A single control system for smooth and saccade-like pursuit in blowflies

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Summary

During courtship, male blowflies perform aerobatic pursuits that rank among the fastest visual behaviours that can be observed in nature. The viewing strategies during pursuit behaviour of blowflies appear to be very similar to eye movements during pursuit in primates: a combination of smooth pursuit and catch-up saccades. Whereas in primates these two components of pursuit eye movements are thought to be controlled by distinct oculomotor subsystems, we present evidence that in blowflies both types of pursuit responses can be produced by a single control system. In numerical simulations of chasing behaviour the proposed control system generates qualitatively the same behaviour as with real blowflies. As a consequence of time constants in the control system, mimicking neuronal processing times, muscular dynamics and inertia, saccade-like changes in gaze direction are generated if the target is displaced rapidly on the pursuing fly's retina. In the behavioural context of visual pursuit, saccade-like changes of the fly's gaze direction can thus be parsimoniously explained as an emergent property of a smooth pursuit system without assuming *a priori* different mechanisms underlying smooth and saccadic tracking behaviour.

Key words: pursuit, control system, visuomotor control, behaviour, computational neuroethology, computer simulation, insect vision, blowfly.

Introduction

When cruising around in an exploratory manner, flies typically change their flight direction and concomitantly the direction of their gaze through a series of short, fast saccadic turns of their entire body and, in synchrony but at a higher angular speed, of the head (Schilstra and van Hateren, 1999; van Hateren and Schilstra, 1999). These stepwise rapid changes of gaze direction have been called, by analogy with human eye movements, body saccades (Collett and Land, 1975). The neural control systems that elicit and steer these body saccades are still unknown. In periods between body saccades flies keep their gaze direction more or less constant (Schilstra and van Hateren, 1998). Gaze stabilisation is assumed to be under the control of both the visual system (Götz, 1975; Land, 1973; van Hateren and Schilstra, 1999) and mechanosensory systems (Chan et al., 1998; Gilbert and Bauer, 1998; Sandeman, 1980; Sherman and Dickinson, 2003). Saccades were concluded to be elicited visually by image expansion in the optic flow pattern across both eyes (Tammero and Dickinson, 2002a,b). Phenomenologically, the viewing strategy of flies is similar to that of humans where, during a variety of tasks, the direction of gaze is shifted by rapid saccadic eye movements (Land and Hayhoe, 2001). The gaze is held almost still during the intervening fixations by reflexes that stabilise the eye even when the head moves (for a review, see Carpenter, 1988).

In primates, including humans, eye movements from a functionally different class catch the image of a moving target and hold it steady in the frontal visual field by smooth pursuit eye movements, even if the observer and thus the visual world moves. Primates were long believed to be the only animals that can perform smooth pursuit. Only recently smooth pursuit has also been revealed in cats (de Brouwer et al., 2001). If target motion is too rapid and displaced outside the frontal visual field, smooth pursuit is interrupted by catch-up saccades which tend to centre the target again (de Brouwer et al., 2002a,b).

Visual pursuit can be found in a number of insect species; dragonflies, for instance, feed on prey caught in flight (Olberg et al., 2000) and males of several fly species chase potential mates or rivals during their courtship behaviour (Collett and Land, 1975; Land, 1993b; Land and Collett, 1974; Wagner, 1986a; Zeil, 1983, 1986). The underlying control system has to solve two important tasks. On the one hand, the chasing insect has to control its forward velocity and its distance to the target. On the other, the insect needs to fixate the target in the frontal visual field. It has previously been shown for blowflies that forward velocity is controlled by the retinal size of the target (Boeddeker et al., 2003). Moreover, it is generally agreed that the retinal position of the target serves as an input variable to the control system that leads to fixation of the target in the frontal visual field. However, how retinal position errors are transformed into turning responses is still controversial, and the objective of the present study is to contribute towards solving this problem.

The housefly *Musca domestica* pursues other flies in a series of rapid discrete turns. It was therefore suggested that chasing behaviour in houseflies is controlled by a discontinuous pursuit system (Wagner, 1986a). The retinal position of the target was assumed to be sampled only from time to time and the output of the chasing system to consist of pre-organised responses, i.e. saccade-like turns without visually driven feedback (Wagner, 1986a). In contrast, the behavioural analysis of chasing behaviour in the small housefly *Fannia canicularis* (Land and Collett, 1974), the dolichopodid fly *Poecilobothrus nobilitatus* (Land, 1993a), the hoverfly *Syritta pipiens* (Collett and Land, 1975) and blowflies of the genus *Lucilia* (Boeddeker et al., 2003) suggested that the tracking system is basically continuous. In such a control system, visual input is transformed to motor output on an instant-by-instant basis. Nonetheless, saccade-like body rotations occur during pursuit in the above-mentioned flies. Because saccade-like and smooth pursuit strategies differ so much in their performance, they might be mediated by separate control systems (Land, 1992, 1993b).

The present study starts from a different perspective. Rather than assuming *a priori* different mechanisms underlying smooth and saccade-like tracking in blowflies, we test to what extent the ‘virtual blowfly’, which was customised for chasing a smoothly moving artificial target in a model analysis (Boeddeker and Egelhaaf, 2003), can also account for pursuit of natural targets, i.e. other flies.

The behaviour of the virtual fly can be manipulated by variation of eight model parameters. Six of these parameters were taken from our preceding study (Boeddeker and Egelhaaf, 2003). The performance of the virtual fly was therefore not specifically tweaked for the pursuit of realistically moving targets as used here. The smooth pursuit system implemented in the virtual fly consists of two subsystems. One module controls the virtual fly’s forward velocity using the retinal size of the target as the input signal. A second subsystem controls the angular velocity of the animal, depending on the retinal target position. In the present study the original version of the smooth pursuit controller is compared to an elaborated version where fixation of moving targets is aided by an accessory controller that uses retinal slip velocity. The use of retinal target velocity, in addition to position error information, was previously found to stabilise the performance of smooth pursuit systems (Land, 1992). A second reason for including an additional controller is that the smooth pursuit system of primates uses target velocity as an important input variable (Rashbass, 1961) and current models of pursuit eye movements include a velocity servo (Churchland and Lisberger, 2001; Krauzlis and Lisberger, 1994; Robinson et al., 1986).

We present evidence that, at least in blowflies, both types of following responses, i.e. smooth pursuit and saccade-like turns that capture the target in the frontal visual field, can be explained by a single control system. We show by numerical simulations of fly behaviour that saccade-like changes of body orientation occur without the need for an extra saccade-generating mechanism. This is mainly a consequence of time constants that mimic neuronal processing times, muscular dynamics and inertia. Thus, saccade-like tracking in blowflies can be seen as an emergent property of a smooth pursuit system under circumstances where the target is displaced rapidly on the pursuing fly’s retina.

Materials and methods

Behavioural analysis

Chasing flights of blowflies (genus *Lucilia*) were filmed using two synchronised CCD video cameras (image acquisition rate: 50 Hz; shutter time 1 ms) and stored in the S-VHS format. The optical axes of the cameras were aligned orthogonally to each other allowing by simple geometric algorithms the computer-aided three-dimensional reconstruction of the flight trajectories and the yaw orientation of flies in an external coordinate system. For further details, see Boeddeker et al. (2003). The experimental data shown in Fig. 2 were obtained and evaluated as described in Boeddeker et al. (2003) except that the chase of two conspecific blowflies was filmed in a 1 m×1 m flight arena, 0.4 m high.

Design of the virtual fly

Overview

As in our previous study (Boeddeker and Egelhaaf, 2003), the mobility of the virtual blowfly is restricted to yaw rotation and to translation in the horizontal plane. These three degrees of freedom are sufficient to enable the virtual fly to generate steering behaviours like real flies chasing a dummy target on a circular track (Boeddeker and Egelhaaf, 2003). Gaze direction is assumed to be equivalent to body orientation. We have refrained, so far, from simulating chases after targets that alter their flight altitude. We implemented two visual pathways in the virtual fly: one for target fixation (Fig. 1A) and one for speed control (Fig. 1B). The retinal size of the target controls the forward speed of the virtual fly. The position and angular velocity of the retinal image of the target determine the fly’s intended flight direction. To mimic lag effects of neuronal processing times, muscle reaction times, and body locomotion dynamics resulting from inertia and viscous air damping we use two low-pass filters as lumped models in combination with a simple locomotion model (Fig. 1C).

To simulate the fly’s rotations about its yaw axis, we boil down the system’s dynamics to one time constant (see Discussion). In accordance with our experimental results (Boeddeker et al., 2003), the time constant in the target fixation pathway was set to 15 ms.

For translational locomotion the fly’s momentum has an even stronger influence, represented by a time-constant of 80 ms in the pathway for speed control. To simulate locomotion in blowflies realistically it is also important to realise that they generate sideward translation and yaw turns relative to the outside world by first rolling their thorax and then pitching the rolled thorax. Hence, the time course of sideward movements and yaw turns in an external coordinate

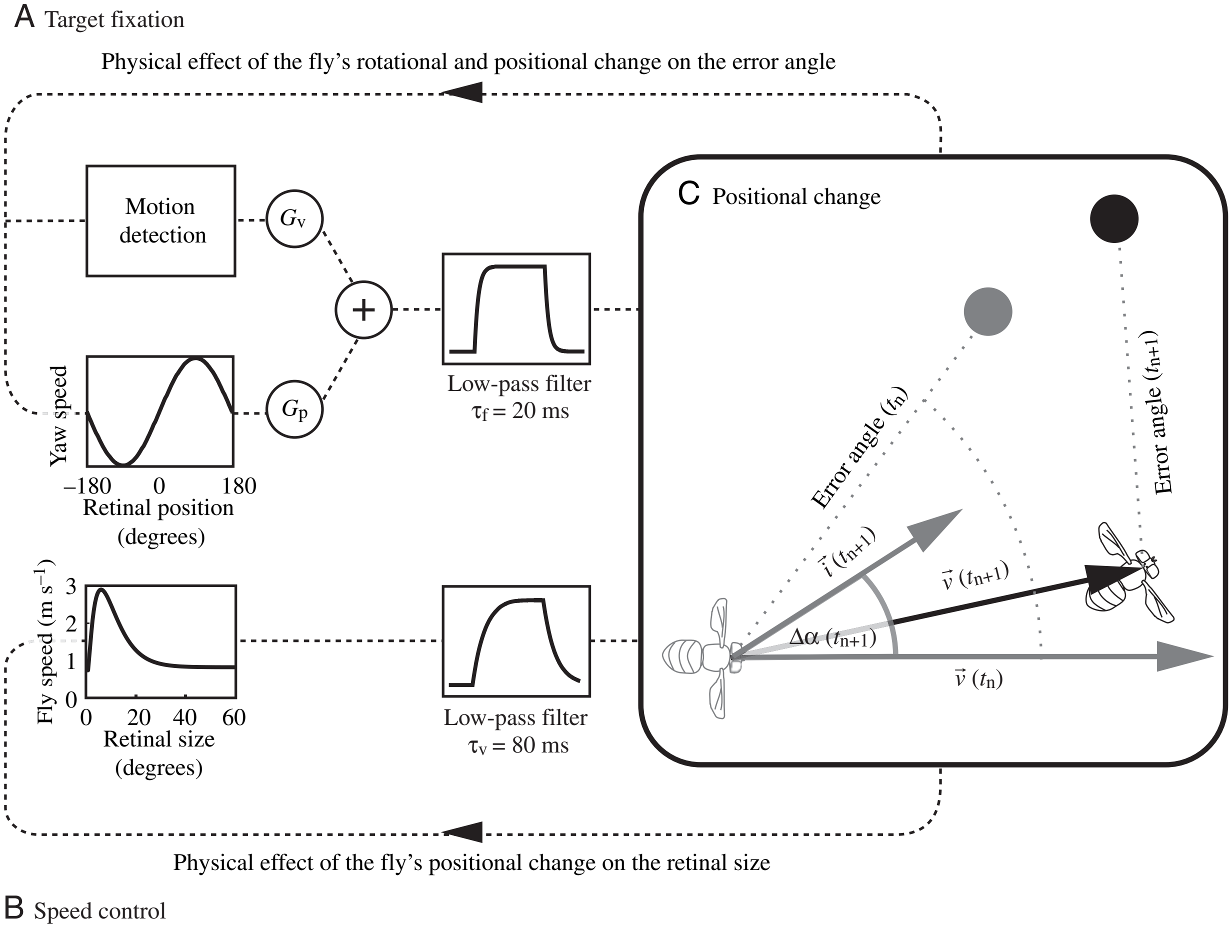

Fig. 1. Signal processing performed by the virtual fly. We implemented two visual pathways in the virtual fly: one for target fixation (A) and one for speed control (B). A further module that receives input from both pathways determines the virtual fly's actual position in the next simulation step (C). In each simulation step the fixation controller, converts the error angle according to the characteristic curve shown in C, weighted by G_p, and the retinal velocity, weighted by G_v, into angular velocity of the pursuing virtual fly $\Delta\alpha(t_{n+1})$. The output of the virtual fly's speed controller depends on retinal target size according to the characteristic curve shown in the box and determines the absolute value of the fly's speed vector for the next simulation step [$s(t_{n+1})$]. First-order low-pass temporal filters are applied to the outputs of both visual pathways, lumping together inertial effects, neuronal processing and muscular reaction time. The filtered outputs from each pathway form the 'intended' vector $\vec{i}\,(t_{n+1})$ of locomotion of the virtual fly. A third module determines the virtual fly's velocity in the next simulation step $\vec{v}(t_{n+1})$ as the sum of the actual fly velocity $\vec{v}(t_n)$ and the 'intended' velocity vector weighted by the movement coefficient M. Six of the free model parameters were taken from our preceding study (Boeddeker and Egelhaaf 2003): the two first-order low-pass filter time constants acting on fixation (τ_f=15 ms) and speed control (τ_v=80 ms), the movement coefficient (M=0.0455), and three parameters characterising the transfer function of the speed controller (S_g=0.8 m s^{-1}, S_v=67, and ρ^*= 0.0865). The gain factor for yaw rotation, depending on retinal target position (G_p), was set to 0.1 and the gain factor for yaw rotation, depending on retinal target velocity (G_v).

system do not, in all situations, coincide with the time course of sideward thrust forces and yaw torque as generated by the fly in a body-centred coordinate system (Schilstra and van Hateren, 1999). Rotational and translational motion components are thus coupled in a non-trivial way. Since the spatial resolution in our movies does not allow reliable resolution of fly roll and pitching rotations, we refrain from simulating translational body dynamics in detail. Instead, we use a kinematic locomotion model (Equation 3) to determine the actual trajectory of the virtual fly (Fig. 1C). From our behavioural study we are able to estimate the maximal possible velocities: rotation was found not to exceed 5000 deg. s^{-1} and maximal translation was below 3 m s^{-1}.

Speed control

The relationship between the retinal size of the target (ρ) and the output of the speed controller (s) is given by Equation 1, with free model parameters S_v and ρ^* that reflect the gain and the location of the maximum of the speed controller's characteristic curve. Since targets at a large distance are too small to be seen by a fly, the controller output should then not be affected by target size, but adjust 'spontaneous' speed (S_g):

$$s(t_{n+1}) = \begin{cases} S_g & \text{if} \quad \rho \leqslant 0.5° \\ \rho(t_n) S_v \, e^{-\rho(t_n)/\rho^*} + S_g & \text{if} \quad \rho > 0.5° \end{cases} . \qquad (1)$$

Target fixation

The angle subtended by the fly's longitudinal body axis and the line connecting the fly with the target represents the deviation of the target position from the frontal midline of the pursuer's head ('error angle'). The error angle is defined in a fly-centred polar coordinate system with 0° pointing directly ahead. A fixation controller, converting in each simulation step error angle (φ) and velocity ($\dot{\varphi}$) into a rotational step of the pursuing virtual fly in the horizontal plane ($\Delta\alpha$), can be formalised as follows:

$$\Delta a(t_{n+1}) = \begin{cases} 0 & \text{if} \quad \rho \leqslant 0.5^\circ \\ G_p \sin[\varphi(t_n)] + G_v \dot{\varphi}(t_n) & \text{if} \quad \rho > 0.5^\circ \end{cases} . \quad (2)$$

G_p and G_v determine the gain of yaw orientation change, depending on the error angle of the target and on the retinal target velocity ('retinal slip'), respectively. The virtual fly does not change orientation if the retinal size of the target is smaller than 0.5°.

Virtual fly kinematics

The kinematics of fly body yaw rotation is lumped into the filter in the target fixation pathway (see above), accounting for the recent finding that inertia is relevant in shaping the dynamics of yaw rotations (Fry et al., 2003). A third module determines the virtual fly's position in the next simulation step, accounting for the fact that translational inertial momentum of the fly has a non-negligible impact the fly's trajectory. The outputs of the above-mentioned pathways form the 'intended' vector of locomotion of the virtual fly ($\vec{i}$). The direction of this vector is determined by the fixation controller, its length by the speed controller. In the physical world, inertia and viscous air damping affect the fly's locomotion. As for rotation, we have strong evidence that inertial forces play a major role in the locomotion dynamics of blowflies (see Discussion). As a result of translational inertia, there is a difference angle (slip angle) between the direction of heading and the direction of the fly's flight trajectory, especially during and immediately after sharp turns. Consequently, the intended vector of locomotion does not exclusively determine the actual trajectory of the virtual fly. To model this effect of frictional and inertial forces, we follow an approach similar to methods that have been used to animate autonomous agents in computer graphics (Reynolds, 1999). Our locomotion model does not consider the details of biomechanical properties or body dynamics – but reduces translational locomotion parameters to a single variable (M) which, in combination with the time constants of the two low-pass filters, was fitted to provide flight trajectories of similar shape to those of real flies in our behavioural experiments (Boeddeker and Egelhaaf, 2003). For each simulation step the new velocity vector $\vec{v}$ is given by Equation 3. The extent to which the intended velocity determines the virtual fly's trajectory and how far the trajectory is determined by the velocity vector in the preceding flight path simulation step can be adjusted by the parameter M. The interplay of time constants in the two visual pathways described above, using the mechanism described by Equation 3, simulates the impact of translational forces generated by the flight motor relative to the effects of translational momentum and viscous air damping on the moving fly:

$$\vec{v}(t_{n+1}) = (1-M)\vec{v}(t_n) + M\vec{i}\,(t_{n+1}) \quad \text{with} \quad 0 < M < 1 \; . \quad (3)$$

Data are updated 1000 times per simulated second. The behaviour of the virtual fly can be manipulated by variation of eight parameters. Six of these parameters were from our preceding study (Boeddeker and Egelhaaf, 2003): the two first-order low-pass filter time constants acting on fixation (τ_f=15 ms) and speed control (τ_v=80 ms), the movement coefficient (M=0.0455), and three parameters characterising the transfer function of the speed controller (S_g=0.8 m s^{-1}, S_v=67, and ρ^*=0.0865). The gain factor for yaw rotation, depending on retinal target position (G_p), was set to 0.1 and the gain factor for yaw rotation, depending on retinal target velocity (G_v), was varied between 0 and 0.005. With this set of parameters the rotational speed did not exceed 5000 deg. s^{-1} and the maximal translational speed was always lower than 3 m s^{-1}. The virtual fly thus locomotes within the constraints set by the behaviour of real flies (Boeddeker et al., 2003).

Results

Behavioural experiments

Male blowflies follow a dummy target moving on a circular track in smooth pursuit (Fig. 2A; Boeddeker et al., 2003). Smooth pursuit is characterised by continuous body rotation (Fig. 2E), matching the fly's yaw velocity to that of the target (Fig. 2G). As a result the target is kept in the frontal visual field (Fig. 2C). However, under natural conditions the trajectories of conspecific flies (Fig. 2B) are much more erratic than the smooth target movements used in our previous behavioural analysis (Boeddeker et al., 2003). When the object moves too rapidly and, as a consequence, is displaced from the central visual field of view to more lateral parts of the visual field, a fast change in body orientation is generated to bring the target back to the front for continued smooth tracking (Fig. 2D,F). These rapid turns go along with brief rotational velocity peaks (see Fig. 2H) and are thus reminiscent of catch-up saccades as found in primates.

Pursuit of a realistically moving target by the virtual fly

A virtual fly, which for locomotion control only uses information on the retinal size and the position error of the target ('position-only servo', G_p=0.1, see Materials and methods) can not only pursue smoothly moving targets (Boeddeker and Egelhaaf, 2003), but also a target that moves like a real fly (Fig. 3A). The trajectory of the virtual fly is similar to that of a real fly chasing another fly on an almost triangular flight path (cf. Fig. 1B). While chasing the target, the virtual fly only manages to fixate the target in the frontal part of its visual field for part of the time; the target is displaced several times towards lateral retinal positions (Fig. 3B).

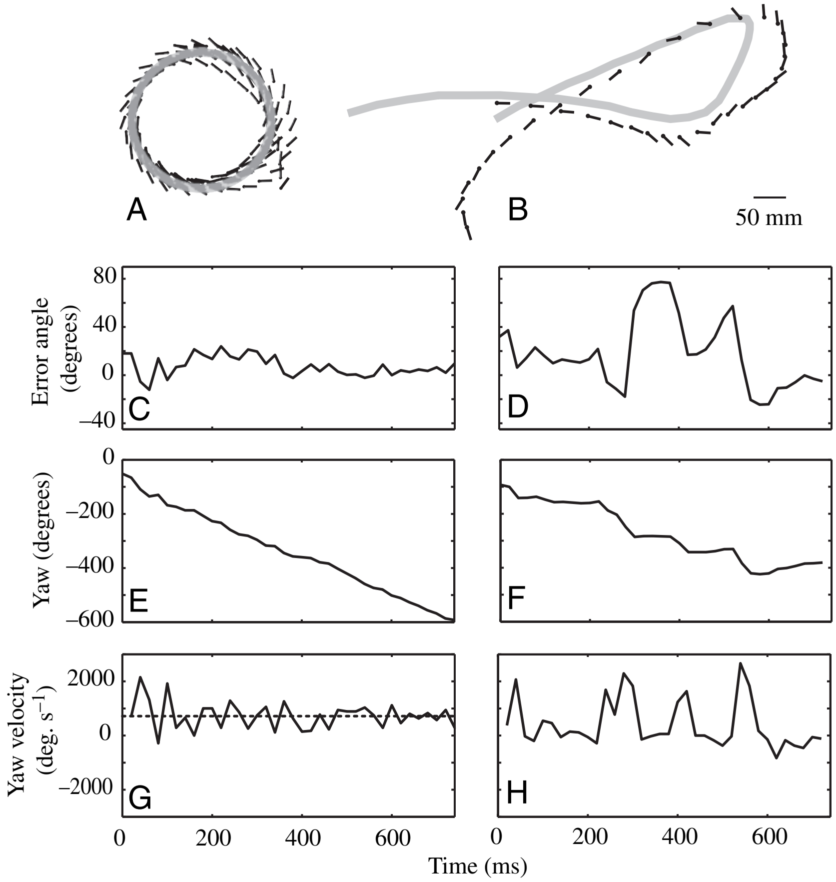

Fig. 2. Saccade-like and smooth tracking during chasing flights of male blowflies. (A) Top view of a flight trajectory of a fly (black markers) chasing a black sphere (diameter: 8.3 mm) moving at a speed of 1.25 m s^{-1} on a circular track in a horizontal plane (grey line). The position (circle) and body axis orientation (lines) of the fly are shown every 20 ms. The fly follows the target for 4 s. (B) Flight trajectory of a fly chasing another fly in top view, plotted as in A. To allow an easier comparison, i.e. to have the same direction of target motion, the trajectories in B were vertically flipped before further analysis. (C,D) Plots of the error angle, (E,F) yaw orientation and (G,H) angular velocity, *vs* time for the chase. In order to use the same time scale in all plots, only the first 740 ms of the chase displayed in A are shown in C, E and G. The rotational velocity of the dummy target (716 deg. s^{-1}) is indicated by the dotted line in G. All traces are affected by noise, primarily due to tape jitter (Boeddeker et al., 2003). Despite this methodical limitation the yaw velocity peaks due to saccade-like body rotations are readily visible in H.

Although a smooth pursuit system is implemented, rapid saccade-like turns occur (Fig. 3C) that re-centre the target in the frontal visual field. These saccade-like turns are characterised by brief rotational velocity peaks (Fig. 3D).

This characteristic behaviour of the virtual fly remains qualitatively the same when the position-only servo is augmented by a velocity input, as long as the gain of the velocity input is relatively small (G_v=0.0015). The additional velocity input smoothes the flight trajectory, reduces the retinal displacements of the target and, concomitantly, somewhat reduces the angular velocities during saccade-like turns (Fig. 3E–H). Increasing the gain of the velocity signal will impair the performance of the virtual fly compared to a real fly (G_v=0.025; Fig. 3I). Fixation of the target in the centre of the visual field is poor and saccade-like turns are absent (Fig. 3J–L). We conclude that fixation control relies strongly on position error and might be improved by taking into account the image velocity of the target, as long as the velocity input is not too strong.

Discussion

Two phenomenologically different chasing modes – one control system

Although in our experimental analysis we found two phenomenologically different chasing modes in the blowfly *Lucilia* – smooth pursuit and saccade-like tracking – we questioned the usual assumption that the dichotomy in behaviour also necessitates two different control systems. Whereas a smooth pursuit control system was inferred by Land and Collett in their seminal studies on chasing behaviour in flies (Collett and Land, 1975; Land and Collett, 1974), a discussion about a saccade-like tracking controller arose when Wagner (1986a) found that tracking in the housefly *Musca* is characterised mainly by sequences of saccade-like turns (see also Land, 1993b). These turns were interpreted as the consequence of a discontinuous control system. Wagner (1986a) suggested that saccade-like tracking was overlooked in the small housefly *Fannia* (Land and Collett, 1974) because, at the time of this early study, it was only possible to resolve the position of the fly and not the orientation of its body axis on each frame of the analysed film sequences. This interpretation was plausible, since Wagner could clearly show that during the pursuit of conspecifics *Musca* changes flight direction by rotation about the vertical body axis at high angular velocities, often separated by periods of little or no turning (Wagner, 1986a). Our experimental data on chases between conspecific blowflies (see Fig. 2B) are fully consistent with the data of Wagner (1986a), although we draw a different conclusion concerning the mechanisms underlying saccade-like tracking in flies.

By using a computer-simulated virtual blowfly we show that catch-up saccade-like body turns can be explained as an emergent property of the fly's smooth pursuit system under certain circumstances. We show that sophisticated visually guided behaviour can emerge from much simpler mechanisms than intuitively expected. The complexity of computational mechanisms needed to explain chasing behaviour can be reduced if one considers not only internal control mechanisms, but also the fact that natural behaviour operates under closed-loop conditions, i.e. under conditions where the system output affects the sensory input.

It is important to stress that the scope of this study is to account parsimoniously for control mechanisms underlying chasing behaviour. Although the smooth pursuit system can produce saccade-like movements under certain circumstances, we cannot exclude that the control system in the blowfly is more complex.

Smooth versus *saccade-like tracking systems*

To transform retinal position errors into angular velocity of the animal, a continuous control system, analogous to the human smooth pursuit system of eye movements, has been proposed for several fly species (Land, 1993b; Land and Collett, 1974; Wehrhahn et al., 1982). According to this scheme, correctional body movements continue until the retinal error is reduced to almost zero. The finding that in tethered flying male houseflies pursuit responses last as long as the target is visible adds further support to the idea of a continuous control system underlying pursuit (Srinivasan and Bernard, 1977). Such a feedback control system is, from an engineer's point of view, a good solution if there are not many time-consuming operations inherent in the system. In

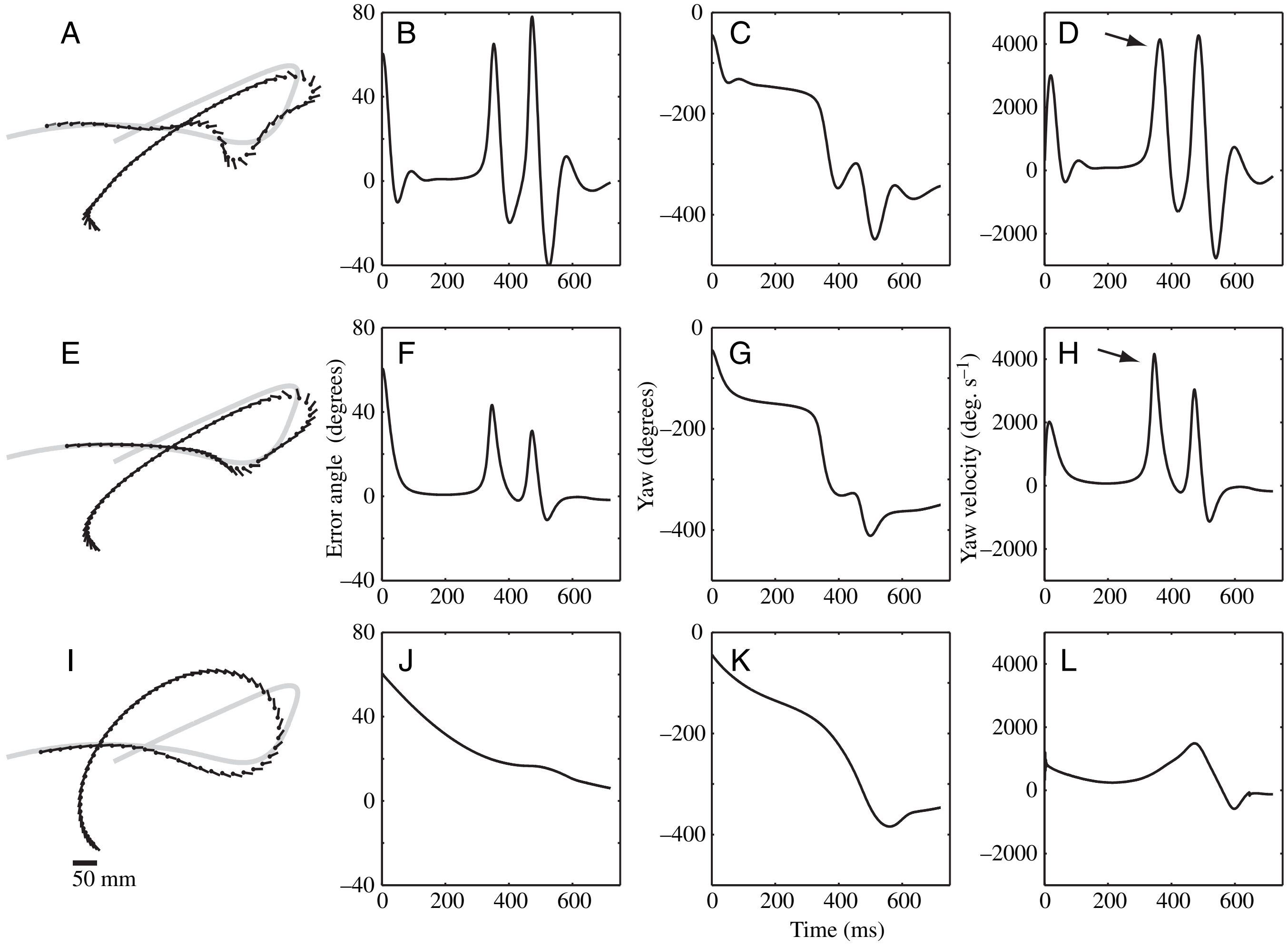

Fig. 3. Chasing a realistically moving target by the virtual blowfly. The gain factor for retinal velocity input relative to the fixation controller is varied. The data shown in A–D are from a virtual blowfly using the 'position-only servo', i.e. the virtual blowfly steers its flight direction only by minimising the error angle. (A) Trajectory of the virtual fly chasing the target (plotted as in Fig. 2A). After sharp turns of the target, the virtual fly makes saccade-like turns, but tends to overshoot the target and then makes a correctional movement. This behaviour leads to a curved path and fluctuations of the error angle (B) and yaw velocity (D). The yaw orientation (C) of the virtual fly changes in a step-like manner similar way to that seen in real flies (Fig. 1A). If the virtual blowfly uses a 'position-plus-velocity servo', i.e. it uses both position and velocity information, (G_v=0.0015), flight performance is stabilised by reducing the overshooting of the target (E–H). Saccade-like turns are characterised by brief yaw velocity peaks (arrows in D,H). Increasing the gain of the velocity signal to higher values (G_v=0.025) leads to rather smooth flight trajectories and an elimination of saccade-like turns. This chasing performance differs greatly from the flight trajectories of real flies (I–L).

technical systems the measuring sensors, the controller and the actuating element also need time to work, which can impair the performance and stability of the feedback control system. This is also true for biological tracking systems, such as those of the fly or of humans. For the chasing system of the blowfly the situation is even more complicated, given that chasing is one of the most rapid and acrobatic behaviours found in the animal kingdom. Targets being pursued by flies can change their direction of motion by more than one order of magnitude more rapidly than targets can be followed by smooth eye movements of primates. The pursuit system may become unstable when the retinal input is very transient, depending on the gain of rotational control and the time it takes to transform the retinal position of a target into rotational body movements. Because blowflies are small and lightweight it might be possible to achieve a shift in flight direction in a relatively short time. Moreover, the neural system in blowflies seems to be able to transform visual input to motor output in a very short time to prevent the control system from getting unstable.

Another solution to improve stability might be to reduce the gain for rotation, but this results in poor tracking performance if the target moves very fast. To catch up with the target, switching to a saccadic tracking strategy can improve performance. Large retinal errors may then be reduced by fast movements, the saccades. Various pursuit strategies and their performance were modelled and compared in a review by Land (1992). Land concludes that mixed pursuit strategies in which position is dealt with by a saccadic system and velocity by a smooth system give the best overall results.

In primates, visual fixation and tracking of targets are suggested to be accomplished by such a mixed strategy: saccades are programmed primarily to correct errors between target and eye position (for reviews, see Moschovakis and Highstein, 1994; Sparks and Mays, 1990). The neural circuit that generates saccadic motor behaviour in primates is concluded to be a central pattern generator distributed within the brainstem and adapted to produce high velocity movements with high precision (e.g. Sparks and Mays, 1990). In contrast, smooth pursuit eye movements are designed to minimise the difference between target and eye velocity (Keller and Heinen, 1991; Lisberger et al., 1987; Rashbass, 1961). The neuronal circuits involved in visual motion analysis for pursuit eye movements have been viewed as largely independent from those for saccade programming, but recent research has revealed functional and anatomical linkage between the two systems (de Brouwer et al., 2001, 2002a; Gardner and Lisberger, 2002; Krauzlis and Stone, 1999).

The origin of rapid turns

Saccade-generation mechanisms are available to flies: *Fannia* makes abrupt turns at more than 1000 deg. s^{-1} when patrolling under landmarks (Zeil, 1986). During cruising flight, houseflies and blowflies change their flight direction mainly by body saccades (Schilstra and van Hateren, 1999; Wagner, 1986b). During target pursuit, the hoverfly *Syritta* makes saccadic turns to new targets, and tracks discontinuously at high target velocities (Collett and Land, 1975).

Currently there are no computational models that can account for the origin of these saccades in flies. Here we show that a continuous smooth pursuit system can generate body turns that are saccadic in character, similar to those seen in real flies during chasing behaviour. It should be noted that this model is not meant to account for saccade-like body rotations in other behavioural contexts, such as during spontaneous cruising flight.

How are saccade-like body rotations during pursuit behaviour generated without an extra saccade-generating mechanism? Saccade-like body movements can be related to specific spatial relations between the target and its pursuer during a chase. Unless the chasing fly is directly heading toward its target, the target may get displaced very rapidly on the retina. Since translational movement leads to large image displacements when the chasing fly is close to the target, it is not surprising that in this situation particularly, saccade-like turns can frequently be found. To understand why saccade-like turns are generated in these situations, one has to consider the geometry of chasing behaviour: the error angle will, in most cases, increase more rapidly for a given translational velocity of the fly the closer it is to the target. Since the error angle is the signal that drives rotational velocity, large and rapid turns are likely to occur if the fly is close to the target. These rapid turns can be regarded, at least phenomenologically, as saccades.

When we analysed the pursuit of real and virtual flies of a target moving smoothly on a circular track, we found fast body rotations, especially during phases of the chase when the blowfly approached the target very closely but missed it, or just before target capture (Boeddeker et al., 2003; Boeddeker and Egelhaaf, 2003). A fixation controller with a combined positional and velocity error input tends to result in an improved performance of the tracking system (Land, 1992). However, to simulate trajectories of the virtual blowfly looking similar to trajectories of real flies, the gain of the velocity servo must be lower than the gain of the positional error signal. This is not surprising, since a pure velocity controller will never manage to centre a target located in the peripheral visual field. However, a moderate velocity input helps to prevent the fixation controller from overshooting and damps oscillations.

Fly head and body dynamics

The virtual fly as used here, though it can account for many features of the chasing behaviour of real blowflies, represents only a crude approximation to reality. Our assumption that gaze direction coincides with body orientation is not exactly valid, since during a saccade the head starts turning only somewhat later than the body and stops moving slightly earlier (Schilstra and van Hateren, 1998; van Hateren and Schilstra, 1999). We have refrained, so far, from simulating this characteristic, because no experimental data on head movements during chasing flights are available. A more realistic treatment of head movements might have implications on the design and, in particular, the time constants in the target fixation controller. The head weighs much less than the fly's body and, as a consequence, has a smaller inertia than the rest of the body. Hence, head movements can be faster than thorax movements and target fixation is likely to be even more precise (van Hateren and Schilstra, 1999) than has been estimated in our studies on chasing behaviour by taking only the orientation of the body axis into account.

To move the fly, its wings have to generate forces to overcome gravity, the inertia of the fly's body and the viscous friction of the air. There is a great deal of knowledge about basic principles of insect flight aerodynamics (e.g. Ellington, 1995; Fry et al., 2003; Lehmann, 2001; Sane, 2003). From measurements of body and wing kinematics during flight it has even been possible to determine the forces that act on the body when turning and to show that, even for small fruit flies, inertia rather than friction is dominating the flight dynamics of these insects (Fry et al., 2003). Hence the earlier assumption that the angular momentum can be neglected (Boeddeker and Egelhaaf, 2003; Land and Collett, 1974; Reichardt and Poggio, 1976) is not valid. Despite the fact that we originally designed the virtual fly according to this assumption, the inertial nature of yaw rotations is indirectly taken into account by the time constant of the fixation controller (see Materials and methods). The time constant and gain for yaw rotation that we used in the present study were estimated from our kinematic studies on chasing behaviour in *Lucilia*. Our assumptions on the maximal yaw acceleration that can be generated by the virtual fly are in accordance with the maximal acceleration measured in free-flying *Calliphora*, a blowfly species related to *Lucilia*, though slightly larger (~10^5 deg. s^{-2}; Schilstra and van Hateren, 1999). A consideration of the forces, masses and inertial momenta involved during turns, reveals that the thorax angular accelerations realized in blowflies appear to be close to the maximum possible (Schilstra and van Hateren, 1999).

The situation is more complicated for non-linear translational locomotion. Blowflies often change flight direction by banked turns (Schilstra and van Hateren, 1999). During turns the fly's translational momentum keeps the fly in its 'old' flight direction even though the flight motor is already producing force that points, in an external coordinate system, sideways. This behaviour is captured by our virtual fly generated trajectories that look very similar to real flies' trajectories.

In conclusion, since the visual mechanisms underlying flight control are the main topic of our study, we refrained from simulating flight dynamics and used a computationally cheap kinematic locomotion model. Nonetheless, the current version of the virtual fly is sufficient not only to account for most features of visually guided chasing behaviour as characterised experimentally, but also to explain the generation of yaw, forward and sideward velocities and the corresponding accelerations, as seen in an external coordination system that closely matches those measured in real blowflies (e.g. Schilstra and van Hateren, 1999; Boeddeker et al., 2003).

The neuronal control of chasing behaviour

The fixation controller of the virtual fly that we propose on the basis of our experimental and modelling analysis (Boeddeker and Egelhaaf, 2003; present study) is somewhat similar to a 'neuronal' model scheme of the control system underlying target tracking as proposed by Land and Collett (1974). Moreover, the properties of male-specific neurons (Gilbert and Strausfeld, 1991; Gronenberg and Strausfeld, 1991; Hausen and Strausfeld, 1980; Strausfeld, 1991) have been suggested to fit well into the scheme proposed by Land and Collett (1974). According to this circuitry two distinct visual pathways act in parallel in the fly's brain when fixating a target in the frontal visual field, in a similar way as proposed here for the fixation controller of the virtual fly (see Fig. 1): one pathway for the processing of target motion and one for the retinal position of the target.

The division of the fixation controller into one pathway exclusively signalling position and another pathway sensitive exclusively to velocity information is convenient for analytical reasons, but is not imperative for implementation at the neuronal level. There are even arguments against such a subdivision: visual neurons signalling the retinal position of an object show different response amplitudes for targets moving with different speeds, and thus, will be ambiguous with respect to these stimulus parameters. This feature may be attributed, for instance, to the spatial and temporal transfer properties of neurons in the early stages of the fly's visual system (Juusola and French, 1997). In addition, any motion-sensitive neuron also provides information about the retinal position of a target, since its sensitivity to visual motion stimuli is not constant over the entire visual field, but has a sensitivity maximum at some retinal location with a decreasing sensitivity at increasing distances from this sensitivity maximum. Again, the responses of motion-sensitive neurons are ambiguous with respect to stimulus parameters (for reviews on motion-sensitive neurons of flies, see Borst and Haag, 2002; Egelhaaf et al., 2002). In any case, the division of the fixation controller into a pure position and a pure velocity servo gets blurred at the neuronal level. Although our knowledge on the functional properties of male-specific neurons of flies is still fragmentary, their known responses appear to be in accordance with this view (Gilbert and Strausfeld, 1991; Gronenberg and Strausfeld, 1991). In particular, none of the described neurons represents either unambiguous position or velocity information. This feature is similar to the receptive-field characteristics of target-selective descending neurons (TSDNs) of dragonflies. TSDNs are good candidates for the chief guiding neurons linking vision to target pursuit behaviour (Frye and Olberg, 1995; Olberg, 1986). The responses of these neurons are jointly determined by the position of the target in the receptive field and by its velocity (Adelman et al., 2003).

Land (1993b) pointed out that a smooth and continuous control system will produce saccades under certain circumstances related to discontinuities in the sensory input. These discontinuities might be due to temporary occlusion of the target, poor contrast or speed-induced motion blur, which is the loss of spatial resolution for moving images. Although moving objects can be resolved even at high retinal velocities, especially by the male retina (Burton and Laughlin, 2003), it is likely that time constants intrinsic to the cells in the peripheral visual system of blowflies may lead to some motion blur that attenuates neural signals to small objects at very high retinal velocities (Burton and Laughlin, 2003; van Hateren, 1992; Juusola and French, 1997; Srinivasan and Bernard, 1975). In a future version of our virtual fly it would be desirable to include a realistic model of the peripheral visual system of male blowflies. It may well be that the behavioural performance of the virtual fly may then become even more realistic. However, it is a distinctive feature of the peripheral visual system of male blowflies that motion blur is kept as small as possible. In male blowflies both optics and phototransduction are specialised to enhance and deblur the neural images of moving targets, enabling male flies also to register target position during fast flight manoeuvres (Burton and Laughlin, 2003).

So far, when implementing our virtual fly, we have not taken into account the specific neuronal hardware of the male-specific part of the fly visual system. This is because the current experimental data are not yet sufficient to constrain the large number of parameters that need to be specified for a realistic neuronal network model. For this reason, we tried to keep the mechanisms implemented in the virtual blowfly as simple as possible while being sufficient to account for the relevant aspects of blowfly chasing behaviour.

From our behavioural experiments and the simulation of chasing behaviour, we now have adequate knowledge of the relevant visual stimulus parameters used by male *Luciliae* to guide pursuit of real flies or artificial targets. Whether or not these input variables are represented in the fly's nervous system and how they might be translated into behavioural responses has yet to be assessed in electrophysiological studies such as are currently conducted in our laboratory with retinal input as is seen by a male blowfly during chasing behaviour. On this basis it may be possible to replace the phenomenological model of the control system for chasing behaviour as implemented in the virtual fly by biologically more plausible networks. Only then will it be possible to understand how the neuronal mechanisms underlying chasing behaviour are adapted to the natural operating conditions of the system.

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