The Smooth (Fixation and Tracking) Control System

Male and female flies fixate (i.e., fly toward) small, contrasted patterns and track moving objects. The theoretical analysis of this control system in females, providing the basis for their behavior, relied almost completely on experiments performed in the laboratory with the flight-simulator device developed by Reichardt and Wenking. Figure 49 shows a diagram of the basic setup, which allows one to simulate free-flight conditions in one degree of freedom, namely, rotation around the vertical axis. Results obtained with this device in which the fly is fixed with the head glued to the thorax can be extended to free-flight conditions, under the assumptions that (1) nonvisual inputs play a negligible role, (2) body control does not depend on the head-movement system, and (3) there are no other degrees of freedom (because these are mechanically blocked).

Figure 50 shows the equivalent free-flight situation that one can study with this experimental setup. In the horizontal plane \( \alpha_f \) designates the instantaneous direction of flight with respect to an arbitrary zero direction, \( \alpha_p \) the instantaneous angular position of an object. The angle \( \psi = \alpha_f - \alpha_p \) is referred to as the error angle (on this plane) and represents the angular position of the object with respect to the coordinate system of the fly. If the head is fixed relative to the thorax, \( \psi(t) \) represents the location of the image of the object on the retina of the fly at instant \( t \). When \( \psi = 0 \), the projection of the fly's long axis on the horizontal plane points toward the object. We neglect translation effects (the object is far away from the fly), and we assume that the flight path of the fly is confined to the horizontal plane.

The flight dynamic is well approximated by the following equation:

\[
\Theta \ddot{\alpha}_f(t) + k \dot{\alpha}_f(t) = F(t),
\]

where \( \Theta \) and \( k \) are the moment of inertia and an aerodynamic friction constant of the fly, respectively, and \( F(t) \) is the instantaneous torque produced by the fly's wings. Since \( \Theta \) is very small compared to \( k \), the angular velocity \( \dot{\alpha}_f \) is essentially instantaneously proportional to the torque \( (\Theta/k = 8 \times 10^{-3} \text{ sec}) \). Equation (1) can be rewritten as
Figure 49. Simplified scheme of the basic closed-loop flight simulator setup developed by Reichardt and Wenking. A fly, fixed to the torque compensator, controls the velocity of a surrounding panorama by its own torque signal through an analog simulation of the flight dynamic.

Figure 50. Polar coordinate system describing the fly's rotational degree of freedom around the vertical axis (on the horizontal plane). \( \alpha_p(t) \) designates the angle between an arbitrary zero direction and the direction of the object in the fly's environment; \( \alpha_f(t) \) is the angle between the zero direction and the fly's direction of flight; \( \psi(t) = \alpha_p(t) - \alpha_f(t) \) is the error angle between the fly's direction of flight and the object. The distance \( \rho \) between the object and the fly is usually assumed to be large in order to neglect translation effects (but see Appendix 6).
where $S(t)$ reflects the trajectory of the object $p$. Thus the fly controls its angular velocity through its torque $F$. The core of the problem here is to determine how $F$ depends on the visual input, that is, which control system is used by the fly. A series of experiments has led to the following conclusions.

1. The underlying torque process is stationary under normal experimental conditions, implying that there is no switching between different control systems.

2. The term $F(t)$ can be approximated as a sum of two terms: a strictly visually evoked response $R_f(\psi(s))$, that is, a functional of the error-angle history, and a component that can be characterized stochastically as a Gaussian process. Thus

$$F(t) = R_f(\psi(s)) + N(t).$$

3. The visually induced response depends in a smooth way on the error-angle history $\psi(s)$. Moreover, because of the low-pass dynamics, the time scale of the torque response, under normal fixation conditions, is much shorter than the time scale characteristic of $\psi(t)$. Under this condition, rigorous theorems (see Coleman, 1971) ensure that $R_f$ can be approximated by a function of $\psi(t)$ and its derivatives. The first-order approximation is

$$R_f(\psi(s)) = D(\psi) + r(\psi)\dot{\psi}.$$  \hspace{1cm} (4)

It has been verified experimentally that Equation (4) is a satisfactory approximation under a wide range of conditions. The terms $D(\psi)$ and $r(\psi)$ are shown in Figure 51. The reaction shows (Reichardt, 1977) a very small delay ($\epsilon = 20$ msec). Thus Equation (2) becomes

$$\Theta \ddot{\psi}(t) + k\dot{\psi}(t) = -D[\psi(t - \epsilon)] - r(\psi)\dot{\psi}(t - \epsilon) + N(t) + S(t),$$  \hspace{1cm} (5)

where $r(\psi)\dot{\psi}$ is the result of a velocity computation; $D(\psi)$ carries the position information and represents the “attractiveness” profile associated with the specific pattern. All these terms have been characterized quantitatively through independent experiments. Equation (5) is a
Figure 51. The functions $D(\psi)$ and $r(\psi)$ (in relative units) characterizing the position and the velocity computation elicited by a narrow vertical black stripe segment in *Musca* females. [Reichardt and Poggio, 1976]

Figure 52. (A) Dynamics of fixation of two different patterns by *Musca* females as measured (upper part) and as predicted (lower part) by Equation (5) with standard values for the parameters. [Poggio and Reichardt, 1973] (B) The trajectory $\psi(t)$ for tracking a black stripe rotating at constant angular velocity as measured (upper part) and predicted (lower part) in a stochastic sense by the same equation.
stochastic nonlinear equation. The mathematics associated with its solution has several interesting aspects (reviewed in Reichardt and Poggio, 1976). Through Equation (5) (and natural extensions of it), the theory can predict nontrivial behavior in quantitative detail.

Interestingly, although connections with physiological and anatomical data are being established (see Hausen, 1977; Wehrhahn, 1979a),* the theory and, in particular, the derivation of Equation (1) are based on behavioral data. Equation (5) describes the basic organization of the smooth fixation and tracking system used by the fly to control its flight. It implies that this control system relies on computations performed on the visual input—extracting movement information and position information—and it states how this information is used to control the flight trajectory. In addition, the equation can account quantitatively for the fly’s behavior in a variety of situations. For the behaviorist or “fly psychophysicist,” Equation (5) represents a satisfactory basis for understanding this control system. For the physiologist or anatomist, the theory could also be a useful starting point, since it explains a relatively complex behavior in terms of simpler modules. Ideally, a physiologist conversant with the theory could look for neural correlates of these modules [movement and position, corresponding to the terms $r(\psi)\dot{\psi}$ and $D(\psi)$]; he would know which characteristic properties to look for. In addition, the physiologist would know that neurophysiological experiments, necessarily carried out under open-loop conditions, can satisfactorily characterize the orientation behavior, in which the visual motor loop is closed [through Equation (5), in which $D(\dot{\psi})$ and $r(\psi)$ are measured under open-loop conditions].

Clearly, a description like Equation (5) could not have been obtained from single-cell recordings or from histology alone. This is clearly an example where there seems to be little predictive extrapolation from the component level to the control-system level. Of course, histology and physiology are necessary in order to understand the system’s circuitry. Although one may argue that, ideally, behavioral analysis has some logical priority, it is clear that analysis has to be carried out at all levels simultaneously.

*Additional data are to be found in Wehrhahn and Poggio, “3-D Flight Control Systems in Houseflies,” manuscript, 1979.
An example of the predictive power of Equation (5) is shown in Figure 52. Equation (5) predicts, in a stochastic sense, the angular trajectory of a fly fixating or tracking patterns. Experimental data agree with the theoretical predictions.

Many more experimental data can be accounted for. For instance, the gaze of the fly toward rather complex patterns is quantitatively predictable by Equation (5) and a superposition rule that determines $D(\psi)$ and $r(\psi)$ associated with a given pattern. The justification for this rule and its range of validity depend on the algorithms for computing $D(\psi)$ and $r(\psi)$ (Reichardt and Poggio, 1976; see also the chapter by Poggio and Reichardt in this volume). The most dramatic validation of the theory is due, however, to free-flight experiments. We turn now to a brief discussion of this topic.

**Free-Flight Experiments**

Land and Collett (1974) were able to film chases in which male flies (*Fannia canicularis*) pursued other flies. These data led them to conclude that the control system used by the chasing fly is a continuous control system that can be described essentially by Equation (5) above. In fact, their Equations (3) and (4) combine to give an equation identical to Equation (5) with $N(t) = 0$ and $D(\psi) = \alpha \psi$ [their data actually support $N(t) \neq 0$; in such a tracking situation, however, $N$ plays a secondary role because it is much smaller than $S(t)$].

Even more dramatically, they have shown that such an equation can correctly simulate the trajectory of the chasing fly, given that of the leading fly. A later analysis of the flight behavior in the hoverfly (Collett and Land, 1975a,b) uncovered different control systems used by this fly in various circumstances. One of them is again a smooth system, phenomenologically identical to the control system in *Fannia* and *Musca*, that relies on (angular) position and movement information to control continuously the flight torque. Thus the control system described by the Reichardt–Poggio theory is equivalent, from the point of view of logical organization and information processing, to the control system used in free flight by male *Fannia* and, often, by
Syritta. This does not mean, of course, that the male tracking system is identical to the female smooth tracking and fixation system at the level of the neural circuitry. The problem of functional equivalence is logically separate from the problem of identity at the circuitry level. As we will see later, the smooth control system underlying chasing in males very probably depends on neural components specific, at least in part, to males.

Although the basic agreement of the data of Land and Collett with the phenomenological description of Reichardt and Poggio is clear, one serious problem still remains: the argument (Collett and Land, 1975b, p. 59) that the control system of male Fannia (and Syritta) must be basically different from the smooth (female) Musca system. Conversely, Reichardt and Poggio (1976) imply that the same theory describes the smooth control system of female and chasing male flies and that, moreover, both males and females track other flies (though with different efficiencies). It is clear from our discussion that the two views are, in fact, basically consistent since the two systems are different, at least in part, at the ethological and neuronal levels, but probably similar from the point of view of information processing. The transient high gain required by effective chasing is certainly triggered only in males by a set of unknown signals and correspondingly specific neural circuitries (Reichardt and Poggio, 1976, p. 364). On the other hand, the same theoretical description and the same equations approximate both systems (Poggio et al., 1977).

Collett and Land's belief that males but not females can track other flies seems to blur the whole argument somewhat. It would, in fact, be disturbing if females could not track other flies at all, since the control system described by Equation (5) is an effective tracking system up to a certain angular velocity {in Musca females the $D(\psi)$ shape and values give an upper limit around 300$^\circ$/sec}, and since tracking has been experimentally demonstrated in restrained females (Virák and Reichardt, 1974). Recently, however, Wehrhahn (1979a) has shown that the free-flying Musca females do indeed track other flies, although not as often or as effectively as their male companions. Figure 53 shows an example of such a tracking episode between female houseflies.

In summary, the validity of the Reichardt-Poggio theory as a phenomenological approximation of the smooth flight-control systems of female and male Musca, Fannia, and Syritta seems now
established (Land, 1977; see also Poggio et al., 1977). It is also clear that Collett and Land are correct in believing that tracking by females is ethologically different from the sexual pursuit displayed by males. The former being a byproduct of the smooth fixation system and probably more concerned with finding some object to land on. From our analysis it is clear that every fixation device having the structure of the *Musca* system, Equation (5), is necessarily a tracking system.

Since tracking in males is characterized by higher angular velocities, we suggest that the term "chasing" be reserved for this behavior and that both males and females be considered to perform "normal" fixation and tracking. A further reason for distinguishing chasing from tracking is the presence of a male-specific system that controls forward velocity in proportion to distance from the target.* Theoretical considerations suggest that a similar control system could optimize in-flight capture of the target (see Appendix 6). The

*Wehrhahn and Poggio manuscript, 1979
velocity–distance control is apparently absent in female tracking, as one would expect since males but not females should optimize capture. If this point of view is correct, chasing would be tracking with the specific aim of capturing the target. However, there is an alternative, although similar, possibility. The distance–velocity control system may only try to keep an optimal distance (around the critical distance $\rho_0$; see Appendix 6) that is optimal for minimizing the probability of loss of target. In this case, capture would not be the immediate goal of chasing.

The difference between chasing in males and tracking in females does not necessarily imply a unique male-specific neural circuit specifically designed for chasing (see Reichardt and Poggio, 1976, p. 364), although there must be, at least, trigger, gain control, and velocity–distance neural circuits. Collett and Land’s conjecture that there should be male-specific visual interneurons in the optic lobe has now been supported by Hauser and Strausfeld (see Hauser, 1977). Wehrhan’s (1979a) recent demonstration that during chasing male flies keep the target in the superior frontal part of the visual field, while female flies track with the inferior frontal part of the eye, is consistent with the anatomical evidence of Hauser and (for females) with measurements of $D(\psi)$ and $L(\theta)$ by Reichardt and Wehrhahn (see Reichardt and Poggio, 1976, p. 352). Furthermore, the fact that males and females use different parts of the eye strongly suggests that the neural circuitry of the male chasing system is distinct from the neural circuitry underlying normal fixation and tracking in females and males. The localization in males of the chasing fovea in the superior part of the eye automatically ensures that a chasing male cannot be chased by a chased male.

**The Smooth Control System: Open Questions**

Although we now have a rather satisfying picture of this control system, our understanding is far from being complete. We outline here some of the open questions presently under study.

1. The phenomenological theory outlined earlier is restricted to one degree of dynamic freedom, namely, rotation around the vertical axis. It has been shown that the vertical degree of freedom, in-
volving the fly’s lift, can be described by an equation similar to Equation (5) (Wehrhahn and Reichardt, 1973, 1975). Wehrhahn (1978) has shown that the two degrees of freedom are, with respect to the position response, essentially independent, as hypothesized earlier (Reichardt and Poggio, 1976). Furthermore, he has studied the 2-dimensional parameterization of the position-dependent torque-and-lift response. The results, which seem to imply some nontrivial restrictions on the underlying mechanisms, allow a quantitative description of fixation and tracking behavior in two degrees of freedom. Experiments are presently under way to confirm that the associated equations appropriately describe free-flight trajectories.

2. One would like to extend this analysis to all six degrees of freedom, including roll, pitch, etc. If Equation (5) is extended to all degrees of freedom, the associated dynamic behavior may become quite complex. For instance, the description of translations involves nonlinear terms, arising from the geometry of the situation, which can lead, in their interplay with the control system of the fly, to a complex series of fixation and tracking behaviors.

Consider Figure 50. If the distance \( \rho \) is not very large, Equation (5) can no longer be applied, and it becomes necessary to take into account the geometrical effect of the fly’s translation on the error angle \( \psi \). The appropriate description is given by adding to Equation (5), where we put \( \Theta = 0 \) and \( \kappa(\psi) = \kappa_0 \), a suitable geometrical term, and by introducing an additional equation that gives the rate of change of \( \rho \):

\[
\dot{\rho} = -\nu \cos \psi,
\]

\[
\dot{\psi} = -\frac{1}{k} D(\psi(t - \epsilon) - \frac{\rho_0}{k} \psi(t - \epsilon) + \frac{\nu}{\rho} \sin \psi + \frac{N(t)}{k}).
\]  

(6)

In order to solve Equation (6) it is clearly necessary to know how the translation velocity \( \nu \) is controlled. Appendix 6 outlines a simple mathematical analysis of Equation (6) and mentions some possible biological implications.

3. The spontaneous “looking-around” torque component \( N(t) \) is characterized by the phenomenological theory in stochastic terms. The stochastic approach only reflects our present ignorance about \( N(t) \), which, in an anthropomorphic language, depends on intentions
and moods of the fly. In principle, a precise knowledge of the internal states of the fly could allow a deterministic treatment of $N(t)$.

Although $N(t)$ might be neglected under chasing conditions, when $S(t)$ is actually much larger, it is always present under artificial closed-loop conditions (and probably in free flight as well) and determines important aspects of the orientation behavior. Thus it is important to characterize better the spontaneous activity of the fly and its dynamic structure. The hypothesis of independence of $N(t)$ from visual input is likely to be only a rough approximation, needing additional experimental and theoretical refinements. It is conceivable, for instance, that $N(t)$ may be switched off when the chasing system (in the male) is active.

4. The analysis must also be extended to include head movements. It is known that the body-control system does not depend on whether the head is fixed to the thorax or not (Reichardt, 1973, and especially Wehrhahn, 1979a). This point is, of course, preliminary to the studies described here and implies that head and body control systems are separate modules. Land's (1973) and Geiger and Poggio's (1977) analysis of head movements in tethered flying flies strongly suggests that head and body movements are independently initiated by central commands. The coordination of the two movements involves sensory feedbacks. It is likely that head-body coordination in flies is organized similarly to the monkey's eye-head coordination (Bizzi et al., 1972).

Much experimental work is still required in order to describe adequately how a fly controls its head position. For instance, the position of the head relative to the body affects the term $D(\psi)$ in a way that is not yet completely known (see Liske, 1977). It is clear, however, that eye movements depend on a mechanism other than the one described by Equation (5). In this sense, the eye-control system is one of several systems that are involved in the flight orientation of flies, in addition to the smooth system described by Equation (5).

5. When large numbers of individual insects, like locusts or mosquitoes, come together and remain together for long periods, one is left with the strong impression that the animals are bound by reactions to one another and often to visual landmarks (Wenck, 1965). In terms of the theory we have outlined, it seems natural to assume that this reaction consists of visual fixation by each individual of the whole or parts of the swarm. According to this conjecture, continued cohesion of the swarm is due to the inward orientation of flies at the
edges of the swarm, in accordance with Equation (5). It is an interesting theoretical problem to develop the “statistical mechanics” of such a “gas” of insects starting from the phenomenological theory outlined here.

**Flight Behavior: Other Visual Control Systems**

The hypothesis that the visual control of movement in flies has a modular structure and that its overall study can be reduced, at first, to the study of functionally independent subsystems is of course central to our approach. This view is supported by evolutionary and, even more convincingly, by epistemological arguments. As a matter of fact, nobody would disagree that the flight behavior of flies must rely on several different control systems. Flies, for instance, are able to land, start, and escape under visual control. The analysis of these and other mechanisms is still, to a great extent, a problem for the future. Appendix 6 gives a brief example of an analysis of this type for the system that controls forward velocity as a function of distance from the target.

Collett and Land (1975a) have shown that orientation behavior in hoverflies depends on three or four different control systems. One of these is essentially equivalent to the *Fannia* and *Musca* smooth system; another accurately directs open-loop body saccades. In *Musca*, however, the available phenomenological evidence indicates that body saccades can usually be neglected. The main criterion for the definition of saccades relies on their much faster time course. In a typical record of human eye movements, saccades appear like sudden discrete jumps, while intersaccadic drift is smooth and slow. Such jumps are usually absent in torque records of (fixating) *Musca*; they are also absent in the time course of the body angle of tethered *Calliphora* and *Musca* (Land, 1973; Geiger and Poggio, 1975), as well as in the body trajectory of free-flying (chasing) *Fannia*. Two processes with widely different time courses should produce multimodal histograms of the body angular velocity. This is the case for human eye movements and for *Syratta* body saccades. Figure 54 shows, however, that it seems not to be so for tethered *Musca*. 
Figure 54. (A) The angular velocity $\dot{\alpha}_f(t)$ of the body axis of a tethered female *Musca* free to rotate on a pivot (see Geiger and Poggio, 1977). (B) Symmetrized histogram of $\dot{\alpha}_f(t)$. There is no evidence for two or more processes with different time scales. $\dot{\alpha}_f(t)$, which is essentially proportional to the torque, seems well characterized in terms of a single low-pass Gaussian process, probably with a corner frequency somewhat higher than 1.5-2 times the corner frequency given for *Musca*’s spontaneous torque by Poggio and Reichardt (1973b, Figure 4b).

Figure 55. A 1440-msec chase between flies (*Musca domestica*) flying freely in a cage. The bottom stereo plot shows the 3-dimensional trajectories of the two flies (*leading fly, chasing fly*). The top stereo pair shows a computer simulation of the flight of the chasing fly, according to the theory described here. The reader should look at the figure with a standard stereo viewer. (Film by H. Wagner)
Recent data by Heisenberg and Wolf (1979) suggest that *Drosophila* also relies on at least two control systems, one being the smooth system and the other a "body" saccadic system. Interestingly, the flight style of *Drosophila* is quite similar to that of the hoverfly. It is possible that hovering flies have developed a saccadic system that fast-translating flies, like *Musca* or *Calliphora*, could not usually exploit. In any case, it is worthwhile to emphasize that Reichardt and Poggio's analysis is restricted to the smooth fixation mechanism of *Musca* and does not pretend to describe the whole orientation repertoire of either *Syrissa* or *Drosophila*. This point, although already explicitly stated in our review paper (Reichardt and Poggio, 1976, p. 365), was perhaps not as clear there as we had wished. We referred, for instance, to "orientation behavior," meaning the specific behavior we were studying. A similar quantitative approach to other control systems is certainly possible; Collett and Land (1975a,b, 1978) have already provided some impressive examples derived from free-flight observations.

The major task for the future is to understand, at the phenomenological level, how the various control systems interact and how switching among various subroutines of behavior occurs. Frame-by-frame analysis of films of flight episodes is now being used in our laboratory to answer this kind of question. Three-dimensional computer reconstruction of flight trajectories and their analysis promises to yield many new and interesting data (see, for example, Figure 55). The best description may turn out to be of the analog-control type at the level of single control systems and of a more symbolic type (in terms of subroutines and logical decisions), at the level of switching between the various control strategies.

**Conclusion**

The analysis of visually guided movements in insects offers a good example of the understanding one can achieve at the highest level of behavioral organization. Our analysis considers the logical organization of a specific control system; it neglects explicit computational analysis since the goal of this system is clear-tracking and fixation. So far, it
also neglects what may be the most difficult problem—a formulation of the likely modularization of a behavior as a set of functionally independent subsystems. Collett and Land (1975a,b) provide this classification for *Syritta*; the *Musca* smooth subsystem is isolated from the start by the experimental techniques. In the future the ethology of a variety of invertebrate behaviors may give insights to a still higher-level problem: How has evolution solved, in the course of time, the common problem of the visual control of movements in many different species?

Discussion

The analysis outlined here of a part of the fly's orientation behavior is independent of lower levels of understanding. Physiological information is not needed to arrive at a successful understanding of the basic information processing that underlies fixation, tracking, and chasing. This analysis, however, is quite important for, and somewhat preliminary to, a study of the algorithms involved. As a matter of fact, its most important aspect is the demonstration that this orientation behavior can be predicted quantitatively from knowledge of the open-loop response of the fly. In addition, it holds that the fly's visual system performs a main computation on the visual input, to abstract movement information and to compute position information. Knowing this, one can then approach these computations at the algorithmic level and at the cellular or circuitry level. An example of the independence of the various levels of understanding is provided here by the sexual dimorphism in orientation behavior. Chasing males may use the same algorithm to control angular velocity as do tracking females. The underlying neural circuitry, however, may be different.
APPENDIX 6
On Mathematical Trajectories of Flies

We will not review here the mathematics of the phenomenological theory, that is, the derivation and study of nonlinear stochastic equations like Equation (5) in the chapter by Reicherdt and Poggio in this volume (see also Reicherdt and Poggio, 1975, 1976). Rather, we will outline briefly a simplified analysis of Equation (6) in that chapter, which contains the geometrical terms corresponding to translation effects. A more detailed treatment of this class of equations can be found in Hadeler, Mottoni, and Schumacher (1979).

We consider the deterministic version of Equation (6), that is, we set $N(t) = 0$. We also choose a coordinate system as in Figure 50, but centered on the object. Thus $S(t) = 0$. In addition we neglect $e$ and $\Theta$, which is usually small compared to $k$, and put $S = 0$. Equation (6) then becomes

\begin{align}
\dot{\rho} &= -\nu \cos \psi = P(\rho, \psi), \\
\dot{\psi} &= -\frac{D(\psi)}{k - r_0} + \frac{\nu}{\rho} \sin \psi = Q(\rho, \psi),
\end{align}

(A1)

where $-\pi < \psi < +\pi$ and $D(\psi)$ is an odd function with positive slope around $\psi = 0$: that is,

\begin{equation}
D(\psi) = -D(-\psi),
\end{equation}

(A2)

\begin{equation}
\lim_{\psi \to 0} \frac{\partial D(\psi)}{\partial \psi} > 0.
\end{equation}

Equation (A1) has two simple equilibrium states, $(\rho_0, \psi_0)$ and $(\rho_0, -\psi_0)$, with

\begin{align}
\rho_0 &= \frac{k + r_0}{D(\pi/2)} \nu, & \psi_0 &= \pi/2,
\end{align}

(A3)
since \( P(\rho_0, \psi_0) = Q(\rho_0, \psi_0) = 0 \) and the determinant

\[
\begin{vmatrix}
\frac{\partial P}{\partial \rho} & \frac{\partial P}{\partial \psi} \\
\frac{\partial Q}{\partial \rho} & \frac{\partial Q}{\partial \psi}
\end{vmatrix} = \begin{vmatrix} 0 & \nu \sin \psi \\
-\frac{\nu}{\rho^2} \sin \psi & \frac{D(\psi)}{k + r_0} + \frac{\nu}{\rho} \cos \psi
\end{vmatrix} \tag{A4}
\]

does not vanish at the equilibrium points.

The origin \( \rho = 0, \psi = 0 \) is not an equilibrium point. Thus the fly cannot land on the object. Moreover, apart from very exceptional initial conditions, the fly will never even fly through the object; in other words, \( \rho \) is almost never 0 for almost all initial conditions. Let us now consider the stability of the equilibrium point \((\rho_0, \psi_0)\); because of the symmetry around \( \psi = 0 \), exactly the same analysis applies to \((\rho_0, -\psi_0)\).

The characteristic equation for the equilibrium point \((\rho_0, \psi_0)\),

\[
\begin{vmatrix}
\frac{\partial P}{\partial \rho} - \lambda & \frac{\partial P}{\partial \psi} \\
\frac{\partial Q}{\partial \rho} & \frac{\partial Q}{\partial \psi} - \lambda
\end{vmatrix} = 0,
\]

is

\[
\lambda^2 + \frac{\lambda}{k + r_0} \left( \frac{\partial D}{\partial \psi} \right)_{\psi = \psi_0} + \frac{\nu^2}{\rho_0^2} = 0, \tag{A5}
\]

which has roots with a negative real part if \( \partial D/\partial \psi \) at \( \psi = \psi_0 \), which we will call \( \alpha \), is greater than zero, and with a positive real part if \( \alpha \) is less than zero. The equilibrium point is a *node* if

\[
\frac{\alpha^2}{(k + r_0)^2} - 4 \frac{\nu^2}{\rho_0^2} = \frac{1}{(k + r_0)^2} \left[ \alpha^2 - 4D^2(\pi/2) \right] > 0, \tag{A7a}
\]
and it is a focus if

\[ \alpha^2 - 4D^2(\pi/2) < 0. \]  

Of course the equilibrium point \((\rho_0, \psi_0)\) is in fact a limit cycle in physical space, corresponding to a circular orbit of the fly around the object at constant speed \(v\), at a distance \(\rho_0 = v(k + r_0)/D(\pi/2)\) and with an angle \(\psi = \pm \pi/2\). This limit cycle is stable if the slope of \(D(\psi)\) at \(\psi = \pm \pi/2\) is positive, and unstable if it is negative.

In particular, the \(D(\psi)\) of *Musca* (see Figure 51) yields an unstable limit cycle, since the slope is negative around \(\psi = \pm \pi/2\), whereas the \(D(\psi)\) characteristic for chasing *Fannia*, as given by Land and Collett (1974), yields a stable limit cycle, since \(D_{Fannia}(\psi) \propto \alpha \psi\) over almost the whole range \(-\pi < \psi < +\pi\). In this case Equation (A7) implies, since \(D(\psi) \approx \alpha \pi/2\), that the stable point is a focus. Thus the approach to the limit cycle in physical space is oscillatory, as shown in the example of Figure A1.

![Figure A1](image-url)
Although Equation (A6) follows directly from Equation (A5), which is known to be a valid biological description, the implications of the analysis outlined here must be considered extra carefully for two main reasons. First, our analysis rests on some simplifying assumptions: Equation (A1) has been obtained neglecting the delay \( \epsilon \) as well as the stochastic term \( N(t) \). The stochastic term should probably be taken into account if we are to interpret experimental data reasonably. The deterministic analysis carried out here can be extended to the stochastic case using, for instance, the stochastic Liapunov function approach. The delay represents a harder problem. The second difficulty concerns the quantitative strategy used by the fly to control its translatory motion. The assumption that \( v \) is constant is, strictly speaking, unrealistic. This hypothesis implies that the fly would never come to rest. Practically, the fly will land on the object whenever its center of gravity is a few millimeters away from the object. Thus, although the fly can never mathematically land, there is always some time \( T \) for which the trajectory is sufficiently close to the object -- with biological estimates for \( D(\psi) \) and \( v \) -- to imply that the fly actually lands on it. This picture corresponds to a very simple control of \( v \): \( v \) is constant except when \( \rho \) is equal or less than a few millimeters (the "legs range"), in which case \( v \) drops to zero. More complex controls of \( v \) are theoretically possible. For instance, if \( v \) is a decreasing function of \( \rho \) (at least for \( \rho \) smaller than a certain distance \( \rho_0 \)) so that

\[
\lim_{\rho \to 0} \frac{v(\rho)}{\rho} = 0,
\]

then the origin \( (\rho = 0, \psi = 0) \) is a stable equilibrium point and the fly can land on the object, even mathematically. If

\[
\lim_{\rho \to 0} \frac{v(\rho)}{\rho} = c
\]

[* of course, \( v(0) = 0 \), then the origin is also a simple equilibrium point. The fly can reach it when the point is a stable node, which happens for \( c < \alpha/(K + r_0) \).*]
It is, of course, interesting to verify experimentally whether a similar control strategy is actually used. An analysis of chases between *Fannia* (and *Muscia*) males suggests that a similar control of $v$ is actually used by the chasing fly.\(^*\) This control strategy could optimize capture, and it therefore makes sense that while chasing males seem to make use of it, female flies apparently do not.\(^*\) In this case the distance $\rho$ would control the thrust $F$ developed by the fly. It seems again likely that an equation like

$$m\dot{v} + kv = F(\rho, \ldots)$$

may be a good first-order approximation of the dynamics of this control system.

An alternative explanation for the observed dependence of $v$ on $\rho$ is that male flies try to keep a constant distance $\rho$ in order to optimize tracking, not too near in order to keep the term $(v/\rho) \sin \psi$ small and not too far in order to keep good visual contact. If this is true, capture would not be the immediate goal of chasing. In this case the fly's control system should try to control $v$ in such a way that

$$\frac{v}{\rho} \sin \psi < \frac{D(\psi)}{k + r_0}.$$ 

Observe that for a resting target the first possibility requires the $v(\rho)$ curve to cross the $\rho$ axis at the origin, while this is not necessarily implied by the second alternative. When the target is moving, however, it is enough that the relative velocity tend to zero as distance approaches zero.

The limit cycle prediction for the linear $D(\psi)$ function is also an interesting property of Equation (A1). According to our data, the smooth control system of *Fannia* may show such a behavior if $v$ is kept constant, as apparently is the case for the female. The question whether the phenomenon is, in principle, observable depends on the quantitative values of $v$ and $D(\psi)$. If *Fannia* uses the $D(\psi)$ function measured for chasing by Land and Collett,

$$\frac{D(90^\circ)}{k + r_0} \approx 1800^\circ/sec,$$

\( \rho_0 \) should be of the order of 1 mm if \( v \) is kept constant (since \( v \approx 1 \) m/sec). With these parameters, the limit-cycle situation cannot have any biological significance.

If, however, *Fannia* normally were to use a smaller-gain \( D(\psi) \) of a similar shape, it might be possible to find indications of closed trajectories around a prominent object. The question is presently open to experimental investigations. These arguments, of course, are only valid for the case in which the smooth control system is active.

As a concluding remark we want to show that all our arguments should be extended to the 3-dimensional case in order to describe reasonably usual free-flight episodes.