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# Chasing Behaviour of Houseflies (*Fannia canicularis*)

## A Description and Analysis

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*Summary.* 1. Chases in which male flies (*Fannia canicularis*) pursue other flies were studied by filming such encounters from directly below. Males will start to chase whenever a second fly comes within 10–15 cm (Fig. 3).

2. Throughout these chases there was a continuous relationship between the angle ($\theta_e$) made by the leading fly and the direction of flight of the chasing fly, and the angular velocity of the chasing fly ($\omega_f$). This relation was approximately linear, with a slope of 20° $s^{-1}$ per degree $\theta_e$ (Figs. 4–7).

3. The maximum correlation between $\omega_f$ and $\theta_e$ occurs after a lag of approximately 30 ms, which represents the total delay in the system (Fig. 8).

4. In the region close to the chasing fly's axis ($\theta_e$ less than about 35°) a second mechanism exists in which the angular velocity of the chasing fly ($\omega_f$) is controlled by the relative angular velocity of the leading fly ($\omega_e$), rather than its relative position. The ratio of $\omega_f$ to $\omega_e$ in this region is approximately 0.7.

5. Using the results in 2–4 above, and an empirically determined relation between the angular and forward velocities of the chasing fly, it was possible to simulate the flight path of the chasing fly, given that of the leading fly (Fig. 11). Because these simulations predict correctly the manoeuvres and outcomes of quite complicated chases, it is concluded that the control system actually used by the fly is accurately described by conclusions 2–4.

6. The physiological implications of this behaviour, and the possible function of chasing, are discussed.

## Introduction

It is quite common to see houseflies engaged in what appear to be short fast chases, which involve many rapid changes of course. If these are indeed chases, in the sense that one fly is trying to catch the other then this implies that the fly which is doing the chasing must possess an accurate and rapid system for determining the course of the leading fly, and for controlling its own flight path accordingly. This paper presents an account of filmed records of such chases, and it is shown that these are cases of real pursuit, and not meaningless displays of aerobatics.

By examining the form of the chases it should be possible to determine the kind of control system the chasing fly uses. There are two basic possibilities. The system might be "continuous" in the sense that some feature of the leading fly's course (e.g. its instantaneous position or angular velocity relative to the chasing fly) continuously controls some aspect of the chasing fly's course (e.g. its angular velocity). Alternatively, the chasing fly might employ a "discontinuous" kind of system in which each manoeuvre of the leading fly is matched by an appropriate but stereotyped reply-manoeuvre.

To anticipate the results somewhat, it seems that this is a continuous system, and that the behaviour of the chasing fly can be described by a quite simple "input-output" relationship. Furthermore, using this relationship it is possible to simulate the chasing fly's flight path, given that of the leading fly. The results of such simulations predict quite accurately the forms and outcomes of chases, and this implies that the "model fly" derived from the observed chases provides an adequate explanation of what is seen to occur.

If this behaviour is visually mediated, and it is difficult to imagine how else it could be controlled, then the information derived from these flights can be used to infer some of the properties to be expected of neurones responsible for the visual control of flight.

## Methods

### *Filming*

There are usually two species of fly found inside houses in England, the common house fly (*Musca domestica*) and the lesser house fly (*Fannia canicularis*). The species are easily distinguished by the sharp upward bend of wing vein 4 iC in *M. domestica* compared with the straight vein in *F. canicularis* (see e.g. Colyer and Hammond, 1951). The other difference which is important for this study is that male *F. canicularis* tend to congregate round prominent objects such as lampshades, making horizontal "patrolling" flights near them for long periods. *M. domestica* on the other hand do not seem to prefer to fly in any particular parts of a room. Males of both species engage in chases, of females or more commonly of other males, but because only *F. canicularis* can be relied upon to perform these at a known location, it has so far only been possible to film this species.

Films were made by positioning the camera (16 mm Bolex with a constant speed motor operating at 50 frames per second) directly beneath a lampshade frequented by *F. canicularis*, and pointing upwards. A reduced shutter sector was used to give an exposure time of 3 ms, which minimised blur. Inspection of chasing flights from the side and below shows that most manoeuvres take place in the horizontal plane, and that vertical components of chases are rather small in comparison. Where there are vertical components to the chases these seem to be mainly in the form of spiralling movements, i.e. ones having a nearly constant upward or downward component, which will reduce the apparent velocity of the flies along the course as seen from below, but will not greatly change their angular relations, which are the important determining features of chasing behaviour. Examination of the flies which had taken part in filmed chases showed that most were males, and the chases analysed here are almost certainly interactions between males. Films were taken on hot days (about 25° C), in normal room daylight (backgrounds about 50 cd $\cdot$ $cm^{-2}$).

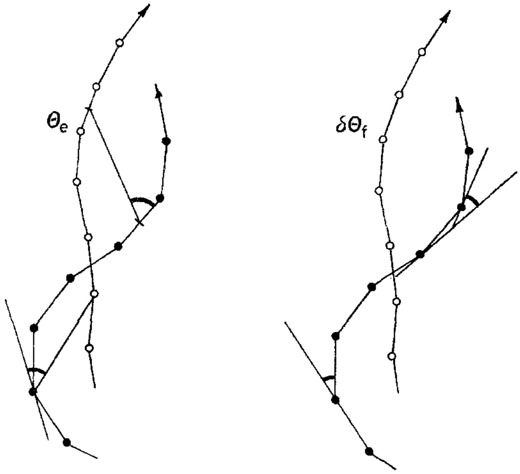

Fig. 1. Alternative ways of measuring the error angle $\theta_e$, and the angular velocity of the chasing fly $\omega_f = \delta\theta_f/\delta t$, at the instants measured on the film, and instants halfway between them

## *Analysis*

The films were analysed frame by frame using a Specto projector, and the courses of the flies in the horizontal plane were plotted. Usually it was impossible to determine the exact direction of the fly's axis, and in subsequent analyses it is assumed that this is the same as the direction of flight. From these course plots three kinds of information were extracted.

(i) The angle made by the line of flight of the chasing fly and a line joining the chasing and leading fly: this is referred to as the error angle ($\theta_e$, Fig. 1), and it is assumed that this represents the location of the leading fly on the retina of the chasing fly at a particular instant. The extent to which flies roll about their long axes during turns is not known ("banking") so this angle cannot simply be interpreted as an angle in the chasing fly's longitudinal plane, but in most instances it is likely that the major component is in this plane, and for the following analysis it does not matter whether or not this is true. The error angular velocity and error angular acceleration ($\omega_e$ and $\dot{\omega}_e$) can be obtained from $\theta_e$ as indicated in Table 1. Two methods of obtaining $\theta_e$ are shown in Fig. 1.

(ii) The angular velocity of the chasing fly ($\omega_f$). This was measured as the change in course angle between two frames of film ($\delta\theta_f$) divided by the sampling time ($\delta_t = 20$ ms). Fig. 1 gives two methods of measuring $\delta\theta_f$. This angular velocity is taken as being appropriate to an instant halfway between the two sampling instants. Angular acceleration ($\dot{\omega}_f$) can be obtained approximately from the difference between successive values of $\omega_f$ divided again by the sampling time.

(iii) The forward velocities of leading and chasing flies ($v_l$ and $v_f$). These are taken as the distances travelled along the flight paths between frames of film, divided by the sampling time. The errors involved in all these estimates increase as the angular velocities of the flies increase, but this is not likely to cause serious errors at angular velocities in the observed range. There does not appear to be any "fine structure" to the records described that is not resolved at 50 frames per second.

Table 1. Symbols

| | |
|---|---|
| $\theta_e$ | Error angle; the angle between a tangent to the flight path of the chasing fly and a line joining the two flies at a particular instant. |
| $\omega_e$ | Error angular velocity; rate of change of $\theta_e$, measured as $\delta\theta_e/\delta_t$ i.e. the change in $\theta_e$ during the sampling time $\delta t$. |
| $\dot{\omega}_e$ | Error angular acceleration; measured as $\delta\omega_e/\delta t$. |
| $\omega_f$ | Angular velocity of the following (chasing) fly; measured as $\delta\theta_f/\delta s$ i.e. the change in course angle during the sampling time. |
| $\dot{\omega}_f$ | Angular acceleration of the chasing fly; measured as $\delta\omega_f/\delta t$. |
| $v_l$, $v_f$ | Horizontal forward velocities of the leading and following fly; measured as the distances travelled along the respective flight paths between sampling instants, divided by the sampling interval. |
| $\delta_t$ | Sampling interval used in measurement and reconstruction of flight paths, usually 20 ms. |
| $d$ | Delay or latency of the response; defined as difference in time between the measurement of an "input" variable (e.g. $\theta_e$) and the time of maximum correlation between this and an "output" variable (e.g. $\omega_f$). |
| sign. convention | All anti-clockwise angles, angular velocities and angular accelerations are taken as positive, and vice-versa. |

## Results

### *General Description of the Flight Pattern of* Fannia canicularis

Male *Fannia* spend much of their time making characteristic "patrolling" flights around prominent objects, and it is in the course of such flights that encounters with other flies take place. Colyer and Hammond (1951) give an excellent description of this behaviour, which they say is characteristic of the genus.

"This flight is made on a series of irregular triangular or quadrilateral courses, an almost imperceptible hovering taking place at the corners and the sides being covered in a rapid dart. When undisturbed and alone, these flies maintain a more or less constant height and regular course, but when more than one decides to patrol the same 'beat,' it usually happens that one darts rapidly towards the other, a sharp flurry and prompt dispersal ensues and eventually one of them recommences the patrolling."

Two examples of such patrolling flights are shown in Fig. 2. The straight segments are about 20 cm long, and the average velocity of the flies is 65 cm $s^{-1}$, about half the speed seen during chases. Sometimes two or even three males manage to co-exist in the same part of the room, but when this occurs the flies are found to be stratified vertically, so that

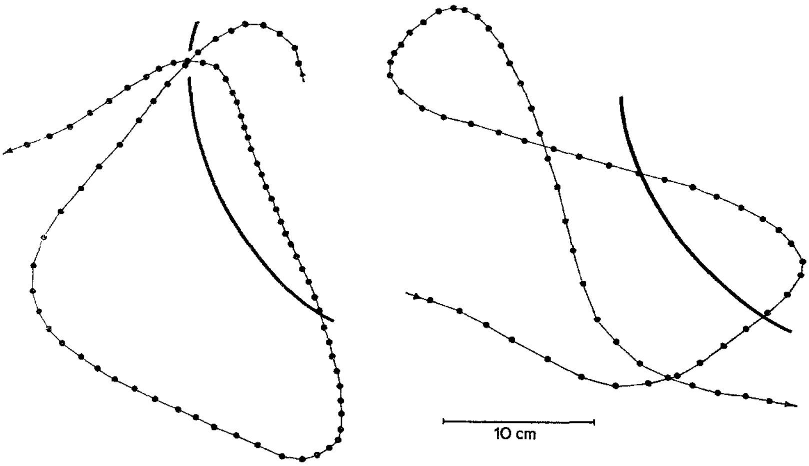

Fig. 2. Two examples of "patrolling" flights made beneath a lampshade, which is indicated by the heavy line. Time interval between points: 20 ms

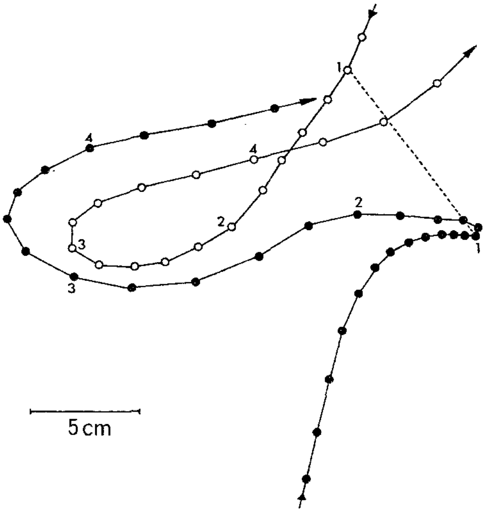

Fig. 3. Patrolling flight ending in a chase. Chasing fly ●, leading fly ○. Points are at 20 ms intervals. Corresponding instants in the two flight paths are numbered at 100 ms intervals. Dotted line indicates relative positions of the flies at the probable instant of visual contact

there is a separation of 10–30 cm between the planes of the various patrolling flights.

From unassisted observation, it seemed that whenever one fly came within a distance of 10–15 cm of another, a chase followed automatically. The beginning of one such encounter is shown in Fig. 3. Here the distance between the flies when the chasing fly makes its first turn is 9 cm, which is probably a slight under-estimate because there must be some latent period. However, if 10 cm is taken as the "visual contact distance," then a 6 mm long fly will occupy a visual angle of 3.4° by 2°, which is comparable with an interommatidial angle of about 2° (in the closely similar housefly *Musca*).

Females rarely strayed into the area occupied by males, although when they did they were chased and sometimes caught, the two flies joining, and flying in tandem to a nearby surface to copulate. Unfortunately, only one instance of what appeared to be a male/female chase was filmed, and this was so brief that little could be learned from it. By far the majority of chases were between males.

### *Flight Paths during a Chase*

Fig. 4 shows the longest and most complete film of a chase that was obtained. The entire sequence lasts just over a second: encounters are often much briefer than this and rarely last more than 2 seconds.

Inspection of Fig. 4 shows that one animal (open circles) is being chased and is taking continuous evasive action, and that the other (closed circles) is trying to follow the first as closely as possible. In the chase the leading animal makes six quite distinct manoeuvres: a sharp left turn after 1, a right turn after 2, a 180° right turn between 3 and 4, a left turn at 4 immediately followed by a right turn, and finally an extraordinary right hand loop which leaves the fly almost on its former course. It is apparently this final manoeuvre that causes the pursuer to lose visual contact. In contrast to this almost random behaviour, the pursuing fly seems to behave in a much more comprehensible manner: it follows each manoeuvre of the leading fly quite accurately, even during the final loop. It gives the impression of trying to keep its course pointing in the direction of the leading fly, as though it were attempting to catch up with it.

In a chase situation like this the leading animal has the advantage in that it makes the manoeuvres first, and the pursuer, because of the limitations of whatever control system it is using, wastes a certain amount of time in making appropriate course changes. This is particularly obvious during the turns between 3 and 4, and 4 and 5, where, in spite of the pursuer's faster forward velocity (1.3 times that of the leading fly, overall) the pursuer's inability to follow each turn instantaneously results in it lagging behind the leader by about 9 cm by 5, although both flies were level at 3. Thus the leading fly can only escape from its pursuer by outmanoeuvring it, since on a straight course the pursuer would, in this case at least, overtake its target.

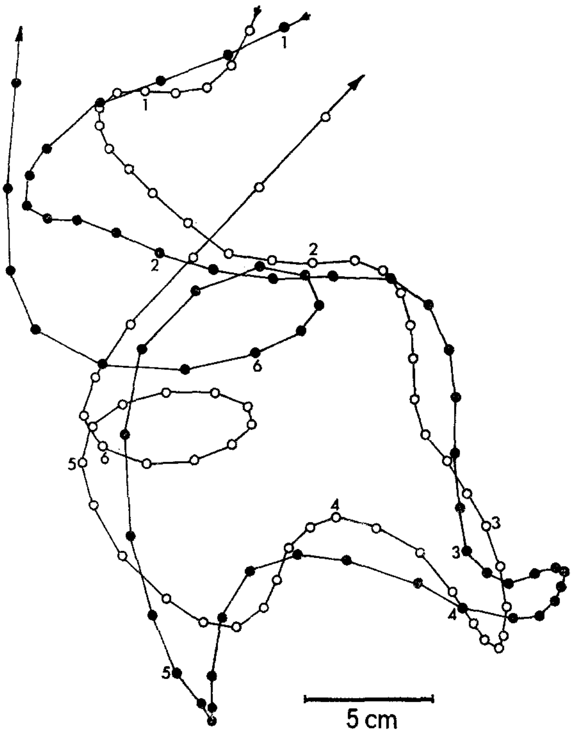

Fig. 4. Flight paths of chasing ( •) and leading ( ○) flies during the longest recorded chase. Points at 20 ms intervals. Corresponding instants on the two paths numbered at 200 ms intervals

The remainder of this paper is devoted to an attempt to unravel the nature of the control system that enables the pursuing fly to follow as closely as it evidently does. It is assumed throughout that the chasing fly is guided by vision, although the validity of the analysis does not depend on this.

## *Input-Output Relations of the Chasing Fly*

In the introduction it was suggested that the chasing fly might either possess a set of stereotyped responses to manoeuvres made by the leading fly, or else that it operated on the basis of a continuously running control system in which some source of information available to it ($\theta_e$, $\omega_e$, or $\dot{\omega}_e$, see Fig. 1) controlled some feature of its behaviour ($\omega_f$, $\dot{\omega}_f$ and possibly $v_f$). The best procedure seems to be to determine whether or not there are any continuous relationships between "input" and "output" variables, if there are to test whether or not they can explain the flight

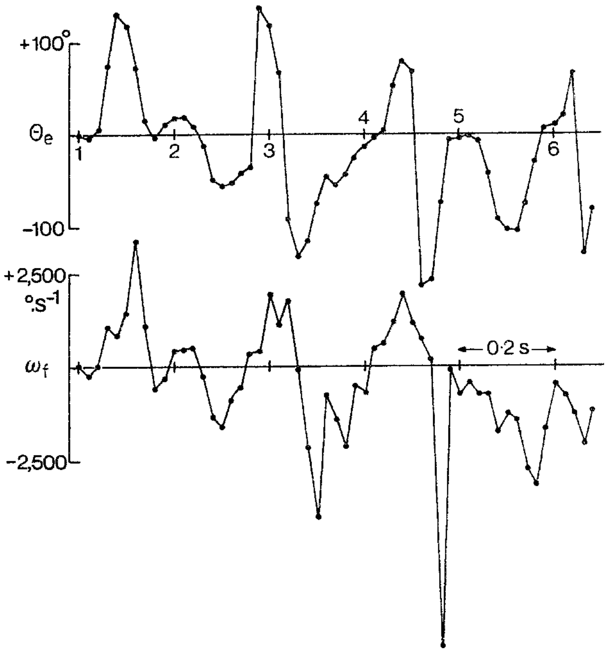

Fig. 5. Plots of error angle ($\theta_e$) and the angular velocity of the chasing fly ($\omega_f$) during the chase shown in Fig. 4, showing the continuous correspondence between the two. Numbers on the time axis refer to the numbered points in Fig. 4

path, and only if this procedure fails to start looking for more complicated kinds of responses.

On comparing input and output variables it became clear that there was a relationship, apparently continuous, between error angle ($\theta_e$) and the chasing fly's angular velocity ($\omega_f$). This is shown in two forms in Figs. 5 and 6a. Fig. 5 shows that whenever the leading fly departed from a position ahead of the chasing fly ($\theta_e = 0$) the chasing fly turned towards it with an angular velocity roughly proportional to the deviation. Comparing the two plots, there seems to be a delay of between 20 and 40 ms between the two, and this will be examined further below. The scatter diagrams in Fig. 6 are all based on the assumption that the input variables maximally affect the output 30 ms later. From Fig. 6a it can be seen that there is a strong and apparently linear relation between $\omega_f$ and $\theta_e$. The correlation coefficient is 0.76 and is highly significant. The relationship can be approximated by the regression line, which has a slope of 21 $s^{-1}$ (the full units are degrees per second per degree $\theta_e$, or simply $s^{-1}$).

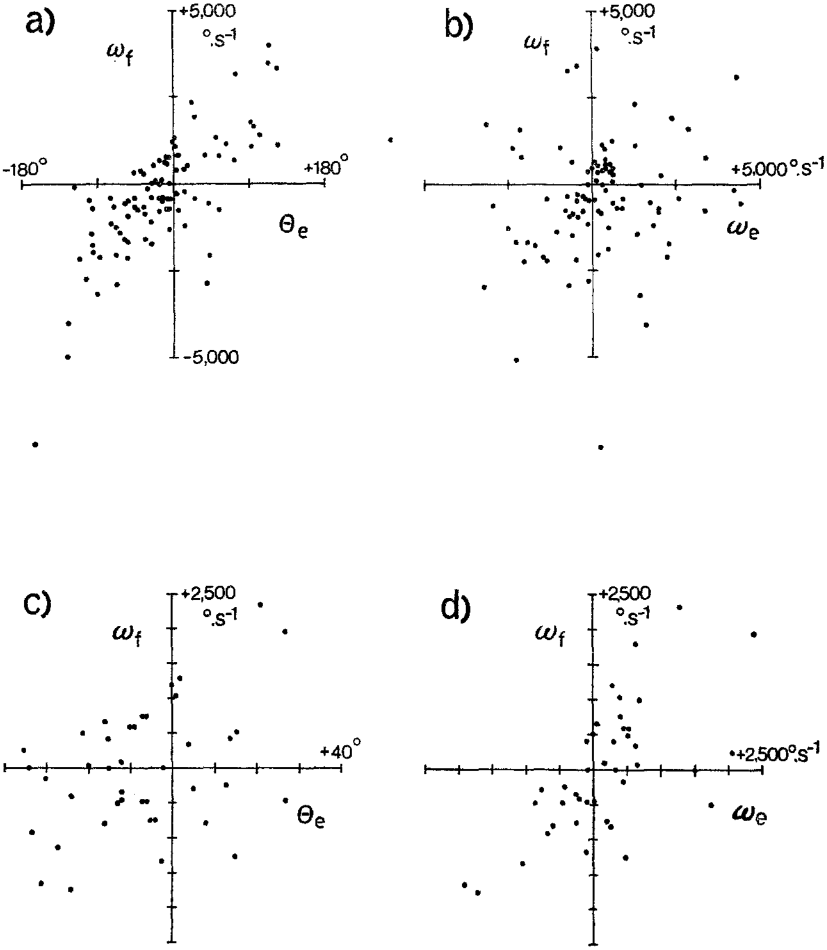

Fig. 6a—d. Scatter diagrams showing the relationships between $\omega_f$ and $\theta_e$, and $\omega_e$ and $\omega_f$ for all points measured on Fig. 4 and 3 shorter chases (a and b), and for only those points for which the error angle ($\theta_e$) lay between $+35°$ and $-35°$ (c and d). In all cases the delay has been taken as 30 ms, i.e. the ordinate of each point corresponds to an instant 30 ms later than that of its abscissa. The correlation coefficients are a) 0.76 ($p < 0.001$), b) 0.09 (n.s.), c) 0.38 ($0.01 < p < 0.02$), d) 0.65 ($p < 0.001$)

Interestingly, there was no correlation between $\theta_e$ and $\dot{\omega}_f$ which indicates that angular position error does not control angular acceleration towards the leading fly, only angular velocity. There was, however, a strong correlation between $\omega_e$ and $\dot{\omega}_f$, which is not surprising since these

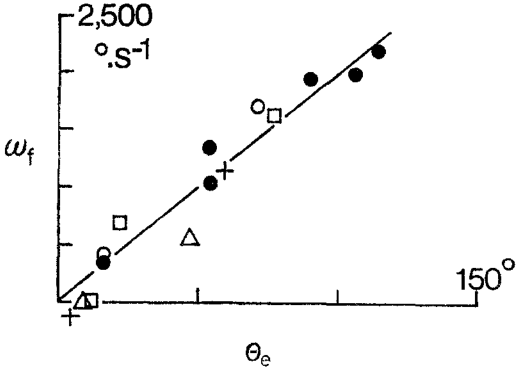

Fig. 7. Relation between $\omega_f$ and $\theta_e$ under conditions that approximate to a steady state. The points are the average values of $\omega_f$ measured during periods of 60 to 100 ms, in which the values of $\theta_e$ were approximately constant. Closed circles are from Fig. 4, other symbols are taken from four other chases. The straight line has a slope of 20 $s^{-1}$

are the first derivatives of $\theta_e$ and $\omega_f$, between which there is a relationship. The question arises as to whether one of these pairs of relationships is causal, and the other its consequence. It seems likely that the $\theta_e$, $\omega_f$ relation is the real one, because there is no reason why the differentiated relationship should be "zero position error seeking." In other words, if $\omega_e$ was actually being used to control $\dot{\omega}_f$ one would not expect the plot of $\theta_e$ vs. $\omega_f$ to pass through zero, which it does.

There is a problem in accepting the value of 21 $s^{-1}$ as the value that the fly actually uses in converting $\theta_e$ into angular velocity $\omega_f$ because of the uncertainty about the exact latency of the response. Ideally, one would like to be able to measure this conversion factor under steady state conditions, that is, to measure the angular velocity of the chasing fly when $\theta_e$ is kept constant. In free flight this is not strictly possible because the angular velocity of the chasing fly tends to reduce $\theta_e$ very rapidly. However during certain manoeuvres, like the loop between 5 and 6 in Fig. 4, a situation does arise in which $\theta_e$ stays approximately the same for 3–5 frames. From such situations a reasonable approximation to the steady state conversion factor can be obtained by plotting the average values of $\omega_f$ during these semi-stable periods against the average value of $\theta_e$ in the period taken as starting 30 ms earlier. Such a plot is shown in Fig. 7. It is well fitted by a straight line whose slope is 20 $s^{-1}$ (i.e. 20° $s^{-1}$ per °$\theta_e$).

From these considerations, the operation performed by the pursuing fly can be defined as the conversion of the *position* of the retinal image of the target (the leading fly) into the *angular velocity* of the pursuer's flight path. Or:

$$\omega_f = k\,\theta_e, \text{ where } k = 20\ \mathrm{s}^{-1}. \tag{1}$$

This, however, is not the only mechanism involved. An examination of certain of the turns in Fig. 4, notably the right turn following 2 and the left turn after 4, shows that the chasing fly begins to turn in the direction of motion of the leading fly, even before the leading fly has crossed the chasing fly's axis. For such turns the above expression cannot be true, and one would expect instead that there would be a closer relation between error angular velocity ($\omega_e$) and the angular velocity of the chasing fly ($\omega_f$). Fig. 6b shows that in general there is no such relation between $\omega_f$ and $\omega_e$: the correlation coefficient is 0.09, and not significant. However, on closer examination it can be seen that there is a cluster of points near the origin that appear to be correlated, and by breaking the distribution down with respect to $\theta_e$ it turns out that nearly all these points are derived from situations in which the leading fly is close to the axis of the chasing fly. There is a highly significant correlation between $\omega_f$ and $\omega_e$ when $\theta_e$ is close to $\pm 30°$ and between these values, but this correlation disappears when $\theta_e$ is $\pm 40°$ or more. This is shown in Fig. 6c and d, which demonstrate the virtual absence of a relationship between $\theta_e$ and $\omega_f$ in this central region, and a strong correlation (0.65, $p < 0.001$) between $\omega_f$ and $\omega_e$. The latter relation is possibly sigmoid, with the response saturating at values of $\omega_e$ around $1500°\ \mathrm{s}^{-1}$, although on the basis of the present data this can only be a guess. In any event, this relation is not badly fitted by the regression line, which has a slope of 0.7, and this value will be adopted.

This can be regarded as meaning that when the leading fly is more or less directly in front, its relative velocity rather than its position determine the angular velocity, and hence the course of the chasing fly. This can be expressed:

$$\omega_f = k'\omega_e, \qquad \text{where } k' = 0.7, \tag{2}$$

provided that $\theta_e$ lies between $\pm 35°$.

The significance of this mechanism will be examined in more detail in the discussion section, where an attempt is made to simulate a chase.

### *Response Time*

Inspection of Fig. 5 indicates a delay (*d*) of 20–40 ms between the appearance of the leading fly at a particular angular position $\theta_e$, and the attainment of the appropriate angular velocity $\omega_f$ by the following fly. To examine this further the cross-correlation coefficients between $\theta_e$ and $\omega_f$ were determined for a range of time differences between the two measurements from $-30$ ms ($\omega_f$ leads $\theta_e$) to $+70$ ms. These are

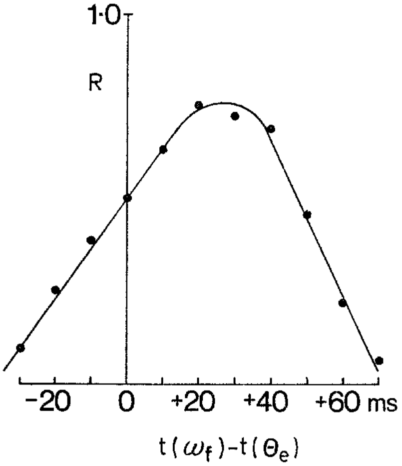

Fig. 8. Correlation ($R$) between $\omega_f$ and $\theta_e$ for different time intervals between the two sets of measurements. Positive time differences mean that the $\theta_e$ measurements lead the $\omega_f$ measurements, by the times shown. The points are derived from the same measurements as those used in Fig. 6. The line has been fitted by eye. The maximum correlation occurs at about +30 ms

plotted in Fig. 8. The results confirm that the maximum correlation occurs after a delay of 20 ms and it remains high up to 40 ms, then falls steeply. The positive correlations throughout the entire period shown merely reflect the fact that both flies tend to be engaged in the same manoeuvre for around 100 ms and a casual correlation between the two variables is to be expected within this range.

The simplest interpretation of Fig. 8 is that the fly has a fixed response time of about 30 ms. Further evidence from simulations (see discussion) indicates that the response time cannot be much greater than this: if it is as long as 40 ms the course would become a series of tortuous knots (Fig. 12).

A similar correlation examination for the $\omega_f$ vs. $\omega_e$ relationship [Eq. (2)] showed that this too has a delay of about 30 ms.

### *Angular Velocity and Forward Velocity*

A problem in trying to analyse and predict the course of the chasing fly is that angular velocity and forward velocity are not independent of each other. There is an obvious slowing down during large angle turns in Fig. 4, which is shown more clearly in Fig. 9. This is a plot of forward velocity vs. angular velocity, both measured in the same 20 ms period, and shows both that there is considerable variation in the horizontal

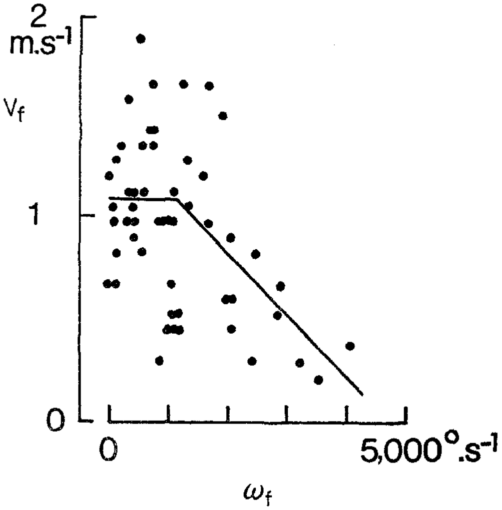

Fig. 9. The relation between the forward velocity $v_f$ and angular velocity $\omega_f$ of the chasing fly measured during each interval between points in Fig. 4. The angled line is an arbitrary attempt to fit the data, and this line is used to adjust course lengths in the simulations in Figs. 11–13

component of forward speed ($v_f$) at low angular velocities (less than 1000° $s^{-1}$), and also that at angular velocities above this the forward speed drops rapidly, and by extrapolation would reach zero at about 5000° $s^{-1}$. There may be several reasons for this, but one is the reduction of net forward thrust during turning caused either by the decreased stroke angle on the side turned to (Nachtigall and Wilson, 1967), or the braking effect of retaining the upstroke attitude of the wing on the side of the turn during the downstroke (Faust, 1952). Some of the variability of the forward speed at low angular velocities may be the result of the time taken to accelerate after turning, and part may be due to departures of the flight path from the horizontal. There is, however, no way of distinguishing these factors from the flight path records, and for the purpose of simulating chases the relation between $v_f$ and $\omega_f$ has simply been approximated by the arbitrarily fitted line shown on Fig. 9.

In addition to the dependence of $v_f$ on $\omega_f$, $v_f$ is also likely to affect $\omega_f$ because the fly's forward momentum will tend to limit the rate at which large turns can be made. There is some indication from the films that the fly actively counteracts this on very sharp turns by actually turning round before its forward velocity has reached a minimum, so that for about 20 ms it is in fact moving sideways. However, the quality of the films was not good enough to examine this in more detail.

### *Other Evidence Supporting a Continuous Relation between $\theta_e$ and $\omega_f$*

While it is most unlikely that the relationship in Fig. 6a could have arisen fortuitously, there is still the remote possibility that it represents the consequence of the chasing fly following a set of pre-set rules, in which each manoeuvre of the leading fly is matched by one from an equivalent repertoire of the chasing fly. It is in fact the case that all but one manoeuvre by the chasing fly in Fig. 4 (the exception being the turn between 3 and 4) has the same general form as the manoeuvre of the leading fly. Thus it is just possible that, provided the chasing fly can somehow detect the kind of manoeuvre made by the leading fly, it can control its flight by matching it.

An example which seems to disprove this conclusively is shown in Fig. 10 in which the manoeuvres made by the two flies are completely different. The leading fly makes a right turn followed by a complete left hand loop, whereas the chasing fly makes a right turn followed by a second very sharp right turn, and finally a sharp left turn. For much of the flight the two flies are actually turning in opposite directions. Nevertheless, when one compares $\omega_f$ and $\theta_e$ (Fig. 10b) it can be seen that there is still a nearly perfect correspondence between the two, in spite of the speed with which $\theta_e$ is changing. Fig. 10c shows the excellent relation between $\theta_e$ and $\omega_f$ 20 ms later. It is not believable either that the chasing fly's manoeuvres are simply replies to those of the leading fly, nor that the relationship in Fig. 10c is accidental.

## Discussion

### *a) An Attempt to Simulate a Chase*

A valuable test of whether or not the behaviour of the chasing fly is adequately described by the relationships given in Eqs. (1) and (2) in the results is to use these expressions to attempt to simulate a chase. If the manoeuvres predicted are similar to those that occur, and the overall result is the same, then it can be concluded that Eqs. (1) and (2) provide a sufficient explanation.

Adding the two equations, and incorporating the delay ($d$) gives:

$$\omega_{f(t+d)} = k\,\theta_{e(t)} + k'\,\omega_{e(t)} \quad (35^\circ > \theta_e > -35^\circ) \tag{3}$$

and this, together with the relation between forward speed ($v_f$) and angular velocity ($\omega_f$) shown in Fig. 9, is used to reproduce the flight path of the chasing fly, given that of the leading fly. In the simulations shown in Fig. 11 the path of the leading fly is taken directly from the chase shown in Fig. 4, so that direct comparison can be made.

The technique used is to start with the first three points of the chasing fly's track as the given initial conditions ($t = t$, $t + 20$ and $t + 40$ ms) and then, by measuring $\theta_e$ at $t + 10$ ms, to calculate the course change that must be made at $t + 40$ ms, if the value of the delay ($d$) is to be 30 ms.

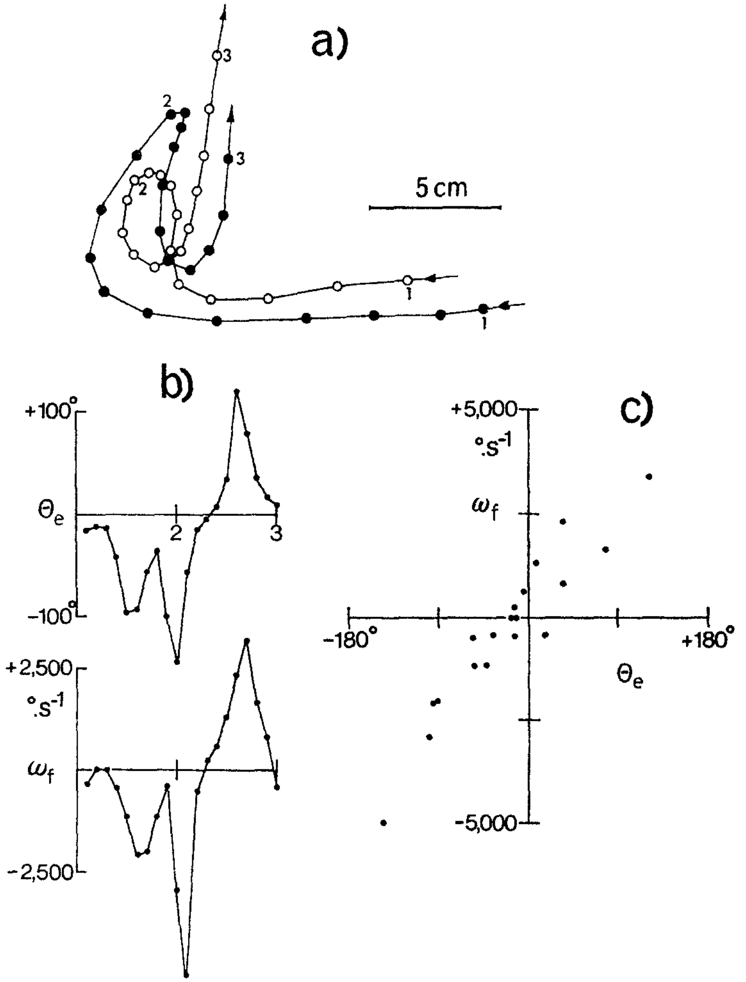

Fig. 10a—c. Instance of a chase in which the two flies execute quite different manoeuvres, but in which the relation between $\omega_f$ and $\theta_e$ is preserved. a) Record of the chase. b) Plots of $\theta_e$ and $\omega_f$. Marks on the time axis correspond to the numbered points on the tracks, and are 200 ms apart. c) Relation between $\omega_f$ and $\theta_e$ measured 20 ms earlier

Since $k\theta_e = \omega_f = (d\theta_f)/dt$, the required change $\delta\theta_f$ is given by $k\theta_e \cdot \delta t$, where $\delta t$, the sampling interval, is in this case 20 ms. Similarly, where the value of $\theta_e$ is appropriate, an angle proportional to $\omega_e$ can be included by measuring the difference between the values of $\theta_e$ at $t=20$ and $t=0$, multiplying this by $k'$ and adding this to course change already obtained. This is the required change because, if $\omega_f = k'\omega_e$, then $(d\theta_f)/dt = k'(d\theta_e)/dt$, or $\delta\theta_f = k'\delta\theta_e$. This now gives the direction of the line between the points at $t+40$, and $t+60$ ms and this is then drawn with a protractor. The length of this line will be $v_f \cdot \delta_t$ and by assuming that $\omega_f$ is equal to the course change divided by $\delta t$, the appropriate value of $v_f$ can be obtained from Fig. 9. This then establishes the fourth point in the course ($t+60$ ms). By repeating these operations (which are simpler than they sound) for successive points, the complete course can be built up. Different values of $k$ and $k'$ can be used, and with slight modifications to the method as described the delay ($d$) and sampling time ($\delta t$) can be altered. The relative speeds of the two flies can also be changed by multiplying the values of $v_f$ obtained from Fig. 9 by a constant factor. In general the smaller the sampling time ($\delta t$) the better, but for most purposes 20 ms was found to be short enough not to introduce appreciable distortion.

In the simulation shown in Fig. 11b, $k=20\ \mathrm{s}^{-1}$, the delay is 20 ms and the velocity term has not for the moment been included. It can be seen that there is a reasonably good match to the actual flight path shown in Fig. 11a. Each manoeuvre of the "real" pursuing fly is duplicated by a corresponding manoeuvre of the simulated fly, even though these differ in detail. The principal difference between the real and simulated fly is that in the former the turns are all rather tighter, and as a result the simulated pursuer appears to stray rather further from the leading fly's course than it should. Nevertheless, if one compares the relative positions of the flies at the marked instants 3, 4 and 5 it can be seen that the simulated fly is not much further behind than the real fly. In the final loop the leading fly does "escape," in both cases, because the distance separating the flies comes to exceed the visual limit of 10 cm. It is concluded from this that the postulated "basic" mechanism, in which error angle is converted by the fly to angular velocity, is able to explain most features of the observed chase, although capable of refinement.

Before considering the effects of adding in the error velocity ($k'$) term, it is interesting to see what the effects of changing $k$ and $d$ are, and important to show that changing them makes the simulation worse in the sense that it looks less like the actual course. Fig. 12 shows a number of simulations of the first two manoeuvres of the same course as in Figs. 4 and 11a. In Fig. 12a it is seen that reducing the delay to zero makes the course intolerably good, so that the trailing fly has caught up with the leader several times after only 0.4 s, and there is virtually no overshoot on the first bend. Equally dramatically, with a 40 ms delay the fly overcorrects wildly on the first bend producing a figure of eight course which wastes time and lets the leading fly get well in front. In Fig. 12b, halving the value of $k$ from 20 to $10\ \mathrm{s}^{-1}$ (20 ms delay) makes the first bend much too wide, while increasing $k$ by a factor of 1.75 clearly makes the bend much too tight and causes some overshoot. From these and similar results it is concluded that realistic simulations of the flight path require that both the delay and the constant $k$ stay close to the values adopted in deriving Fig. 11b.

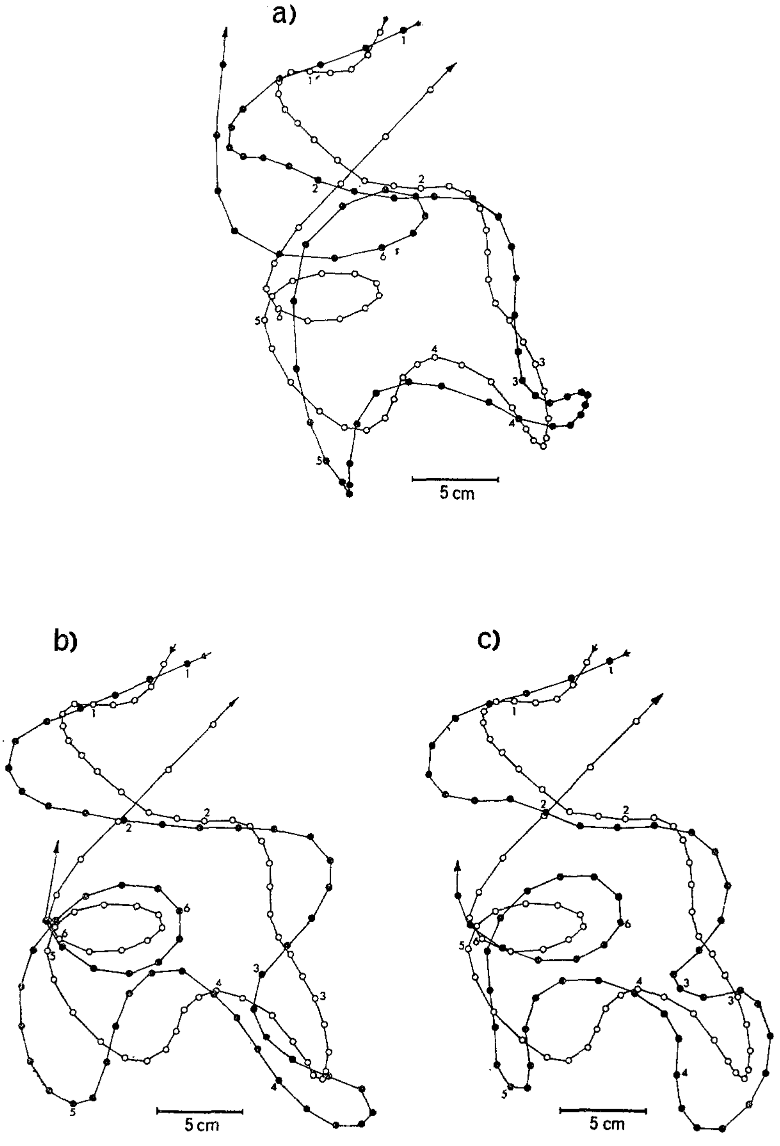

Fig. 11a—c. Attempts to simulate the chase shown in Fig. 4. The course of the leading fly is taken from Fig. 4, and the course of the chasing fly is plotted by the method given in the text. a) Actual chase; b) Simulation using only the $\theta_e$, $\omega_f$ relationship: $k = 20\ \mathrm{s}^{-1}$, $d = 20$ ms. c) As b) but incorporating the relationship between $\omega_e$ and $\omega_f$: $k = 20\ \mathrm{s}^{-1}$, $k' = 0.7$, $d = 30$ ms. The sampling time used in the simulations was 20 ms in b) and 10 ms in c) although for clarity only every second point is shown

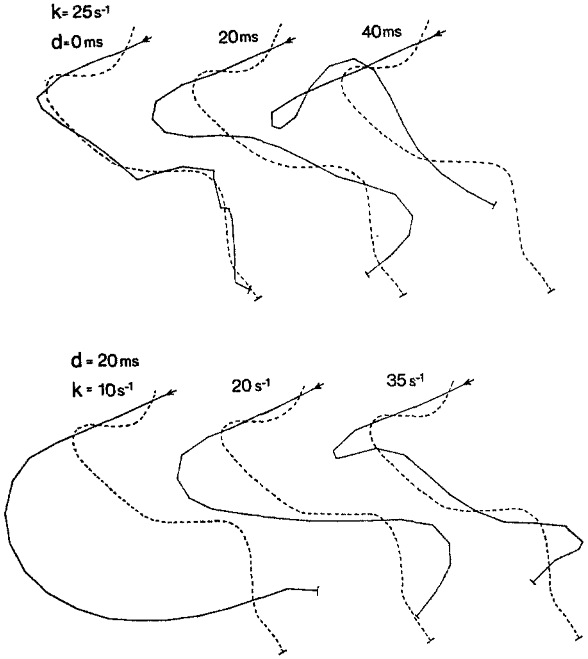

Fig. 12. Effects of changing the parameters *k* and *d* on the form of the simulation of the first two bends in the course shown in Fig. 4. All courses start in the same way, and the cross line indicates where they would have reached when the track of the leading fly ends. It can be seen that reasonable approximations to the actual flight path are only obtained when *k* and *d* are close to values estimated in the results

The inclusion of the error velocity term (Fig. 11c), while not much improving the overall appearance of the course, does have two very important effects. Firstly it "stabilises" the simulated fly somewhat, especially on abrupt turns, and the indirect effect of this is that the delay adopted in the simulation can be increased from 20 to 30 ms, without this producing much overshoot. A 40 ms delay is, however, still unacceptable. This is an important point because the delay obtained in the results section (Fig. 8) seems to be nearer 30 than 20 ms, and also from a physiological point of view 30 ms is already a very short total response latency, and 20 ms probably unrealistic. The second feature, which is better illustrated in Fig. 13, is that the inclusion of some velocity component makes it possible to simulate some turns which are not even qualitatively correct without it. In the real chase, during the right turn between points 2 and 3, the chasing fly has actually begun to turn right

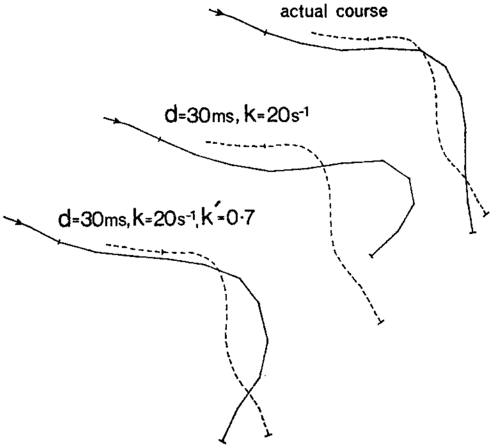

Fig. 13. The effect of including the error velocity term ($k'\omega_e$) on simulation of the second bend in the chase shown in Fig. 4. The middle plot shows the path without this term, and the lower left the improvement resulting from its inclusion. The overshoot is reduced and the turn "anticipated" as in the actual track (upper right)

while the leading fly is still on the left, though moving right. A similar situation occurs in the left turn after 4, and the right turn into the loop after 5. This clearly cannot be simulated with only the position error system, but as shown in Fig. 13 the inclusion of the angular velocity term makes this possible by opposing the effect of the position term while the leading fly is approaching the chasing fly's line of flight, and augmenting it once the line of flight has been crossed. Thus an effect that almost looks like anticipation is explicable.

### *b) Comments on the Nature of the Control System*

#### The Geometry of Chasing Behaviour

It is clear that by turning towards the leading fly the chasing fly will tend to follow it, and if fast enough to overtake it. However, this cannot be viewed simply as a feedback system in which the leading fly provides the input, and the following fly the correcting output. The reason is that changes in the course of the following fly have two consequences: one is to reduce the error angle ($\theta_e$) but the other is to alter the respective positions of the two flies, which changes the angle of the line $FL$ and hence the angle $\phi$ (Fig. 14) in very complicated ways. This second effect is particularly important when the two flies are close together, as a small displacement of either fly can then result in a very rapid change in $\theta_e$, and several instances of this can be seen in Fig. 4. In Fig. 14 an

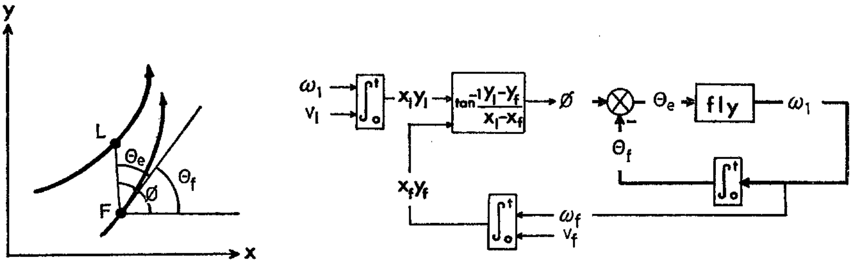

Fig. 14. Left: the geometrical relations between the leading ($L$) and following fly ($F$) at an instant during a chase (represented here as two dimensional). Right: diagram showing the double effect on $\theta_e$ of changes in the angular velocity of the following fly ($\omega_f$). The heavy line indicates the straightforward feedback loop in which changes in course angle of the following fly ($\theta_f$) reduce the error angle ($\theta_e$). The thin lines indicate that $\omega_f$ also affects the relative positions of the two flies at time $t$, and hence the angle $\phi$ of the line joining them ($LF$). In this diagram the relation between $\omega_e$ and $\omega_f$ and the delay have been ignored

attempt has been made to illustrate the complete system for the simplified case of two dimensional flight. The essential point is that the angle $\phi$ is the angle of the line between $F$ and $L$ at any instant, and the coordinates of these points are the resolved vector sums of all the elements ($\omega \cdot dt$, $v \cdot dt$) that went to make up the respective courses since the beginning of the chase. These vector sums are represented by the two integrals in the outer loop in Fig. 14. The problem of working out the effects of changes of $\omega_f$ on $\phi$, the input to the "straightforward" loop, are beyond the scope of this paper, and will be ignored. However, this does mean that the conclusions which follow are only strictly applicable to conditions in which the two flies are well separated, and the effect of $\omega_f$ on the angle $\phi$ is small.

### Stability

In feedback systems containing delays there is always the potential problem of instability. It is therefore worth inquiring whether there is a special reason why the fly should use the particular value of $k$ (20 $\mathrm{s}^{-1}$) that is observed. In a system like this there will be a value of $k$ above which any attempted manoeuvre will result in continuous oscillations of increasing amplitude. It can be shown theoretically and graphically that this occurs when $k > \Pi/2d$, or in this case ($d = 30$ ms) when $k > 52\ \mathrm{s}^{-1}$. For lower values of $k$ the fly will oscillate after each course change, but these oscillations will gradually die out. At lower values still there is no oscillation, and the new course is smoothly, but relatively slowly approached. The ideal value for $k$ would presumably be that at which there were just no oscillations; this is the "aperiodic limit" and is given by $k = e^{-1}/d$, i.e. $0.368/0.03 = 12.3\ \mathrm{s}^{-1}$, if $d = 30$ ms. The value of $k$ used by the fly is slightly greater than this, and indeed simulations like that in Fig. 11b using a value of $d$ of 30 ms do show slight "hunting" around each new course; if $d = 40$ ms (see Fig. 12) these overshoots become very pronounced indeed. However, for a step input graphical estimates show that the size of the overshoot when $k = 20\ \mathrm{s}^{-1}$ and $d = 30$ ms is only about 7%, i.e. the sudden appearance of an object at 100° from the fly's axis would result in an initial turn of 107°, and this error is probably not important. In any case, the small amount of instability introduced is effectively damped out by the error rate feedback [the $k'\omega_e$ term in (3)] that operates in the region close to the axis. From these considerations it seems that the operation of the chasing fly is critically and elegantly adjusted to its task—turning as fast as possible without becoming unstable.

An interesting sideline to this is that one would expect $d$ and $k$ to vary inversely with temperature, if this critical relationship is to be maintained. It would be interesting to know whether cold flies can chase effectively, or whether the breakdown of the critical conditions for effective chasing abolishes this kind of behaviour.

## Relations between Torque, Acceleration and Velocity

Interesting questions arise out of the way the chasing fly changes from one angular velocity to another. Clearly it must accelerate or decelerate in order to do so, and yet acceleration does not seem to be under the control of $\theta_e$, but rather angular velocity itself. This apparent contradiction is resolved if we accept that the initial output of the fly is torque (rotational force about a vertical axis) and consider what happens to that torque. As Reichardt has pointed out (Reichardt, 1973; Poggio and Reichardt, 1973) the fly's rotational dynamics can be approximated by:

$$T = I\dot{\omega} + F\omega,$$

where $T$ is the torque (dyne · cm), $I$ is the moment of inertia of the fly (g · cm$^2$) and $F$ the aerodynamic friction opposing rotation (gm · cm$^2$ · s$^{-1}$). In other words, at any instant part of the torque is taken up in accelerating the fly and part in overcoming air friction. If $I$ is very large compared with $F$ one would expect that $\dot{\omega}$ would correlate well with $T$ (which we are assuming is linearly related to $\theta_e$). The reverse, however, seems to be the case: $\theta_e$ and hence $T$ correlate well with $\omega_f$ and not $\dot{\omega}_f$ so $F$ must be large compared with $I$.

For a step change in torque, the above equation is solved by:

$$\omega = T/F\,(1 - e^{-t/(I/F)}).$$

This expression indicates that when the fly produces torque, it accelerates to an asymptotic angular velocity ($T/F$) with a time constant $I/F$ (s), and this time constant specifies how long the fly will take to reach its final angular velocity. In general, if $I/F$ is similar to or longer than the periods of movements during a chase, the chasing fly will show instabilities of tracking, and attempts to simulate its behaviour will be poor. It is easy, by graphical construction, to determine how $\omega_f$ changes with time when $\theta_e$ changes, for different values of $I/F$, and these constructions can be compared with the "real" results shown in Figs. 5 and 10b. The results of this exercise show that constructed and actual time courses of $\omega_f$ only begin to become importantly different when $I/F$ is greater than about 20 ms, and that any value of $I/F$ below this value will give a good approximation to the courses shown in Figs. 4 and 10a.

It is interesting that Poggio and Reichardt (1973) have estimated indirectly, by methods quite different from those given here, that the value of $I/F$ for female *Musca* lies between 4 and 8 ms. There is no reason for not accepting their conclusions, since *Fannia* and *Musca* are of similar size, and both $I$ and $F$ are related to linear dimensions, and not to any property of the control system governing a particular form of flight.

These times mean in practice that although the course of the fly is similar to that of one with zero moment of inertia, there will be some delay between the application of torque and the attainment of maximum angular velocity. These delays will vary with the kind of manoeuvres made, but from the graphical reconstructions of Figs. 5 and 10b they appear to be in the range 0.5 to 1.0 times the time constant ($I/F$). Using Poggio and Reichardt's estimates this suggests acceleration delays between 3 and 6 ms, and they should not in any case be greater than 15 ms, using the maximal estimate of $I/F$ of 20 ms.

### c) Physiological Inferences

If male flies track each other in the way that has been described, they must have neural mechanisms for converting certain specific kinds of stimuli into appropriate output patterns. The response time of the fly is very rapid, about 30 ms, which includes every process from seeing the stimulus to accelerating to an appropriate velocity. Thus it seems likely that number of neural operations involved will be small, and that it is sensible to inquire how the systems might be organised with as few neurones as possible. The two operations that need explanations are (i) the conversion of stimulus position into angular velocity, and (ii) the conversion, in the anterior regions of the eye, of stimulus velocity into angular velocity. For the moment we shall assume that there exist neurones passing to the thorax whose discharge rate specifies the fly's

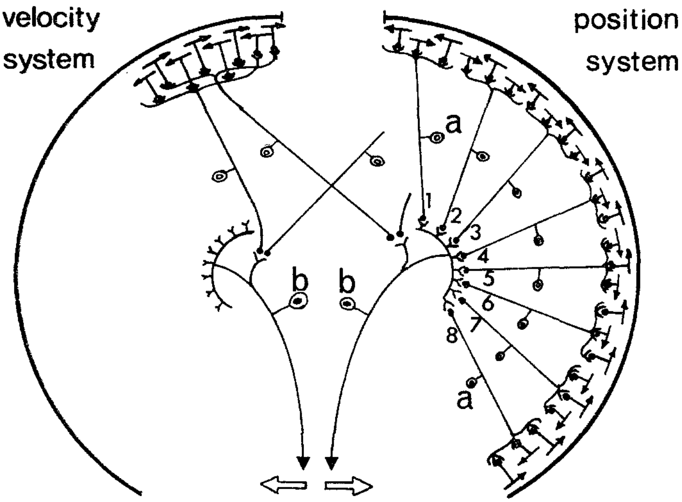

Fig. 15. Possible scheme by which position and velocity information might be extracted. The semicircles represent the two eyes, and it is assumed that each contains an array of small-field movement detectors (represented by arrows). On the right these feed onto interneurones (a) whose effect on the output neurone (b) increases in the numbered order shown, from anterior to posterior. On the left the movement detectors feed onto two units which collect selectively from the clockwise and anti-clockwise "on"-direction sets. These units in turn connect to the output neurones. For further explanation see text

ultimate angular velocity, and concentrate on how the inputs to these neurones might be arranged.

A suggestion as to how the first operation might be performed is given in Fig. 15. This assumes that there are neurones which detect movement and collect from restricted regions of the eye (a). These feed onto a collector neurone (b) which could be the neurone to the wing muscles. The (a) neurones must have the following properties.

(i) They must respond optimally to quite small objects. During the filmed chases the average separation of the two flies was 3.7 cm, and there was no sign of loss of visual contact at distances less than 10 cm. The relevant stimulus angles on the retina for a 6 mm long fly are 9.3° and 3.4°, for the longest dimension of the stimulus.

(ii) They must be capable of responding to objects moving at angular velocities up to at least 2500° $s^{-1}$. This is a conservative estimate based on the distribution of values of $\omega_e$ (Fig. 6) which actually extend to twice this figure. In the case of a 5° object passing ommatidia spaced at 2°, this represents a total "exposure time" of about 2.8 ms per ommatidium, which is not incompatible with flicker fusion frequencies of around 300 $s^{-1}$ (*Calliphora*; Autrum, 1950).

(iii) These cells must be able to distinguish background movement from target movement. During chases the chasing fly turns at angular velocities that cover the same range as the target velocity (Fig. 6b), and so the cells must be capable of ignoring movements of large patterns over the same range of velocities as they respond to small objects.

(iv) The output of these cells should not be a function of stimulus velocity, or stimulus size. Ideally they should fire at maximum velocity if there is a target in their field of view, and not at other times. Finally, the outputs of each (a) cell must be "weighted" according to its location, so that the (b) cell fires in proportion their position. This could be achieved either by a gradation of the firing rate of the (a) cells according to their position, or by differential weighting of their synaptic effectiveness on the (b) cells. It would be premature to speculate at present whether any of the visual interneurones so far recorded in dipteran visual systems have properties compatible with the (a) cells postulated here, not least because most workers have used females for electrophysiological work, and except for the predatory Asilidae and Empidae (Richards, 1927), females do not track other flies. The small-field non-directional interneurones described by Mimura (1971) in the medulla of flies have some of the properties required, notably an indifference to the actual velocity of target motion (iv above), although the angular velocity range given (0.2–2 rad $s^{-1}$) is much smaller than that required here (up to 45 rad $s^{-1}$). McCann and Dill (1969) describe what are probably the same fibres as those Mimura found (class Ia) but they say these have minimum latencies in the range 20–30 ms, which is too great for use in a system whose total latency is 30 ms. Visual interneurones with the essential property of distinguishing small target motion from background motion (iii) have been found in moths (Collett, 1971, 1972) but not so far in flies. Perhaps this emphasises the need to look for electrophysiological properties of neurones in stimulus situations that are behaviourally realistic, and in this case it is likely that realistic conditions will be sex specific.

The other operation, converting angular velocity to output, is a familiar one, since it is similar in many ways to the optomotor response studied by Fermi and Reichardt (1963), and for which there already exist plausible neural candidates in the class II and class IV units (the latter descending to the thorax) described by Bishop *et al.* (1968) and McCann and Foster (1971). These unidirectional motion detectors are maximally sensitive to movements occurring about 20° from the fly's axis, which would account elegantly for the positional restriction on the angular velocity response seen in chasing behaviour. However, these units, like the (a) units postulated above, must also meet the condition that they distinguish small target motion from background motion. It could simply be that a small target ahead of the animal is a more powerful stimulus to these cells than the rest of the field moving in the opposite (or the same) direction, but this is not yet clear. It is also possible that the velocity system (Fig. 15) is distributed over the whole eye, but that it is only detectable in front, where the position system has its smallest effect.

Finally, the total response delay raises difficulties. Using available data, we have McCann and Dill's (1969) estimate of 20 ms as the minimum latency for visual interneurones. Mulloney (1969) has shown in *Calliphora* that the total conduction time from optic lobe stimulation to the appearance of an action potential in the "take-off jump muscle" (tergo-trochanteral muscle) is only 3.6 ms. This is agreeably short and includes one central synapse and a neuro-muscular junction. Heide (1968) found that the direct (non-fibrillar) flight muscles likely to be responsible for yaw give a fused tetanus when stimulated at 60 Hz, which suggests that contraction and relaxation times cannot be much less than 17 ms (*Calliphora*). Acceleration time has already been discussed and could be as short as 2 ms. Even using these optimistic estimates, the total delay should be at least 43 ms, compared with the 30 ms found here. Either visual latencies are rather shorter than existing measurements suggest, or direct flight muscles operate more rapidly, or both.

### *d) Function of Chasing*

Male flies of many species will chase any moving object of about the right velocity and dimensions. Houseflies (*Musca* and *Fannia*) will chase both males and females of their own or other species: for example it is quite common to see *Musca* chasing *Calliphora* twice their size. It is easy also to lure *Musca* off a wall, or *Fannia* from their patrolling flights by throwing small objects past them (e.g. peas). Provided the missile does not pass too close, the animal's response is to fly *towards* it, and to follow its trajectory for a while. This is thus pursuit and not evasion. Greenbottles (probably *Lucilia* sp.) are especially spectacular. They will sit on a particular leaf, and respond to small (1 cm) stones thrown just above them by darting up to intercept, and then flying with the stone for several metres before returning to the *same* leaf. One fly repeated this performance 27 times in succession. Interestingly, a tendency to chase thrown or flying objects turns out to be an excellent indicator of sex. We have never seen a female muscid or calliphorid fly chase anything.

Chasing thus seems to be confined to males and the stimuli that elicit it are not very specific. There are really only two plausible functions for this behaviour: sex—"marriage by capture" to use Richards, (1927) pretty expression—or some kind of territorial defence. Territoriality implies either the defence of a breeding site, or a food-gathering locality, and neither of these possibilities fit the fly's situation. *Fannia* neither feed nor deposit eggs near lampshades. The function of male pursuits must then be to catch females, and indeed this often happens. And, since males of one species all have preferences for the same kind of locality, male—male chases are also inevitable. Although proof of this is lacking, males presumably manage to escape from each other, but females do not—either because they are slower or less good at evasive tactics.

The mechanism of chasing, as described in this paper, raises the interesting possibility that not only sex selection but also species selection may be in a sense "coded" in the chase itself. For example, a small slow fly will never catch a large fast fly, but equally the fast fly with considerable momentum will not be able to catch the slower one if the latter always makes a sharp turn as the fast fly approaches. Appropriate mating could thus arise if the evasion strategy of the female was matched to the manoeuverability of the "correct" male, and thereby provide an effective species sorting system that operates prior to actual contact. Given the large number of different fly species to be found in gardens in summer, some mechanism of this kind seems an attractive possibility.

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