

Visual Fixation and Tracking by Flies: Mathematical Properties of Simple Control Systems

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Abstract. The study of the orientation behavior of flies requires the consideration of a few simple control systems for fixation and tracking. In this paper two such control systems are analyzed, in terms of the corresponding difference and differential equations. The first control system corrects with a delay ε the angular trajectory proportionally to the error angle ψ ; the second control system also corrects proportionally to the error angle ψ but only when the absolute value of ψ is increasing. The differential equations are

$$\dot{\psi}(t) = -\alpha' \psi(t - \varepsilon) + A' \quad (0)$$

and

$$\dot{\psi}(t) = -\alpha' \psi(t - \varepsilon) \cdot u[\psi(t - \varepsilon) \dot{\psi}(t - \varepsilon)] + A' \quad (*)$$

$u[\]$ being the step function ($u[x] = 1$ if $x > 0$, otherwise $u[x] = 0$). Under suitable restrictions on the parameters it is proved (a) that the difference equations

$$x_{n+1} = x_n - \alpha x_n + A \quad (0')$$

and

$$x_{n+2} = x_{n+1} - \alpha x_{n+1} \cdot u[x_{n+1} \cdot (x_{n+1} - x_n)] + A, \quad (*)'$$

which can be associated to Eqs. (0) and (*), are "asymptotically equivalent" (for large n) if the time scale is "smoothed" over two time units and (b) that the second equation, with $0 < \alpha < 2$, always converge to a set of oscillating solutions of period 2 for arbitrary initial conditions. Numerical simulations show that the delay-differential equations behave in a similar way. We have also demonstrated with computer simulations that both control systems can satisfactorily predict the 3-D trajectory of a fly chasing another fly. The main biological implications of the analysis are: (1) The two control systems are practically equivalent descriptions of the fly's control of flight on a "coarse" time scale (2 times the fly's delay), consistently with an earlier more general derivation of Eq. (0) (Poggio and

Reichardt, 1973). (2) On a fine time scale the second control system is characterized by an asymptotic oscillation with period twice the fly's delay. It is conjectured that a wide range of control systems of the same general type must have a similar oscillatory behavior. Finally, we predict the existence of asymptotic oscillations in the angular trajectory and the torque of tracking flies (if a control system of the second type is involved to a significant extent). Such oscillations should have a basic period of twice the effective reaction delay, and should be best detectable outside the binocular region. Closed loop experiments and the analysis of free flight trajectories may provide critical tests of this prediction.

1. Introduction

1.1. Biological Background

1.1.1. The Fixation Control System: An Approximate Description. Houseflies visually control their flight course during fixation, landing and tracking of moving objects. A theory proposed by Reichardt (1973) a few years ago led to a phenomenological model of a control system used by the fly which can describe quantitatively a variety of fixation and tracking instances. According to the theory (for a review see Reichardt and Poggio, 1976) the fly controls its angular velocity $\dot{\theta}_f$ through its torque T , according to a simple approximation of the flight dynamics

$$\Theta \ddot{\theta}_f(t) + k \dot{\theta}_f(t) = T(t), \quad (1)$$

where Θ and k are the moment of inertia and an aerodynamic constant (of the fly), respectively. The situation in which the fly fixates or (tracks) a stationary (moving) target is described, in its simplest one dimen-

sional form, if $\Theta \ddot{\alpha}_f = 0$ and translation effects are neglected, by

$$k\dot{\psi}(t) = -[R_t\{\psi(s)\} + N(t)] + S(t), \quad (2)$$

where $S(t)$ reflects the angular motion of the target [if the target moves at constant angular speed $S(t) = \text{const.}$]. The fly's torque, in square brackets, is approximated by the sum of two terms: $R_t\{\psi(s)\}$, the visually induced response is a functional of the error angle history $\psi(t)$; $N(t)$, about which ignorance is professed, is characterized stochastically as a gaussian process. Reichardt and Poggio (1976); see also Poggio and Reichardt (1973) have shown that if a) the fly's response depends in a smooth way on the error angle history and b) $\psi(t)$ is not changing too fast [if $S(t) = 0$ this is automatically satisfied] then $R_t\{\psi(s)\}$ can be approximated in terms of two functions of ψ and $\dot{\psi}$

$$R_t\{\psi(s)\} \simeq D[\psi(t-\varepsilon)] + r[\psi(t-\varepsilon)] \cdot \dot{\psi}(t-\varepsilon), \quad (3)$$

where ε is the delay in the response of the fly.

Thus the overall equation describing the "trajectory" of a fly is

$$k\dot{\psi}(t) = -D[\psi(t-\varepsilon)] - r[\psi(t-\varepsilon)] \cdot \dot{\psi}(t-\varepsilon) + N(t) + S(t). \quad (4)$$

The various terms in the approximate Eq. (4) can be measured quantitatively by appropriate experiments. Notice that Eq. (4) is, up to this point, only an approximate description, valid only on a "slow" time scale (slower than the fly's reaction time scale). As a matter of fact, Eq. (4) has been mainly used with $\varepsilon = 0$ to describe situations in which the delay ε is negligible. It is important to stress that its derivation and its validity are independent of the specific form of the fly's visual response $R\{\psi(s)\}$ and thus of the underlying neural mechanisms.

1.1.2. What is the Exact Form of the Fly's Visual Response? Since the formulation of the theory, the question of the precise form of the visual response of the fly $R_t\{\psi(s)\}$ and correspondingly about the nature of the underlying mechanism has been often addressed. Two main hypotheses have been considered:

a) The flicker detector hypothesis: position information is measured independently of movement. Equation (3) is not only just an approximate but also a faithful description, at the level of the mechanisms, if the reaction is nonzero at zero flicker frequency. This hypothesis stresses the importance of the position term relative to the velocity term. In its extreme form, it leads to

$$R_t\{\psi(s)\} \simeq D[\psi(t-\varepsilon)] \quad (5)$$

and thus to the equation

$$k\dot{\psi}(t) = -D[\psi(t-\varepsilon)] + N(t) + S(t). \quad (6)$$

For $\varepsilon = 0$ and $r = \text{const.}$ the form of Eq. (6) coincides with Eq. (4): remember that Eq. (4) is valid on a time scale over which the delay ε is usually negligible.

If flicker detectors are assumed to be active only when $|\dot{\psi}| \neq 0$, the control system is essentially of the type of hypothesis b).

b) The progressive-regressive hypothesis: reaction to progressive motion (front to back) is larger than to regressive motion. The reaction is parametrized by ψ . Perhaps the simplest formulation of this idea is

$$R_t\{\psi(s)\} = D[\psi(t-\varepsilon)] \cdot u[\psi(t-\varepsilon)\dot{\psi}(t-\varepsilon)] \quad (5')$$

with $u[x] = 1$ if $x > 0$ and 0 otherwise, leading to

$$k\dot{\psi}(t) = -D[\psi(t-\varepsilon)] \cdot u[\psi(t-\varepsilon) \cdot \dot{\psi}(t-\varepsilon)] + N(t) + S(t). \quad (6')$$

Thus position information is mediated by movement computation¹. Equation (3) is no longer a faithful description of the reaction of the fly. As a consequence, the decomposition of Eq. (3) into 2 terms, depending respectively mainly on position and velocity does not reflect separate mechanisms.

Although Reichardt (1973; Poggio and Reichardt, 1973; see also Geiger, 1974) originally proposed hypothesis b), which is also supported for *Drosophila* by many data (Götz and Wenking, 1972; Götz, 1975; Götz et al., 1979), later experiments by Pick (1974) suggested that a) was a better description of at least a part of the fly's reaction (Pick, 1976; Poggio and Reichardt, 1976). Very recently Wehrhahn and Hausen (1980) have convincingly argued on the basis of careful experiments with transient stimuli that hypothesis b) is fully adequate to describe several instances of fixation and tracking behaviour in female houseflies (but see Geiger, 1980).

As a consequence, it is again interesting to analyze and compare the properties of Eq. (6) and (6'). It is important to stress that these 2 equations describe extreme versions of hypothesis a) and b), respectively. In particular, Eq. (6) is different from the original Reichardt-Poggio Eq. (4). For $r = \text{const.}$ the form of Eqs. (4) and (6) coincide if the delay is zero ($\varepsilon = 0$), which is roughly equivalent to the conditions under which Eq. (4) was derived and mainly used. Even for delays different from zero (but small), Eq. (4) (with $r = \text{const.}$) behaves essentially as Eq. (6), as an examination of the associated characteristic equation immediately reveals (compare an der Heiden, 1979; Hale, 1977). If the delay is small, solutions of Eqs. (4) and (6) can be considered practically equivalent. For these reasons, we will be concerned in this paper with Eq. (6)

¹ Notice that a decomposition of the fly's response into a direction sensitive (y_{ds}) and a direction insensitive component (y_{di}) is always formally possible, as long as the fly's response is an (arbitrary) function of object position and velocity (Geiger and Poggio, 1975).

(the "normal" equation) and Eq. (6') (the "progressive-regressive" equation), representing extreme forms of the two control systems a) and b).

Various mathematical aspects of Eq. (4) (for $\varepsilon=0$) and its extensions have been already characterized (Poggio and Reichardt, 1973; Reichardt and Poggio, 1975) with special emphasis on stochastic properties and more recently on free flight trajectories (Hadelar et al., 1980; Reichardt and Poggio, 1980).

To anticipate the results somewhat, the analysis in this paper shows that although Eqs. (6) and (6') have a characteristically different fine behavior, they are equivalent on a smoothed time scale, in accordance with the more general derivation [of Eq. (4)] of Reichardt and Poggio. In addition, it is proved that the fine structure of the solutions of Eq. (6') exhibits asymptotically a typical oscillatory behavior. Thus, considered as two different control systems, Eqs. (6) and (6') are both similarly effective in fixation and tracking, with a different fine dynamics but equal time smoothed properties. The control system Eq. (6) can be considered also as an approximation of control system Eq. (6'), the approximation being valid on a smoothed time scale.

Much of this paper is devoted to the analysis of the difference equations which can be associated with the differential equations Eqs. (6) and (6') by discretizing time. One reason is mathematical convenience. It is in fact possible to provide a satisfactory characterization for the difference equation, whereas an equivalent analysis of the differential equations seems more difficult. On the other hand numerical simulations show that the behavior of the difference equations closely reflects in this particular case the behavior of the corresponding differential equations. There is an additional reason for emphasizing the difference equations. From the biological point of view, there is scant evidence for believing that the differential equations Eqs. (6) and (6') should describe the fly's control system better than the corresponding difference equations. This is because the delay involved (20–40 ms) is small compared with the time scale over which the fly's response can be considered smooth and continuous (and it is comparable with the basic time constant associated with the aerodynamics of flight $\frac{\Theta}{k} \simeq 8 \text{ ms}$).

At present both types of description can be considered legitimate first order approximations.

1.2. The Mathematical Problem

Consider stripped-down versions of Eq. (6) and (6') as

$$\dot{\psi}(t) = -\alpha'\psi(t-\varepsilon) + A', \quad (7)$$

$$\dot{\psi}(t) = -\alpha'\psi(t-\varepsilon) \cdot u[\psi(t-\varepsilon) \cdot \dot{\psi}(t-\varepsilon)] + A', \quad (7')$$

where the constant A' represents the angular velocity of the target. ψ is an angular coordinate, i.e. $-\pi \leq \psi \leq \pi$ with $\psi + 2\pi = \psi$.

Although very simple, these equations preserve the important characteristics of Eqs. (6) and (6'), and again we will refer to them as the normal [Eq. (7)] and the progressive-regressive equation [Eq. (7')].

We can associate a difference equation to the differential equation Eqs. (7) and (7'), respectively, by discretizing time in the following way. We substitute

$\dot{\psi}(t)$ with $\frac{x_n - x_{n-1}}{\varepsilon}$ and obtain

$$\Delta x_{n+1} = -\alpha x_n + A \quad (8)$$

$$x_{n+1} = x_n + \Delta x_{n+1} \quad n=0, 1, 2, \dots$$

$$\Delta x_{n+1} = -\alpha x_n \cdot u[x_n \cdot \Delta x_n] + A \quad (8')$$

$$x_{n+1} = x_n + \Delta x_{n+1} \quad n=0, 1, 2, \dots,$$

where $\alpha'\varepsilon = \alpha$, $A'\varepsilon = A$, $\alpha > 0$, $\varepsilon > 0$. Notice, as pointed out by Hadelar, that this way of discretizing the differential equation is by no means unique. Although the first order difference Eq. (8) and the second order difference Eq. (8') can be interpreted as defining dynamical systems on the real line (via the map $\varphi: \mathbb{R} \rightarrow \mathbb{R}$ and $\varphi': \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R} \times \mathbb{R}$, respectively), the biological situation requires x to be interpreted as an angular coordinate, i.e. is to be understood mod 2π with the convention $-\pi \leq x < \pi$. More precisely Eq. (8') defines a dynamical system with a periodic coordinate in the following sense: the state space is $S \times \mathbb{R}$, i.e. $[x_n, \Delta x_n]$: the first equation (in 8') is in \mathbb{R} ; Δx_n is real and $x_n \in [-\pi, +\pi]$; the second equation is to be understood mod 2π ($-\pi \leq x_{n+1} < +\pi$). Equation (8) may be interpreted in a similar way. In this sense we will be able to define with Eq. (8) a dynamical system on S (via the map $\Phi: S \rightarrow S$) and with Eq. (8') a dynamical system on $S \times \mathbb{R}$ (via the map $\Phi': S \times (\mathbb{R} \rightarrow S \times \mathbb{R})$). The interpretation of Eqs. (8) and (8') as dynamical systems on the circle introduces in general a number of complications. They are not, however, relevant neither for the biological situations nor for the analysis of this paper. We could in fact restrict our mathematical analysis to the dynamical systems defined by Eq. (8') on the real line. We chose, however, to consider in Theorem 1 the coordinate to be cyclical in the above sense. We avoid most of the complications by restricting our parameter values [for Eq. (8')] in such way that $\Delta x_n < \pi$, from some n . Corresponding restrictions for Eq. (8) could be $A/\alpha < \pi$ and $\alpha < 1$ (then $\Delta x_n < 2\pi$).

Whereas Eq. (7) is a well known linear retarded functional differential equation, Eq. (7') is more pathological in several respects, even when it is considered as a dynamical system on the real line. It is a

neutral equation (with delay in the derivative), containing the non continuous function $u[\]$. Standard results in the theory of functional differential equations cannot be directly used to characterize completely the behavior of Eq. (7') (see, for instance, Hale, 1977). Notice that Eq. (6) (with $\varepsilon \neq 0$) is also a neutral equation.

The situation is quite different for the difference Eq. (8) and (8'), which will be analyzed in the next section. Properties of the Eqs. (7') and (8') will be compared by means of computer simulations. It turns out that the biologically relevant properties of the difference equation are also valid for the differential equation.

2. Mathematical Analysis

2.1. Main Results for the Difference Equations

The dynamical system defined by Eq. (8) on the real line (instead of the circle) is well known. For small enough delays, the solution decays "exponentially" to the equilibrium value $\hat{x} = A/\alpha$ for all initial conditions.

With the restrictions $\left| \frac{A}{\alpha} \right| < \pi$ and $\alpha < 1$ the corresponding dynamical system on the circle behaves in basically the same way, since, if

$$|x_n| < \pi, \quad |x_{n+1}| = |x_n - \alpha x_n + A| < \pi.$$

We start from a few instructive facts about the function $f: R \rightarrow R$ defined by [compare Eq. (8')]

$$f(x_n, x_{n+1}) = -\alpha x_{n+1} \cdot u[x_{n+1} \cdot (x_{n+1} - x_n)] + x_{n+1} + A. \quad (9)$$

Lemma. a) If $A=0$ every state (x, x) is a stationary state, i.e. $f(x, x) = x$.

b) If $A \neq 0$ there is no stationary state, i.e. $f(x, x) \neq x$ for every x .

c) If $A \neq 0$ there exists only 2 numbers $\hat{a}, \hat{b} \in [-\pi, \pi)$ with $\hat{a} \neq \hat{b}$ such that $f(\hat{a}, \hat{b}) = \hat{a}$, $f(\hat{b}, \hat{a}) = \hat{b}$. The two numbers are $\hat{a} = 2A/\alpha$, $\hat{b} = 2A/\alpha - A$.

In a certain sense these properties suggest that Eq. (8') with $A=0$ is not "structurally stable". Equation (8) is immune from this singularity.

We prove now the following theorem for the dynamical system defined by Eq. (8') on the circle (see Sect. 1.2).

Theorem. We assume $2A/\alpha < \pi$. Then, if $1 \leq \alpha < 2$ Eq. (8'), defined on the circle, has a global stable attractor with period 2, namely (\hat{a}, \hat{b}) . If $0 < \alpha < 1$ in addition to the attractor (\hat{a}, \hat{b}) some trajectories approach asymptotically (only from below) the value $\hat{c} = A/\alpha$, although

\hat{c} is not a stationary state. This artefact can be removed by a small perturbation of the function $u[\]$ in Eq. (8').

Proof. We only sketch the main points of the proof. We assume $A > 0$, since the argument for $A < 0$ is equivalent. Since $2A/\alpha < \pi$ and $\alpha < 2$, it follows that $A < \pi$. If for some n , $\Delta x_n < 0$ Eq. (8') implies that $\Delta x_{n+1} > 0$, where Δx_{n+1} is interpreted as a real number (and not mod 2π). Thus there always exists a n for which $\Delta x_n > 0$; then $|\Delta x_{n+1}| < \pi$. In the following, therefore, we choose n such that $\Delta x_n > 0$. We distinguish between $\alpha < 1$ and $\alpha \geq 1$.

$$0 < \alpha < 1$$

The 1-D coordinate space is divided into four regions:

$$\mathcal{A} = \{x: \pi > x > 3A/\alpha\}$$

$$\mathcal{B} = \{x: 3A/\alpha > x > A/\alpha\}$$

$$\mathcal{C} = \{x: A/\alpha > x > 0\}$$

$$\mathcal{D} = \{x: 0 \geq x \geq -\pi\}.$$

Observe that \mathcal{A} may be empty if A/α large. We consider now the fate of the coordinate point depending on its location at time n .

Case \mathcal{A}

If $x_n \in \mathcal{A}$, $x_{n+1} = x_n - \alpha x_n + A$ and $x_{n+2} = x_{n+1} - \alpha x_{n+1} + 2A$. Thus $x_{n+2} \in \mathcal{D}$ or \mathcal{B} (because x modulus 2π) and $\Delta x_{n+2} > 0$.

Case \mathcal{D}

If $x_n \in \mathcal{D}$, $x_{n+1} = x_n + A$. Thus at the next time point $\Delta x > 0$ and $x \in \mathcal{D}$ or \mathcal{C} . There is some $m > n$ at which $x_m \in \mathcal{C}$, $\Delta x_m > 0$.

Case \mathcal{C}

If $x_n \in \mathcal{C}$ then

$$x_{n+1} = x_n - \alpha x_n + A, \quad \Delta x_{n+1} = -\alpha x_n + A > 0.$$

Thus x , increases monotonically, approaching (exponentially bounded) the limit $\hat{x} = A/\alpha$. This value is an attractor but only from below. It is not stable for arbitrarily small perturbations. We can remove this artificial singularity defining instead of $u[\]$ the function

$$u_\varepsilon[x] = 1 \quad \text{if } x > \varepsilon,$$

$$u_\varepsilon[x] = 0 \quad \text{if } x \leq \varepsilon.$$

Then for ε arbitrarily small ($\varepsilon > 0$), there exist n such that $x_n(x_n - x_{n-1}) < \varepsilon$ determining $x_{n+1} = x_n + A$ at which point the barrier is crossed and $x_{n+1} \in \mathcal{B}$.

Case \mathcal{B}

If $x_n \in \mathcal{B}$ then writing $x_n = \hat{a} + \eta$ with $\hat{a} = 2A/\alpha$, $|\eta| < A$ one obtains, since the condition $2A/\alpha < \pi$ ensures that $x_{n+1} < \pi$,

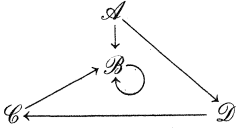
$$x_{n+2} = \hat{a} + (1-\alpha)\eta, \quad x_{n+2} \in \mathcal{B}, \quad \Delta x_{n+2} > 0.$$

Thus the subsequence $x_{2n} = a_n$ if in \mathcal{B} remains in \mathcal{B} , approaching the limit $\hat{a} = 2A/\alpha$ according to

$$a_{n+1} = a_n + (2A - \alpha a_n).$$

Correspondingly, the sequence $b_n = x_{2n+1}$, approaches the limit $2A/\alpha - A = \hat{b}$.

Thus, once in \mathcal{B} , the coordinate point remains there, asymptotically oscillating between \hat{a} and \hat{b} . Once removed the singularity in \mathcal{C} (at $x = A/\alpha$), \mathcal{B} is a global attractor, in the sense that all trajectories end up in \mathcal{B} irrespectively of initial conditions. The following diagram summarizes some of the results, illustrating the ("asymptotic") "transition path" for the sequence a_n ($0 < \alpha < 1$):



$$1 \leq \alpha < 2$$

The 1-dimensional coordinate space is now divided into 5 regions:

$$\mathcal{A} = \{x: x \geq 3A/\alpha\}$$

$$\mathcal{B}'' = \{x: 3A/\alpha > x > 2A/\alpha\}$$

$$\mathcal{B}' = \{x: 2A/\alpha \geq x > A/\alpha\}$$

$$\mathcal{C} = \{x: A/\alpha > x > 0\}$$

$$\mathcal{D} = \{x: 0 \geq x \geq -\pi\}.$$

Case \mathcal{D}

If $x_n \in \mathcal{D}$ there is some m such that ($m > n$)

$$x_m \in \mathcal{B}' \text{ or } \mathcal{B}'', \quad \Delta x_m > 0.$$

Case \mathcal{A}

If $x_n \in \mathcal{A}$ then $x_{n+2} \in \mathcal{B}'$ or \mathcal{D} .

Case \mathcal{C}

If $x_n \in \mathcal{C}$, $x_n = 2A/\alpha + \eta - A/\alpha > \eta \geq -2A/\alpha$

$$\Delta x_{n+1} = -\alpha x_n + A > 0$$

$$x_{n+1} = x_n - \alpha x_n + A = (1-\alpha)x_n + A, \quad A/\alpha < x_{n+1} < 2A/\alpha$$

and for $1 \leq \alpha < 2$, $x_{n+1} \in \mathcal{B}'$, $\Delta x_{n+1} > 0$.

Case \mathcal{B}'

If $x_n \in \mathcal{B}'$, $x_n = 2A/\alpha + \eta$, $0 > \eta > -A/\alpha$

$$\Delta x_{n+1} = -\alpha x_n + A = -2A/\alpha + \alpha|\eta| + A \leq 0.$$

Thus $x_{n+2} = \hat{a} + (1-\alpha)\eta$, $x_{n+2} \in \mathcal{B}'$ and $\Delta x_{n+2} > 0$ and $a_n = x_{2n}$ approaches, if $|1-\alpha| < 1$, asymptotically $\hat{a} = 2A/\alpha$, while the sequence $b_n = x_{2n+1}$ approaches $\hat{b} = 2A/\alpha - A$.

Case \mathcal{B}''

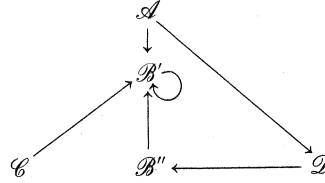
If $x_n \in \mathcal{B}''$, $x_n = 2A/\alpha + \eta$, $0 < \eta < A/\alpha$

$$\Delta x_{n+1} = -\alpha x_n + A < -2A/\alpha + A = -A < 0.$$

Thus $x_{n+2} = a + (1-\alpha)\eta$ and $A/\alpha < x_{n+2} < \hat{a}$, implying that

$$x_{n+2} \in \mathcal{B}' \text{ and } \Delta x_{n+2} > 0.$$

Thus \mathcal{B}' is an attractor region for the sequence $a_n = x_{2n}$. The transition graph for the sequence a_n is (for $1 \leq \alpha < 2$)



Remarks. (a) Theorem 1 can be extended to the case in which x is not an angular coordinate. The corresponding dynamical system is then defined by a map $\varphi': \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R} \times \mathbb{R}$ [from Eq. (8')]. In this case the upper bounds of regions \mathcal{A} and \mathcal{D} change to $+\infty$ and $-\infty$, respectively (region \mathcal{A} can actually merge with \mathcal{B}). The (asymptotic) transition $\mathcal{A} \rightarrow \mathcal{D}$ disappears. The stability condition $0 < \alpha < 2$ is then the same as for Eq. (8) (on the real line).

(b) The asymptotic behavior of Eq. (8') is the same as of Eq. (8) under a smoothing operation over 2 time units [the equilibrium value is, however, different, being $(2A/\alpha - A/2)$ vs. A/α for the "classical" equation]. The transient behavior, if smoothed, is mostly but not always the same, depending on the initial conditions (for $\alpha < 1$ it is the same if $x \in \mathcal{A} \cup \mathcal{B}$; it is not the same if $x_0 \in \mathcal{D}$). The period of the asymptotic oscillation is 2.

(c) The peak-to-peak amplitude of the asymptotic oscillations [in Eq. (8')] is A and is in turn proportional to the average x value $(2A/\alpha - A/2)$. The oscillation amplitude can be made arbitrarily small with small A .

2.2. Numerical Results

All numerical simulations of Eqs. (8) and (8') have been performed with angular coordinates. For the parame-

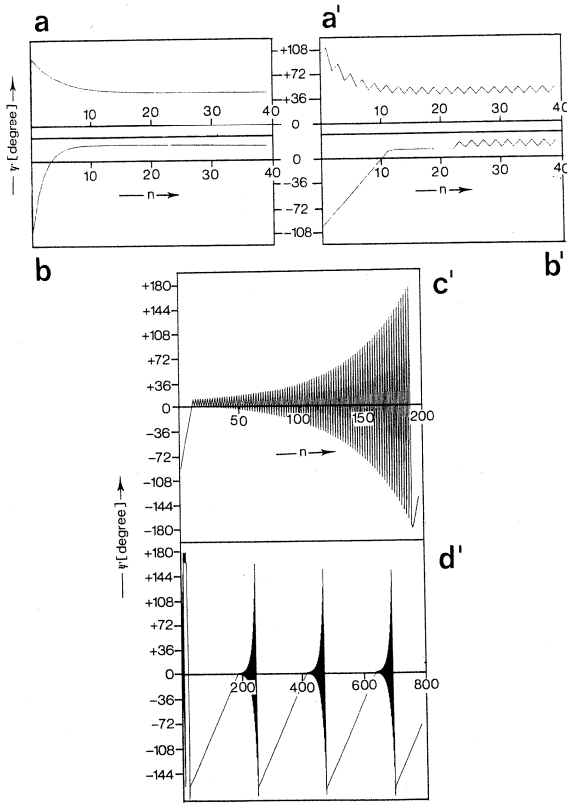


Fig. 1a-d. Comparison of the difference equations Eq. (8) – the usual equation – and Eq. (8') – the progressive-regressive equation. The figures with primed letters show simulations with the latter equation. In **a** $\alpha=0.2$, $x_0=100^\circ$, $A=10^\circ$; in **a'** $\alpha=0.4$, $x_0=100^\circ$. In **b** $\alpha=0.4$, $x_0=-100^\circ$, $A=10^\circ$; in **b'** $\alpha=0.8$, $x_0=-100^\circ$. In **c** $\alpha=2.02$, $x_0=-100^\circ$, $A=10^\circ$. **d'** is the same as **c'** on an extended time scale; it is the only case shown here where the angular coordinate plays a role. In the case of Eq. (8') the initial condition includes $x_1=x_0$. See text

ters and initial conditions used in the examples shown here, the cyclic coordinate does not play any role with the exception of Fig. 1d'.

Numerical simulations of the difference Eqs. (8) and (8') are shown in Fig. 1 to illustrate some of the

analytical results of the previous section. The asymptotic and the transient behavior of the subsequence a_n [for Eq. (8')] is equivalent to the solution of Eq. (8), because the initial condition does not lie in \mathcal{C} or \mathcal{D} (Fig. 1a'). Figure 1b shows that when x_0 lies in \mathcal{D} , the transient behavior of Eq. (8'), which is determined only by the constant A , differs from the initial transient of Eq. (8), dominated by the value of α . The unstable equilibrium at the \mathcal{C} - \mathcal{B} boundary, which exists for $\alpha < 1$, is approached faster for larger α . The "stability" condition $\alpha < 2$ is valid for both equations: Fig. 1c' and 1d' show a case in which the solution is unstable.

Computer simulations (with a simple Euler integration algorithm, checked by making the integration steps ten times smaller) suggest that the differential equation shows a behavior similar to the difference equation. Figure 2 summarizes the main results. The transient and asymptotic behavior of the differential equations are equivalent to the difference equations (Fig. 2a, b). The computed solution of Eq. (7) oscillates around $(2A/\alpha \pm A\varepsilon/2)$, whereas the asymptotic value for Eq. (7') is A/α . Thus, in the differential equation case, averaging over 2 time units the asymptotic trajectory of Eq. (7') seems to provide the solution of the classical Eq. (7) with $\alpha/2$ [to compensate for the fact that the "force function" $\alpha\psi$ is active in Eq. (7) only half of the time, asymptotically].

From the biological point of view it is interesting to know how the two equations behave when the constant A is substituted by a sample function of a gaussian process $N(t)$ (Poggio and Reichardt, 1973). Figures 2c and 2c' compare the equation

$$\dot{\psi}(t) = -\alpha\psi(t-\varepsilon) \cdot u[\psi(t-\varepsilon) \cdot \dot{\psi}(t-\varepsilon)] + N(t) \quad (10)$$

with the "classical" equation

$$\dot{\psi}(t) = -\alpha\psi(t-\varepsilon) + N(t), \quad (11)$$

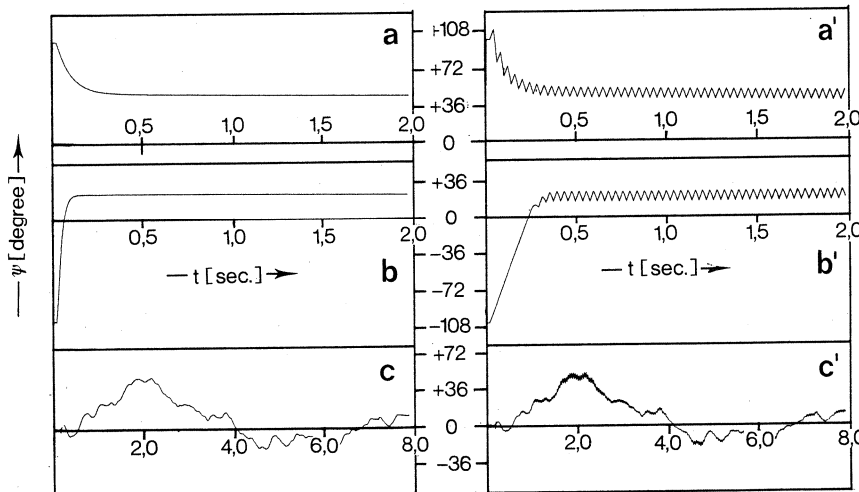


Fig. 2a-d. Comparison of the differential equations Eq. (7) – the usual equation – and Eq. (7') – the progressive-regressive equation. The figures with primed letters show simulations with the latter equation. In **a** $\alpha'=10$, $\psi(0)=100^\circ$, $A'=500^\circ/\text{s}$, $\varepsilon=0.02 \text{ s}$. In **a'** the parameters are the same, apart $\alpha'=20$. In **b** $\alpha'=20$, $\psi(0)=100^\circ$, $A'=500^\circ/\text{s}$, $\varepsilon=0.02 \text{ s}$. In **b'** parameters are the same apart $\alpha'=40$. In **d** $\alpha'=10$, $\psi(0)=0^\circ$, $A'=0^\circ/\text{s}$, $\varepsilon=0.02 \text{ s}$; a low-pass noise term is added. In **d'** parameters are the same apart $\alpha'=20$; again a low-pass noise term is added. In the case of Eq. (7') the initial condition includes $\psi(t)=\psi(0)$, $0 \leq t < \varepsilon$. See text for more details

where $N(t)$ has been generated by low-pass filtering a gaussian "white-noise" process. As expected, the solution of Eq. (11) is a smoothed version (over the oscillation period, i.e. 2ϵ) of the solution of Eq. (10), with twice α . Notice that in all these simulations the amplitude of the asymptotic oscillations increases with increasing ψ values (see remark c) in the previous section).

The criteria for stability of the solutions are of course different: in the case of Eq. (7) defined as a dynamical system on the real line, stability is ensured if $\alpha\epsilon < \frac{\pi}{2}$. Numerical simulations suggest that the same condition is sufficient but not necessary to ensure practical "stability" for the solutions of Eq. (7').

It is finally interesting to ask whether modifications of Eq. (7') still yield the same characteristic (asymptotically oscillatory) behavior. Assume, for instance, that the response to regressive movement is not zero, although smaller than for progressive movement. This hypothesis may be translated into the equation

$$\dot{\psi}(t) = -\alpha\psi(t-\epsilon) \cdot u\{\psi(t-\epsilon) \cdot \dot{\psi}(t-\epsilon)\} + \alpha^*\psi(t-\epsilon) \cdot u\{-\psi(t-\epsilon) \cdot \dot{\psi}(t-\epsilon)\} + A \quad (12)$$

with $\alpha > \alpha^* > 0$.

Observe that progressive and regressive responses follow the motion (i.e. have the same sign as $\dot{\psi}$).

Figure 3a shows that Eq. (12) has, with $\alpha^* = \alpha/2$ again the same qualitative behavior, with a larger oscillation amplitude, as intuitively expected. Computer simulations suggest that other more complex versions of Eq. (7') still show the same asymptotic oscillation, as long as there is an asymmetry in the "force term" $\alpha\psi$ for progressive vs. regressive movement. More accurate description of the fly's reaction should, for instance, take into account that the fly's reaction also depends on the speed $\dot{\psi}$ of the stimulus. For instance, as suggested by Hausen, the fly response may grow proportionally to $\dot{\psi}$ up to a certain value of $\dot{\psi}$. This leads to

$$\dot{\psi}(t) = -\alpha\psi(t-\epsilon)\sigma(|\dot{\psi}|) \cdot u\{\psi(t-\epsilon) \cdot \dot{\psi}(t-\epsilon)\} + A, \quad (13)$$

where $\sigma(|\dot{\psi}|) = |\dot{\psi}|$ for $|\dot{\psi}| \leq |\dot{\psi}_c|$ and $= |\dot{\psi}_c|$ for $|\dot{\psi}| > |\dot{\psi}_c|$.

Figure 3b shows that the behavior of Eq. (13) is again similar, although the oscillation pattern is somewhat more complicated. Notice that asymptotic oscillations are present also when the u function is dropped altogether in Eq. (13).

The "equivalence" over a coarse time scale between Eqs. (7) and (7') seems to apply also for the case in which a more complex function than $\alpha\psi$ is used, as for instance, the function $D(\psi)$ (Reichardt, 1973; Poggio and Reichardt, 1973) associated with the fly's reaction to one or more stripes.

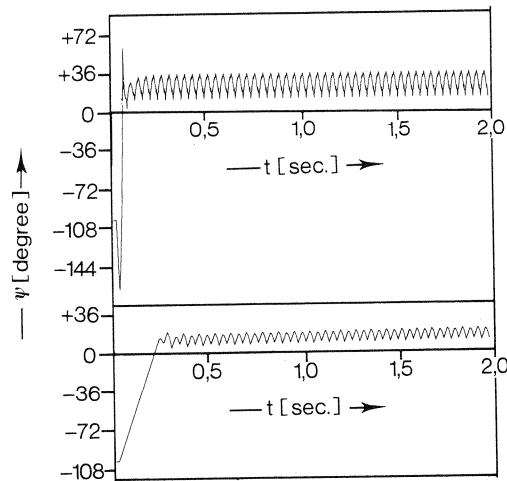


Fig. 3a and b. In a the equation simulated is Eq. (12) with $\alpha' = 40$, $\psi(0) = 100^\circ$, $A' = 500^\circ/\text{s}$, $\epsilon = 0.02$ s. Equation (13) is simulated in b, where $\dot{\psi}_c = 2000^\circ/\text{s}$, $\alpha' = 0.2$, $A' = 500^\circ/\text{s}$, $\epsilon = 0.02$ s, $\psi(0) = -100^\circ$

2.3. Simulations of 3-D Chases and Landings

Evidence has been accumulating in recent years that Eq. (3) represents the starting point for a successful description not only of the closed loop fixation and tracking experiments but also of free flight chases between flies and landing of a fly on a target (Land and Collett, 1974; Reichardt and Poggio, 1980; Bühlhoff et al., 1980 and in preparation; Wagner, 1980). Figure 4 and 5 show 3-D simulations of the trajectory of the chases between *Musca* flies shown on the top of Figs. 4a and 5a, respectively, from the trajectory of the leading fly. The set of equations used for the simulation is based on

$$k\dot{\alpha}_f(t) = -D[\psi(t-\tau_1)] + r\dot{\psi}(t) \quad (14a)$$

for the torque, with α_f being the horizontal angle of the fly

$$\eta\dot{z}(t) = -L[\vartheta(t-\tau_2)] + s\dot{\vartheta}(t) \quad (14b)$$

for the lift, with ϑ being the vertical error angle and z the vertical coordinate;

$$h v_{xy}(t) = -T[\varrho(t-\tau_3)] \quad (14c)$$

for the thrust, with ϱ being the 3-D distance between the chasing fly and the leading fly and v_{xy} the forward velocity on the xy plane. Notice that the equations are coupled [$\psi(t)$ for instance depends on the coordinates of the leading fly at time t and the coordinate of the chasing fly at time t]. Input to the equations are the xyz coordinates of the leading fly. With initial conditions given by the first τ_3 seconds of the true trajectory of the chasing fly, Eq. (14) reconstruct the rest of the trajectory. $\dot{\alpha}$, \dot{z} and v_{xy} determine at each t the "new" xyz coordinates of the chasing fly. More

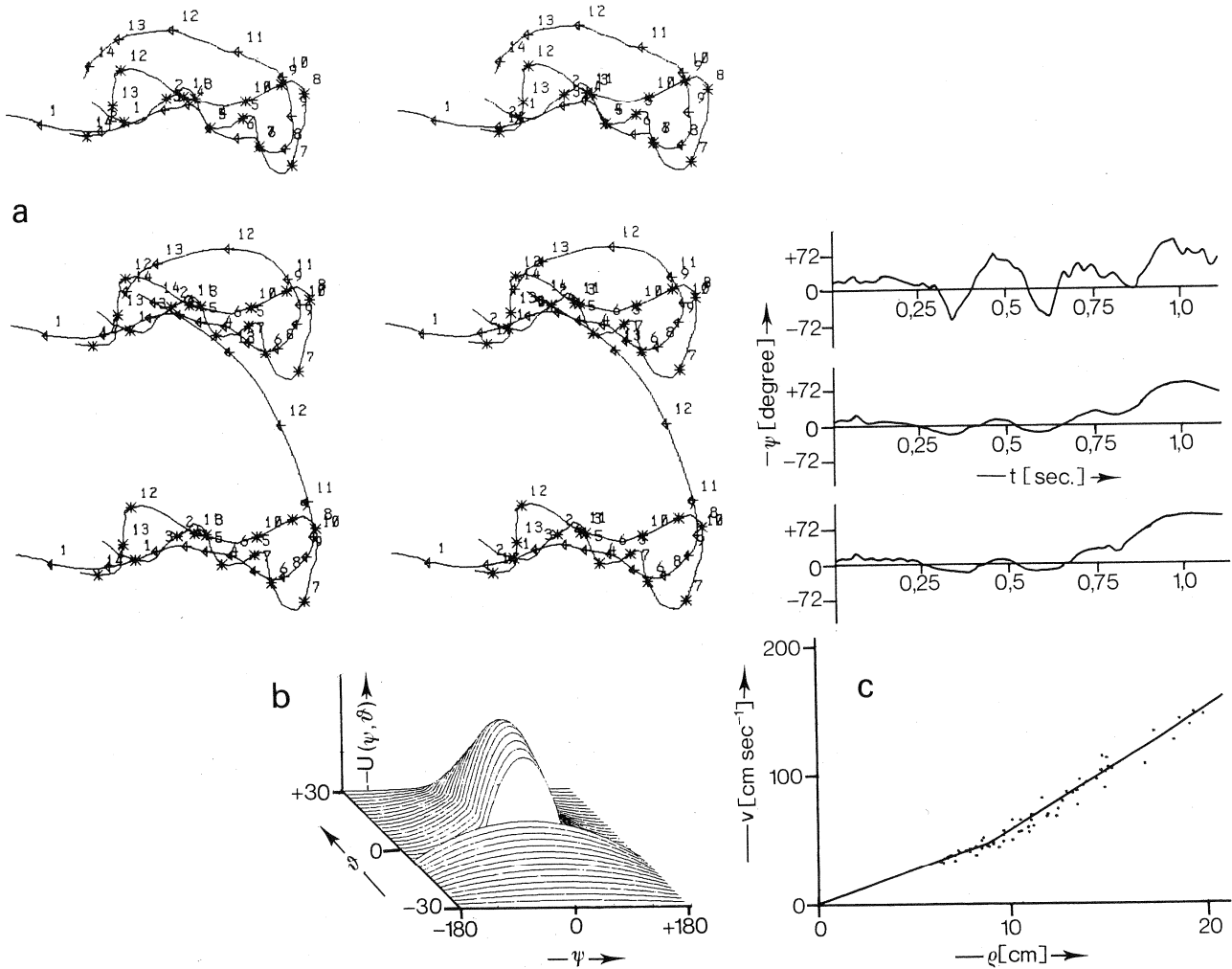


Fig. 4a-c. A stereo plot of a 3-D chase between flies *Musca domestica* is shown in the top of **a**. It should be observed with standard stereoglasses. The middle figure shows a simulation of the same chase according to an algorithm based on Eq. (14). The algorithm computes from the xyz coordinates of the leading fly (*) and of the chasing fly (Δ) the future torque, lift, and thrust of the chasing fly, translates them into angular velocity, vertical velocity and forward velocity and integrates them into a 3-D trajectory. The bottom figure is another simulation with Eq. (15a) instead of Eq. (14a). 1 cm corresponds to 16 cm in space (see also Reichardt and Poggio, 1980). The parameter values used for this simulations are $k = 0.0031 \text{ g} \cdot \text{cm} \cdot \text{s}^{-1}$, $r = 0.001 \text{ cm}^2 \cdot \text{s}^{-1}$, $\tau_1 = 20 \text{ ms}$, $\eta = 0.5 \text{ g} \cdot \text{cm}^{-1}$, $s = 0.0001 \text{ g} \cdot \text{cm} \cdot \text{s}^{-1}$, $\tau_2 = 60 \text{ ms}$, $h = 1 \text{ g} \cdot \text{cm}^{-1}$, $\tau_3 = 40 \text{ ms}$. The insets on the right show $\psi(t)$. Notice the (slight) oscillatory behavior of $\psi(t)$ in the “progressive” simulation. **b** shows the “potential” $U(\psi, \theta)$, used to compute torque and thrust from the error angles ψ and θ respectively. The simulations shown could be improved by better parameter fitting. **c** shows the scatter diagram between 3-D velocity v and distance ρ for the middle simulation (delay = 70 ms). The continuous line corresponds to the function $T(\rho)$ used in this simulation.

details about the methods used for the 3-D computer analysis and their limitations can be found in Bulthoff et al. (1980, and in preparation).

The specific parameter values and functions $D(\psi)$, $L(\theta)$, $T(\rho)$ used for the simulation are inferred from experimental data (Reichardt, 1973; Wehrhahn and Reichardt, 1975; Wehrhahn, 1978; Bulthoff et al., in preparation; Wagner, unpublished) and are given in the legend. Figure 4 shows the “potential” $-U(\psi, \theta)$ used in the simulation

$$D_s(\psi) = \frac{\partial U(\psi, \theta)}{\partial \psi}, \quad L_\psi(\theta) = \frac{\partial U(\psi, \theta)}{\partial \theta}$$

and Fig. 4c shows the function $T(\rho)$. In a similar way Figs. 5b, 5c, and 5d show the functions used in the simulation of the chase shown in Fig. 5a, top.

The core of the simulation is represented by Eq. (14a), corresponding to our normal Eq. (6). The basic equivalence between Eqs. (5) and (6) suggests that the simulation should be also successful in the case of the progressive hypothesis. This corresponds to substituting Eq. (14a) with

$$k\dot{\alpha}(t) = -D[\psi(t - \tau_1)] \cdot u[\psi(t - \tau_1)\dot{\psi}(t - \tau_1)] + r\dot{\psi}(t). \quad (15a)$$

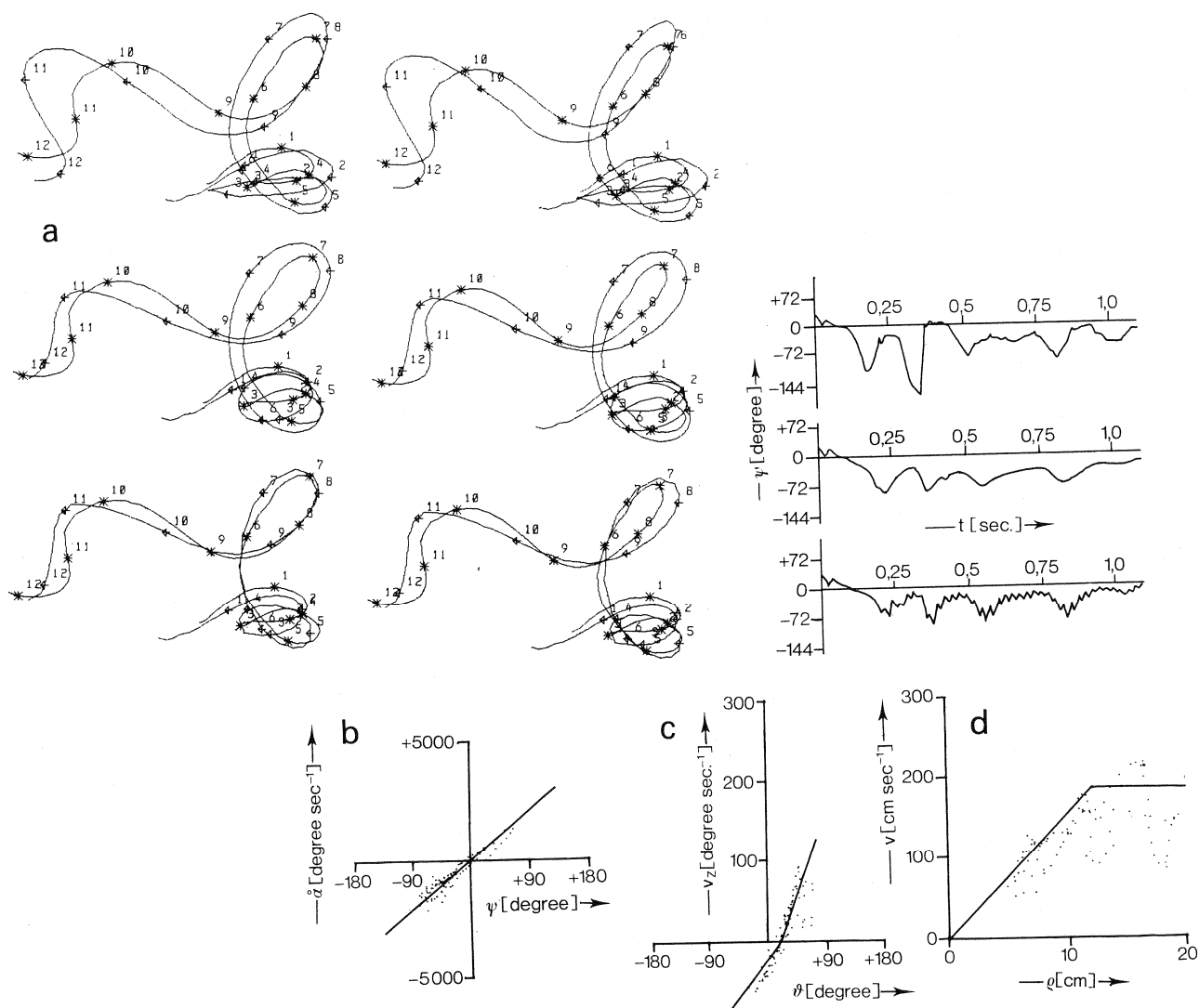


Fig. 5 a Another stereoplot of a chase between *Musca* males (top). The middle figure shows a simulation according to the "normal" Eq. (14) and the bottom figure shows another simulation according to the "progressive" Eq. (15a) [instead of Eq. (14a)]. The scale is the same as in a. The insets on the right show $\psi(t)$. The "progressive" simulation shows a clear oscillatory behavior. The parameters used are as for Fig. 4, except $\tau_1 = 12.5$ ms. **b** A scatter diagram (with a delay of 12.5 ms) of the angular velocity $\dot{\alpha}_j$ of the chasing fly (proportional to the torque) vs. ψ for the middle simulation. The continuous line gives (modulus $1/k$) the $D(\psi)$ function assumed for the simulation. For the "progressive" simulation, the $D(\psi)$ used is twice as large, to compensate for the lack of response during regressive movement of the target's image. **c** A scatter diagram (with a delay of 50 ms) of the vertical component of the velocity of the chasing fly vs. the angle θ for the (middle) simulation. The continuous line corresponds to the $L(\theta)$ used in the simulation (modulus the parameter η). **d** A scatter diagram of the forward 3-D velocity of the chasing fly vs. the distance between the two flies (with a delay of 80 ns), for the (middle) simulation. The continuous line corresponds to the function $T(\rho)$ used in the simulation. The chase has been filmed by Wehrhahn and will be analyzed in details in a forthcoming paper (Bülthoff et al., in preparation)

The lower portions of Figs. 4a and 5a show that the resulting simulations (otherwise with the same parameters) are indeed satisfactory. Notice that we don't imply that males *Musca* use this control system during chasing. It is possible, in fact, that the chasing system is more similar to Eq. (14a) than to Eq. (15a). We merely want to show the adequacy of a progressive-regressive control system to achieve successful tracking and to illustrate its properties. The oscillatory behaviour of $\psi(t)$ with a period which equals twice the delay is clear

also in this more complex situation. We have neglected, in these simulations, the additional term $N(t)$, representing (Reichardt and Poggio, 1976), in a stochastic sense, the "free will" of the fly. Various simulations have shown that $N(t)$ (with physiological parameter values) may often affect the simulated trajectories, even in a "qualitative" sense. We have, for instance (with Wagner) examples in which the term $N(t)$ may change a successful landing on an object into a "near miss". Trajectories in landing situations are

much more affected than trajectories in “chasing” cases.

It must be stressed that these 3-D simulations assume that the fly has only 3 degrees of freedom (the fly is treated as a point in space), short of the 6 degrees of freedom available to a rigid body. In addition, head and legs movements are neglected. Figure 5a, for instance, suggests that although the simulation may be improved by better parameter fitting, its shortcomings lie in the approximation of the fly as a point.

The model described here only refers to the smooth control system involved in chasing. The role of saccades will be discussed elsewhere (Bülthoff et al., in preparation; Wehrhahn, in preparation).

3. Discussion

3.1. Main Results

The main result of this paper is the demonstration that the two control systems described by the normal Eq. (6) and by the progressive-regressive Eq. (6') are in a certain sense equivalent on a smooth time scale [i.e. a time resolution which is long compared with the fly's reaction delay (20–40 ms)]. This is encouraging because it validates for this particular case the more general derivation of Eq. (4) by Poggio and Reichardt (1973). The equivalence suggests that the theoretical results obtained for Eq. (4) can be used also to describe approximately, on a coarse time scale, a control system of the type of Eq. (6).

In addition we have shown that solutions of either Eq. (7') or Eq. (8') always have a characteristic asymptotic oscillatory behavior with a period that depends on the delay. This is the main difference on a fine time scale between the “classical” Eq. (7) and the “progressive” Eq. (7'). In the following, we discuss in more detail some implications of the results of this paper.

3.2. Control Systems for Fixation and Tracking: Implications

In a future paper we hope to discuss control systems for fixation and tracking from a general point of view, characterizing theoretically some of them within the universe of known tracking systems. In this section we only mention some implications of the results of this paper from the point of view of guidance systems.

Equation (2) describes the bones of what is the simplest and most used control system for tracking a target. A term depending on the error angle directly determines the correcting output of the system (in the fly's case its torque, roughly proportional to the result-

ing angular velocity). The resulting position control [see for instance Eq. (5)] can be exhaustively characterized, even for stochastic inputs.

In the simple, 1-dimensional framework described by Eq. (2) position control is needed to achieve successful tracking. For instance, simple proportional navigation corresponding to

$$\mathbb{R}_t\{\psi(s)\} = r\dot{\psi}(t - \varepsilon)$$

cannot achieve asymptotic stable tracking of targets moving at constant angular velocity. This statement can be detailed in the following terms. If $\varepsilon = 0$ and the stochastic term $N(t)$ replaces A , Eq. (2) suggests

$$[k + r(\psi)]\dot{\psi}(t) = N(t) \quad r(\psi) > 0, \quad k > 0,$$

where $N(t)$ is a white gaussian process with spectral density $2D$ and $r(\psi)$ describes the ψ dependent optomotor (proportional) control. The asymptotic probability distribution of the error angle can be found to be (interpreting the equation as a Stratonovich and not as an Ito equation)

$$P(\psi) \propto \frac{r(\psi)}{D}$$

and may therefore show a maximum for $\psi = 0$ [if $r(\psi)$ is maximum there]. This behavior may be characterized as pseudofixation. Observe now that if the target drifts with angular velocity proportional to δ the resulting equation

$$[\kappa + r(\psi)] \cdot \dot{\psi}(t) = N(t) + \delta$$

leads to an average slip speed $|\dot{\psi}|$ larger than 0. The situation may be different if translation effects are not negligible. In this case proportional control can effectively control a pursuer homing on a target.

The control system Eq. (6') is therefore quite interesting because position information is critically controlled by movement information (for instance, when $\dot{\psi} = 0$ the reaction R is zero for every position ψ). It has been long realized that asymmetric movement detection, parametrized by position, can provide the necessary position information, which is required for tracking [see, for instance, Reichardt (1973) and Poggio and Reichardt (1973), p. 198]. The results of this paper make in fact explicit the basic equivalence between the two control systems. On a coarse time scale the progressive control system reduces to the classical position control system. On a very fine time scale the progressive system shows a new asymptotic oscillatory behavior. It seems likely that these conclusions hold for a wide class of control systems of the same basic type. Thus, we conjecture that for control systems in which position information is at least in part mediated (with a delay), by differences between

reactions to progressive and regressive motion the following 2 properties hold

- a) there is a characteristic asymptotic oscillatory behavior (possibly of small amplitude) with half period in the order of the system's effective delay;
- b) there is an (asymptotic) equivalence with the corresponding "classical" position controlled system, if the trajectory $\psi(t)$ is smoothed over time intervals in the order of twice the system's delay.

Several questions remain open. For instance, it is not clear to what extent and in which sense the differential equation (7') is more stable for large delays than the classical differential equation (7). From a more general prospective, it remains to compare the two types of control in terms of optimal strategies (differential games) for the pursuer. It is also clearly interesting to characterize control systems which are a mixture of Eqs. (6) and (6'). We hope to analyze these problems in a future paper.

3.3. The Fly's Control of Flight: Experimental Predictions

The main biological implication of the analysis is that most tracking and fixation experiments performed so far and successfully described by equations of the type of Eqs. (5) or [(4) with $\varepsilon=0$] (see Reichardt and Poggio, 1980) are consistent with a progressive-regressive control system [as Eq. (6')], since on the time scale usually involved the two control systems are indistinguishable.

In addition, we predict that the spectrum of $\psi(t)$ should show a strong peak at a frequency of around $f=1/2\varepsilon$, whenever a progressive control system is involved to a significant extent. There are several reasons that could make the detection of such an oscillation quite hard, like for instance intrinsic variability in the delay ε . The period of the oscillation may also depend significantly on the specific dynamics of the response of the fly. On the whole, however, it seems difficult to escape the conclusion that a progressive-regressive control system must show an oscillatory behavior in the error angle $\psi(t)$ (and in the fly's torque)².

In this connection, it is important to realize that a simple progressive-regressive description like Eq. (7') cannot be expected to hold strictly for those ψ values that represent a region of binocular overlap between the two eyes. Therefore, oscillations in $\psi(t)$ (or in the

fly's torque) should be better searched outside the region of binocular overlap. In addition our analysis shows that the amplitude of the oscillations increases with A and therefore with the average offset. As a consequence, optimal closed loop conditions to detect progressive-regressive oscillations require a) tracking and not fixation experiments, b) target's velocity as high as stable tracking allows (see Reichardt and Poggio, 1976). Interpretation of eventual experimental oscillations will require some care, since the normal Eq. (7) can also be expected to produce oscillations, though not asymptotically, if the delay is not negligible.

Computer based analysis of free flight episodes may also reveal whether these predictions are valid for tracking *Musca*³ (Bülthoff et al., in preparation).

3.4. Conclusions

It is clear that the problem of the detailed control system used by the fly is essentially a problem at the level of the neural algorithms and mechanisms responsible for the transduction between visual stimuli and torque output. The basic equivalence of the classical and progressive control systems as judged from the "trajectory" $\psi(t)$ shows in fact that it is not easy to distinguish between these control mechanism only on the basis of phenomenological observations of closed loop situations (either in the laboratory or in free flight).

In addition, a flicker based control system that depends on $|\dot{\psi}|$ may be equivalent to a form of "progressive" control system and show asymptotic oscillations. Open loop experiments aimed at the underlying mechanism (behavioral and physiological) are more likely to provide a clear cut answer to the question (Wehrhahn and Hausen, 1980; Hausen and Wehrhahn, in preparation; Geiger, in preparation). This difficulty of extrapolating from one level of understanding to another is common in the analysis of complex systems.

The critical problem is represented here by the time scale involved. The oscillations induced by a progressive control system take place on a time scale over which the torque produced by the fly may not be described as a continuous process. Its fine structure remains in any case to be analyzed on this time grain.

2 The amplitude of the oscillations certainly depends on the specific form of the progressive-regressive control system eventually used by the fly. Thus the oscillation amplitude may be much smaller than for the simple Eq. (8') studied in this paper

3 It is conceivable that male and/or female flies use in fact a mixture of (a) (formally) 1-input detectors and of (b) progressive-regressive asymmetric movement detectors in order to compute position information. The relative role of one mechanism versus the other one may for instance depend on the velocity $\dot{\psi}$ of the target. Whether this "flicker" effect may be related to the position dependent torque saccades detected in *Drosophila* during regressive stimuli (Heisenberg and Wolf, 1979) is of course an interesting possibility

Control systems like Eq. (6') act in an almost bang-bang way; the resulting oscillations could be interpreted in the limit as a series of saccadic "spikes". On the other hand, it is quite possible that the "open loop" torque itself has a "grained", "spiky" structure on this time scale. We may reach here the limits of a phenomenological description like Eq. (6'). At this point a more detailed analysis at the level of wing muscles and neurons is clearly needed and will lead to more accurate descriptions probably different from Eq. (6') or (6).

Unlike several biologists worrying about theory, one should appreciate that theories do not themselves provide definitive answers to biological questions. Mathematics is, after all, the science of all possible worlds. Models, like the ones analyzed in this paper, are useful tools for generating a chain of thoughts and experiments that might not otherwise have occurred. Their specific level of description and range of validity (like time scale) should always be kept in mind while applying them to a specific biological problem. In particular, terms in an equation do not have to correspond to specific neurons.

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