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Asymptotic Oscillations in the Tracking Behaviour of the Fly *Musca Domestica*

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Abstract. From recent theoretical work (Poggio and Reichardt, 1981), high frequency oscillations are expected in the angular trajectory of houseflies tracking a moving target if the target's retinal position controls the flight torque by means of a stronger optomotor response to progressive than to regressive motion. Experiments designed to test this conjecture have shown that (a) asymptotic non-decaying oscillations are found in the torque of female houseflies tracking targets moving at constant angular velocity; (b) the magnitude of the oscillations grows monotonically with mean retinal excentricity of the target; (c) the period of the oscillation is around 180–200 ms. The experimental findings are consistent with the hypothesis that a "progressive-regressive mechanism" plays a significant role in the tracking behaviour of female houseflies. From this phenomenological point of view a flicker mechanism that is active only for non-zero motion is equivalent to a progressive-regressive system. The relatively long period of the oscillation requires more complex reaction dynamics than a pure single dead-time delay. As a specific example we show that a model where the reaction to progressive motion is "sticky", holding for a longish time after the ending of the stimulus, is consistent with the experimental data.

1. Tracking in the Fly: A Prediction

Female houseflies are able to track moving targets and, in particular, other flies. An analysis of the control system used by the fly has revealed that its flight torque depends in a characteristic way on the angular position of the target's image on the eye (Reichardt, 1973). A quantitative theory can account for the fly's behaviour in a variety of situations (Reichardt and Poggio, 1976), including free flight chasing episodes.

The phenomenological theory leaves open the question of whether movement is necessary to mediate position information (but see Poggio and Reichardt, 1976). Recently Wehrhahn and Hausen (1980) have strongly argued (for female *Musca*) in favour of a hypothesis originally proposed by Reichardt (1973), according to which the torque reaction for progressive (front to back) motion on the retina is greater than for regressive (back to front) motion. On a coarse time scale (at least twice the reaction's delay) systems of this type are equivalent to controls where position information is independent of movement (Poggio and Reichardt, 1973, 1981). Furthermore, Poggio and Reichardt have conjectured that a large class of systems of the progressive-regressive type is characterized by high frequency asymptotic oscillations during tracking. In the case of a simple progressive-regressive system with one dead-time delay the period of the oscillations was proved to be twice the reaction delay. In this paper we report evidence in favour of asymptotic oscillations of this type during closed loop tracking of *Musca domestica*.

2. Methods

A flying female *Musca domestica* fly was tethered to a torque-thrust transducer (Geiger et al., 1981) and placed at the centre of a translucent vertical cylinder of 56 mm diameter illuminated evenly from the outside. The stimulus consisted of a black stripe with a visual contrast of 96%, a width of 5° and a length of 100°, which was driven by a servomotor and moved close to the inside of the cylinder. This apparatus was used in two modes, an "open-loop" mode in which the experimenter set the motion of the stripe while the fly's torque response was measured, and a "closed-loop" mode, in which the fly's torque signal is coupled to the motor driving the motion of the pattern via an electronic device which simulates the fly's free flight dynamics (for details see Reichardt and Wenking, 1969; Reichardt, 1973). The angular velocity of the stripe was

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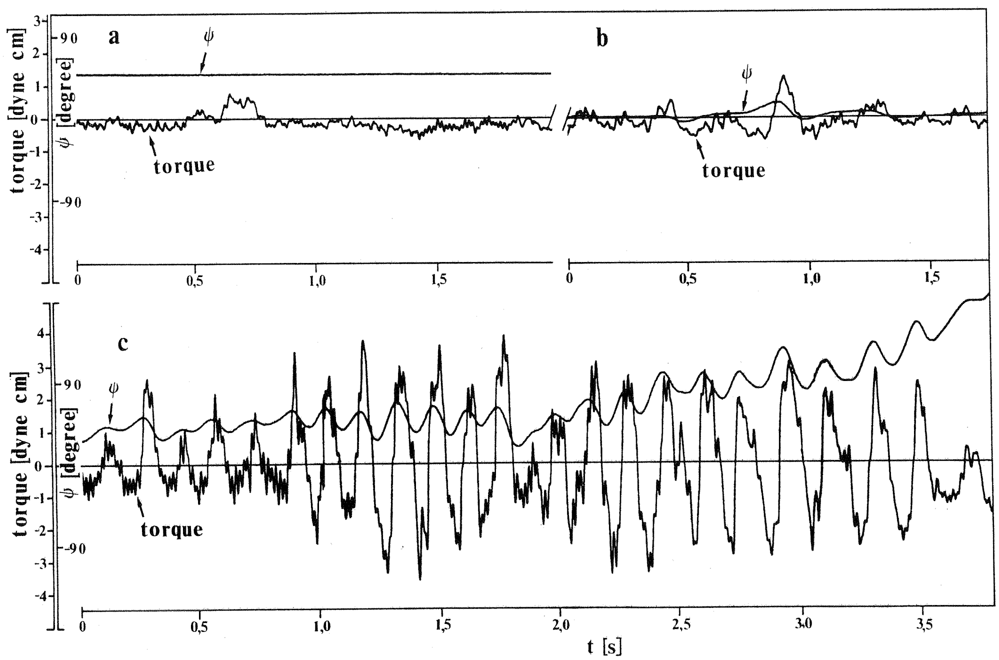

Fig. 1. a The torque response of the fly in an open loop situation. The graph shows that the stripe does not move. **b** Closed loop fixation without additional voltage (equivalent target's velocity is zero). The fly gazes at the stripe right in front ($\psi=0$). No oscillations are obvious. **c** Closed loop tracking. An additional voltage has been added: if the fly did not act against it, the stripe would move with a constant velocity around the fly. Under these conditions clear oscillations in both ψ and the torque become obvious. The velocity of the target is quite high: loss of target takes place every few seconds. Although the oscillatory behaviour is particularly clean in this record, oscillations with the same frequency are usually present under these conditions

then roughly proportional to the torque produced by the fly and opposite in direction. For more details see Geiger et al. (1981).

3. Evidence of Non-Decaying Oscillations in Closed Loop Tracking

The theory (Poggio and Reichardt, 1981) suggests that closed loop oscillations arising from a progressive-regressive control system are maximally magnified under tracking conditions with a constant target's velocity as high as possible. We have accordingly examined the closed loop behaviour of female houseflies for a target's velocity such that the stripe position on the fly's eye was kept around 30–40° laterally. Higher target velocities lead to larger angular errors and to immediate loss of target. Figure 1c shows the result of a typical experiment. The fly's torque, as well as the angular error usually show oscillations with a frequency around 5–6 Hz. Several properties of this oscillatory behaviour are consistent with the theoretical predictions:

a) The oscillatory behaviour is restricted to closed loop conditions.

b) Oscillations do not apparently decay but maintain a roughly constant amplitude for long times.

c) There is a trend for the oscillation amplitude to increase for larger offsets, i.e. for greater targets velocities.

The oscillatory behaviour is rather similar to computer simulation of very simple control systems of the progressive-regressive type (Poggio and Reichardt, 1981). Figure 2 shows some examples. Sometimes the oscillatory behaviour is somewhat buried by the stochastic component of the fly's torque (see Reichardt and Poggio, 1976), in the simulation (Fig. 2d) as well as in the experimental data. Notice that a control system where the position dependent response is only active for non-zero absolute value of the velocity must be considered, in a phenomenological sense, of the progressive-regressive type and shows asymptotic oscillations (Fig. 2c).

4. The Period of the Oscillations

The frequency of the oscillations during tracking is always around 5–6 Hz. Poggio and Reichardt (1981) have studied in detail what is probably the simplest progressive-regressive system. This control has a single delay for the reaction. It is described by

$$\dot{\psi}(t) = -\alpha\psi(t-\varepsilon) \cdot u[\psi(t-\varepsilon)\dot{\psi}(t-\varepsilon)] + A\,, \tag{1}$$

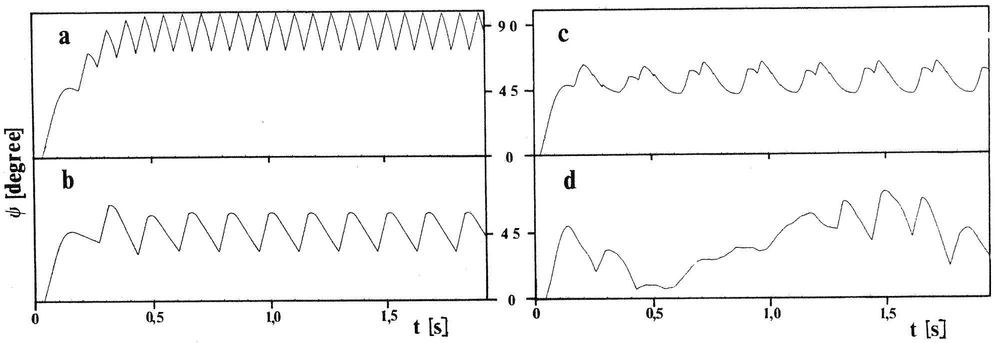

Fig. 2. **a** A computer simulation of Eq. (1) with the following parameter values: $A = 700°/s$, $\alpha = 15$, $\varepsilon = 40$ ms. The period of the asymptotic oscillations is $T = 2\varepsilon = 80$ ms. **b** A computer simulation of Eq. (2) with the following parameter values: $A = 700°/s$, $\alpha = 15$, $\varepsilon = 40$ ms, $\eta = 80$ ms. The period of the asymptotic oscillations is now 160 ms, corresponding to a frequency $f = 6.25$ Hz. **c** A computer simulation (suggested by W. Reichardt) of the equation $\dot{\psi}(t) = -\alpha\psi(t-\varepsilon)f(|\dot{\psi}|) + A$, where $f(|\psi|) = s|\dot{\psi}|$ for $|\dot{\psi}| \leqq 100°/s$, otherwise $f|\psi| = s100°/s$. The parameter values are $A = 700°/s$, $\alpha = 15$, $\varepsilon = 40$ ms, $s = 0.01$. **d** A low-pass gaussian noise has been added to the right hand side of Eq. (2), to simulate the stochastic component of the fly's torque (Reichardt and Poggio, 1976; Poggio and Reichardt, 1981). Other parameters as in Fig. 2b

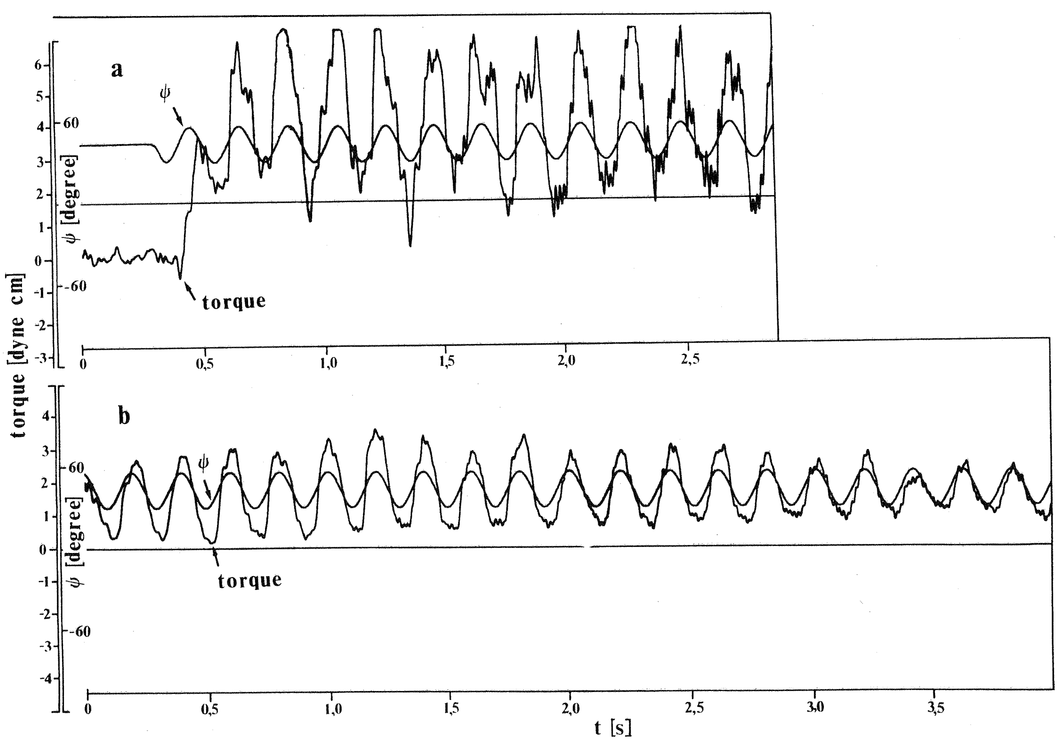

Fig. 3a and b. A stripe (5° wide) is oscillated sinusoidally with a frequency of 5 Hz and an amplitude of 36° around $\psi = 40°$ under open loop conditions. **a** shows the fly's torque at the onset of the stimulus. **b** represents the average of 4 flies. The "effective" delay in the torque reaction for this stimulus is no larger than 50 ms (compare the turning point in the torque reaction with the switch from regressive to progressive movement). The parameters have been chosen to make this open loop visual stimulus similar to that arising in the closed loop situation of Fig. 1

where $u[\,]$ is the step function. Notice that there is no reaction at all for regressive motion. The period of the asymptotic oscillations characteristic for Eq. (1) can be shown to be exactly $T = 2\varepsilon$. Thus if the fly's control were described exactly by Eq. (1), a frequency of 5–6 Hz would imply a pure reaction delay around $\varepsilon = 90$–100 ms. A delay of this size is inconsistent with most existing estimates (Reichardt and Poggio, 1976; Wehrhahn and Hausen, 1980), which suggest a value closer to 40 ms (but see Geiger et al., 1981). In any case we have decided to measure the open loop reaction of the fly to sinusoidal oscillations of the target with the parameters – i.e., frequency, amplitude and center position – which characterize our closed loop oscillations. Figure 3 shows typical torque records. The response of the fly has a rather complex structure, whose main properties like adaptation and age dependence will be presented elsewhere. For the purpose of our present argument, it is sufficient to notice that under conditions essentially equivalent to the closed loop situation of Fig. 1 the delay in the fly's reaction to progressive motion is no longer than about 50 ms. A control system like Eq. (1) is thus inconsistent with a closed-loop oscillation frequency of 5 Hz. There are, however, somewhat more complex control systems of the same type with longer oscillation periods. For instance, a low pass type of dynamics – possibly nonlinear – can make the effective delay of the system longer than the pure dead-time ε. One of the possibilities is the following. The fly's reaction does not have a single dead-time delay: the reaction to progressive motion does not only set in with a delay ε but is, in addition, "sticky", holding on for a longer time than ε after the ending of the progressive stimulus. Perhaps the simplest such system is:

$$\dot{\psi}(t) = R\{\psi(t)\} + A\,, \tag{2a}$$

where R, the fly's reaction, is given by

$$\begin{aligned} R\{\psi(t)\} &= -\alpha\psi(t-\varepsilon)u\{\psi(t-\varepsilon)\dot{\psi}(t-\varepsilon)\} \\ &-\alpha\psi(t-\varepsilon-\eta) \\ &\cdot u[-\psi(t-\varepsilon)\dot{\psi}(t-\varepsilon)]\cdot u[\psi(t-\varepsilon-\eta)\dot{\psi}(t-\varepsilon-\eta)] \end{aligned} \tag{2b}$$

with ε and η being the reaction delay and the "sticking time", respectively. In the hypothesis that asymptotic oscillations exist, their period can be easily proved to be $T = 2\varepsilon + \eta$. In other words, the "effective delay" is $\varepsilon + \eta/2$. A rigorous demonstration for the difference equation corresponding to Eqs. (2) could probably be carried out similarly to the proof given by Poggio and Reichardt (1981) for Eq. (1). Numerical simulations suggest that Eqs. (2) behave quite similarly to Eq. (1) with asymptotic oscillations of period $T = 2\varepsilon + \eta$. Figure 2 shows a computer simulation of Eqs. (1) (Fig. 2a) and (2) (Fig. 2b and d). The latter case (with $\varepsilon = 40$ ms and $\eta = 80$ ms) yields an oscillatory behaviour with a frequency of the correct order. As in Eq. (1), there is no reaction to regressive motion.

Although a "sticky" progressive-regressive system is not the only possibility, two arguments can be listed in its favour. Firstly, since Zimmermann's work (Zimmermann, 1973), it is known that the reaction to progressive motion may hold on for a considerable time after the stimulus has stopped, quite differently from the regressive reaction. A second point relies on data of the type of Fig. 3: the form of the reaction is consistent with the hypothesis of a sticky reaction to progressive motion. Figure 3 shows that at the onset of the stimulus (a stripe oscillating on the right side) the fly torque jumps to a positive value around which it follows the movement. This behaviour is exactly what a pure position control [$R = -\alpha\psi$ in Eq. (2)] would provide. It is, however, inconsistent with a simple (progressive-regressive) model like Eq. (1), without any dynamics. Integrator-like properties of a "sticky" progressive response could, however, account for an open loop behaviour as shown in Fig. 3 (compare Poggio et al., 1981). A mixture of such a system and a position control would be, of course, consistent with the observed behaviour. A pure position control completely independent of $\dot{\psi}$ (and corresponding to flicker detectors active also at zero flicker frequency) cannot lead to asymptotic oscillations in closed loop (Poggio and Reichardt, 1981).

Conclusion

In summary we have found that tracking in female houseflies is characterized by asymptotic non-decaying oscillations. This finding supports a significant role of a progressive-regressive control system in non-foveal tracking. The period of the oscillations, around 200 ms, can be accounted for by integrator properties of the dynamics, for instance by a "sticky" reaction to progressive motion. Reconstruction of chases between flies has already provided some hints of similar oscillations in the angular trajectory of chasing flies. Further work (with head fixed) is needed, however, to clarify the existence and the eventual properties of such oscillations for female and male houseflies.

One final point must be stressed. The data presented in this paper do not imply that a progressive-regressive mechanism is the only basis for position dependent reaction in the tracking behaviour of the fly. All our data are fully consistent with a "mixed" control system where the fly's torque depends on the angular error via two different mechanisms, the first one being independent of the direction of retinal motion and the second one relying on a stronger direction selective response to progressive than to regressive motion. In addition, a position control where the reaction depends on the absolute value of the velocity, but not on its sign, can also show asymptotic oscillations.

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