is observed. This result has been interpreted as evidence for a further visual control system (Wehrhahn *et al.* 1982). However, closer inspection leads to another interpretation: in figure 10*a* the time course of the three-dimensional translation velocity of the pursuing male in the chase of figure 2 is shown together with that of the distance to the target. Obviously both variables fluctuate in a similar manner (compare the timing of the extreme values of the two variables). By a comparison of the time course of the translation velocity with that of the angular velocity about the vertical axis (figure 6*a*) and by inspection of the trajectory, it becomes obvious that the decrease of velocity occurs simultaneously with or shortly after the turns (the arrows in figure 10*a* correspond to turns numbers 3, 4, 5 of figure 6*a*). This observation has been interpreted as being a consequence of the flight motor organization of houseflies (paper I). Thus, the fluctuations seem to be due to aerodynamic constraints and not due to the action of a visual control system. A high correlation between translation velocity and distance at a delay of

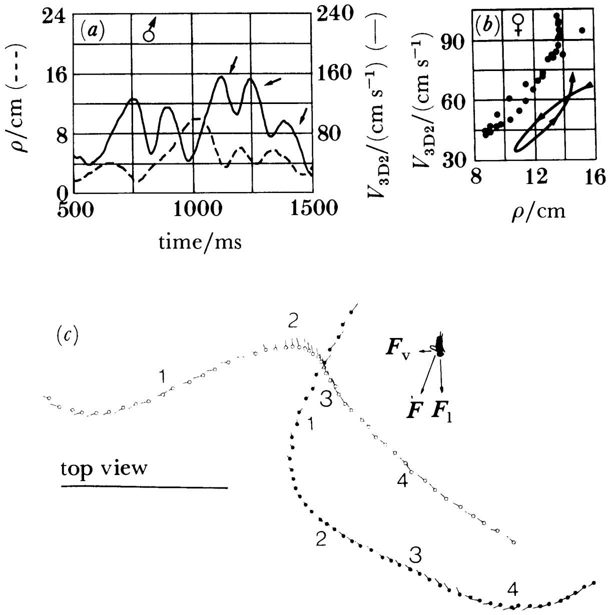

FIGURE 10. The relation between three-dimensional translation velocity of the pursuer and the distance between target and pursuer. (*a*) Part of the male chase of figure 2; solid line, V_{3D2}; broken line, ρ. Both variables show similar fluctuations in time. The arrows indicate the influence of the turns with numbers 3, 4, 5 in figure 6*a*. (*b*) The same variables plotted for a female track in a scatter diagram. The values of V_{3D2} are delayed 110 ms with respect to the values of ρ. The solid line and the arrows give time information. Although a high correlation is obvious, it is also a consequence of angular movement. (*c*) The trajectory corresponding to (*b*). The leading female is indicated by the filled circles, the tracking one by the open ones. Inset shows hypothetical orientation of body and legs and the components of the motor force. Numbers denote the time in 0.1 s and the bar 10 cm.

60–100 ms (Wehrhahn *et al.* 1982; own observations) probably results from the behaviour of the male: during the approach, which often takes place without a noticeable decrease of the velocity, the distance becomes smaller. It increases after the target has been missed due to overshooting. Translation velocity decreased during the turn and increases afterwards again (figure 10*a*, 0.7–1.0 s, figure 2, top view at 0.8 s).

A similar observation is made in female tracks. In figure 10*b* the translation velocity of a tracking female is plotted versus the distance to the target. The high correlation is obvious. However, in this case, too, the translation velocity decreases due to a turn about the vertical axis (figure 10*c*). Distance decreases in the period of the approach before the turn, it increases shortly after the turn and decreases again in the period of the fly's acceleration.

In the close vicinity, shortly before the target is caught by the male, the use of distance information cannot be excluded. This situation is not examined here. However, in the examples of figure 10 and apparently all other ones, a visual control of the translational velocity by the distance to the target could not be detected during the period of approach.

In many cases a sideways movement results from the inertial forces acting on the translational movements during the turns (figure 2 and 3). In some examples, however, a sideways motion is found independently of a turn about the vertical axis during straight flight.

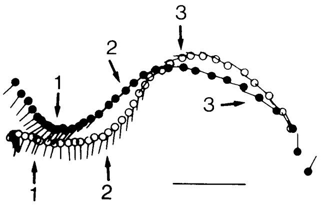

FIGURE 11. Tracking by sideways motion. The movements of two females are viewed from above. Numbers denote the time in 0.1 s. The time interval between two frames is 10 ms. In the beginning the tracking fly (○) follows the target's trajectory by translational movement alone (0–0.25 s; then it performs a turn about the vertical axis to closely match the flight path of the target. Bar, 2.5 cm.

Figure 11 shows an extreme case viewed from above. The tracking female fly starts to move at an angle of nearly 90° to its long axis from a stationary aerial position. This sideways movement is most probably due to rolling about the long axis (paper I). In the first 0.25 s the fly closely follows the target's movement solely by translational movement at a distance of about 2 cm. After this period it continues tracking by turning about the vertical axis. Although this is the only example of 'sideways' tracking, it is shown here because it clearly demonstrates the capability of houseflies to follow the movements of the target by translation alone. However, this strategy does not play an important role either in females or in males.

Males fly underneath the target and attack it from below, whereas females are positioned above the target in most cases (figures 2 and 3). This indicates that the vertical movement has to be controlled too. Owing to the relatively fixed direction of the force vector, males may come underneath the target in two ways only: (i) by reducing the force generated by the flight motor and sinking due to the action of gravity and (ii) by rotating about the transverse axis. As shown in figure 2 (0.8 and 1.15 s, side view), the latter strategy seems to be dominant. From (5) it can be read that the angular velocity about the transverse axis and the upward velocity may be important parameters in controlling the vertical error angle. In fact, a positive correlation between upward velocity and the vertical error angle was found in some examples. However, it is not clear, and will not be analysed further here, whether this correlation represents an independent control system because the upward velocity depends on the pitch (body) angle, which is normally also changed by a turn about the transverse axis (see also §3.6.3.).

4. Discussion

In this part the visual guidance during pursuit in houseflies has been phenomenologically described. Obviously only a beginning in the understanding of the visual control underlying the aerobatic chases and tracks of houseflies is achieved. However, it seems necessary to 'accumulate' data of the manoeuvres during pursuit before a thorough theoretical analysis can be attempted. Although both sexes pursue targets, a marked difference between the chasing of males and the tracking of females is evident. Houseflies mainly control the rotational body movements with information obtained from the target. A control of the translation velocity by the distance to the target is observed neither in males nor in females. Instead, males attack the target at high translation velocities.

4.1. *Consequences of the turning behaviour for the methods used for the analysis*

Hoverflies seem to control the torque output during foveal tracking by the target's deviation from the midsagittal plane in a continuous manner (Collett & Land 1975; Collett 1980*a*, *b*). Every value of the angular velocity can, thus, be related to the value of the error angle measured 10 ms before. In contrast, the large-amplitude turns are the main component of angular tracking in houseflies. The turns of *Musca* are similar to the body saccades sometimes interspersed with tracking in hoverflies and marchflies (Zeil 1983*b*). For the analysis of angular tracking and chasing in *Musca* the following method is applied: the turning amplitudes and not the angular velocities are correlated with the input variables. As has been mentioned in the Introduction, a control system may be characterized by the reaction time between input and output (delay) and the factor converting an input value to an output value (gain). The quantitative characteristics of the control systems could not be unravelled because clear criteria for relating the output to the input, which were available in using continuous correlation, cannot yet be defined. Problems in this context are: (i) exact delay measurements are possible only under defined stimulus conditions. The fast and irregular fluctuations in retinal target position, however, do not meet this criterion; (ii) on the other hand, absence of fluctuations would decrease the value of a correlation analysis, too, because the position of the maximum of the correlation coefficient becomes smeared. Thus, the delay, indicated by this measure, cannot be precisely determined and also the gain, which probably varies with the assumed delay, remains uncertain.

One can compute ('simulate') the flight path of the pursuing fly by using the properties of the control systems acting during pursuit or aerodynamic constraints as they are revealed by a linear correlation analysis (Land & Collett 1974; Poggio & Reichardt 1981; Wehrhahn *et al.* 1982). The same is possible for body movements in three-dimensional space (H. Wagner, unpublished). However, as Buchner (1984) has mentioned, the simulations are very unspecific. The main constraints seem to be to find an equation for each output variable that relates it to an input or another output variable irrespective of a visual control mechanism being present or not. Then, if the target coordinates of (1)–(3) are included, a simulation will be successful. The simulations performed so far used the results of the linear correlation analysis. Thus, they implicate inadequate mechanisms of pursuit in houseflies. Therefore, these simulations are of weak significance and should no longer be performed, unless the mechanisms underlying chasing and tracking are incorporated.

4.2. *Organization of rotational control systems and related problems*

The control systems for yaw and pitch are organized in a complex way. The retinal positions and velocity of the target influence the turning behaviour. The influence of the latter variable improves fixation (Land & Collett 1974) in that the dependence on the direction of target motion phenomenologically leads to a 'prediction'. These two cues seem to be straightforward input variables for any rotational control system that has to bring about fixation. At least in male houseflies further factors improve the control. However, it is not clear how this is achieved. As has been considered above, these cues should be related to the translational components (distance, translation velocity of the pursuer).

A simple answer to the question of how the visual input controls the fly's movement during the pursuit is not yet possible. Four reasons for this will now be discussed.

(i) The geometry of pursuit in three-dimensional space is complex. Thus, control of one degree of freedom may cause 'negative' influences on some other degree. This is especially true for the control of pitch (§3.6.3.). Thus it might be necessary to ask other, probably more complex, questions than is done here, or analyse only specific manoeuvres. For this, however, much more data than those that are analysed here seem to be necessary. That such a 'dissecting' might be successful is indicated in figure 9*c*, where a specific fraction of turns is marked by circles. The turning amplitudes of these turns seem to be related to the vertical error angle, whereas the whole sample provides a very confusing picture.

(ii) Even with the improved resolution of the flies on the films, not all movements could be computed. Head movements are not visible on the films. Although during cruising flights the head is better oriented in the horizontal plane than the body (H. Wagner and C. Wehrhahn, unpublished), this might not be so during pursuit. In addition, the head can be turned about its transverse and vertical axis leading to other retinal target positions and target velocities than those assumed here. These deviations can only be estimated from the study of head and body coordination in free flight.

(iii) A spherical coordinate system is only a crude approximation to the real eye geometry (Braitenberg 1967; Franceschini *et al.* 1981). The values of the eye coordinates may considerably deviate from spherical values.

(iv) The target has been regarded as a point here. This seems to be a good approximation only at distances greater than about 8 cm, because the angular subtense of the target is then less than 5°. It is not known, however, which point of the target is fixated by the flies at smaller distances.

4.3. *Comparison of free and tethered flight*

Tethered flying houseflies not only fixate a single stripe, but also follow the movement of different objects in their environment (Reichardt 1973; Virsik & Reichardt 1976). This is similar to the results of the free-flight behaviour. The yaw-torque response of tethered flying flies to different stimuli can be predicted quite well (Reichardt & Poggio 1976; Virsik & Reichardt 1976; Reichardt *et al.* 1983; Egelhaaf 1985). However, tethered flies seem to react in a smooth and continuous way (Reichardt & Poggio 1981). Therefore, according to the theory of Reichardt & Poggio it is assumed that the visual induced response has a much shorter time constant than the 'error angle history'. Whether this condition is met in free flight cannot be decided. The fluctuations of both the input and output signal lie in the same range of frequencies. Further implications of the free-flight behaviour and their relations to the experiments in tethered flight are examined in paper III.

4.4. *The relation of the free-flight data to morphological and electrophysiological investigations*

Sex-specific differences are found in the eye morphology, the arrangement of the photoreceptors and the optic lobes (Beersma *et al.* 1977; Franceschini *et al.* 1981; Hardie *et al.* 1981; Hausen & Strausfeld 1980). In males and females an 'acute zone', showing an increased resolution, is found (Land & Eckert 1986). This zone is directed frontally in females and dorsofrontally in males. The male 'acute zone' corresponds well with the region in which male-specific receptor cells are found (called 7r, Hardie *et al.* 1981). In fact, the target is fixated in this region during 80% or more of the time (see figures 6 and 8). The different photopigments of houseflies are sensitive from the ultraviolet to yellow light. Obviously ultraviolet light is not necessary for pursuit to take place, because males and females pursue targets under conditions in which no ultraviolet light is present (indoors under artificial illumination in glass cages).

The results of this study are not specific enough to attribute them to a certain class of cells at higher visual neuropiles. However, one can derive some constraints that have to be fulfilled by the neuronal networks underlying chasing and tracking. Firstly, the position as well as the velocity has to be encoded for both the horizontal and vertical direction. Secondly, there has to be some variability, because the flies do not pursue targets all the time and at least the males change between fixation and non-fixation when starting a retreat. This variability is most probably introduced after the level of the lobula plate cells, because the latter respond in a very stereotyped way to stimulation (Hausen 1984; Egelhaaf 1985). Thirdly, the networks that are active during the periods of pursuit and the attacks mainly have to drive the rotational outputs.

Anatomically the control systems of males and females are most probably represented by different networks. This is concluded from the different eye regions in which the target is fixated by the two sexes. It is very interesting that male-specific neurons with receptive fields in the dorsal part of the eye have been found in the lobula. MLG-cells have large receptive fields, whereas COLC- and COLD-cells are columnar and have smaller receptive fields (Hausen & Strausfeld 1980). The response properties of these cells have not yet been investigated. However, it is tempting to attribute to them a role in chasing. Egelhaaf (1985) functionally characterizes small field-selective cells in females. These cells seem to be part of a network that accomplishes figure-ground discrimination (Reichardt *et al.* 1983) and induces a fixation of the target in tethered flight. They are one of the candidates of the control of yaw-torque during tracking.

4.5. *On the biological significance of pursuit*

Males seem to chase targets in the air to get a mate. In this context the behaviour on the ground may be regarded as a prechasing reaction. If the target starts to fly before the jump, the male chases and attacks it in the air. The sudden attacks seem to be a good strategy for aerial capture, because the target is reached in a very short time. This may also be the reason why a control of the translation velocity by the distance to the target does not take place. Such a 'homing-in' strategy would only be a successful alternative, if the target does not perform evasive reactions. The periods of approach, pursuit and attacks are sometimes interrupted by retreats from the target. In some cases the target stops its evasive reactions if the pursuer retreats (figures 2 and 4). Thus, the significance of the retreats may be that they increase the probability of a hit during the next attack. Indeed, the percentage of contacts with the target seems to increase with the numbers of attacks (table 2). In accordance with the strategy of the chasing male, a reversal of chasing fly–chased fly is very rarely observed. Thus, houseflies do not perform 'games' in the air, but really chase each other with clearly assigned 'roles'.

The male is able to distinguish between females and males. However, so far, the nature of the information it obtains remains speculative: (i) the pursuer could extract information from the target's translation velocity or acceleration, since they are different in males and females; (ii) males or females could produce a signal (for example, a pheromone) that repels or attracts the pursuer when it comes close to the target. A male attractant produced by female houseflies (Rogoff *et al.* 1964) as well as a male deterrent produced by male houseflies has been described (Schlein *et al.* 1981). However, nothing is known about the role of these pheromones during pursuit.

While it is easy to attribute a biological significance to male chasing, one can only speculate about the meaning of female tracking. By computing relative motion, females are able to detect objects in an environment with contrast. In tethered flight they turn towards these objects (Reichardt *et al.* 1983). They could use this information for course control, foraging or landing. On the other hand, tracking could serve to fixate the moving target for some time in the frontal part of the eyes, where resolution is improved (Beersma *et al.* 1977; Land & Eckert 1986). Since the flight motor cannot produce a sidethrust, a turn towards a target at a non-zero translation velocity always leads to some matching of the flight paths. It is an open question, however, why females sometimes follow the vertical movements of the target and perform such complicated manoeuvres as shown in figure 11.

4.6. *Pursuit in houseflies and hoverflies*

Male houseflies attack targets and try to catch them in the air. In contrast, the hoverfly *Syritta* shadows targets in the air and catches them when sitting on flowers (Collett & Land 1975). *Syritta* males control the rotational and translational movements during the pursuit to fixate the target frontally and to keep a certain distance to the target. Houseflies seem mainly to control the rotational movements during pursuit. They do not control the translation velocity by the distance to the target. Hoverflies seem to prefer smooth tracking at low angular velocities (Collett 1980*b*), whereas in *Musca* large amplitude turns are dominant. These behavioural differences are paralleled by differences in the organization of the flight motors of these species. Whereas hoverflies are able to adjust forward and sideways movements independently of each other and of rotations about the vertical axis, houseflies do not produce an active sidethrust and do not fly backwards. Their strategy seems to be coadapted to the organization of the flight motor. Shadowing would be risky. If the target approaches the pursuer it has to perform a time-consuming turn and might lose the target. The retreats from the target cannot be taken as a contradiction to this consideration, because they have to be regarded in the context of the attacks that probably increase the chance of capture so much that this general strategy is evolutionarily stable. Thus, it seems that the strategies of pursuit and the organization of the flight motor mutually influence each other. However, this does not exclude that flies with a flight motor similar to *Syritta*, for example *Eristalis* (Collett & Land 1978) and *Bibio* (Zeil 1983*b*), may also attack targets in the air.

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APPENDIX

The derivation of (4)–(6) will be shown here. I follow Rieger (1983) with the exception that my θ is $90-\theta$ in his equations. Equations (1)–(3) are rewritten here:

$$\psi = \arctan\ (y_t/x_t) \text{ defined from } -180 \text{ to } +180°, \tag{A 1}$$

$$\theta = \arctan\ (z_t/\sqrt{(x_t^2+y_t^2)} \text{ defined from } -90 \text{ to } +90°, \tag{A 2}$$

$$\rho = \sqrt{(x_t^2+y_t^2+z_t^2)}. \tag{A 3}$$

x_t, y_t and z_t are the coordinates of the position of the target in a fly-centred cartesian coordinate system. ψ, θ and ρ are the spherical coordinates. The time derivatives denote in component form

$$\dot{\psi} = \frac{1}{\rho \cos\ (\theta)}\ (v_{fr} \sin\ (\psi) - v_{sr} \cos\ (\psi)) + \tan\ (\theta)\ (\dot{\alpha}_l \cos\ (\psi) + \dot{\alpha}_t \sin\ (\psi)) - \dot{\alpha}_v, \tag{A 4}$$

$$\dot{\theta} = \frac{1}{\rho}(-v_{fr} \sin\ (\theta) \cos\ (\psi) - v_{sr} \sin\ (\theta) \sin\ (\psi) + v_{ur} \cos\ (\theta)) + \dot{\alpha}_l \sin\ (\psi) - \dot{\alpha}_t \cos\ (\psi), \tag{A 5}$$

$$\dot{\rho} = -(v_{fr} \cos\ (\psi) \cos\ (\theta) + v_{sr} \sin\ (\psi) \cos\ (\theta) + v_{ur} \sin\ (\theta)), \tag{A 6}$$

where $\dot{\alpha}_v$, $\dot{\alpha}_t$, $\dot{\alpha}_l$ are the angular velocities of the fly and v_{fr}, v_{sr}, v_{ur} the relative translation velocities between fly and target. Since target and fly are both moving, the translation velocities are composed of two parts: one from the motion of the target and one from the motion of the fly. These can be summed since the motion of target and fly are independent of each other.

$$v_{ir} = v_i(\text{tr}) + v_i(\text{ta}), \tag{A 7}$$

where i is an index, (tr) denotes the motion of the tracking fly and (ta) the motion of the target. The values of target motion result from a transformation of the values of target motion in external coordinates $(x,\ y,\ z)$ to fly-centred coordinates $(x_b,\ y_b,\ z_b)$ with the 3×3 matrix of paper I (equation (A 1)):

$$M = \begin{bmatrix} \cos\beta_{xy}\cdot\cos\ (-\beta_{xz}) & \sin\beta_{xy}\cdot\cos\ (-\beta_{xz}) & -\sin\ (-\beta_{xz}), \\ \cos\beta_{xy}\cdot\sin\ (-\beta_{xz})\cdot\sin\beta_{yz} & \sin\beta_{xy}\cdot\sin\ (-\beta_{xz})\cdot\sin\beta_{yz} & \cos\ (-\beta_{xz})\cdot\sin\beta_{yz} \\ -\sin\beta_{xy}\cdot\cos\beta_{yz} & +\cos\beta_{xy}\cdot\cos\beta_{yz} & \\ \cos\beta_{xy}\cdot\sin\ (-\beta_{xz})\cdot\cos\beta_{yz} & \sin\beta_{xy}\cdot\sin\ (-\beta_{xz})\cdot\cos\beta_{yz} & \cos\ (-\beta_{xz})\cdot\cos\beta_{yz} \\ +\sin\beta_{xy}\cdot\sin\beta_{yz} & -\cos\beta_{xy}\cdot\sin\beta_{yz} & \end{bmatrix}. \tag{A 8}$$

Then

$$\begin{bmatrix} v_f(\text{ta}) \\ v_s(\text{ta}) \\ v_u(\text{ta}) \end{bmatrix} = M\cdot \begin{bmatrix} v_x(\text{ta}) \\ v_y(\text{ta}) \\ v_z(\text{ta}) \end{bmatrix}, \tag{A 9}$$

$v_x(\mathrm{ta})$, $v_y(\mathrm{ta})$, $v_z(\mathrm{ta})$ are the translation velocities in the fixed earth-related coordinate system with respect to the axes x, y, z. In summary, the geometrical relations between retinal target velocity and the movement of the target and the pursuer can be denoted as

$$\dot{\psi} = \frac{1}{\rho \cos(\theta)}((v_\mathrm{f}(\mathrm{tr}) + v_\mathrm{f}(\mathrm{ta}))\sin(\psi) - (v_\mathrm{s}(\mathrm{tr}) + v_\mathrm{s}(\mathrm{ta}))\cos(\psi)) + \tan(\theta)(\dot{\alpha}_\mathrm{l}\cos(\psi) + \dot{\alpha}_\mathrm{t}\sin(\psi)) - \dot{\alpha}_\mathrm{v}, \quad (\mathrm{A}\ 10)$$

$$\dot{\theta} = \frac{1}{\rho}(-(v_\mathrm{f}(\mathrm{tr}) + v_\mathrm{f}(\mathrm{ta}))\sin(\theta)\cos(\psi) - (v_\mathrm{s}(\mathrm{tr}) + v_\mathrm{s}(\mathrm{ta}))\sin(\theta)\sin(\psi) + (v_\mathrm{u}(\mathrm{tr}) + v_\mathrm{u}(\mathrm{ta}))\cos(\theta)) + \dot{\alpha}_\mathrm{l}\sin(\psi) - \dot{\alpha}_\mathrm{t}\cos(\psi), \quad (\mathrm{A}\ 11)$$

$$\dot{\rho} = -((v_\mathrm{f}(\mathrm{tr}) + v_\mathrm{f}(\mathrm{ta}))\cos(\psi)\cos(\theta) + (v_\mathrm{s}(\mathrm{tr}) + v_\mathrm{s}(\mathrm{ta}))\sin(\psi)\cos(\theta) + (v_\mathrm{u}(\mathrm{tr}) + v_\mathrm{u}(\mathrm{ta}))\sin(\theta)). \quad (\mathrm{A}\ 12)$$

This can be reduced here, since roll movements cannot be measured. Thus $\beta_{yz} = 0$, $\dot{\alpha}_\mathrm{l} = 0$:

$$\dot{\psi} = \frac{1}{\rho \cos(\theta)}((v_\mathrm{f}(\mathrm{tr}) + v_\mathrm{f}(\mathrm{ta}))\sin(\psi) - (v_\mathrm{s}(\mathrm{tr}) + v_\mathrm{s}(\mathrm{ta}))\cos(\psi)) + \tan(\theta)\dot{\alpha}_\mathrm{t}\sin(\psi) - \dot{\alpha}_\mathrm{v}, \quad (\mathrm{A}\ 13)$$

$$\dot{\theta} = \frac{1}{\rho}(-(v_\mathrm{f}(\mathrm{tr}) + v_\mathrm{f}(\mathrm{ta}))\sin(\theta)\cos(\psi) - (v_\mathrm{s}(\mathrm{tr}) + v_\mathrm{s}(\mathrm{ta}))\sin(\theta)\sin(\psi) + (v_\mathrm{u}(\mathrm{tr}) + v_\mathrm{u}(\mathrm{ta}))\cos(\theta)) - \dot{\alpha}_\mathrm{t}\cos(\psi), \quad (\mathrm{A}\ 14)$$

$$\dot{\rho} = -((v_\mathrm{f}(\mathrm{tr}) + v_\mathrm{f}(\mathrm{ta}))\cos(\psi)\cos(\theta) + (v_\mathrm{s}(\mathrm{tr}) + v_\mathrm{s}(\mathrm{ta}))\sin(\psi)\cos(\theta) + (v_\mathrm{u}(\mathrm{tr}) + v_\mathrm{u}(\mathrm{ta}))\sin(\theta)). \quad (\mathrm{A}\ 15)$$

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