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Chasing a dummy target: smooth pursuit and velocity control in male blowflies

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Male blowflies chase and catch other flies in fast acrobatic flights. To unravel the underlying control system, we presented a black moving sphere instead of a real fly as a pursuit target. By varying the size and speed of the target, we were able to systematically analyse the decisive visual determinants that guide chasing behaviour. Flies pursue targets of a wide range of sizes and velocities. The percentage of pursuits resulting in target capture decreases with increasing target size and speed. Chasing male flies adjust their forward velocity depending on the retinal size of the target, indicating that retinal size is a relevant input variable of the control system. The chasing fly focuses the target with great accuracy in the frontal part of its visual field by means of a smooth pursuit control system using the retinal position of the target to determine the flight direction. We conclude that for a comprehensive understanding of chasing control different time lags in the control systems of angular and forward velocity together with the impact of inertia on fly movements need to be taken into account.

Keywords: vision; sensorimotor control; fly; visual pursuit; pursuit behaviour; smooth pursuit

1. INTRODUCTION

To catch females and to mate with them, male flies engage in high-speed aerial chases involving virtuosic visually guided behaviour (Land & Collett 1974; Wehrhahn *et al.* 1982; Wagner 1986*b*). Given the great expenditure of neuronal resources and energy that is required to accomplish such an extraordinary form of mating behaviour, chasing appears to be a way of selecting the fittest males. The functional significance of chasing behaviour is underlined by sexual dimorphisms in eye design and in brain structure, most probably being the neural substrate for chasing control (Hardie *et al.* 1981; Hornstein *et al.* 2000; Hausen & Strausfeld 1980; Zeil 1983*a*; Strausfeld 1991). We analyse the chasing behaviour of the blowfly *Lucilia* (genus *Lucilia*), because it permits both filming of free-flying flies in relatively small flight arenas with sufficient spatial resolution and electrophysiological recordings of visual interneurons (Kimmerle & Egelhaaf 2000; Kern *et al.* 2001).

Apart from large hoverflies, which may reach their target via shortcuts by adopting an interception course (Collett & Land 1978), males of other fly genera fixate their target in the frontal visual field by body rotations, thereby virtually copying the track of the leading fly (Land & Collett 1974; Wehrhahn *et al.* 1982; Wagner 1986*b*). It is generally agreed that the retinal position of the target is an input variable of the fixation control system. The way the retinal position error is transformed into torque is, however, not yet fully understood. On the one hand, continuous tracking analogous to human smooth pursuit eye movements has been proposed (Land & Collett 1974; Wehrhahn *et al.* 1982; Land 1993*b*). On the other hand, a saccadic tracking strategy reminiscent of human fixation saccades has been put forward (Wagner 1986*b*).

Without shortcuts, chasing males will not reach their target unless they are faster. Still, it is not yet clear whether the fly controls its forward velocity relative to the target or chases the target in flat-out pursuit (Collett & Land 1975; Wehrhahn 1979; Wehrhahn *et al.* 1982; Wagner 1986*b*).

The analysis of chases after real flies is complicated by the irregular flight manoeuvres of the target fly. Therefore, we simplified the conditions by using a dummy fly as the target instead of a real fly. Flies have already been observed to chase moving targets, such as black painted peas (Collett & Land 1978; Zeil 1983*b*, 1986). By precisely controlling the movements of the target, we were able to unravel phenomenologically the major constituents of the control system underlying chasing behaviour.

2. MATERIAL AND METHODS

(a) *Experimental procedure and set-up*

The experiments were carried out on at least 7-day-old male blowflies of the genus *Lucilia* from laboratory stocks. For each set of experiments 10 flies were kept in the flight arena for 2–7 days. The experiments were carried out with five different sets of male flies at temperatures between 25 and 35 °C. Black painted glass spheres (diameters of 5, 8.3 and 13 mm) served as dummy flies. They were glued to a thin transparent glass rod (length of 100 mm) and moved on a circular track (radius of 100 mm; speeds of 1, 1.25 and 1.5 m s^{-1}) in the x–y plane (figure 1*a*). The dummy speeds were in the range of the speeds of real flies. Combinations of dummy size and speed were randomly chosen during filming sessions of 15–30 min.

The side walls of the cubic flight arena made of glass (length of the edges = 500 mm) were covered with randomly textured tracing paper and illuminated from outside by four 500 W halogen lamps (luminance of 1200 cd m^{-2} in the arena centre). The floor was transparent and the ceiling was homogeneously white. Chasing flights were filmed with two synchronized CCD-video cameras (image acquisition rate of 50 Hz; shutter time of 1 ms) and stored in the S-VHS format. One camera viewed the

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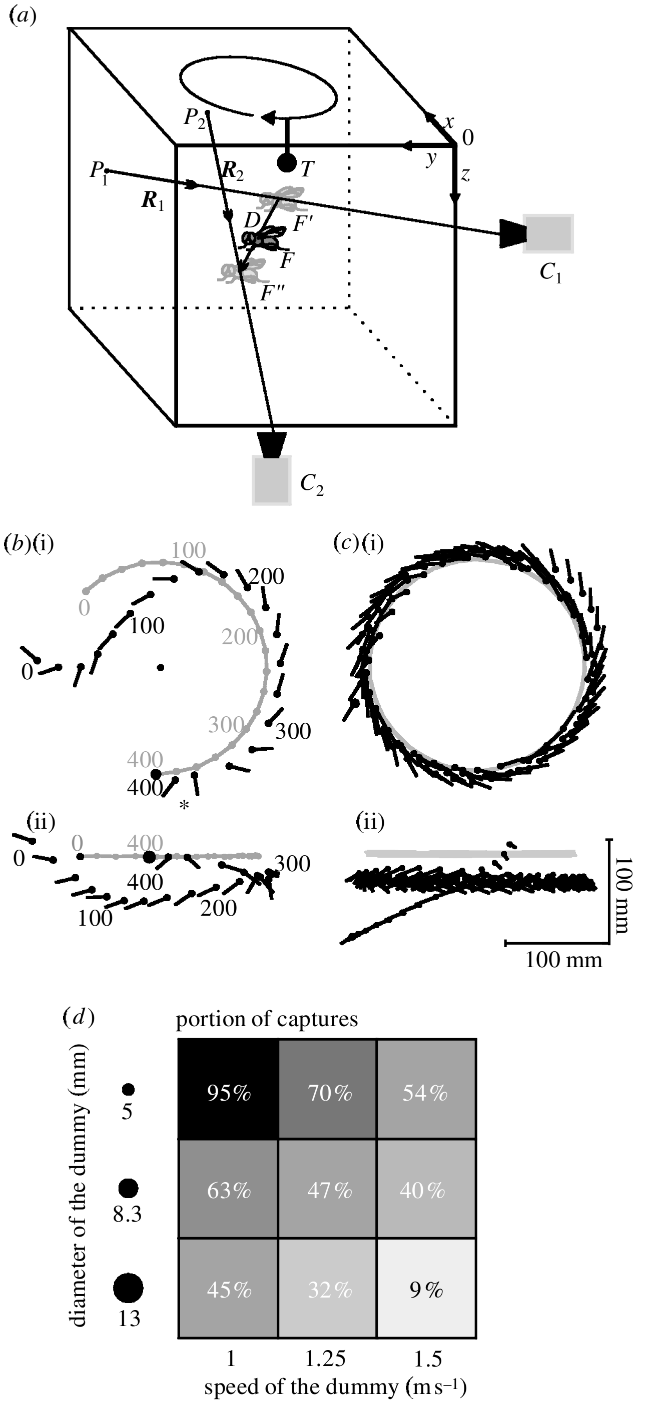

Figure 1. (*a*) Experimental set-up and reconstruction of 3D trajectories. Two cameras (C_1 and C_2) provide perspective views of the flight arena. The image coordinates are transformed into an orthographic 3D coordinate system to avoid systematic positional errors in the excerpted flight trajectories. The procedure used for this coordinate transformation requires the determination of the view reference point (VRP) in each camera view, which coincides with the camera position (C_1 and C_2). The VRPs were calculated with the aid of a removable translucent cube (not shown) with nine markers on the front and on the bottom, the arena coordinates of which were known. The image coordinates of the fly in both camera views (F' and F'') were projected onto the back and top sides of the arena (P_1 and P_2) in 3D flight-arena coordinates according to markers on the cube. Two vectors ($\boldsymbol{R}_1$ and $\boldsymbol{R}_2$) connecting P_1 and P_2 to the VRPs of the corresponding views were constructed in the arena coordinate system. The two vectors should intersect but owing to small measurement errors they are skew. There is a point on each line that is closest to the other line. The midpoint of the segment connecting these points (D) gives the position of the fly (F) and can be calculated by solving the following 3D set of simultaneous linear equations ($P_1 + t\boldsymbol{R}_1 + D = P_2 + u\boldsymbol{R}_2$) with two unknown variables t and u. The same procedure is used to determine the arena coordinates of the target (T). (*b*) Example of a reconstructed flight trajectory of a fly (black markers) capturing the target (grey markers) in plane view (i) and side view (ii). The fly is indicated by the position of its centroid (circle) and the orientation of its body axis (line). The numbers denote corresponding positions of the fly and the target every 100 ms. The asterisk denotes a sudden turn of the fly, before it catches the target. (*c*) Pursuit of the target without capture, plotting as in (*b*). (*d*) Dependence of target capture on target size and target speed. The percentage gives the portion of captures out of all chases for a given combination of target parameters. The number of chases for each combination of target parameters ranges between 22 and 65. The total number of chasing flights is 354.

arena from below, the other from the side through a hole in the wall texture. The optical axes of the cameras were aligned orthogonally to each other.

(b) *Data analysis*

Sequences of interest were digitized with a DT 3155 (Data Translation Inc.) frame-grabber and stored as TIFF files. We included 170 flights resulting in target capture into the analysis. Pursuits without capture ($n = 184$) were defined as chasing flights if the male fly followed the target on its circular track for at least one lap. The position and orientation of moving objects in each image were detected by specifically designed software, using standard image-processing algorithms. The reconstruction of the three-dimensional (3D) trajectories (figure 1*a*) and all further data processing were done using MATLAB 6.0 (The MathWorks, Inc.).

Although blowflies can move their heads (Land 1973; Hengstenberg 1993), it is possible to estimate gaze shifts from body movements without recording the head movements. Yaw head rotations are usually in phase, though somewhat faster than yaw body rotations. Rotations of the head relative to the surrounding area about the pitch and roll axes are generally small during flight (Schilstra & Van Hateren 1998). The angle subtended by the fly's longitudinal body axis and a line connecting the fly and the target, therefore, represents an appropriate approximation of the azimuthal fixation error ('error angle') in a spherical fly-centred coordinate system.

(c) *Errors*

The detectability of the fly and dummy in video images is affected by:

(i) inhomogeneous illumination of the flight arena;
(ii) reflections on the wings and the fly's metallic-green body surface;
(iii) lens aberrations of the camera objectives; and
(iv) noise in the CCD chip of the camera.

Videotape jitter during digitization adds to these error sources. To assess methodological errors, we reconstructed the given position and orientation of a perched fly. The yaw orientation of the fly was reconstructed with *angular errors* below 3° interquartile range (IQR) over time for stationary and for moving flies. When the same video sequence was repeatedly digitized, the time course of the reconstructed body orientation was different for each trial (IQR of 3°). Hence, the angular error is primarily caused by tape jitter rather than other sources. By contrast, the *position error* is not dominated by tape jitter, because it was possible to reconstruct the position with minimal errors (< 0.1 mm) between repeated digitizations of the same frames. The position error increased with increasing eccentricity of the fly in the flight arena, but was always below 1.5 mm. This position error is supposedly caused by distortions in the camera optics or by inhomogeneous illumination.

Time-dependent data (e.g. error angle, angular velocity) were not smoothed, because we do not have *a priori* knowledge about the frequency ranges of the relevant signals and the noise.

3. RESULTS

Male flies chase targets of various sizes and speeds from below and behind. The target is either caught after a short pursuit (median duration of 340 ms; example in figure 1*b*) or is followed, sometimes for longer than 7 s, without capture (figure 1*c*). Therefore, chasing flights might be classified into two categories: capture flights (C chases) and pursuit flights without capture (P chases). After the target has been captured, the male may stick to it for up to 50 laps. Whether or not the target is caught depends on its size and speed (figure 1*d*). Targets much larger than a real fly were chased some of the time, but were caught only occasionally. Targets of the size of a conspecific (5 mm) were captured more often than larger targets. This was true for all tested target speeds. With increasing target speed, the frequency of capture decreases. Pursuit of targets moving at $2\ \mathrm{m\ s^{-1}}$ occurred only occasionally and never resulted in the capture of the target (data not shown).

While chasing the target, the fly continuously changes the orientation of its body long axis (figure 2*a*(i),*b*). Rapid saccade-like turns, which are characteristic of cruising flights and are correlated with large and brief yaw rotational velocity peaks (figure 2*a*(ii); Wagner 1986*a*; Schilstra & Van Hateren 1999), happened only occasionally during chases. Consequently, the distribution of yaw velocities has its peak around the angular velocity of the dummy target (figure 2*b*). There is no pronounced peak at a speed of $0°\ \mathrm{s^{-1}}$, which would be expected if body rotations were saccadic with straight flight sequences between saccades. Hence, when chasing a target that changes its direction continually, the chasing behaviour is reminiscent of a smooth pursuit system.

The chasing fly fixates the target in the frontal visual field during both P and C chases (figure 2*c*). There is no significant difference in the error angle between the two chasing modes. The median error angle is 1.5° in P chases (IQR of 20°) and 6° in C chases (IQR of 21°). Thus, in both modes the target is slightly shifted in the direction in which it would move on the eye if it were not fixated.

To characterize the system controlling yaw rotations, the time lag between retinal error angle and the fly's yaw velocity was analysed by cross-correlation (figure 2*d*) for six particularly long sequences of smooth pursuit (lengths of between 1.5 and 7.5 s). The time lag cannot be resolved precisely, because it is of the same order of magnitude as the temporal resolution of the video technique (20 ms). In any case, the time lag is short, indicating a quick transformation of the retinal error into body rotations. Periodicity in the cross correlograms can be interpreted as oscillation of the underlying control system.

The fly's speed is correlated with the retinal size of the target; this is most noticeable during long P chases (figure 3*a*). To test whether the forward velocity relative to the target is controlled by the retinal target size, we measured the distance between the fly and the target for different target sizes and velocities. The larger the target, the larger is the distance between target and fly (figure 3*b*(i)); this is mainly caused by variation in the horizontal distance (x–y plane, see figure 1*a*) between fly and target (figure 3*b*(ii,iii)). As a consequence, the retinal target size is kept constant for a given speed (figure 3*c*(i)). A control system with retinal size as an input variable and the fly's speed as the output can lead to this result. A time lag of 60–80 ms between input and output of this hypothetical control system was determined for six long P chases by cross correlating the time-dependent retinal target size and the speed of the fly (figure 3*d*). Hence, forward velocity control operates with a larger time constant than turning velocity control. In P chases a target of given size is followed at a distance that increases with increasing target velocity, and, thus, the retinal target size decreases (figure 3*c*(ii)).

The chasing male frequently flies slightly outside the circular track of the target (figure 1*b*,*c*). In C chases, the fly eventually approaches the target from outside its track before capture. The fly's distance from the centre of the target's trajectory is larger for big targets than for small ones (figure 4*a*). During P chases the male may fly inside the circular target track for some time, but, on average, the distance from the fly to the centre of the target track is moderately larger than the radius of the target track, without significant dependency on target size or speed (median difference of 0.5–8 mm, data not shown).

The fly's speed is faster before catching large targets than before catching small targets (figure 4*b*). This finding is surprising, since, at first glance, there is no need to approach large targets faster than small ones. It should be noted that large targets are not always followed at higher speeds than small targets, but only in those cases where the target is caught. As already stated, capture of large targets happens only occasionally (figure 1*d*).

Before catching the target, the chasing fly changes its orientation in the horizontal plane and, concomitantly, deviates from the target's direction of movement by sometimes more than 90° (see asterisk in figure 1*b*). To quantify this behaviour, we calculated δ, which is the angle subtended by the fly's longitudinal body axis and the target's instantaneous flight direction in the horizontal plane (see inset figure 4*c*); δ increases with increasing retinal target size and, thus, with decreasing distance between fly and target before the dummy is caught (figure 4*c*). Similar changes in δ are found during P chases when the fly approaches the target and the retinal target size thus increases (figure 4*c*).

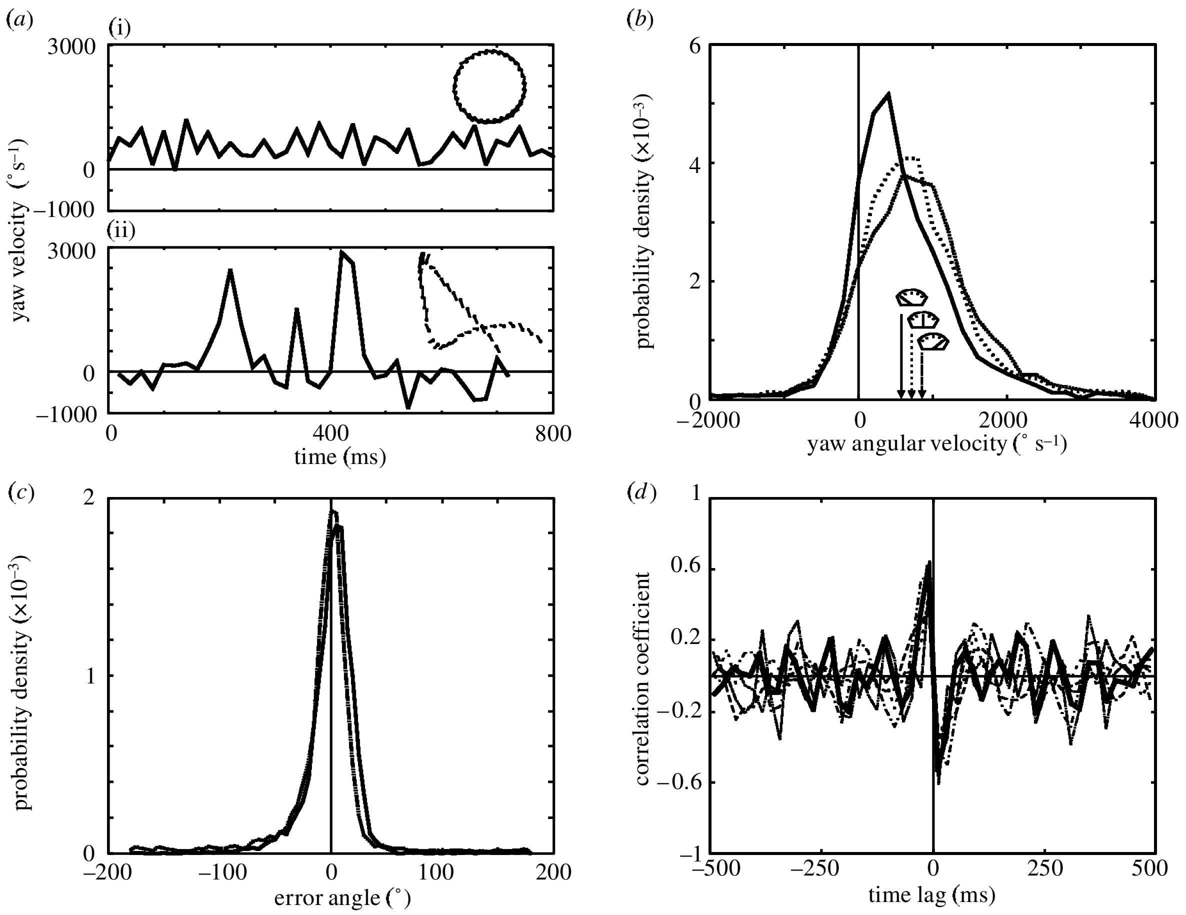

Figure 2. Control of yaw rotation. (*a*) (i) Yaw velocity of a fly during an 800 ms excerpt from the steady-state phase of the P-chase example shown in figure 1*c*. (ii) Yaw velocity of a fly during a cruising flight in the flight arena. Both yaw velocity traces are affected by noise as described in § 2. Despite this methodical limitation the velocity peaks in the bottom trace resulting from body saccades are easily detectable. Insets: body position and orientation of the longitudinal body axis of the fly every 20 ms. (*b*) Probability density of the yaw velocity for all chasing flights grouped by target speed (indicated by arrows). A target moving at 1 m s^{-1} on the circular track changes its yaw orientation at 573° s^{-1} (1.25 and 1.5 m s^{-1} are equivalent to 716 and 859° s^{-1}, respectively). (*c*) Probability densities of the error angle for 170 C chases (solid line; 3169 data points) and 184 P chases (dotted line; 8234 data points). In each mode, data points of the error angle were pooled for all target speeds and sizes, because no obvious difference in the fixation performance was detected between different target conditions. (*d*) Cross correlation of error angle and yaw velocity for each of six particularly long P chases (target size of 8.3 mm; speed of 1 m s^{-1}). The time lag that gives the highest correlation coefficient is near the temporal sampling interval of 20 ms in each of the six chases. The cross correlogram that reveals the most pronounced periodicity is indicated by a solid line. The peaks in the cross correlograms shown are not the consequence of tape jitter (see § 2), as tape jitter on its own leads to a much smaller correlation peak (not shown).

4. DISCUSSION

Male blowflies exhibit two behavioural modes when chasing a dummy fly. Either the target is caught after relatively short pursuit flights (‘C chases’) or the target is followed for up to several seconds on precisely controlled tracks without being caught (‘P chases’). Since male flies chase not only females but also other males (Wagner 1986*b*) as well as black spheres, they are probably unable to distinguish between the different types of target without close contact. This is not surprising if one considers the coarse spatial resolution of the fly’s eye (Land & Eckert 1985).

Other fly species also exhibit two modes of chasing behaviour, although these seem to play a different functional role from those of *Lucilia*. Male *Poecilobothrus* pursue females at close distance during courtship behaviour (‘shadowing’), whereas other males are chased in pursuits resulting in head-on clashes (Land 1993*a*). Chasing of *Syritta* includes shadowing that often culminates in a rapid dart towards the leading fly after it has settled (Collett & Land 1975).

The two chasing modes of *Lucilia* can parsimoniously be explained as the consequence of a single control system. This system is calibrated to control the capture of targets of the proper size and velocity, but can be deluded if the target is either larger or faster than conspecifics. Under the artificial conditions of our experiments targets larger or faster than conspecifics often resulted in prolonged pursuits without capture. Since in natural situations potential targets usually do not move on regular tracks as the artificial target in our behavioural experiments did, they may not be followed for a long time. The proposed pursuit system controls in parallel the rotational velocity and the forward velocity of the fly.

(a) *Control of yaw rotation*

The control of yaw rotation in male *Lucilia* is organized in a similar way to that proposed for the male-

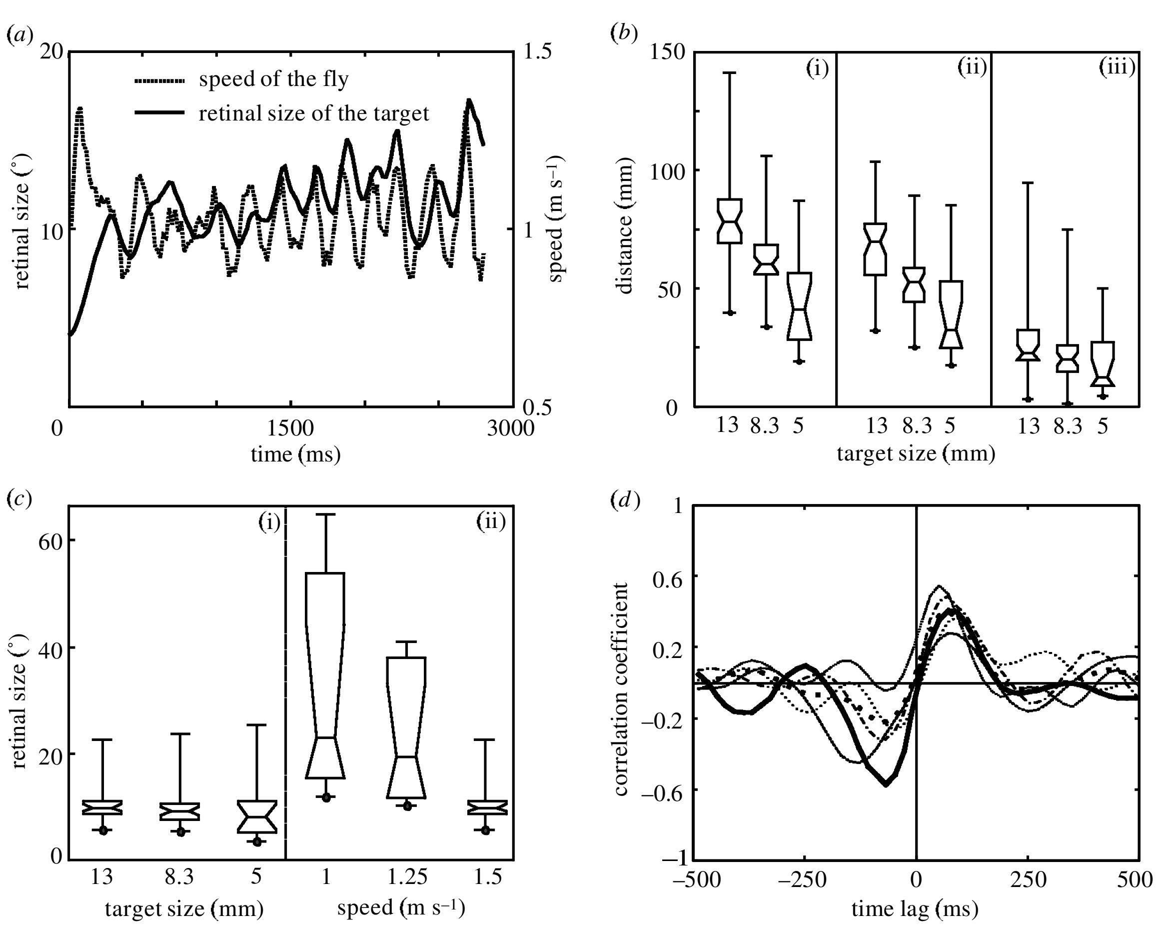

Figure 3. Control of forward speed. (*a*) Retinal size (solid line) and speed of the fly (dotted line) during the P chase shown in figure 1*c*. The speed of the chasing male fluctuates, which to some extent cause fluctuations in the distance between fly and target (not shown). Consequently, the retinal size of the target also oscillates between local minima and maxima. (*b*) Box-and-whisker plots of the minimal distance between fly and target in each P chase after the 5, 8.3 and 13 mm targets at a speed of 1.5 m s^{-1}. The box has horizontal lines at the lower quartile, median and upper quartile values. The lines extending from each end of the box show the extent of the rest of the data. The medians (central lines) of two box-and-whisker plots are significantly different ($p < 0.05$) if the corresponding notches do not overlap (McGill *et al.* 1973). We did not calculate the mean distance to the target over the total flight episode, because this measure would have been much affected by the first approach to the target and the departure from the target, especially in short chases. We therefore calculated the median of all local minima of the time-dependent distance in each chase. (i) 3D distance, (ii) distance in the x–y plane and (iii) difference in the z coordinates of fly and target. For each target size between 48 and 65 P chases were included. (*c*) Box-and-whisker plots of the maximal retinal size (visual angle) of the target in each P chase. The retinal size was calculated as the median of all local maxima of the time-dependent retinal size for each chase. (i) Differently sized targets at a speed of 1.5 m s^{-1} (same chases as in (*b*)). (ii) Pursuits after the 13 mm target at the three different speeds. (*d*) Cross correlation between retinal size and fly speed for the same P chases as in figure 2(*d*). The cross correlogram that reveals the most pronounced periodicity is indicated by a solid line.

specific pursuit systems of other flies (Land & Collett 1974; Collett & Land 1975; Srinivasan & Bernard 1977; Poggio & Reichardt 1981; Wehrhahn *et al.* 1982; Wagner 1986*b*; Land 1993*b*). Moreover, the yaw control of female *Musca* in fixation tasks has been attributed to a similar mechanism (Virsik & Reichardt 1976). In all these systems, the target is detected at some retinal position, which elicits a turning response towards the target. Within certain limits, the turning response increases with increasing deviation of the target from the frontal midline of the head ('error angle'). In order to maintain fixation of a moving target, the error angle is converted into yaw rotation. Occasional deviations of the body-axis direction from the flight direction (figure 1*b*) can be attributed to inertia (Wagner 1986*a*; Boeddeker & Egelhaaf 2003).

Chasing flies are able to change their flight direction gradually when following a target moving on a smooth track. However, during cruising flight flies usually change course by short and rapid body saccades (Schilstra & Van Hateren 1999). The gaze shifts of male flies, therefore, might be accomplished in a similar way to those in primates and humans, that is, smoothly when pursuing a target and by saccades when exploring a visual scene. None the less, saccade-like turns of flies also occur during the pursuit of real flies (Wagner 1986*b*) and occasionally during the smooth pursuit of dummy targets. We will show in a subsequent paper (Boeddeker & Egelhaaf 2003) that these saccade-like turns are not necessarily generated by a saccadic tracking system, but can be explained as the consequence of a smooth pursuit system, provided that time constants and the inertia of the fly are taken into account.

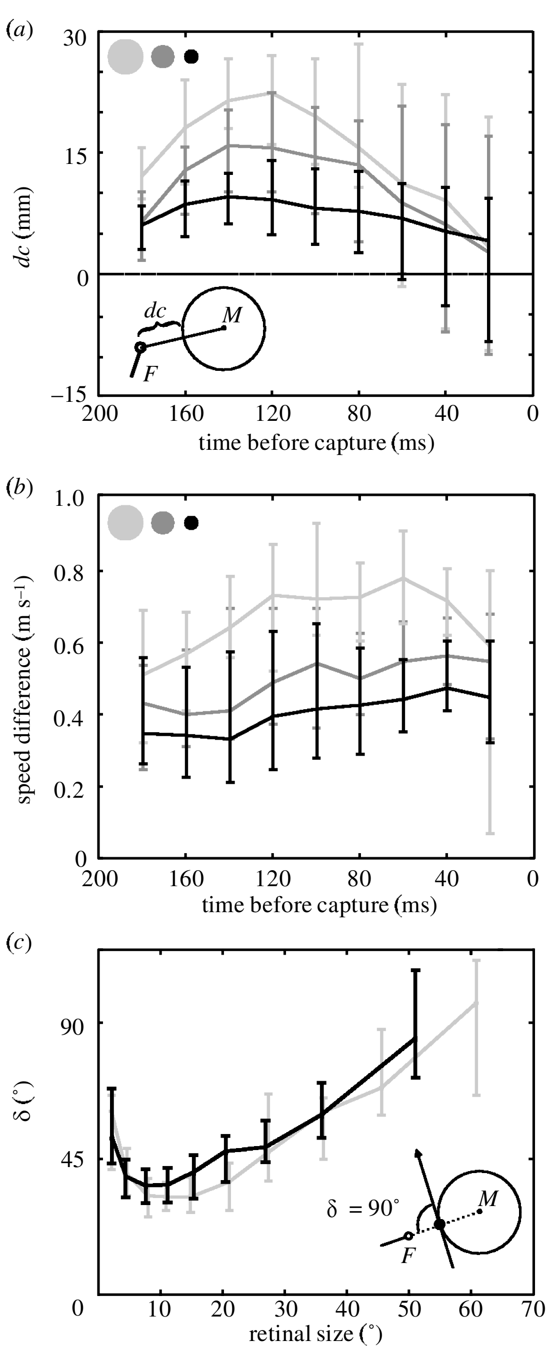

Figure 4. Features of the flight trajectories. (*a*) The variable *dc* quantifies whether the fly (*F*) is inside or outside the circular target track. It is calculated by subtracting the radius of the target track from the distance between the fly and the midpoint (*M*) of the target track (see inset). As we found no significant relation with target speed, the medians and quartiles of *dc* of all C chases ($n = 170$) were grouped with reference to the absolute target size and plotted versus time for every sampling point during the last 180 ms before capture. The absolute size of the target is indicated by the grey level of the lines (see inset). (*b*) Speed difference between fly and target in C chases during the last 180 ms before capture, for differently sized targets. The data pooling and plotting are as in (*a*). (*c*) δ is the angle subtended by the fly's longitudinal body axis and the target's instantaneous flight direction in the horizontal plane. If the fly (*F*) flies tangentially to the target's track, δ is 0°; if the fly's long axis points towards the centre of the track, δ is 90° (see inset). δ is plotted against retinal size of the target averaged over all C (black) and P (grey) chases.

(b) *Control of forward speed*

Male *Lucilia* always approach the target from behind and from outside the circular track (figure 4*a*). Hence, *Lucilia* has to fly faster than its target to catch it. During P chases, male flies, on average, do not fly faster than their targets, although their flight motors would enable them to do so. Instead, the forward velocity goes down when the retinal size exceeds a certain threshold and increases when the retinal size of the target is small. Hence, the retinal size of the target appears to be a decisive input variable for forward velocity control in chasing behaviour. The smaller retinal size of fast targets than of slow targets during P chases can also be traced back to the relation between the retinal size of the target and the speed of the fly. If a target of given absolute size moves at a higher velocity, the fly needs to fly faster to follow it. As flight speed and retinal size are thought to be inversely related, this can only be achieved at a smaller retinal size.

At first sight, the conclusion that the chasing fly decelerates at a critical retinal target size raises the question of how the chasing fly will ever be able to catch its target. As catching females is a prerequisite of mating, a velocity control system resulting in P chases where the target is only followed and not caught seems paradoxical. Can targets of the size and speed of conspecifics be caught only by inactivating the control of translational velocity during the final approach to the target? To answer this question one has to remember that any neuronal control system requires time for information processing and, thus, the response is delayed relative to the stimulus. Moreover, inertia prevents the fly from adjusting its velocity immediately to the current retinal target size. Consequently, after the motor command for deceleration is given when the retinal size exceeds a critical value, the chasing fly retains its velocity for a while. This implies that a fly approaching a small target may be able to reach and catch it before the command to decelerate becomes effective. By contrast, when approaching a large target, deceleration is initiated at a larger distance, though at the same retinal target size as in the case of a small target. As a consequence, deceleration may be effected too early, and the target is followed without being caught because the fly is 'trapped' by its control systems.

5. CONCLUSIONS

The existence of C and P chases does not necessitate separate control systems. Several experimental findings allow us to underline this conclusion.

(i) Small targets are caught most often, as the speed control system 'allows' a closer approach.
(ii) Large targets are caught only, if the fly is much faster than the target during the final approach. This might be essential, since only at a high velocity is the pursuer able to overcome the distance to the target before the motor command to decelerate becomes effective. Otherwise, the target will not be caught, which results in a P chase.
(iii) The flight manoeuvre quantified by δ can be explained in both chasing modes as the consequence of interaction between target fixation, motor force reduction and the remaining impetus of the fly.

> When the retinal size increases during P chases, δ (see figure 4*c*) increases in a similar way to during C chases. This takes place at a larger distance, which results in missing the target.

In a subsequent paper we will show by model simulations that a control system with retinal size and position as input variables can account for most features of *Lucilia* chasing behaviour and we will discuss this hypothesis in the context of the available literature (Boeddeker & Egelhaaf 2003).

What may be the advantage of a translational control system that initiates deceleration of the chasing fly at a critical retinal target size, which may prevent the male from catching targets? On the one hand, this peculiar feature prevents the fly from catching targets that are too large (such as hornets). On the other hand, capture of an appropriate target might be improved if the male does not crash into it at full speed but rather slows down before contact. This deceleration may facilitate a graceful embrace of the potential 'Ms Right'.

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