MASSACHUSETTS INSTITUTE OF TECHNOLOGY
ARTIFICIAL INTELLIGENCE LABORATORY
and
CENTER FOR BIOLOGICAL AND COMPUTATIONAL LEARNING
DEPARTMENT OF BRAIN AND COGNITIVE SCIENCES

A.I. Memo No. 1512 December, 1994
C.B.C.L. Paper No. 103

Cooperative physics of fly swarms: an emergent behavior

M. Poggio and T. Poggio
This publication can be retrieved by anonymous ftp to publications.ai.mit.edu.

Abstract

We have simulated the behavior of several artificial flies, interacting visually with each other. Each fly is described by a simple tracking system (Poggio and Reichardt, 1973; Land and Collett, 1974) which summarizes behavioral experiments in which individual flies fixate a target. Our main finding is that the interaction of these simple modules gives rise to a variety of relatively complex behaviors. In particular, we observe a swarm-like behavior of a group of many artificial flies for certain reasonable ranges of our tracking system parameters.

This report describes research done at the Artificial Intelligence Laboratory and within the Center for Biological and Computational Learning in the Department of Brain and Cognitive Sciences at the Massachusetts Institute of Technology. This research is sponsored by grants from ONR under contract N00014-93-1-0385 and from ARPA-ONR under contract N00014-92-J-1879; and by a grant from the National Science Foundation under contract ASC-9217041 (this award includes funds from ARPA provided under the HPCC program). Additional support is provided by the North Atlantic Treaty Organization, ATR Audio and Visual Perception Research Laboratories, Mitsubishi Electric Corporation, Sumitomo Metal Industries, and Siemens AG. Support for the A.I. Laboratory's artificial intelligence research is provided by ARPA-ONR contract N00014-91-J-4038. Tomaso Poggio is supported by the Uncas and Helen Whitaker Chair at MIT's Whitaker College. Martino Poggio is with the Roxbury Latin School, St. Theresa Ave., West Roxbury, MA

1 The Problem

Two decades ago researchers proposed a simplified model of the visuo-motor control systems used by flies (Musca domestica for instance) to fixate contrasted targets (Reichardt and Wenking, 1969; Reichardt and Poggio 1975, 1976, 1980; Poggio and Reichardt, 1973; Geiger and Poggio, 1975; Wehrhahn and Poggio, 1976) and to chase other flies (Land and Collett, 1974; Poggio et al., 1977; Buelthoff et al., 1979; Reichardt and Poggio, 1980; Poggio and Reichardt, 1981; Wehrhahn et al., 1982; Collett and Land, 1975; Collett and Land, 1978). The models describe the motion of a fly as it is tracking a visual target. The basic equation of motion is somewhat similar to a point mass in a nonlinear force field. The models were used to simulate free-flight behavior; the simulations were compared with actual flight data recorded through high-speed 3D movies. In the simulations of chases, the trajectory of a leading fly was given to the model which then used that data to predict the trajectory of the chasing fly. Simulations were also made of a fly approaching a stationary target (a landing situation).

Simulations were never made, however, of two or more flies interacting with each other using the model of the visuo-motor control system for tracking. The purpose of this paper is to conduct such simulations. In particular, we are especially interested in finding out whether the interaction of two or more model flies can lead to trajectories showing indications of chaotic behavior, from equations governing the motion are fully deterministic and rather simple. In addition, this project may be a first step in studying the complex behavior arising from the interaction of many flies in a swarm, each one described by a simple model.

2 Background

Male and female flies fixate – that is fly towards – small contrasted patterns and track moving objects. A simple, mathematical model developed by Reichardt and coworkers (see for instance Reichardt and Poggio, 1976; Reichardt and Poggio, 1980) were based on so-called closed-loop experiments in which a flying fly was fixed to a torque compensator, capable of measuring its torque about the vertical axis. The torque was controlling the motion of the environment around the fly by a real-time electronic simulation of the flight dynamics.

In this paper we restrict ourselves to the an idealized situation with a restricted number of degrees of freedom. In particular, we assume that the flight trajectories are on the horizontal plane. The models can be extended to the 3D situation (see Reichardt and Poggio, 1981; Wehrhahn et al., 1982; Buelthoff, H. et al., 1979). Figure 1 shows the equivalent free-flight situation. ψ is the error angle between the direction of flight α_f and the direction of the target α_p, both relative to the "zero" direction ; it represents the position of the image of the target on the eye of the fly under the assumption – not completely correct – that the fly's head is always looking straight ahead in the direction of flight. The flight dynamics, neglecting translational effects, is approximated by

$$k\dot{\alpha}_f = F(t) \tag{1}$$

where $F(t)$ is the torque generated by the fly and $\dot{\alpha}_f$ is the angular velocity of the fly. The torque $F(t)$ depends on the visual input; it was found (see Reichardt and Poggio, 1976) that it can be approximated, under situations of tracking and chasing, as a function of the angular error (see Fig.1). The angular velocity also contributes but in a small way: we will neglect here the angular velocity term (see Reichardt and Poggio , 1980). We approximate $F(t)$ as

$$F(t) = D(\psi) + N(t) \tag{2}$$

$D(\psi)$ has been described as either a linear function of the angular error over the domain $(-\pi, \pi)$ (see Fig. 2a) or as a nonlinear function of it (see Fig. 2b), depending on whether the fly is male or female and on whether it is engaged in free-flight chasing or in simple fixation. In this paper we will examine both forms of $D(\psi)$ as two different, but plausible control systems. $N(t)$ is a so-called zero-mean, gaussian process characterized by its autocorrelation function. It can be thought of as low-pass white noise. Since in most of our simulations we did not use the noise term $N(t)$, unless otherwise specified we will set $N(t) = 0$. Note that $N(t)$ reflects our ignorance (in the model) of the fly's will and intentions. The model, which describes the smooth tracking system and neglects a possible "saccadic" system (see Land, 1977 and Poggio et al, 1977), is of course an oversimplification. Heisenberg and Wolf (1990) among others have described evidence pointing to necessary extensions of it. We also assume that flies move at constant translational velocity v; in some cases we will make the assumption that the velocity v is controlled by the distance to the target and refer to this control choice with $v(\rho)$. The specific forms of $D(\psi)$ and of $v(\rho)$ are in Figures 2a, 2b, and 2c.

3 The Model

We model a fly in most of our simulations by using the following equations of motion

$$k\dot{\alpha}_f = F(t) \tag{3}$$

$$F(t) = D(\psi(t-\epsilon) \tag{4}$$

where is the delay in the fly's reaction (about 30 msec); the translational equations, which account for the change in angle due to the translation of the fly relative to the target, are

$$\dot{x} = v(\rho) sin\alpha_f \tag{5}$$

$$\dot{y} = v(\rho) cos\alpha_f \tag{6}$$

Instead of this set of differential equations we simulate on the computer the corresponding set of difference equations by discretizing the differential equations at time intervals of Δt. Notice that a change in Δt in our difference equations corresponds to scaling appropriately parameters such as k and v. We neglect the delay (the "equivalent" delay in our difference equation model is Δt).

4 The Simulations

4.1 One fly, one fixed target

The first simulated experiments consist of one fly fixating a single fixed target. We first run the simulation using $D_l(\psi)$ and a constant velocity (see Fig. 3). The (simple) theory (see Reichardt and Poggio, 1980) predicts a periodic attractor in which the fly orbits the target in a fixed circular path. The fly cannot land because the velocity is constant. It keeps the target at an error angle of $\pi/2$. The orbit is stable because the slope of $D_l(\psi)$ around $\pi/2$ is positive (see Fig. 2a) . The result of the simulation confirms that prediction. When we use $v(\rho)$ of Fig. 2c to control the fly's velocity and the same $D_l(\psi)$, the fly is able to land, as expected.

Using $D_n(\psi)$ and a constant velocity we observe a locally unstable situation, since in $D_n(\psi)$ around $\pi/2$ the slope is negative (see Fig. 4). Figure 4 also represents the first observation of a "flower-like" periodic attractor. This attractor shows up again in later simulations with multiple flies. The fly makes "bowtie-like" loops by fixating the target, passing through it, and then fixating it again and so on. It makes these loops in one direction for a certain amount of time, depending on the initial conditions, then it gets stuck in one loop apparently ad infinitum. The attractor is unstable and can be destroyed by small amounts of noise.

If we use $v(\rho)$ to control the fly's velocity and again $D_n(\psi)$ for the torque the results are similar to those using $D_l(\psi)$ as the torque function. As expected, the fly's behavior for $|\psi| < \pi/6$ is virtually the same for both $D_n(\psi)$ and $D_l(\psi)$ since the slope of the two functions is similar in that range.

4.2 One fly, one moving target

In the next set of experiments we simulate a fly tracking a moving object: therefore in all of the following simulations the velocity is controlled by $v(\rho)$ with the speed of the target as the lower bound. Whether we use linear or nonlinear $D(\psi)$ the observed behavior are qualitatively similar. Fig. 5 is a specific example showing tracking of a target moving with random direction.

4.3 Two flies chasing each other

At this point we begin to simulate the cases that have not appeared previously in the literature. In the next two simulations the two flies have the same constant velocity and are both tracking each other. When we use $D_l(\psi)$ to control the torque in both flies we observe two attractors by randomly changing the initial positions of the two flies. The first attractor, and far more frequent one (see Fig. 6), consists of the two flies always settling into the same circular orbit, one chasing the other, and keeping each other at a $\psi = \pi/2$ error angle. This behavior is similar to the single fly orbiting around a target. It is a stable attractor because in $D_l(\psi)$ the slope around $\pi/2$ positive. This attractor – like the single fly, single target attractor – is not easily destroyed by small amounts of noise. The second, far more rare attractor (see Fig. 7) exists only with certain restricted initial conditions (i.e. both flies must initially face in parallel directions and be positioned on the same line perpendicular to their direction of flight). The flies begin to weave around each other while making their loops progressively smaller and smaller ad infinitum until they seem to be travelling along the same straight line.

However, when the fly's torque is controlled by $D_n(\psi)$ the resulting attractor is very unstable (see Fig. 8). Small amounts of noise will significantly alter the fly's behavior. This attractor closely resembles the single fly fixed target attractor seen in Fig. 4. After forming the typical "flower-like" pattern the flies settle into a periodic attractor. Instead of progressively rotating each new loop slightly from the last as they do while creating the "flower-like" pattern, the flies remain in the same loop. Once trapped in the periodic attractor, the flies fixate each other, pass through each other, and fixate each other again while retracing the same path ad infinitum. The time between the beginning of the simulation and the beginning of the periodic attractor (roughly proportional to number of loops made before "getting stuck") depends on the initial conditions.

4.4 More than two flies chasing each other

In simulations in which a fly has more than one target we assume, based on experimental data from Reichardt and Poggio (1976), that the fly's total torque is approximated by the sum of the torques generated by each target individually. In formula:

$$F_{total} = D(\psi_1) + D(\psi_2) + \cdots + N(t) \qquad (7)$$

where $\psi_1, \psi_2, \cdots$ are the error angles of the fly relative to each target. We also assume that the absolute value of the torque produced by the fly cannot exceed an upper limit. For this reason we introduce a saturation nonlinearity operating on F_{total}

$$F_{sat} = \sigma(F_{total}) \qquad (8)$$

where σ is the function defined here as

$$\sigma(x) = \begin{cases} x & \text{if } |x| \leq 4 \\ \pm 4 & \text{otherwise.} \end{cases} \qquad (9)$$

Notice that this means that nonlinear saturation never occurs with less than 4 flies if the nonlinear $D_n(\psi)$ is used.

4.4.1 Three flies chasing each other

Three flies chasing each other show different types of behavior depending on their initial conditions, Δt, and on the values of their parameters.

Using the "linear" control equation $D_l(\psi)$ (with the nonlinear saturation) we observe several different types of behavior depending on Δt. With small Δt values ($.06 > \Delta t > .003$) we observe several different periodic and apparently chaotic attractors. One of these attractors simply consists of the three flies merging their flight paths and flying off in a straight line (this occurs around $\Delta t = .06$). The other two are variations of the general "weaving" behavior (see Fig. 9), one being almost chaotic (it shows almost periodic behavior over a very long time scale), the other periodic. Using very small Δt's ($\Delta t < .003$) we observe only the apparently chaotic "weaving" pattern of Fig. 10. With large and moderate values of Δt ($\Delta t > .06$) we observe an attractor in which the three flies, after an initial transient, apparently random flight pattern, suddenly fly apart in straight lines at $2/3\pi$ from each other. This phenomenon occurs because each fly puts itself in a position such that the error angles ψ for the other two flies are equal and opposite, producing equal and opposite torques, which lead to this equilibrium situation. As a general, but by no means unequivocal rule, the "120° equilibrium" phenomenon occurs at higher Δt's and variations of the "weaving" behavior occur at lower Δt's.

It is interesting to note that making Δt greater or smaller is equivalent to making the flies' torque F and translational velocity v greater and smaller respectively as we alluded to earlier. With a large Δt ($\Delta t > .2$) and the $D_n(\psi)$ control system complete chaos reigns. This behavior is due to the fact that a large Δt is equivalent to a large torque F which would cause the fly to over-rotate leading to chaos. As one reduces Δt more and more ($.1 > \Delta t > .07$) the flight pattern apparently remains chaotic but all three flies stick to each other and take the same path. Their path becomes smoother and less rough than with large Δt's yet it remains riddled with chaotic loops. As Δt is lessened even further ($.07 > \Delta t > .05$) the flies split up their flight path (see Fig. 11). One fly goes on its own while the other to remain attached together. These two groups (of 2 flies and 1 fly) continue to fly towards each other, pass through each other, and then fly towards each other again ad infinitum. In doing so they form loops but no apparent pattern. Their behavior apparently remains chaotic. When Δt is very small ($\Delta t < .05$) then the flies remain grouped as before and they loop in the same way, however patterns begin to surface in their behavior. Flight paths begin to resemble the "bow-tie loops" discussed earlier, and the error angle ψ between two flies begins to follow a quasi periodic pattern. The behavior, however, is not completely periodic. The repetition of patterns is not as exact as in the simulation involving only two flies. Chaos still may be present. For larger Δt there is also another more rare attractor in which all three flies follow the same straight-line path.

4.4.2 Two flies chasing, one fleeing

In the next set of simulations, we used three model flies, two of which chased (or were attracted by) the other flies, and one of which fled from (or was repelled by) the other flies. The behavior, like in the previous simulations, depends on Δt and on which of the two control equations was used.

Using the linear function $D_l(\psi)$, at large Δt ($\Delta t > .2$) we observed several different types of apparently chaotic attractors. In some cases the fleeing fly may fly off in a straight line with the two chasers following in a chaotic way. In other cases a "V" shape was formed by the paths of the two chaser flies while the fleeing fly is chaotically in the middle of the "V" (similar to "120° equilibrium"). In still other cases the flies simply follow apparently random "zig-zag" paths. But as Δt was decreased ($\Delta t < .1$) the flies always displayed the same type of behavior (see Fig. 12). The two chaser flies weave around each other, making "U" shaped loops in a curved path, and gradually increasing the size of the loops. At the same time the fleeing fly follows a curved path on the inside of the curved path of the two chaser flies. This behavior occurs in small to very small Δt's and seems to be the only behavior at these Δt's (observed as low as $\Delta t = .0005$).

Using the non-linear function $D_n(\psi)$, we also observed that as dt decreases just one type of behavior seems to take over. For large Δt ($\Delta t > .5$) we observed only apparent chaos. But as we decreased Δt ($.5 > \Delta t > .1$) the behavior became less and less chaotic until the fleeing fly flew off in a straight line with the two chasers following immediately behind it in the same straight line. This behavior occurred in small to very small Δt's and seems to be the only behavior at these Δt's (observed at as low Δt as $\Delta t = .0005$).

4.5 A swarm of flies

10 flies with the nonlinear $D_n(\psi)$ (and saturation) show a periodic behavior for $\Delta t < 0.03$. With $\Delta t > 0.03$ there seems to be onset of chaos (see Fig. 13). The behavior of the swarm starts to resemble the rapid imploding and exploding motions of actual swarms of mosquitos. We notice a global stability of the swarm itself which is glued together and moves relatively slowly as a whole, at a much slower rate than the individual flies. The glue that holds the swarm together is the reciprocal attraction that fly exert on each other. There is no leader though all the flies follow one of them for some interval of time before the onset of a phase of chaotic flight. The behaviour seems to be relatively independent of the number of flies.

5 Discussion

Our simulations of artificial flies suggest that the interaction of very simple control systems may account for some of the complex behavior observed in real swarms of flies or mosquitoes. The model of the fly which we use is a vast oversimplification. Therefore in the following we discuss some limitations of the model and some of the most important (possible) extensions.

5.1 Limitations of the model

The original Reichardt and Poggio model is a simplification of the tracking of real-life flies. It does not take into account the motion of the individual fly's head relative to its body (Land, 1973; ; Geiger and Poggio, 1977; Wagner, 1986). It does not model the apparent ability of the fly to control in some circumstances the "noise" term, $N(t)$ (Heisenberg & Wolf, 1990). It also concentrates on the smooth pursuit control system. In addition our simulation uses difference equations in the place of differential equations with delay. Furthermore our simulated flies are simply points on a screen and can pass through each other, unlike real flies. Finally, we make the assumption that all flies can see all the other flies regardless of the distance between them (clearly unrealistic). In fact one may assume that a fly becomes visible to another fly under normal conditions only for distances below $50cm$ or so (Collett & Land, 1978). We should also notice that the systems involved in tracking and chasing are almost certainly different from each other with respect to the underlying neural substrate; they are also different in male and female flies (Wehrhahn, 1978; Poggio et al., 1977).

5.2 Extensions of the model

There are several obvious extensions of the model. We have mentioned earlier examples such as taking into account the visibility of flies as a function of distance and of occlusions (by other flies). Clearly an extension to three dimensions would be desirable. A full model of the dynamics of flight – including lift, roll, yaw and pitch – is relatively challenging, especially if one would like to take into account the degrees of freedom associated with the movements of the head relative to the body. More interesting is the idea of modeling different simple behaviors in the individual flies. It is likely that a fly has at very least a small repertoire of routines or behaviors that can be switched on in different situations: the landing reaction, the chasing behavior and the tracking behavior are such examples. From our simulations it seems that the swarm behavior of a group of flies may be an emergent property of a simple control system for tracking. It is quite possible however that the parameters of the control system active during the swarm behavior may be different from the control system active during chasing and that they may correspond to different neural structures. Notice that the slope of $D(\psi)$ is much greater in male flies than in female flies and that only male flies "swarm". Our simulations pose the question of whether the swarm behaviour is a side effect of an existing tracking system. We believe that a positive answer to the question is unlikely. We believe, however, that the swarm behaviour may depend on a relatively simple tracking system similar to – even if separate from – the chasing system described in this paper. The alternative hypothesis is of course that the swarm behaviour depends on a completely different control system.

The most interesting aspect of our simulations is to show that the interaction of a few very simple control systems as we described for flies can generate complex behavior. Under some conditions this behavior appears to be chaotic. We did not test whether the solution of our (difference!) equations has all the characteristics of deterministic chaos but at least in some of our simulations this is quite likely and not too surprising. Even more interesting is the observation that the chaotic behavior of groups of flies has a qualitative similarity with the swarm behavior sometimes observed in mosquitos or similar flies. It is instructive how many different behaviors a few of these simple equations can generate: the figures show a few of them but do not exhaust the number of interesting attractors we have observed. The figures do not do justice to the richness of the simulations which should be observed dynamically to appreciate them fully.

Acknowledgements. We are grateful to H.Bülthoff for having helped us develop the idea for this work, to F. Girosi and C. Wehrhahn for several useful suggestions and especially to K. Goetz for many constructive comments. Thanks also due to G. Geiger and to R. Dower. It was up to Marney Smyth to take care of the most difficult step: transferring text and figures from the Windows environment to Latex, WWW and PS.

References

[1] H. Bülthoff, T. Poggio, and C. Wehrhahn. 3-D analysis of the flight trajectories of flies (Drosophila melanogaster). *Z. Naturforsch*, 235c:811–815, 1979.

[2] T. S. Collett and M. Land. Visual control of flight behavior in the hoverfly, Syritta pipiens. *J. Comp. Physiol.*, 99:1–66, 1975.

[3] T. S. Collett and M.F. Land. How hoverflies compute interception courses. *J. Comp. Physiol.*, 125:191–204, 1978.

[4] G. Geiger and T. Poggio. The Muller-Lyer figure and the fly. *Science*, 190:479–480, 1975.

[5] G. Geiger and T. Poggio. On head and body movements of flying flies. *Biol. Cyber.*, 25:177–180, 1977.

[6] K. G. Goetz. The optomotor equilibrium of the Drosophila navigation system. *J. Comp. Physiol.*, 99:187–210, 1975.

[7] M. Heisenberg and R. Wolf. Visual control of straight flight in Drosophila melanogaster. *J. Comp. Physiol.*, A, 167:269–283, 1990.

[8] M. F. Land. Head movement of flies during visually guided flight. *Nature*, 243:299–300, 1973.

[9] M. F. Land. Visually guided movements in invertebrates. In G. Stent, editor, *Life Sciences Research Report*, volume 6, pages 161–178, Berlin, 1977. Dahlem Konferenzen.

[10] M. F. Land and T.S. Collett. Chasing behaviour of houseflies (Fannia canicularis): A description and analysis. *J. Comp. Physiol.*, 89:331–357, 1974.

[11] T. Poggio and W. Reichardt. A theory of pattern induced flight orientation of the fly, musca domestica. *Kybernetik*, 12:185–203, 1973.

[12] T. Poggio and W. Reichardt. Visual fixation and tracking by flies: mathematical properties of simple control systems. *Biol. Cyber.*, 40:101–112, 1981.

[13] T. Poggio (Rapporteur), E. Bizzi, R. E. Eckmiller, A. M. Greybiel, K.G. Gotz, M. Ito, M. F. Land, F. A Miles, W. Reichardt, D.A. Robinson, D. C. Sandeman, P. H. Schiller, and G. Westheimer. Visually guided movements. In G. Stent, editor, *Function and Formation of Neural Systems*, pages 309–327, Berlin, 1977. Dahlem Konferenzen.

[14] W. Reichardt and T. Poggio. A theory of the pattern induced flight orientation of the fly, Musca domestica, II. *Biol. Cyber.*, 18:69–80, 1975.

[15] W. Reichardt and T. Poggio. Visual control of orientation in the fly. part i: A quantitative analysis. *Quart. Rev. Biophys.*, 3:311–375, 1976.

[16] W. Reichardt and T. Poggio. Visual control of flight in flies. In *Theoretical Approaches in Neurobiology*, pages 135–150. M.I.T. Press, Cambridge, MA, 1980.

[17] W. Reichardt and H. Wenking. Optical detection and fixation of objects by fixed flying flies. *Naturwissenschaften*, 56:424–425, 1969.

[18] H. Wagner. Flight control and visual control of flight of the free-flying housefly (Musca domestica). Part III. *Philosoph. Trans. Royal Soc. London*, B(312):581–595, 1986.

[19] C. Wehrhahn. Sex specific differences in the orientation behaviour of houseflies. *Biol. Cybernetics*, 29:237–247, 1978.

[20] C. Wehrhahn and T. Poggio. Real-time delayed tracking in flies. *Nature*, 261:43–44, 1976.

[21] C. Wehrhahn, T. Poggio, and H. Bülthoff. Tracking and chasing in houseflies (Musca): an analysis of 3D flight trajectories. *Biol. Cyber.*, 45:123–130, 1982.

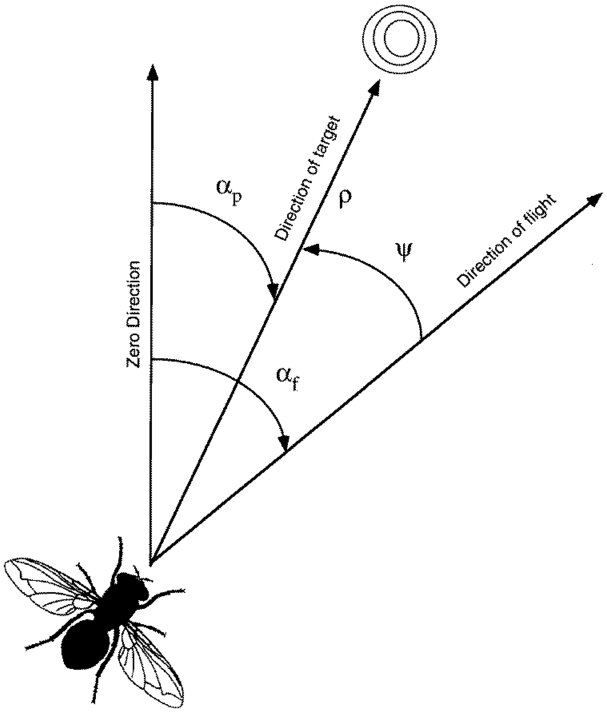

Figure 1. The angles used in our model and ρ , the distance of the fly to the target. α_p is the direction of the target relative to the vertical; α_f is the direction of flight relative to the vertical; $\psi = \alpha_p - \alpha_f$ is the error angle.

(a) (b) (c)

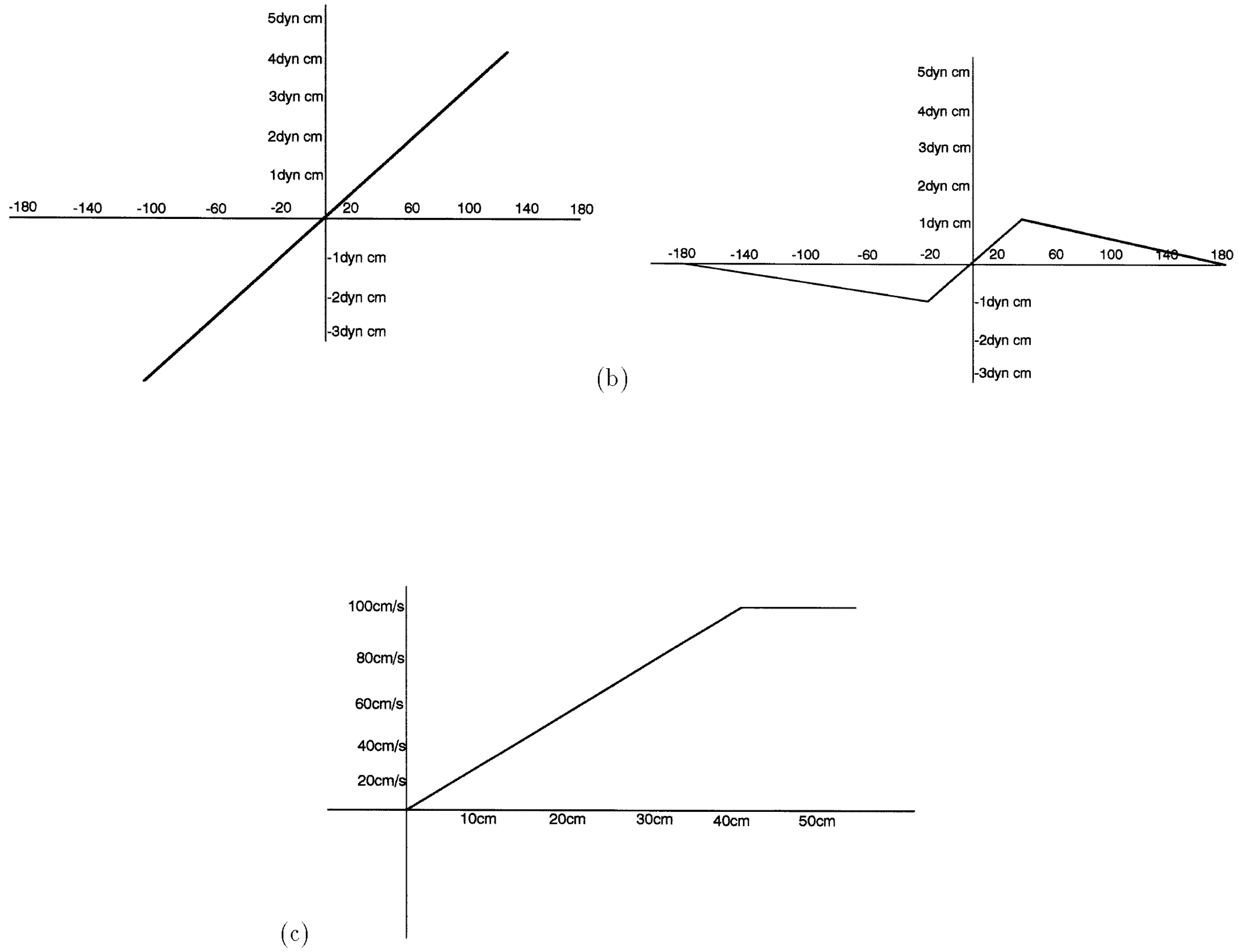

Figure 2a. The linear $D_l(\psi)$ function describing how the torque generated by the fly depends on the error angle . This function seems to describe free-flight chasing by male flies Musca domestica (see Reichardt & Poggio, 1981). The ordinate is torque (dyn cm); the abscissa is degrees of visual angle. 2b) The nonlinear $D_n(\psi)$ function describing how the torque generated by the fly depends on the error angle . This function seems to describe tracking in female flies Musca domestica (see Poggio & Reichardt, 1981). The ordinate is torque (dyn cm); the abscissa is degrees of visual angle. 2c) The function $v(\rho)$ describing how the forward velocity is controlled depending on the distance to the target in chasing situations (see Poggio & Reichardt , 1981).

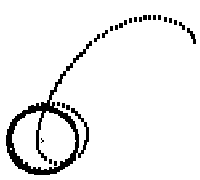

Figure 3. The trajectory of a simulated fly tracking a stationary target. In our difference equation we used the linear $D_l(\psi)$, $v = 100$ and $\Delta t = 0.01sec$. The simulation shows a periodic attractor, as predicted by the (simple) theory. The same attractor is found over a wide range of Δt.

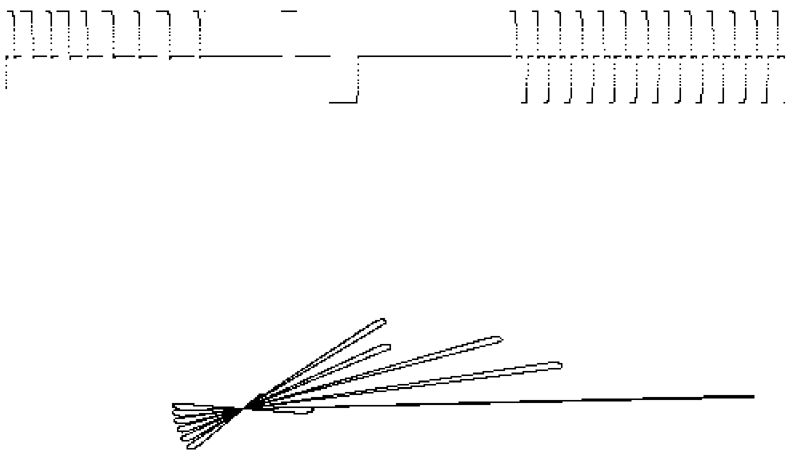

Figure 4. The trajectory of a simulated fly tracking a stationary target with nonlinear $D_n(\psi)$, and $\Delta t = 0.01 sec$. The velocity is constant. After a transient bow-tie trajectory the model fly settles in one of the loops (the smallest one in the figure) with a periodic behavior (see inset). The same behavior is observed for different dt (from 0.1 to 0.001). Here, as in several of the following figures, the inset above the figure shows the error angle as a function of time. The ordinate is from $-\pi$ to π , the abscissa starts at time 0.

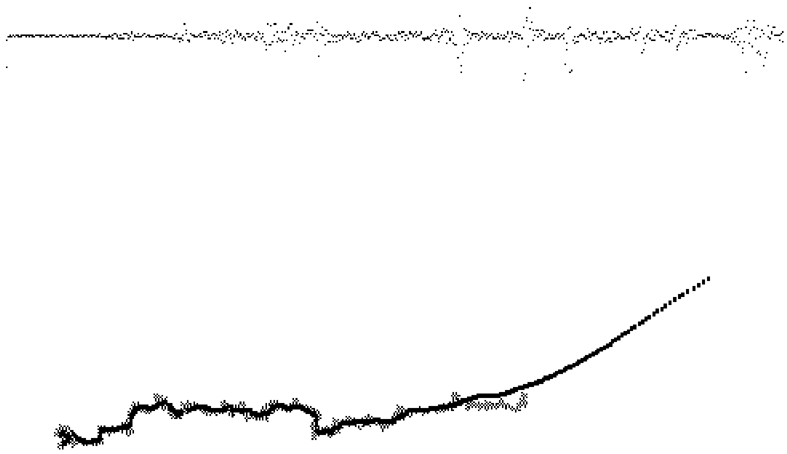

Figure 5. A typical chasing behavior of a simulated fly tracking a moving target. The target moves at constant speed with random directions. The same basic behavior is observed with nonlinear and linear $D(\psi)$, and a wide range of Δt. The velocity decreases with the distance from the target according to the function $v(\rho)$. The inset above the figure shows the error angle as a function of time. The ordinate is from $-\pi$ to π , the abscissa starts at time 0.

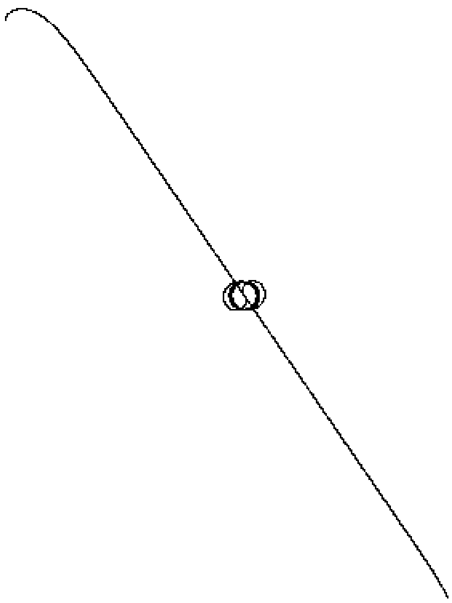

Figure 6. The behavior of two flies chasing each other. We use the linear $D_l(\psi)$. The velocity is constant for both flies. In this simulation $\Delta t = .001$ but the same behavior is observed for a broad range of Δt.

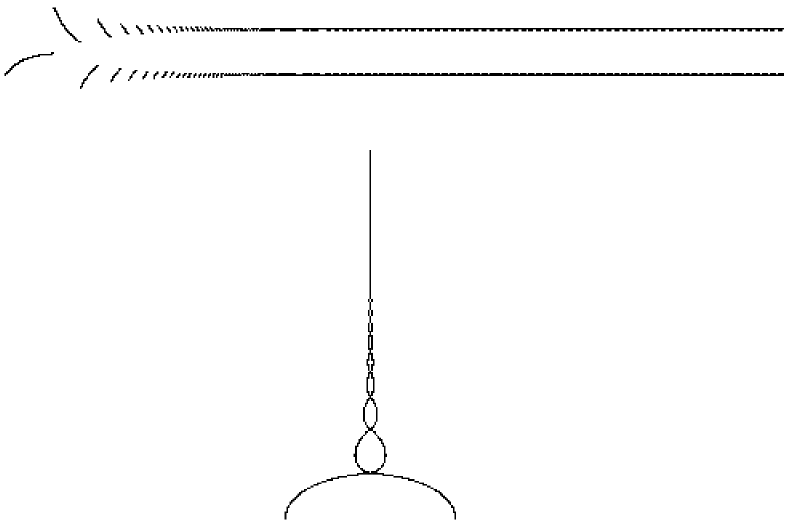

Figure 7. The second, far more rare attractor for the case of two flies chasing each other with a linear $D_l(\psi)$ exists only with certain restricted initial conditions (both flies must initially face in parallel directions and be positioned on the same line perpendicular to their direction of flight). In this simulation $\Delta t = .001$ but the same behavior is observed for a broad range of Δt. The inset above the figure shows the error angle as a function of time.

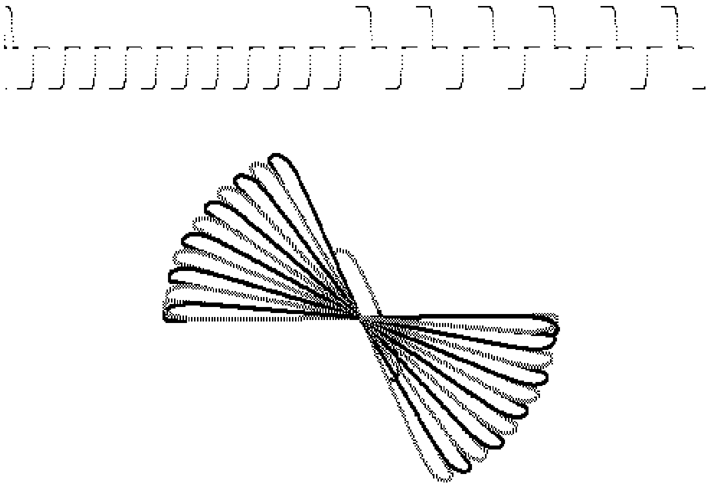

Figure 8. The behavior of two flies chasing each other. Both flies use now the nonlinear $D_n(\psi)$. The velocity is constant for both flies. In this simulation $\Delta t = .001$ but the same behavior is observed for a broad range of dt. As usual, the upper inset shows the error angle of one fly relative to the other plotted as a function of time.

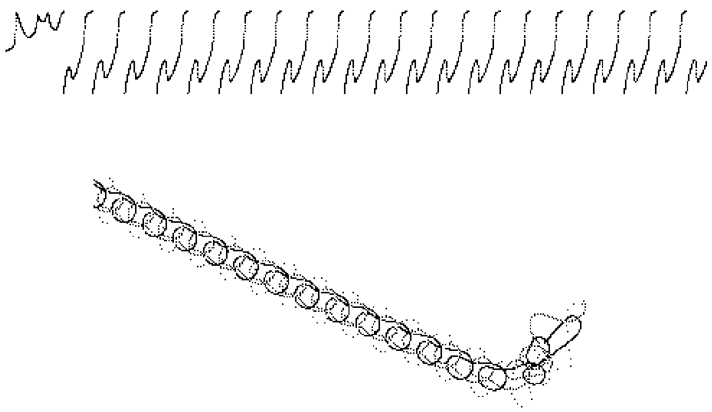

Figure 9. The behavior of three flies chasing each other. All the flies are controlled by the linear $D_l(\psi)$. The velocity is constant. This behavior is observed for a wide range of parameters (see later figures). The inset above the figure shows the error angle as a function of time.

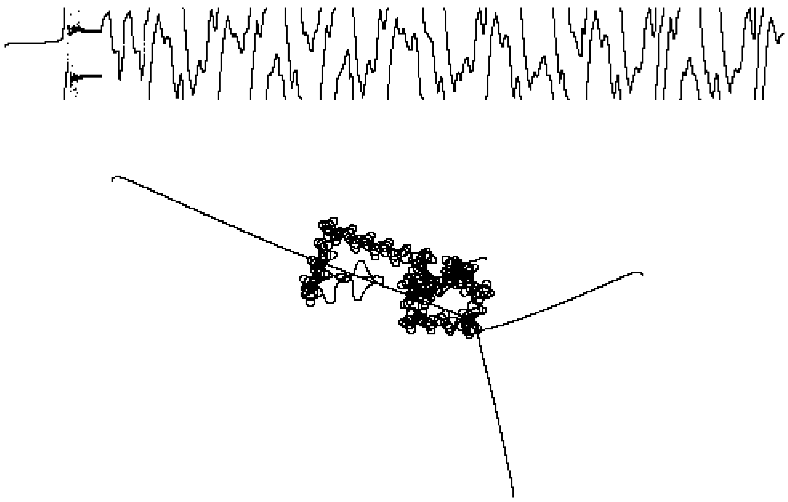

Figure 10. Three flies chasing each other. All the flies are controlled by the linear $D_l(\psi)$ with nonlinear saturation of the total torque of each fly (see text). The velocity is constant. This apparently chaotic behavior is observed for small Δt (such as for instance $\Delta t = .001$). The inset above the figure shows the error angle of one of the fly relative to one of the other two as a function of time.

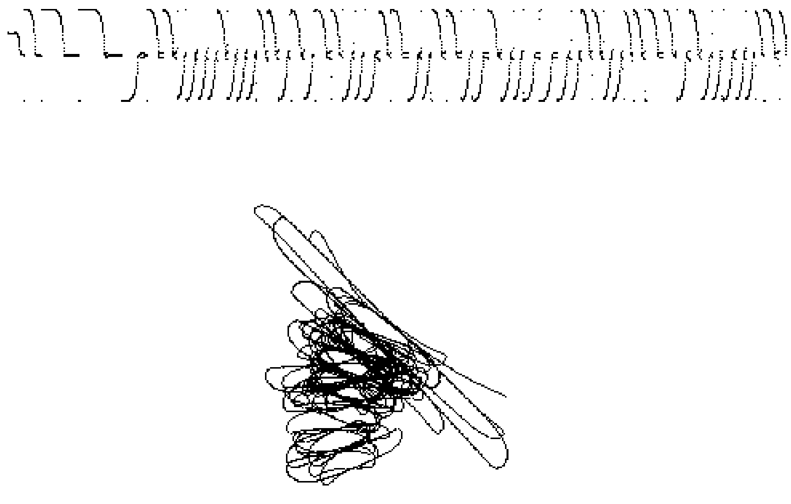

Figure 11. Three flies chasing each other using the nonlinear $D_n(\psi)$. This particular behavior depends on a large Δt (here $\Delta t = .05$). The velocity is constant. The inset above the figure shows the error angle of one of the fly relative to one of the other two as a function of time.

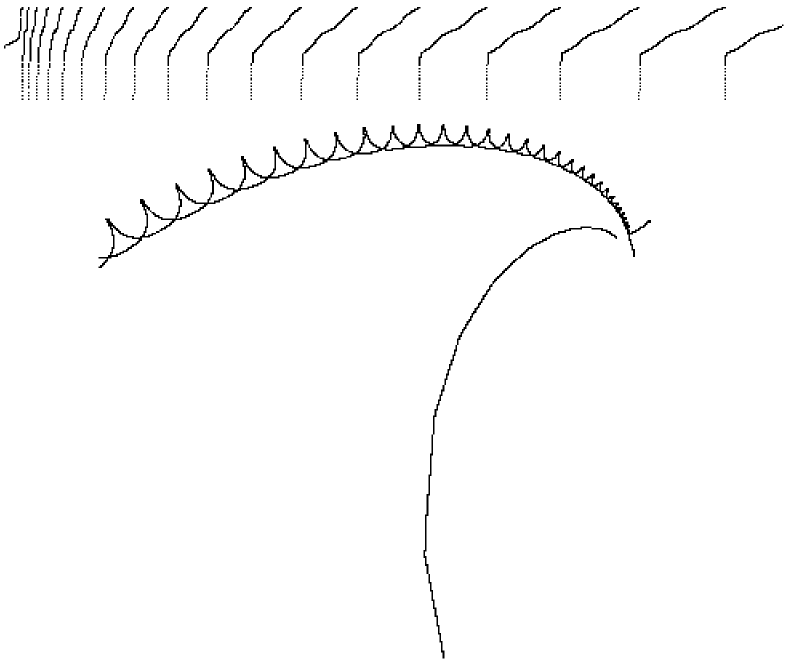

Figure 12. Three flies, two of which are chasing the others while one is escaping (its $D_l(\psi)$ appears with a negative sign, see text). All the flies are controlled by the linear $D_l(\psi)$. The velocity is constant. This behavior is the most frequent and has been observed for a wide range of Δt's (from 0.1 to 0.001). The inset above the figure shows the error angle of one of the chasing flies relative the other chasing fly as a function of time.

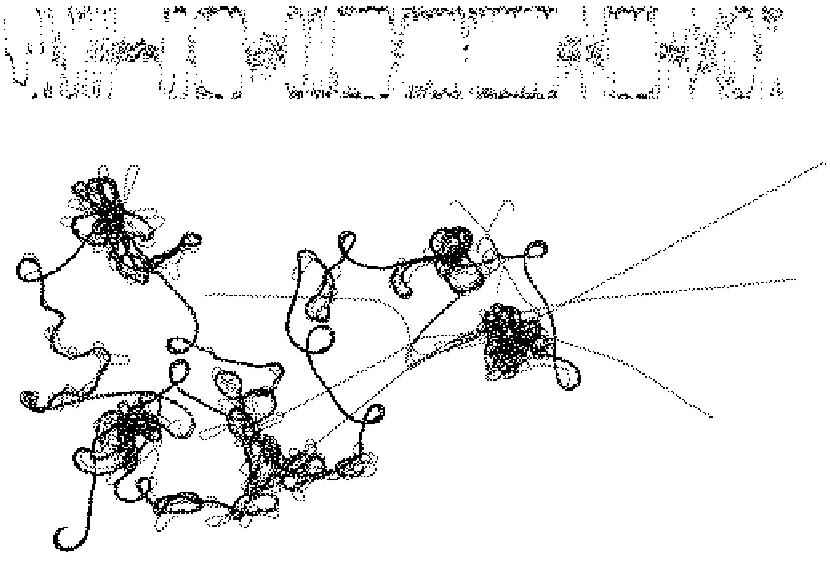

Figure 13. "Swarm behavior". 10 flies, chasing each other, with nonlinear $D_n(\psi)$, torque saturation, $\Delta t = 0.035$: the behavior is chaotic and resembles the swirling pattern of a real swarm of mosquitos. The behavior disappear for sufficiently small Δt. The inset above the figure shows the error angle of one of the fly relative to one of the others as a function of time.