3-D Analysis of the Flight Trajectories of Flies (*Drosophila melanogaster*)

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We have developed a computer system for reconstructing and analyzing three dimensional flight trajectories of flies. Its application to the study of the free flight behaviour of the fruitfly *Drosophila melanogaster* is described. The main results are: a) *Drosophila* males only occasionally track other flies; b) in such cases the fly's angular velocity is a function of the error angle under which the leading fly is seen; c) body saccades can be demonstrated during cruising flights; d) high angular velocities are strongly correlated with low forward velocities, probably reflecting an aerodynamic constraint of flight. The 3-D technique described may provide an adequate tool for studying the organization of the systems present in flies and for relating the free flight behaviour to previous analyses of tethered flies.

Visual control of flight in flies has been approached in recent years by studying either the behaviour of tethered flies [1–4] or the trajectories of free flying flies [5–7]. Until now neither approach has encompassed all dynamical degree of freedom enjoyed by a free flying fly. The analysis of free flight episodes has been carried out by filming only projections onto one plane of three dimensional trajectories. Although houseflies have been filmed simultaneously from above and from the side, lack of synchronization between the two cameras prohibited a precise 3-D reconstruction [7]. In order to overcome these limitations, we have developed a computer based system to reconstruct and analyze the trajectories of free flying flies in three dimensions. In this paper we briefly describe this technique and its use in a preliminary analysis of the 3-D trajectories of *Drosophila melanogaster.*

Flies were placed in a rectangular glass cage (58 × 28 × 28 cm) homogeneously illuminated from two sides by dc-driven fluorescent light bulbs (1000 cd/m^2). The flies were filmed with a high speed camera (Redlake Locam, model 51-0002) simultaneously from one side (x-z plane) and from above (x-y plane) through a mirror leaning forward at 45 ° over the box. The data presented in this paper were obtained with a frame rate of 100 frames/s and an exposure time of 3 ms; the 16 mm film used was Kodak (Eastman Ektachrome Video News Film 7240 Tungsten, 125 ASA). The films were projected frame by frame on a digitizing tablet (Summagraphics-ID) with a single-frame projector (L-W International, Model 224; or Vanguard Motion Analyzer M-16C). For each frame the xy- and the xz-coordinates of each fly were digitized, together with a pair of fixed reference points, used by the computer (PDP-11/34) to correct possible errors of frame positioning. After perspective corrections, the "true" xyz-coordinates of each fly in each frame or even between frames (as given by a spline interpolation routine) were available for further processing by other programs. It is, for instance, possible to obtain stereoplots of the fly trajectories (see Fig. 1) and to perform translation and rotation in 3-D space. The time history of several parameters characterizing flight – for example angular velocity, forward velocity etc. – can also be plotted, together with their histograms, scatter diagrams (see 5), crosscorrelation and autocorrelation functions. In this way, relationships between visual input variables (such as the instantaneous error angle at which a fly sees a target) and output variables (such as the angular velocity of the tracking fly) may be discerned and analyzed. Characterization of input-output relations in all six degrees of freedom (three of rotation and three of translation) is thus in principle possible, although at present the rotation of a fly around its long axis (as well as head movements) cannot be resolved. Since in our analysis we consider the fly as a point in 3-D space, we

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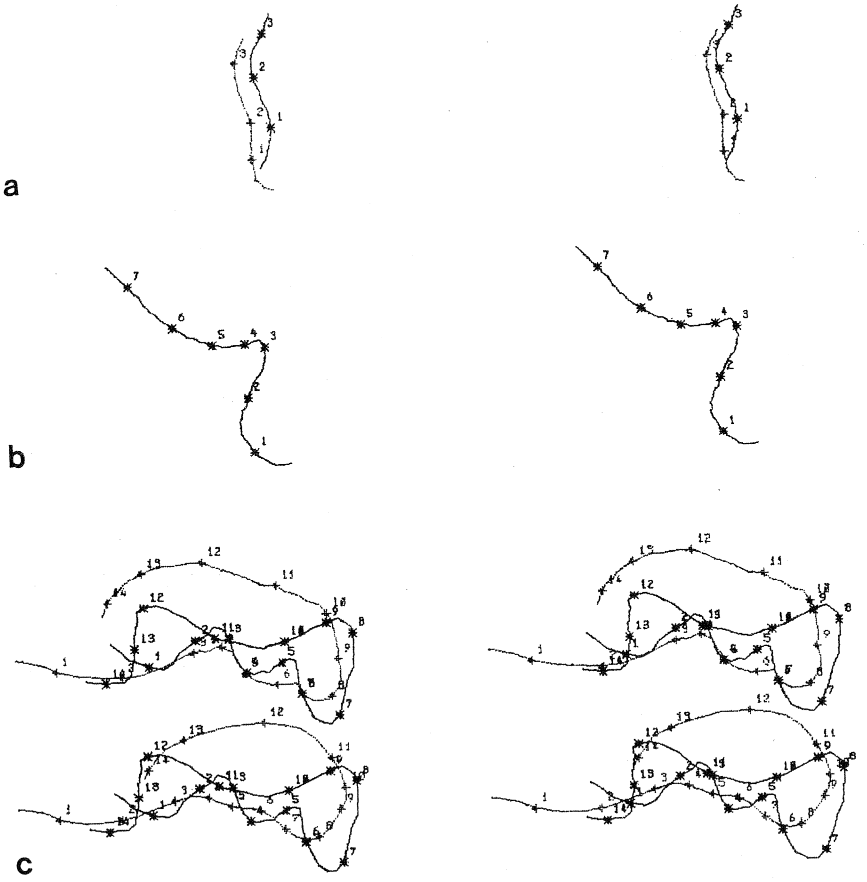

Fig. 1. Stereo plots of 3-D flies trajectories are shown in Fig. 1. They should be observed with standard stereoglasses. Fig. 1 a shows a flight interaction in which a *Drosophila* male (←) apparently tracks another male (∗). Corresponding instants in the two flight paths are numbered at 100 ms intervals. Fig. 1 b shows in 3-D a cruising flight of a "single" *Drosophila* male. Turns are almost never completely horizontal: they are often associated with significant vertical components to the flight. For comparison, Fig. 1 c (top) shows a chase of *Musca domestica* (very probably males). The following fly is able to follow accurately even sharp turns of the leading fly. Fig. 1 c (bottom) show a stereo pair of the simulation of the same *Musca* chase. The stereo pair demonstrates that a 3-D extension of previous models to describe simultaneously the torque, thrust and lift control system leads to a satisfactory prediction of the behaviour of the chasing fly [4]. 1 cm corresponds to 16 cm in space for Fig. 1 c and to 8 cm for Figs. 1 a, b.

are at present able to take into account only 3 degrees of freedom (out of the six + head movements) needed for a complete description. Because of this limitation our analysis of the control systems involved in a 3-D control of flight should be considered as a first order approximation.

Tethered flying *Drosophila melanogaster* under artificial laboratory conditions show tracking behaviour similar in some respects to *Musca* [3, 8, 9]. Although free walking *Drosophila* males follow female flies during courtship and females track other females under certain conditions [10], no analogous behaviour in flight has been yet described. Whilst chasing episodes can be readily observed amongst captive male houseflies, in *Drosophila* the situation is less clear. Careful observation of about 15 minutes (98684 frames) of film has confirmed this impression. We did not observe a single chasing episode comparable in accuracy and rapid changes of course with chases observed in male houseflies. In several instances, however, a fly was apparently able to follow for short periods of time (maximum 500 ms) the course of another fly. One such short tracking-like episode is shown in Fig. 1 a. The almost straight path of the leading fly is a common characteristic of these flight interactions; sharp turns of the leading fly (as in Fig. 1 b) were never followed by the other fly. In contrast, Fig. 1 c shows a rather typical chase between houseflies (digitized from a film kindly provided by H. Wagner) with its many rapid changes of course. From closed-loop tracking experiments with both *Drosophila*, and *Musca*, it is known that a fly controls the torque around its vertical axis as a function of the horizontal error angle ψ. The ψ we have measured does not represent of course the horizontal position of the target on the fly's eye (as in closed loop experiments), because of uncertainity about body rolling and head position. It may be assumed, however, that it provides an approximative indication of the target's position [5]. Closed loop experiments [3] and free flight observations [5] of houseflies suggest that the angular velocity $\dot{\alpha}$ in a horizontal plane is proportional, to a first approximation, to the torque around the vertical axis, since the inertia of the fly is negligible compared to its (aerodynamic) "friction" coefficient. Independent measurements on tethered flies free to rotate around the vertical axis have confirmed these estimates [14]. It seems plausible that for *Drosophila* the inertia is even more negligible.

In addition we expect that acceleration components may also be negligible for the remaining degrees of freedom. For these reasons (and since our data are limited to 3 degrees of freedom) we will consider the angular velocity of the fly around its vertical axis as a first approximation of its torque. As a consequence, we expect that the presence of a tracking system controlling the torque as a function of the error angle should be reflected in a correlation between ψ and $\dot{\alpha}$ with a certain delay ε (for *Musca* and *Fannia* males $\varepsilon = 20-30$ ms

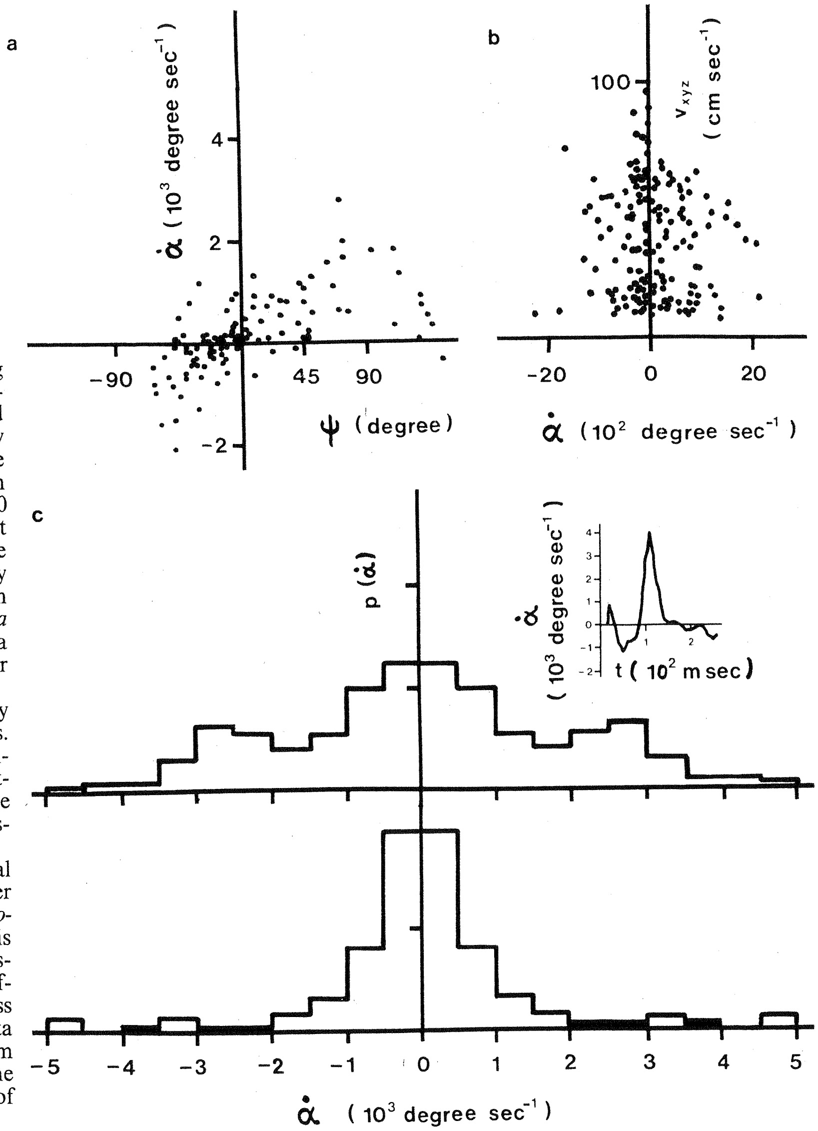

Fig. 2. a) Scatter diagrams showing that the angular velocity of the following flies (*Drosophila* males) $\dot{\alpha}$ (and therefore the torque) is controlled by the horizontal error angle ψ. The maximum of the correlation between ψ and $\dot{\alpha}$ occurs for a delay of between 20 and 30 ms. The correlation coefficient for this delay is 0.76. The slope of the regression line is about $18 s^{-1}$ (roughly the same value has been measured in tethered Musca, in free flying *Fannia* and in free flying *Musca*). The data are taken from 6 tracking episodes for a total of about 2000 ms flight.
b) Relationship between 3-D velocity and angular velocity for various flies. The maximum of the correlation always occurs for 0 ms delay. The scatter diagrams are basically the same for either leading, tracking or "cruising" flies.
c) Histograms of the 2-D horizontal angular velocity $\dot{\alpha}$ for chasing (lower plot) and "single" (upper plot) *Drosophila*. In this last case the histogram is multimodal, consistently with the presence of two processes with quite different time courses, a slow process and a fast saccadic process. The data are taken from 4 flight episodes (from a total of 1700 ms), each showing one saccadic-like turn. The time course of such a turn is shown in the inset.

[5, 16]). The scatter diagram of Fig. 2 shows that for *Drosophila* there is indeed a significant relationship between ψ and $\dot{\alpha}$. This relationship is roughly linear for $-50° < \psi < +50°$; the maximum of the cross-correlation between ψ and $\dot{\alpha}$ indicates a delay in the order of 20–30 ms. All this suggests that the short interactions observed in free flying *Drosophila* may show a tracking behaviour similar to the one inferred from closed-loop experiments in *Drosophila* and from closed-loop and free flight data in houseflies [8, 9]. Similar scatter diagrams show that *Drosophila* (either male or female) are probably unable to effectively control their forward velocity as a function of the distance from the target, similarly to female *Musca* and unlike male *Musca.* This seems again to suggest that tracking episodes in *Drosophila* flights are a (necessary) byproduct of a fixation system perhaps more concerned with fixation of objects to land on [7]. The correlation between the vertical velocity (associated with the fly's lift [1, 2]) and the vertical error angle ϑ is rather poor in *Drosophila.* In *Musca* this degree of freedom is controlled almost as efficiently as rotation around the vertical axis [16]. For male *Drosophila* most tracking episodes we have digitized [9 out of 11] show that the following fly is at the same level as the leading fly or below.

These results confirm the observation that courtship tracking is neither initiated nor maintained by flying pairs of *Drosophila melanogaster.* It is possible, however, that flight is important for courtship in other respects. Courtship stimulating chemicals may be preceived by males during flight, and they could determine gross course control and even a landing site.

As already observed in *Fannia* [5], forward velocity (associated to the fly's thrust) is coupled to angular velocity. Scatter diagrams (Fig. 2b) reveal a maximum in the cross-correlation for 0 ms delay, for all flies (leading, chasing and singles), as one would expect for a pure aerodynamic phenomenon. The data can be interpreted in the following way: there is an upper bound to the 3-D forward velocity and this bound decreases monotonically with angular velocity (from about 100 cm s^{-1} at $\dot{\alpha} = 0° s^{-1}$ to 10 cm s^{-1} at $\dot{\alpha} = 2000° s^{-1}$). Interestingly the observed maximal angular velocities are larger than the values expected from the torque values measured in tethered flies. From closed loop experiments an estimate of the relation between torque and angular velocity leads to an upper bound of 87 ° s^{-1} per 10^{-9} Nm [8, 9]. Published peak values of *Drosophila* torque are below 4×10^{-9} Nm [8, 9], corresponding therefore to peak angular velocities of less than 400 ° s^{-1}. Significantly higher angular velocities seem possible in free flight (2000 ° s^{-1} in Fig. 2a and 4000 ° s^{-1} in the inset of Fig. 2c). Although this may in part be due to noise in our digitized data (amplified in the angular velocities, which correspond to second derivatives of the trajectories), in free flight additional mechanisms probably increase the effective torque produced by the fly. Firstly the torque measured in still air may be effectively increased by aerodynamic effects under streaming air conditions [11]. In addition steering by posture of the legs and the abdomen [2] and one sided braking by posture of the wing internal to the turn [12, 13] may produce in free flight torque components absent under tethered conditions because of the absence of streaming air. The torque component associated with braking would be generated mainly at the expenses of forward thrust, consistently with the dependance of v on $\dot{\alpha}$. Steering by posture of the legs and of the abdomen has been shown to be under visual control [2]. It is interesting to speculate whether the torque component possibly provided by braking by a wing may be controlled by the visual input according to rules somewhat different from the ones obeyed by the torque component measured in tethered flying flies.

It has been recently proposed that tethered *Drosophila* perform body torque saccades around their vertical axis [9]. The standard criterion for the definition of saccades, as used for vertebrate eye movements, relies on their much faster time course [4, 6, 14]. According to this criterion the presence of body saccades in free flight could be revealed by a multimodal histograms of $\dot{\alpha}$, indicating the presence of 2 processes (the normal one and a saccadic one) with widely different time courses. While histograms of $\dot{\alpha}$ during tracking interactions are unimodal for both flies (Fig. 2c), the situation is different for some "cruising" (non tracking) flights especially chosen because of their sharp turns. Fig. 2c shows that in this case $\dot{\alpha}$ has a multimodal distribution, strongly suggesting the presence of a fast process in addition to the slow, roughly gaussian stochastic torque process [3]. The saccadic nature of the associated turns can be seen from the time course of $\dot{\alpha}$ (inset Fig. 2c) and can be compared with the saccades observed in *Syritta* [6] and the torque pulses described in *Drosophila.* The duration of the saccades varies between 50 and 100 ms and their peak velocity values between 2000° s^{-1} and 5000° s^{-1}, each one leading (in the observed cases) to a total angular shift of about 100°. They are therefore quite different from the much smaller and longer torque pulses measured in tethered *Drosophila* but similar to the body saccades generated by tethered *Drosophila* free to rotate around their vertical axis [9]. The apparent absence of saccades during tracking reflects the fact that the fixation system is most of the time a nonsaccadic, continuous system (our tracking data are then automatically biased against saccadic trajectories of the leading fly, because a saccade would immediately disrupt tracking). Our data rule out the possibility that these sharp turns in the x-y projection of the trajectory are an artefact of the 3-D nature of the flights. The additional analysis of 3-D angular velocity ($\dot{\alpha}$ is the 2-D angular velocity on the x-y projection) supports these conclusions and indicates the presence of a fast process for "cruising" flies but not for chasing flies.

The technique introduced in this paper promises to be a adequate tool for the analysis of the control systems used by flies for visual guidance of flight, including tracking, fixation and landing, making feasible a complete 3-D description of the input-output relations involved in visually guided behaviour. As a consequence it will also be possible to compare the behaviour of flies in free flight to that displayed by tethered flies. Similar 3-D data for *Musca* [16] will allow to extend a theory of tracking behaviour in *Musca* to describe the additional degrees of freedom involved in 3-D flight. For instance, Fig. 1 c (bottom) shows a 3-D simulation of the flight shown in Fig. 1 c (top). The model [3, 4, 15] can produce the trajectory of the chasing fly from the trajectory of the leading fly with a satisfactory degree of agreement. This does not prove the correctness of the specific model, especially because computer simulations show that addition of a "looking around" or "noise" term [3] in the phenomenological equations strongly affects the simulated trajectories. For instance, it may lead to either correct landings or near-misses (Poggio, Reichardt and Wagner, unpub.).

In summary, our 3-D analysis of flight trajectories show that *Drosophila melanogaster* males are able to track other flies. These tracking episodes are, however, infrequent and short. In addition, saccadic changes in angular velocity have been clearly identified during cruising but not during tracking flights.

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