Simultaneous Recordings of Torque, Thrust and Muscle Spikes from the Fly *Musca domestica* during Optomotor Responses

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A new torque/thrust meter is described. Torque, thrust, wing-beat frequency and spike activity in direct flight muscles are recorded simultaneously during optomotor responses of the fly *Musca domestica*.

In earlier studies on the optomotor response of flies torque, thrust and spike activity in direct flight muscles have been recorded and analysed in separate experiments. To gain further information about the flight control system it is advantageous to correlate these parameters with one another. This paper describes an experimental set-up that allows both the above mentioned parameters and the wing-beat frequency to be recorded simultaneously while the fly is stimulated by the motion of stripe patterns.

Torque as well as thrust is measured using two semiconductor force transducer elements (Akers AE 801). This force transducer has already been applied to the measurement of torque by Sandeman *et al.* [1], Liske [2], and Srinivasan and Bernard [3]. The torque/thrust meter shown in Fig. 1 works on the following principle: The fly is fastened to the connector (c) that is clamped between the torque transducer (d) and the thrust transducer (i) without any other bearing. The torque transducer (d) is suspended on plate-springs (f) that adapt to movements in the direction of thrust whereas they do not yield to forces transferred by the lever (k) during torque reactions. The axis of rotation is determined by the points of two insect pins (g) that are pressed against the thrust transducer (i) by the tension of the plate-springs. During generation of torque and thrust the transducer beams are deflected in the directions indicated by arrows in the enlarged drawings of the suspension points. These are the directions of strain-sensitivity of the transducer beams.

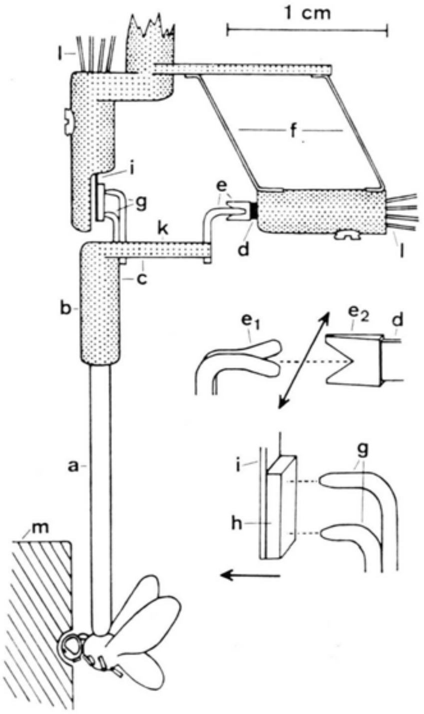

Fig. 1. Design of the torque/thrust meter. The glass capillary (a) carrying the fly is inserted into the tightly fitting balsa tube (b) of the connector (c). The connector is coupled firmly to the silicon beam of the torque transducer (d) by two forks that are at right angles to each other (e). The torque transducer is suspended on plate-springs (f) so that by spring tension the blunt tips of the two insect pins (g) are secured to the rubber cushion (h) that is glued to the silicon beam of the thrust transducer (i). When the fly generates thrust and torque the beams of the transducer elements are deflected in the direction indicated by arrows. The deflection is sensed by a strain-sensitive resistor on either side of the transducer beam. (k) balsa lever of connector, (l) leads of transducer elements, (m) screen.

For an experiment the fly is mounted dorsally to the sealed end of a glass capillary by cyanoacrylate adhesive. The head is fixed to the thorax by a small drop of a mixture of beeswax and collophonium. To keep the fly from tearing out the electrode leads and to prevent inhibition of flight by tarsal contact all legs are cut off in the middle of the femura. Stainless steel wires (diameter 20 μm), electrolytically sharpened to a tip diameter of about 10 μm, are used for recording of spikes from direct flight muscles. The reference electrode lead is placed in the abdomen. Then the fly is positioned in the torque/thrust meter. The fly is stimulated by horizontal motion of two stripe patterns in front of the fly (method by Götz [4]). A screen (Fig. 1, m)

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placed in the median plane directly in front of the fly's head narrows the visual field of each complex eye to its ipsilateral region. The wing-beat frequency is recorded by sensing the modulation of the intensity of an IR light beam that is interrupted by one of the swinging wings (method by Heide [5]). – The torque and thrust recordings taken in this experimental set-up do not show any perceptible interference with each other provided that the fly's yaw axis is in sufficiently good line with the axis of rotation of the torque/thrust meter.

An example of a set of recordings is given in Fig. 2. Just before the experiment both halteres of the fly were extirpated since longer and steadier flights can be initiated under this condition. (Turning reactions of flies without halteres correspond to those of flies with intact halteres, but usually the reactions of the former are weaker.) Muscle spikes were recorded from the right and left direct flight muscle III1 (numbered according to Heide [6]).

It has already been shown that in most cases each direct flight muscle III1 is active only during spontaneous or induced turning reactions to the contralateral side (Heide [5, 7]). In some flies, however, the muscles III1 may spike continuously or simultaneously on both sides (Fig. 2 A, B and Spüler [8]). In Fig. 2 B the left muscle III1 is activated during stripe motion to the right (second period of pattern motion) while at the same time the spontaneous activity in the right muscle III1 is decreased (Fig. 2 A). This demonstrates that excitation as well as inhibition is involved in the generation of the motor output pattern activating the muscles III1 (Spüler [8]). During the stripe motion to the right a considerable torque to the right is produced (Fig. 2 C). Diverging from the usual findings no marked increase in spike frequency in the right muscle III1 and no torque to the left is produced during pattern motion to the left (third period of pattern motion). This corresponds to Heide's [7] findings that the response activity of direct flight muscles can vary considerably or may even be fully suppressed in spite of constant visual stimuli. McCann and Mac Ginitie [9] point out the high variability of torque reactions during the first seconds after the onset of pattern motion and the greater uniformity after 30 – 60 seconds. Thus, small or absent responses to short-time pattern motions are not inconsistent with the rather uniform torque reactions obtained by Fermi and Reichardt [10] and by Götz [4] using pattern motions lasting 1 or 2 minutes. – In Fig. 2 the recordings of torque and thrust show completely different courses (C and D). This confirms the "principle of independent torque and thrust con-

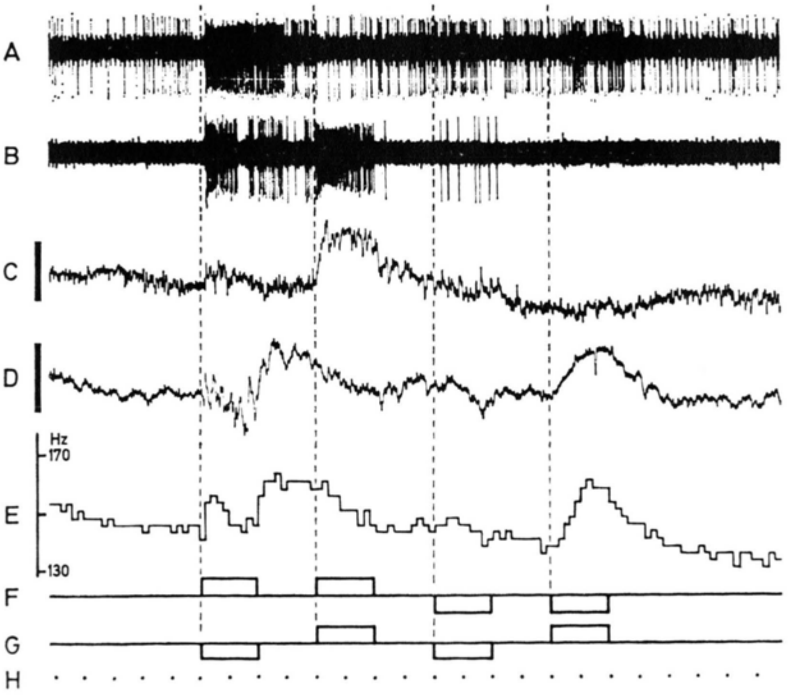

Fig. 2. Simultaneous recordings of the activity of direct flight muscles, torque, thrust and wing-beat frequency. *A*: Spikes recorded from the right muscle III1, high-pass filtered (cut-off frequency 1 kHz). *B*: Spikes recorded from the left muscle III1, high-pass filtered (1.5 kHz). *C*: Torque. Torque to the right is indicated by an upward deflection of the trace; the recording is low-pass filtered to eliminate oscillations due to wing-beat vibrations (20 Hz), calibration bar: 5×10^{-7} Nm. *D*: Thrust, band-pass filtered to eliminate slow drift and oscillations due to wing-beat vibrations (0.02 Hz – 20 Hz), calibration bar: 10×10^{-5} N. *E*: Wing-beat frequency, computed with an Ortec Time Histogram Analyser, binwidth 200 msec. *F*: Graph indicating motion of the stripe pattern in front of the right eye; rectangle above centre line: motion to the right, rectangle below centre line: motion to the left, centre line only: no motion. *G*: The same as in F, but indicating motion in front of the left eye. *H*: Time marks: period 1 second.

trol" described for *Drosophila* and *Musca* by Götz [4].

In Fig. 2 large fluctuations of the wing-beat frequency correlated to changes of thrust can be seen (E and D). This contrasts with the findings of Götz [4] in *Drosophila* that changes in wing-beat frequency are too small to be responsible for large changes of the force of flight. However, during the first period of pattern motion in Fig. 2 (progressive motion in front of both eyes) there is a significant rise in wing-beat frequency but no marked increase in thrust. At the same time both muscles III1 are active (A and B). This suggests that other flight parameters not measured here (lift?) are changing. It has already been shown (Spüler [8]) that a large short-time increase in wing-beat frequency of about 15 percent is strongly correlated to simultaneous activity in both muscles III1 and that these synchronous variations can occur spontaneously or can be induced by pattern motion. As yet the type of flight behaviour resulting from these changes is not known.

The torque/thrust meter can be a useful aid when dealing with the complexity of the optomotor system of flies. Using the set-up described here experiments are in progress to study the folowing: the way in which the activity of several direct flight muscles depends on visual input; how these muscles contribute to the generation of torque and thrust; the part played by variations in wing-beat frequency.

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