

AERODYNAMIC CAPABILITIES OF FLIES, AS REVEALED BY A NEW TECHNIQUE

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SUMMARY

Forces and torques exerted by fixed flying *Calliphora erythrocephala* were monitored with strain gauges. *Calliphora* was shown to have independent control of all possible parameters of motion (lift, thrust, side-slip, roll, yaw, pitch). During voluntary manoeuvres, the fly modulated several or all of these parameters simultaneously. Modulations of certain parameters were strongly correlated. Possible applications of the strain gauge apparatus and limitations in the use of open-loop experiments for the study of flight behaviour are discussed.

INTRODUCTION

A flying body can rotate or translate in each of the three coordinates of space (Fig. 1). Little is known of the abilities of the vast majority of birds and insects to make use of these six degrees of freedom.

Most experiments concerning flight control in insects are based on the observation of only one flight parameter: yaw, lift, thrust or roll. Some studies have been made of the relationships between these parameters. For instance, it has been shown that thrust and lift are not independently modulated during tethered flight of *Drosophila* (Götz, 1968) whereas thrust and yaw are independent in this fly (Götz, 1968) and *Musca domestica* (Spüler & Heide, 1978). Lift and yaw are independent in tethered *Drosophila* (Götz, 1968).

Existing instruments that are capable of recording two flight components simultaneously are those of Nachtigall & Wilson (1967), Nachtigall & Kogge (1975) and Spüler & Heide (1978). Each is prone to cross-talk, and only the latter responds fast enough to record the transient responses of the animal.

In the present paper, an instrument is described which simultaneously monitors sustained and transient responses of a stationary, flying *Calliphora erythrocephala*, in all six degrees of freedom. From the forces and torques that were measured, deductions are made about the aerobatic capabilities of the fly.

MATERIALS AND METHODS

Animals

Experiments were carried out with females of *Calliphora erythrocephala* from the Institute's stock. The animals selected were 6-10 days old, weighed 55-65 mg, showed flight activity in the breeding cages and looked completely undamaged.

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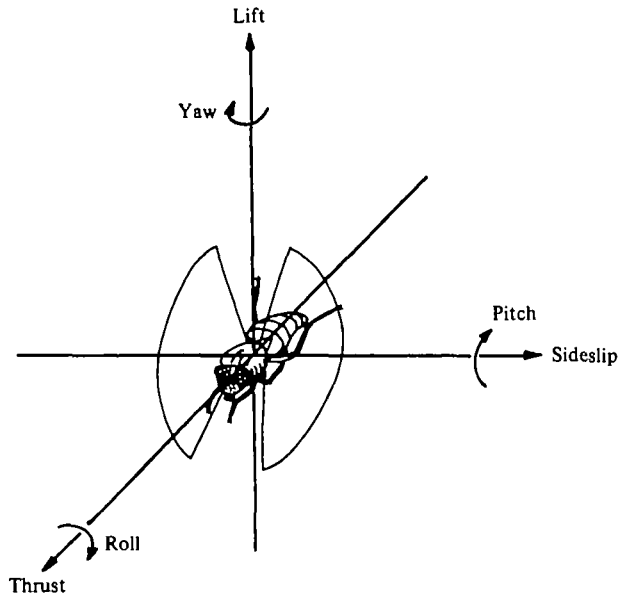


Fig. 1. The six degrees of freedom of a flying body. Translation is possible in three independent directions and rotation around three independent axes. For the sake of simplicity, and also in the hope of remaining close to nature, an orthogonal reference system was chosen where rotational axes coincide with translational axes. The names of the different movements were derived from aviation vocabulary.

Room conditions

All experiments were carried out at 19–21 °C and 50–70% relative humidity. Ambient illumination of the room was 60 to 150 lx.

Preparation of the animals

The flies were briefly anaesthetized with carbon dioxide (for about 5 s and glued to a cardboard triangle by means of a molten mixture of beeswax and resin (2:1), or, as a control of the influence of the heated wax, with a dental epimine cement (Scutan-Espe). The cardboard triangle was cemented to the front of the thorax in the median sagittal plane in such a way that the fly was held horizontally once clamped. Wing and head movements were unhindered.

Recording apparatus

Forces in any direction and torques around any axis were recorded by using a symmetrical arrangement of plastic leaf springs, each of which was fitted with two semiconductor strain gauges (Philips PR 9862), one on each face of the spring (Fig. 2). The fly was fixed in the centre of the system by means of a table-like rack, the legs of which were flexible steel needles (N) (diameter 0.3 mm, length 30 mm) that rested in a tiny half-spherical excavation on the ends of the four central springs. The needles decomposed the torques into forces that were transmitted to the springs. The mechanical and electrical symmetry of the device resulted in low mechani

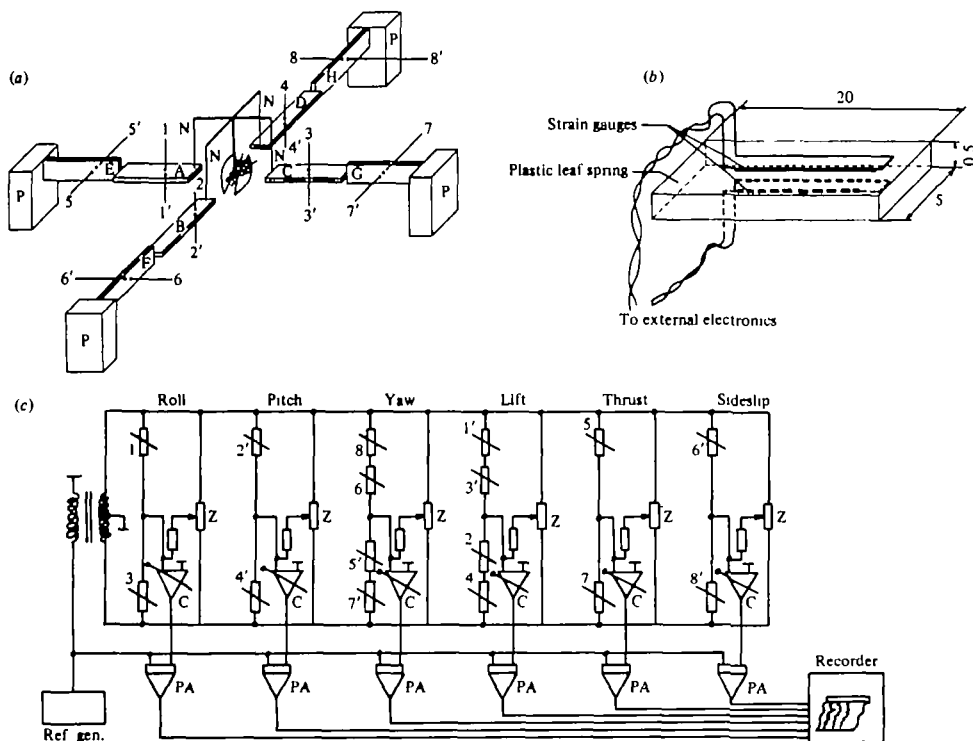


Fig. 2. Strain gauge apparatus for open-loop flight measurements. (a) General view of mechanical construction. The fly is fixed in the symmetry centre of a cross made out of eight plastic leaf springs (A to H). Each arm of the cross consists of two springs, the length axes of which are horizontal; the inner springs have their face horizontal, the outer ones vertical. The animal is fixed to a table-like rack, the legs (N) of which are slender steel needles. The tips of the needles are resting on the free ends of the innermost leaf springs (A–D). (b) Detailed view of an isolated leaf spring. Each leaf spring is fitted with a strain gauge on each face. (c) Electrical circuitry of the apparatus. Each strain gauge forms one arm of a bridge circuit. Each bridge contains two gauges such that it reacts to forces or torques in only one coordinate. To minimize noise, the bridges are fed with alternating current at a frequency of about 1000 Hz and the following amplification stages are phase locked to the feeding frequency. Ref. gen., reference frequency generator; Z, zero adjust; C, calibration; PA, phase locked amplifier with low pass filter (20 Hz).

cross-talk between the different channels and low sensitivity to temperature. The electrical output was recorded on a six channel chart recorder (Oscillomink–Siemens) as shown in Fig. 4. These traces are corrected for remaining drift and the base line is interpolated from the non-flight periods.

The functioning of the apparatus is exemplified here for the measurement of the thrust. If the fly exerts a pure thrust force, it will bend the springs E and G (Fig. 2a) forward. This, in turn, causes the gauges 5 and 7' to be compressed and the gauges 5' and 7 to be extended. The ohmic resistance of 5 and 7' will fall while the resistance of 5' and 7 will rise. The bridge which is built out of strain gauges 5' and 7, which is the measuring bridge for thrust (Fig. 2c), will be moved out of balance. Forces in the other directions influence different pairs of gauges, and hence unbalance different bridge circuits.

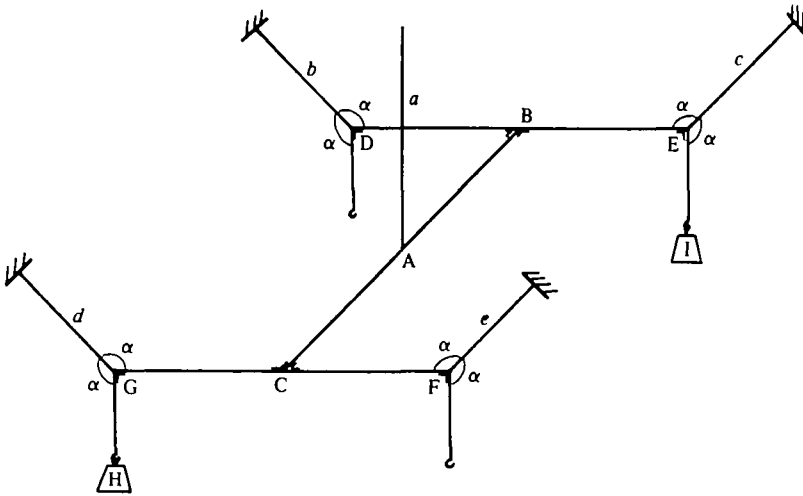


Fig. 3. Calibration of the setup; principle of the virtual pulleys; generation of force-free torques (example, yaw). A lever (BC) of known length was fixed to the axis (a) of the strain gauge apparatus (in the position that is normally occupied by the fly). 4 thin synthetic threads are bound to the extremities of the lever (BD, BE, CF, CG). Other threads (b, c, d, e) were knotted to them at one end and to a fixed support at the other end. Equal weights (H, I) were hung to the threads d and f . Each of the threads b, c, d, e was positioned at an angle ($\approx 135^\circ$) to the two other threads to which it was knotted and was located in the same vertical plane as them. The knots in D, E, F and G have like pulleys as long as the movements imposed by the weights to the system remain negligibly little (virtual movements). The vertical forces F applied by the weights are hence transmitted to the horizontal threads and create a torque BC. F around the vertical axis (a). The remaining threads, which do not carry weights were used to compensate for the weight of the threads themselves.

Test and calibration

Microscope control showed that the fly's body movements caused by its own forces never exceeded $3.5 \mu\text{m}$ or $8 \cdot 10^{-3}$ degrees. This guaranteed a satisfying open-loop situation.

Static calibration was carried out according to a procedure developed earlier for the calibration of a torque compensator (Götz, 1964), using weights and very thin synthetic threads of almost negligible weight, connected to form virtual pulleys (Fig. 3). Calibrations are given in the results. Linearity of the measurements was not determined directly, but it was inferred from the linear characteristics of the strain gauges and from the smallness of the deformations imposed to the springs (see above) that the non linearity would hardly be measurable in the range used. Cross-talk was too little (less than 1% of the calibration bars in the diagrams) to be measured. No attempt was made to calibrate the apparatus dynamically. The lowest resonant frequency of the apparatus was about 350 Hz.

Stimulation

Visual stimulation was chosen to elicit flight manoeuvres. The stimuli consisted of arbitrarily moving black or white pieces of cardboard and also of lights turned on and off at arbitrary positions around the fly. The range of stimuli was made as wide as the experimenter's imagination and spontaneous skill allowed in order to evoke a broad spectrum of reactions.

Interpretation of results

In this preliminary work, the interpretation of the fly's patterns of forces was made by visual inspection of the records. No statistical methods were used. Two parameters were considered independent when it was possible to find modulations of one parameter that were not correlated with variation of the other. Nonreciprocal relations were not considered as dependencies and were examined separately.

RESULTS

Flight was recorded successfully from 12 flies (in about 300 spurts), but all the results presented here come from a single fly in unmodified position in the apparatus (27.4 min of flight in 89 spurts).

Recordings of typical flight behaviour are shown in Fig. 4.

Duration of flight periods

Flight periods did not generally (80% of all cases) last longer than 25 s (Fig. 4), which agrees with the period observed by Heide (1971) but is less than that reported by Liske (1977).

Polarity of flight parameters

Lift and thrust were always positive, i.e. lift was oriented upwards and thrust was directed forwards (Fig. 4). Pitch was almost always positive (i.e. front up), but some rare and weak episodes of negative pitch were observed (e.g. Fig. 4*b*) (4 cases out of 89). Negative pitch never exceeded half the maximum amplitude of positive pitch for the same fly.

Stability of flight parameters

Lift was the only parameter to consistently reach a steady level (Fig. 4). Other parameters were less steady and showed a tendency to increase in amplitude during the flight period. This may reflect a period of analysis of sensory feedback.

Coupling between flight parameters

No strict coupling was observed between flight parameters, indicating a potentiality for good manoeuvrability. However, the parameters were very often modulated simultaneously and, furthermore, not all of them occurred in both polarities with equal frequency.

(a) One way coupling between lift and thrust

While strong modulations of the lift force were rare, every fluctuation of this force was paralleled by a modulation of thrust (Fig. 4). This relationship was not reciprocal **not** every modulation of thrust was accompanied by a modulation of lift. Indeed **only** strong modulation of thrust could happen without being paralleled by any disturbance of lift (Fig. 4*d*).

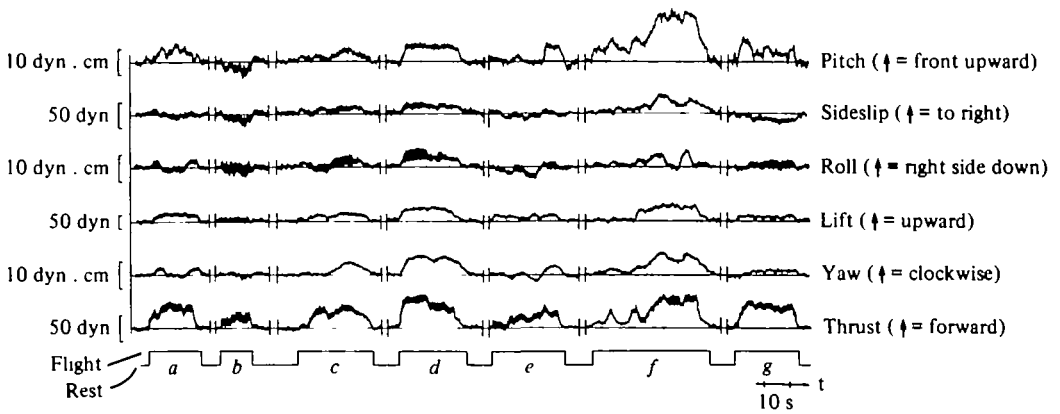


Fig. 4. Recordings of some typical flight episodes. (a) Flight sequence with positive pitch; there is little modulation of lift as compared with other flight parameters. (b) Sequences like this where the pitch is negative (the fly tries to dive) are rare, negative pitch does not reach the strength of the positive episodes. During the negative pitch periods, the lift force decreases strongly, but never gets negative. (c) Modulations found in the lift trace have parallels in the thrust but, (d) not every modulation of the thrust finds a parallel in the lift. (e) Yaw and roll mostly follow fairly parallel courses. (f) The yaw and roll parallelism is not an absolute rule. (g) In this unique case, sideslip had its polarity oriented against yaw and roll.

(b) Relation between pitch and lift

Although pitch and lift were not always modulated in parallel, lift was always positive when pitch was positive. When the fly tried to dive (i.e. negative pitch), the lift force was strongly reduced and in some instances went down to zero, but never got negative. In all the episodes of negative pitch, thrust was reduced too, but never vanished (Fig. 4*b*).

(c) Roll and yaw

Since roll and yaw often followed different time courses (Fig. 4), these parameters are principally to be considered independent. In the vast majority of flight spurts (96%), however, they were modulated in parallel. In most cases, roll tended to pull down the side of the fly that was at the inside of the turn imposed by the yaw torque (Fig. 4), implying a voluntary manoeuvre similar to that of an aeroplane turning in flight.

(d) Sideslip

The sideslip force was always weak. The recordings of many flight spurts did not show any recognizable sideslip at all. In most instances during which sideslip occurred, it was strongly coupled with yaw and, to a lesser extent, with roll. This indicates that during a turn to the right, for instance, the fly would have applied a sideward force also to the right. In a unique case, sideslip had its polarity against roll and yaw (Fig. 4*g*). This time the sideward force was applied to the left while the fly tried to turn and roll to the right. The possible use of these combinations of force and torques is mentioned in the Discussion.

DISCUSSION

Properties of the strain gauge apparatus

The above experiments have shown that the strain gauge apparatus provides a simultaneous record of all flight parameters of a fly. This device, through its simple geometry, is relatively easy and cheap to build yet delivers accurate measurements if quasi static forces are applied to it. The dynamic range of the apparatus is limited by its inertia, which is about 500 times larger than that of the fly. Nonetheless, the mechanical part of the setup, including the strain gauges, transmits the individual wing beats (about 150 Hz). In the traces shown (Fig. 4) the wing beats are eliminated by the low pass filters (20 Hz, see Fig. 2c) of the subsequent electronic amplification stages in order to improve the readability of the recordings.

Even in the most rigid instrument, movements result from forces produced by the fly. To allow open loop measurements with *Calliphora*, these displacements have been kept below the movement detection threshold of the fly's visual system. The minimal angular displacement that has been reported to elicit an activity change in the fly's nervous system is $6 \cdot 10^{-2}$ degree (Zaagman, 1977). The maximal angular displacement that *Calliphora* can undergo by exerting its torque at the strain gauge apparatus is $8 \cdot 10^{-3}$ degree. This value produces just significant signal/noise ratios in the strain gauges. For experiments with *Musca*, slightly thinner springs would be required. Measurements with flies as small as *Drosophila* can hardly be realized with a similar apparatus because of the brittleness of the silicon transducers: a setup of sufficient sensitivity would be very fragile.

Applications of the strain gauge apparatus

In the present study, the measurements of flight behaviour were limited because *Calliphora* flew for only brief spurts, apparently because of a lack of sensory feedback (a head-on air current could prolong flight). Also, the large amplitudes of forces and torques and the comparatively slow modulations in the flight patterns are probably due to the restrained situation of tethered flight. Despite these limitations the recordings indicate that *Calliphora* is capable of many flight manoeuvres. These will be discussed in more detail.

Parallelism of yaw and roll

Although it is able to control independently yaw and roll, the fly makes little use of this freedom: roll and yaw act mostly in a concerted way to incline the fly into the turn. This behaviour makes sense in the frame of *Calliphora*'s flight patterns. This fly is heavy and flies fast; if it were to use only yaw in order to turn, it could describe only very wide curves and would be unstable around the roll axis.

The lift - thrust relation

The results show that lift and thrust are asymmetrically coupled: when lift is modulated then thrust is also, whereas lift can remain steady while thrust is modulated. This could be because the lift vector of *Calliphora* is inclined forward, and hence has a positive thrust component (Fig. 1). This lift-thrust relation is quite

different from the strong coupling described by Götz (1968) for the fruitfly and probably more like the situation found by R. W. Rodieck (unpublished observations) for *Musca*.

Correlation between pitch, lift and thrust

It seems probable that *Calliphora* has a certain speed range at which it can exert optimal control, and that it tries to remain in this speed range. This could be the reason why lift and thrust are considerably reduced during diving. The very scarce occurrence of diving should be a consequence of the fixed position of the fly. At the start of the flight, it is normal for *Calliphora* to try to rise. The failure to achieve take-off might also be a partial explanation for the brevity of the flight episodes.

Sideslip – linkage to yaw and roll

Because of the weakness of sideslip and its almost complete coupling to yaw, this force might be considered as a side effect of the state of other parameters like yaw and roll. However, the existence of one single but clear sequence where the polarity of sideslip is opposed to roll and yaw excludes this interpretation. Such a manoeuvre, with little or no thrust, would allow the fly to circle around a target while keeping its head pointed toward it, as found by Collett & Land (1975) for *Syrirta pipiens*. (Note: in the example of fig. 7, the thrust is not close to zero, so that in free flight the fly would have described a steep spiral instead of a circle.) In the normal situation, where sideslip has the same polarity as yaw, its use would be to introduce a supplementary push toward the centre of the turn, rendering it sharper.

Conclusion

The description of fly aerobatics on the basis of the six degrees of freedom of motion is incomplete as long as body posture is not taken into account. Body posture may play two different roles. Firstly, certain flight manoeuvres may be performed by the fly only in a particular posture. Negative lift might have been observed if the fly had been fixed head down in the recording apparatus. Secondly, it seems most plausible that flies also use aerodynamic steering. After all, aerodynamic steering has been predominantly adopted in flight technology. Such flight manoeuvres cannot be fully studied with tethered flies at the strain gauge apparatus.

It is also very important to keep in mind that the fly's position in the strain gauge apparatus was chosen arbitrarily and varied slightly from animal to animal. The rotation centre of the device probably does not coincide with the (maybe variable) focal point of the static and aerodynamic forces in the fly's body and this mismatch could readily introduce torques in a partially uncontrolled way. The imprecision of the positioning of the animal also poses some problems in the estimation of the independency of flight parameters. In principle, only traces obtained from the same animal in an unmodified position can be compared safely.

Research in several laboratories is currently directed towards the relationship between properties of giant neurones in the lobula plate and visual flight control behaviour. It is obvious from the present study that *Calliphora* modulates several flight parameters at a time during flight manoeuvres. Since there is no reason

Believe that this would be different in response to defined visual stimuli, one would like to know the main features of course control before trying to interpret the properties and interactions of neurones mediating them.

Limited as the strain gauge apparatus may be for recording true flight manoeuvres, in the open-loop experiments on visual flight control it may tell us more about the underlying behaviour than the uni- or two-dimensional techniques used so far.

I dedicate this paper and the preceding one (Blondeau, 1981) to my wife Gabi. They describe part of a doctoral thesis made in the Max-Planck-Institut für biologische Kybernetik in Tübingen (W.-Germany).

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