The Flight of the Dipterous Fly Muscina stabulans Fallen

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THE FLIGHT OF THE DIPTEROUS FLY *MUSCINA STABULANS* FALLÉN

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As a preliminary step in the study of a system consisting of a flying insect and the air surrounding it, a comparison is made between the system under natural conditions of free flight and under experimental conditions (when the insect is held stationary), in order to ascertain under what conditions conclusions reached with the insect held stationary would hold for free flight. To avoid the difficulty of making this comparison directly in respect of each of the many factors involved, the resultant force which, acting continuously on the body of the insect, would most nearly replace those cyclicly changing forces that normally maintain or modify the state of motion in flight, is taken as an index of what is occurring in the system.

When the insect is held stationary in 'still air' it is found in most cases that this resultant, though of sufficient magnitude to support the insect in flight, does not act through the centre of gravity: the line of action of the resultant intersects the body axis at some point behind the centre of gravity. The position of this point depends on the amplitude of wing beat. When the insect is exposed in a wind tunnel to a stream of air of appropriate speed and direction, however, the resultant acts through the centre of gravity, as in free flight.

The forward displacement of the point of intersection between the line of action of the resultant and the body axis, when the insect is exposed to a stream of air, is analysed further, and it is found: (1) that the effect of the stream of air on the body of the insect is negligible in this connexion as compared with the effect on the wings; (2) that changes in amplitude of wing beat do not account for the forward displacement of the resultant; and (3) that when the insect is exposed to a stream of air the path travelled by the wing tip on its downward beat is displaced forwards along the body axis in a direction which would tend to produce the observed displacement of the resultant force. This forward displacement of the path travelled by the wing on its downward beat converts the elliptical course, characteristic of wing movements when the insect is held stationary in 'still air', into the figure of '8' course commonly associated with insect flight, and is dependent on the movement or position of the third antennal joint relative to the second, which in turn is determined by the action of the stream of air on the third joint with its arista.

The characteristic attitude of the legs in flight, and the continued vibration of the wings when air is blown at the insect from in front also depend on the sensory inflow from the antennae. The maintenance of the figure of '8' path involves the interaction of the sensory inflow both from the antennae and from the halteres.

CONTENTS

1. INTRODUCTION

There are three main lines of approach to the study of flight in any insect. One is to regard the insect as an aerodynamic machine of peculiar interest. Another is concerned with structure and function in a living organism, the mechanisms by which all the movements of the insect associated with flight are performed and controlled. The third considers a product of evolution, an adaptation of a type which can be analysed in detail and described with precision in terms of the static and dynamic factors involved.

Adopting the first of these lines of approach one meets at the outset with a major difficulty. If the investigation is to be based solely on observations of living insects held stationary, the 'flight system', that is, the living insect and the surrounding air, may differ considerably under these conditions from that of free flight; what is observed in the one may not be assumed implicitly to occur in the other. On the other hand, many useful methods of investigation can be applied to insects held stationary which could not be used if the insect were flying freely, methods on which one is dependent for certain quantitative data, which cinematography, for example, does not supply. An escape from this difficulty would be to proceed in two stages. First, a comparison would be made between the flight system under natural conditions in free flight, and under experimental conditions with the insect held stationary, and the relationship of the one to the other would be established. Secondly, the flight system with the insect held stationary would be studied under such conditions (defined by the relationship already established) that any conclusions reached would hold for free flight.

The object of this present communication is to approach the aerodynamic aspect of the subject by attempting the first of these steps in a detailed study of the flight of females of the dipterous fly *Muscina stabulans* Fallén. At the same time the role of the airflow in determining behaviour and the importance of the antennae in flight are demonstrated.

2. Material and methods of mounting living insects

In selecting a species for this study it was considered desirable: (1) that the insect chosen should be one of the Diptera, in order to avoid the complication of a second pair of wings or of elytra; (2) that it should breed readily in the laboratory; (3) that it should prove amenable to the experimental conditions imposed upon it; and (4) that it should not be too small. *Muscina stabulans*, with an average wing length of only 7 mm., barely qualifies on the score of size, but is preferable to *Calliphora vomitoria* since it maintains strong, regular flight movements over a wide range of experimental conditions. The adult flies were fed on sugar and water. The larvae were reared in a medium of cooked alfalfa leaf-meal, cooked soyabean meal and dried skim milk, with a little yeast sprinkled on the surface. Normally females oviposited readily on this, though at times they failed to do so for reasons which have not been satisfactorily explained. It was then necessary to establish another stock from individuals collected in the field. In this way it has been possible to maintain stocks over a period of several years. Individuals proved to be hardy and suitable for experiments. In spite of its small size, therefore, *M. stabulans* was selected for the present part of this work, while it was regretted that of those species already used in studies of insect flight none satisfied the above conditions. All observations were made at a temperature between 20 and 25°C. Unless otherwise stated observations were confined to females; these were not used for experiments until two weeks after emergence.

Diverse methods have been employed in the past for mounting insects which were to be held stationary. It has long been recognized that the legs should remain free, and that wing movements normally cease if the tarsi make contact with any support. In practice this restricts the region suitable for attachment to the upper part of the thorax or abdomen. It has been argued by Voss (1914) that the insect should be supported by holding the tip of the abdomen, so that the major part of the weight of the insect is carried by the vibrating wings themselves, as in free flight. In estimating the importance of this point, two sets of forces have to be considered: the stresses within the insect's body and the aerodynamic forces acting on the wings. The distribution of stress within the body may surely be expected to be most natural when the position of artificial attachment is as close as possible to the region of natural support of the body in free flight, that is, the wing bases. The aerodynamic forces acting on the wings will not differ greatly from their normal value as a result of artificial attachment in this region, provided that there is but little displacement of the body in a vertical plane during each wing beat in free flight. In this species, where frequencies of wing beat between 115 and 220 beats per second have been observed, it is unlikely that any appreciable displacement of this sort occurs. Furthermore, the method of attaching the insect by the abdomen has the disadvantage that the whole of the thorax, with the wing mechanism, is free to be inclined by the insect at different angles relative to the observer or to any recording apparatus used. Attachment by the upper surface of the thorax is preferable, therefore, provided that

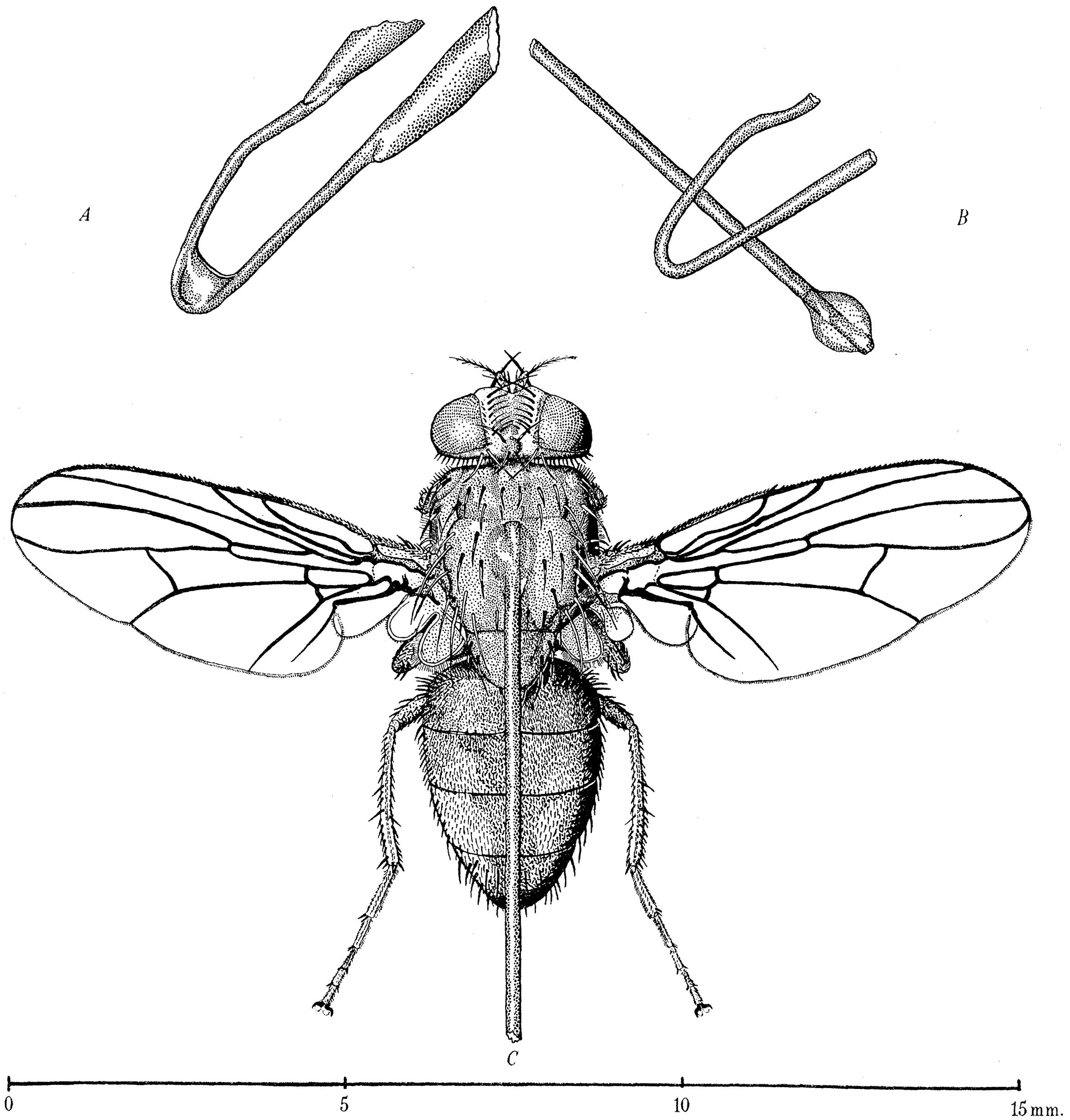

Figure 1. Illustrating the method of mounting the living insect. A, a drop of melted wax held in the loop of the cautery. B, the wax transferred to the supporting wire and C, a female of *Muscina stabulans* with the legs in the attitude of flight mounted on the supporting wire.

this does not appreciably disturb the airflow of the system, or interfere with the natural vibration of the wings. A comparison of the speed and direction of the airflow, and the angular movements of the wings in individuals supported by the thorax or by the abdomen showed that in these respects attachment by the abdomen possessed no advantage over the other method, if a suitably delicate method of mounting was employed. Attachment by the thorax was, accordingly, adopted, and the living insect was mounted as shown in figure 1 by the method described in Appendix I.

One effect of the wing movements performed by the insect when held stationary is to produce a flow in the surrounding air. This has been studied in other insects by Demoll (1918) with a frame of owl's feathers, and by Magnan (1934) with smoke, hot air, and anemometer. The main mass of the surrounding air, however, remains at rest relative to the insect, and in the account that follows, this condition will be referred to as 'still air', in contrast to that condition in which the main mass of the surrounding air moves backwards relative to the insect, as in free flight, or (with the insect held stationary) in an airflow produced in a wind tunnel. The insect is then said to be exposed to a stream of air. This stream is defined in terms of the magnitude and direction of the vector which must be introduced to convert the flight system in 'still air' to that in the given airflow, other factors remaining unchanged.

Flies were normally used between 1 to 4 hr. after being mounted. Though very variable in this respect, some individuals maintained a vigorous vibration of the wings, allowing observations to be made over a period of 2 or 3 hr. These vibrations were regular under certain conditions, irregular under others. For any set of conditions, however, a certain basic behaviour can be recognized, to which the insect returns after each brief excursion. In this present study we shall be concerned only with this basic behaviour.

3. Comparison of the flight system when the insect is held stationary with normal free flight

(i) *The basis and method of the comparison*

A moment's consideration will suggest an embarrassing profusion of features in respect of which the flight system when the insect is held stationary may be compared with normal free flight: the posture of the insect; the frequency and amplitude of its wing beats; the attitude of the wing as a whole and that of different parts of the wing, since it is a flexible structure; the path and speed of the wing relative to the insect, and the path and speed of the air relative to the wing. Differences in these and in other factors may occur, but for the immediate purpose of the present phase of this inquiry all that is significant will be found to be summed up in three values: the magnitude, the direction of action, and the position of the 'resultant force', which acting continuously on the body of the fly would most nearly replace those cyclicly changing forces which normally maintain or modify the state of motion in flight. By taking this resultant as an index of what is occurring, and assuming that for any particular flight speed one set of values for this index is equivalent to but one set of conditions in the system, a comparison involving so many aspects is at once reduced to manageable dimensions. The application of this method rests, however, upon being able to determine these values for an insect held stationary. For this purpose a balance was constructed, designed to measure the vertical and horizontal components of the resultant force to the nearest milligram over a range of 60 mg. and to enable the position of its line of action to be determined to the nearest half millimetre. A description of this balance and the way in which it was used is given in Appendix II.

(ii) *The flight system with the insect held stationary in 'still air'*

Of fifty flies used in this analysis, thirty-two maintained consistently regular wing movements for a sufficient length of time to allow the requisite measurements to be recorded. The weight of these individuals ranged from 20 to 48 mg. with an average weight of 31 mg. It is noteworthy that all, with but four exceptions, maintained wing movements in which the magnitude of the resultant force generated was equal to or greater than the weight of the insect. The magnitude of the resultant for any individual usually varied from time to time, and the averages of steady maximum and minimum values (as opposed to momentary excursions) were 35 and 30 mg. respectively. Although the magnitude of the resultant was not constant in each individual, changes in the inclination of its direction of action relative to the insect's body, as determined from the values of vertical and horizontal components, did not amount to more than 4°. On an average the force acted along a line inclined forwards and upwards at 48° to the body axis of the insect.

These values for the magnitude and direction of the resultant are such as one might expect for insects held stationary, performing wing movements similar to those of normal forward flight; but the determination of the *position* of the resultant emphasized that in a majority of cases the system was incompatible with stable forward flight. These data for the thirty-two flies investigated—giving the position of the resultant expressed in terms of the distance from the centre of gravity of the point of intersection of its line of action with the body axis—are presented in figure 2. By measuring the vertical and horizontal components of the resultant with the insect inclined at different angles, it was found that both the magnitude and direction of the resultant relative to the fly were independent of the inclination of the body axis to the horizontal. For the following determinations in 'still air' the insects were therefore held as was most convenient, with the body axis approximately horizontal. At the bottom of figure 2, the body axis of a fly, whose outline is drawn to scale, is marked out in half-millimetres from the centre of gravity as zero. The histogram at the top represents the numbers of individuals in which the resultant force intersected the body axis within each half-millimetre of its length. Thus, of these thirty-two flies, in one individual only was this point of intersection within ±0·25 mm. of the centre of gravity, and in half of the total number the resultant crossed the body axis between 0·75 and 1·75 mm. behind it. A distance from 1·75 mm. in front to 3·25 mm. behind the centre of gravity included the observed points of intersection for all the individuals studied.

It is clear that in free flight in a straight line the resultant force must act through the centre of gravity of the insect. The condition of the flight system in the individuals

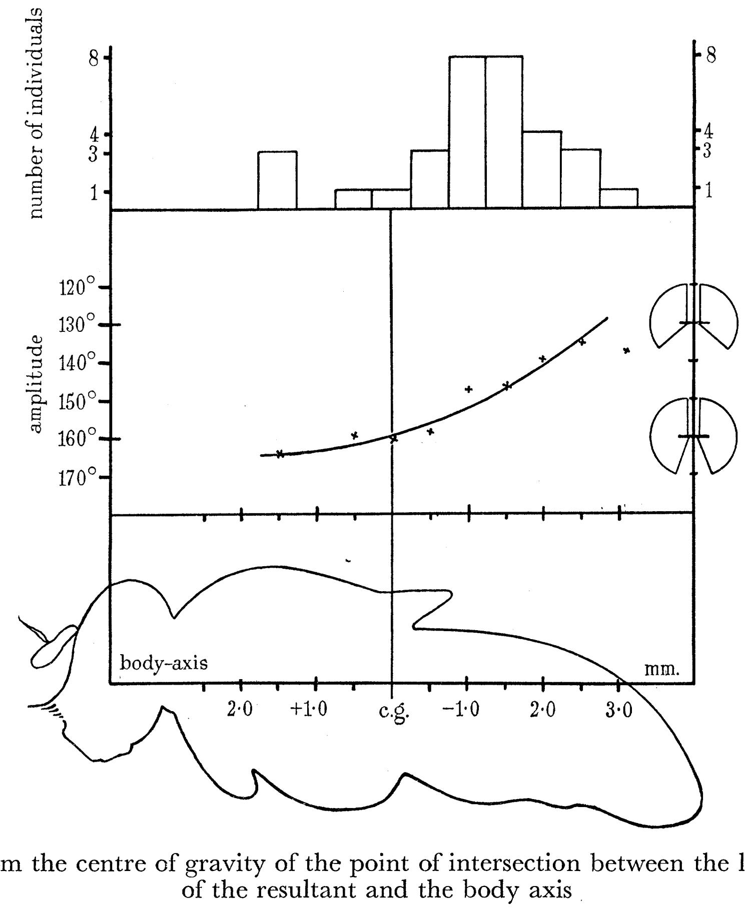

FIGURE 2. Diagram showing the relation of the amplitude of wing beat to the position of the 'resultant force' relative to the centre of gravity, for thirty-two individuals held stationary in 'still air'.

we have been considering was, therefore, with one exception, incompatible with free flight. This incompatibility lay in the position of the resultant rather than in its magnitude, which suggests that, in pursuing further the comparison of the system with that of free flight, special attention should be paid to those factors which determine the position of the line along which the resultant acts.

In this connexion it is interesting to compare the amplitude of wing beat in the thirty-two individuals just considered. Neglecting for the present the details of the paths travelled by the wing tips, the wings may be regarded as beating upwards and backwards, downwards and forwards, in a plane inclined backwards at about

50 degrees to the body axis. With the exception of insects which were fatigued or anaesthetized, the wings almost touched one another at the top of the beat and showed little variation in this respect. If it be assumed that the leading edge of the wing of each side is in a vertical plane at the top of the beat, then the amplitude of wing beat may be expressed as that angle which the leading edge of the wing makes with this plane at the bottom of the beat, in the plane of movement. This angle was measured by viewing the insect through a circular aperture in a disc graduated in degrees, with a cross-wire and pointer which could be rotated so as to be seen in line with the leading edge of the wing at the bottom of the beat. It was best observed against a black background, with the fly illuminated from behind. The average of these values for each group of individuals represented at the top of figure 2 is given in the middle of that figure, and the curve drawn through these points indicates the relation between the amplitude of the wing beat and the position of the line of action of the resultant force relative to the centre of gravity for these individuals held stationary in 'still air'.

Two effects are likely to follow from an increase in amplitude, as the following considerations show. It is probably correct to regard the insect in flight as moving under the influence of cyclicly changing forces, which, during the greater part of the cycle, tend to rotate it about a horizontal transverse axis passing through the centre of gravity. The forward and upward components of the aerodynamic force acting on the wings in flight are almost certainly positive during both the downward and, as emphasized by Magnan and Sainte-Laguë (1933), the upward beats, and their values are likely to be maximal at the end of the downward stroke, when the wings are performing the lower curve of their trajectory. Bull (1910), using cinematography, found that there was maximum forward and upward acceleration of the body during this phase of the beat in the dragonfly *Agrion*, where the wing movements are in many ways similar to those of *M. stabulans*. One effect of an increase in amplitude would be to displace forwards the line of action of these important forces associated with the close of the downward beat. A second effect of an increase in amplitude is likely to be that the resultant of the forces momentarily acting will pass in front of the centre of gravity during *a greater proportion of time* in the period of each cycle. It may be expected, therefore, that the greater the amplitude of the wing beat, the further forward relative to the insect is the line of action of the resultant which, acting continuously, would most nearly replace the repeated cycle of forces generated.

The accuracy of these observations was roughly confirmed in the following manner. A series of flies were each mounted on a short length of stiff horse-hair in place of the usual heavy wire support. The horse-hair carrying the fly was gripped in forceps, suitably mounted so that they just held it firmly. Between the upper part of the two arms of the forceps a small soft-rubber bulb was pressed: this was connected to a large bulb by a length of tubing. Squeezing the large bulb inflated the small bulb, forced apart the two arms of the forceps and suddenly liberated the insect without imparting to it any jerk. Individuals maintaining regular wing vibrations through an amplitude of about 160° or over, flew straight forwards without faltering perceptibly on being liberated in this way. The majority of flies tested in this manner maintained an amplitude of wing beat of 140° to 150° and these on sudden liberation plunged straight into a nose dive.

A simple but instructive photographic record of what occurred was made by previously focusing a camera on the insect and the plane in which it would travel on liberation, and illuminating the insect from in front. The shutter was opened, the fly liberated, and after it had passed, the shutter closed. Since the wing at the top and bottom of its beat undergoes a considerable rotation about its long axis, light was reflected from the wing surface towards the camera at some phase of this rotation, so that a record of the wing in these two positions in successive beats was superimposed upon the trace of the insect's body on the negative.

From such a record it was seen, first, that associated with the downward path on liberation was a sudden forward rotation of the insect about a transverse horizontal axis. This agreed with the observed values given in figure 2 for the position of the resultant of those forces which, acting on the fly, would determine its state of motion in free flight at the moment of liberation. This figure shows that the line of action of the resultant passes behind the centre of gravity in the individuals maintaining wing beats of this amplitude (140–150°). Recalling the magnitude of this resultant, it seems probable that the downward path travelled on liberation resulted from the observed rotation rather than from inadequacy of the 'lift' generated. The deficiency lay in the distribution of forces in the system rather than in their magnitude. Secondly, it was clear that the rotational tendency was lost as soon as forward speed had been acquired. In fact, if the forceps holding the insect were travelling forwards at an appropriate speed, the state of motion of the insect remained unchanged on liberation. This was demonstrated by mounting the forceps holding the insect on a small trolley, drawn along two horizontal wires by a cable from an electric motor. The trolley travelled for about 3·0 m. prior to the release of the insect, whose path on liberation was observed directly against a squared background. The speed of forward movement of the insect at the moment of release was calculated from the time taken to cover 1·0 m. immediately prior to the point of liberation. In horizontal free flight it had been found in general that females of this species, timed over distances of 3·0–5·0 m. in a straight course, travelled at average speeds of 1·6–3·0 m. per sec., and, furthermore, the impression was gained that at the lower speeds the body axis of the fly was inclined backwards at 20–30° to the horizontal. It has already been noted in determinations with the insect held stationary in 'still air', that the inclination of the body axis to the horizontal is then of purely arbitrary importance, but this is clearly no longer the case when the insect (held stationary) is exposed to a stream of air or when, as here, the insect is moving forwards. Observations were therefore made of the sudden liberation of flies with the body axis similarly inclined to the horizontal, and travelling at speeds of 1·0–3·3 m. per sec.

In sixty-five observations over this range of speeds it was found that only between speeds from 1·6 to 2·3 m. per sec. did any fly continue to travel along a horizontal path on liberation. At 1·0 m. per sec. the path travelled in free flight was inclined markedly downwards. Liberated at 3·3 m. per sec. the insect instantaneously lost speed, and the path was irregular. It is reasonable to assume, therefore, that the flight system was essentially similar to that of free flight in a straight line, when the insect was mounted in the way described and travelling forwards at the speed of normal flight. At lower speeds of forward movement the system chiefly differed from this in that the resultant acted somewhat behind the centre of gravity, while when held stationary the line of action of the resultant was still further back. In this way the gap has been bridged between the system in free flight, whose direct investigation presents so many technical difficulties, and the flight system with the insect held stationary. In comparing these it is now possible to pass more readily from the one to the other.

(iii) *The flight system with the insect held stationary and exposed to a stream of air*

In the previous section it was seen that the chief difference between the condition when the insect was held stationary and that of free flight lay in features connected with the position of the line of action of the resultant rather than its magnitude, and that the amplitude of the wing beat and the forward movement of the insect were both closely concerned with the position of the resultant. We have now to decide whether this difference can be accounted for in terms of the difference in the airflow as compared with that normally associated with forward flight.

This was investigated by using the balance already described in conjunction with a small wind tunnel. This wind tunnel, which was circular in section with a working section 6 in. in diameter, was constructed of celluloid and had a shaped intake of turned wood. In order to reduce turbulence to dimensions negligible for the present inquiry, the entrance was fitted with a honeycomb of artificial straws, tightly packed and glued in position. The other end of the tunnel led by an expanding section to a suction fan of eight blades, driven by a half-horse power, D.C. motor. The speed of the motor was controlled by a rheostat, using a circuit described by Schmitt (1938), which reduced the variation of motor speed with changing voltage and was found to be most satisfactory. A hot wire anemometer, forming one side of a Wheatstone-bridge circuit, was used to measure the speed of airflow in the working section of the tunnel. The anemometer was made of platinum wire, $\frac{1}{1000}$ inch in diameter, welded to platinum supports. The current necessary to maintain the wire at a constant temperature at about 58° C was measured with a Universal Avo Meter, and at this low temperature the instrument was found to give reliable readings down to 4 cm. per sec. The anemometer was calibrated up to 420 cm. per sec. by swinging it on a whirling arm round an enclosed circular track.

Determinations of the position of the line of action of the resultant were attempted in a series of twenty-five individuals exposed to a stream of moving air (velocity

50–250 cm. per sec.) and inclined at angles of 0–45° to the direction of flow. Although flies in 'still air' may not continue to vibrate their wings for long periods of time, when they do so the movements are on the whole regular. Unfortunately the behaviour of the insect when exposed to a stream of air varies continually. This variation is probably due to natural turning movements and greatly increases the difficulty of using the balance and of obtaining the series of readings necessary for each determination. The practical difficulty is somewhat comparable with having to determine the aerodynamic properties of an aeroplane, without being able to eject a pilot who, at irregular intervals, manipulates the controls in an entirely erratic fashion. The twenty-five determinations in 'still air' and the thirty-six determinations successfully concluded under wind-tunnel conditions are not sufficient to define in detail the relation between the position of the resultant, the inclination of the body axis, and the speed of the stream of air to which the insect is exposed. The chief features of these relations, however, are shown by the average values given in table 1. The data have been divided according to the inclination of the body axis to the general stream of the air at approximately 0°, 15–29°, or 30–45°. In columns I, IV and VII the horizontal distance of the line of action of the resultant from the centre of gravity, with the wing vibrating in 'still air', is given for the individuals of each group. The error given as ±0·3 mm. is the maximum error expected in any individual determination under the conditions of this experiment. The thirty-six determinations with the insect exposed to a stream of air are arbitrarily divided into those in which the speed of the stream was over 200 cm. per sec., and those in which it was less. It will be seen that, after introducing this vector into the airflow of the flight system with the insect held stationary, the line of action of the resultant moves forwards and comes to lie close to the centre of gravity. The magnitude of this shift is found by subtracting the horizontal distance between the centre of gravity and the line of action of the resultant in 'still air' from the corresponding figure in an airflow. Comparing these values for roughly similar air-

TABLE 1

Column ...	I	II	III	IV	V	VI	VII	VIII	IX
Inclination of body axis	0°			15–29°			30–45°		
Number of determinations	9	5	7	9	6	6	7	10	2
Average speed of the stream of air to which the insect is exposed, in cm. per sec.	0	134	219	0	105	217	0	114	204
Horizontal distance in mm. of line of action of resultant before (+) or behind (−) the centre of gravity	−2·3 ±0·3	+0·16 ±0·3	+1·3 ±0·3	−1·7 ±0·3	−0·2 ±0·3	+0·3 ±0·3	−1·6 ±0·3	−0·97 ±0·3	−0·45 ±0·3
Distance in mm. of advance of line of action of resultant when the insect is exposed to a stream of air	—	2·4	3·6	—	1·5	2·0	—	0·6	1·1

speeds in columns III, VI and IX, it is evident that the advance tended to be greater at smaller angles of inclination. It also appears that at the smaller inclinations, the advance tended to be greater when the insect was exposed to a stream of air at a higher speed. At larger angles of inclination, 30–45°, the data are of doubtful significance in this respect.

From observations of free flight and from the liberation experiments described above it is likely that the behaviour of individuals mounted as illustrated in figure 1 corresponds to that of individuals in free horizontal flight at speeds between 160 and 230 cm. per sec. Bearing in mind the figures in table 1, it may be expected that, when the insect is exposed to a stream of air having a velocity within this speed range, with the body axis inclined at 0°, the resultant will act in front of the centre of gravity, while at 30–45° inclination the resultant will pass behind it. Within this speed range and at inclinations between 15° and 29°, a combination of speed and inclination may be expected to occur in which the resultant passes through the centre of gravity.

In free flight, the path travelled may be horizontal, or inclined upwards or downwards. In the equivalent behaviour under wind-tunnel conditions the horizontal component of the resultant, as measured by the balance, will represent the difference between the propulsive force and the resistance to motion in the direction of flight, and will be zero, positive or negative respectively, since in free flight a zero, negative or positive component of the insect's weight will be added, so that the algebraic sum of these components will be zero if the speed and direction of flight is constant. For the purposes of our comparison, horizontal flight may be taken as a median in the range of normal behaviour. Measurements of the horizontal component of the resultant in five individuals inclined at 20–26° to the direction of flow showed that, for the range of behaviour exhibited, this component was zero between the speeds of 124 to 204 cm. per sec. This broadly overlaps both the observed range of speeds of horizontal free flight, and the range of airspeeds to which the insect was exposed, over which the resultant is expected to pass through the centre of gravity (the insect being held stationary at similar inclinations).

A more exhaustive analysis along these lines might well narrow down still further the range of experimental conditions for each individual which includes those conditions consistent with a particular type of free flight, though in practice the frequency of excursions from the insect's basic behaviour would make this so difficult, that the attempt would not at present be justified. Even without carrying the analysis further, however, there are good grounds for the statement that the deficiency in the flight system with the insect held stationary in 'still air', which we have been considering, can be accounted for by the difference between the airflow in this condition and in that of normal free flight. Furthermore, in so far as the resultant considered here has rightly been regarded as an index of the whole system (that is, the flying insect together with the surrounding air), it follows that, so far as steady flight is concerned, all deficiencies from the aerodynamic point of view can be accounted for similarly.

The system with the living insect held stationary in a wind tunnel and exposed to a stream of air of appropriate speed and direction therefore provides the conditions we have been seeking. Conclusions reached by a study of this system may be expected to hold for free flight.

4. THE ACTION OF A STREAM OF AIR IN DETERMINING THE POSITION OF THE RESULTANT FORCE

(i) *The direct action of a stream of air on the body of the insect*

The body of a wingless insect was held in the wind tunnel and exposed to a stream of air at speeds over the range with which we are concerned. Using the balance, no couple could be detected tending to rotate the insect about a horizontal transverse axis passing through the centre of gravity. The change in position of the resultant with airflow when the wings were intact was not due primarily, therefore, to the direct action of the air on the insect's body, but was an effect involving the wings. It has already been shown that the position of the resultant is dependent upon the amplitude of the wing beat; we may now inquire whether this amplitude is in turn dependent on the airflow, and, if so, whether this relationship accounts satisfactorily for the changes in position of the resultant which have been noted.

(ii) *The effect of a stream of air on the amplitude of wing beat*

It is not practicable to measure the amplitude of wing beat by inspection, under conditions in which the behaviour is so frequently changing. It was therefore necessary to construct a small rectangular wind tunnel, with plate glass top and bottom through which photographic records of the wing amplitude could be made. The chief features of this apparatus are described in Appendix III.

The amplitude of wing beat was determined in 'still air' and with the insect exposed to a stream of air at speeds of 140, 220 and 320 cm. per sec. for ten flies inclined at 0, 15, 30 and 45° to the direction of the stream. Two photographs were taken for each set of conditions and two photographs of the wing vibrations in 'still air' were made after every six exposures to serve as a control. More frequently than not the amplitude of wing beat on the two sides was different. (It is interesting to note, in passing, that associated with this, the metathoracic leg on the side of lesser amplitude always extended further laterally than the other—an observation in contrast to those of Stellwaag (1916) on various insects in free flight, where no compensating leg movements were detected.) The angle between the two wings at the bottom of their beat was therefore taken as the best available substitute for what one would have preferred to be determinations of amplitude with the wing movements bilaterally symmetrical. The range of behaviour is illustrated by the histogram in figure 3, which shows the frequency of different values for this angle in the control determinations for the ten individuals in 'still air'. The average of the values for all these control determinations was 67°, and two-thirds of these lay within the range from 60° to 88°. In figure 4, the average value for the angle between the wings at the bottom of their beat has been plotted against the inclination of the body axis at different airspeeds. Each point on the graph is the average of twenty determinations. The average value for 'still air' is indicated at 67° and the standard deviation is represented by the two transverse broken lines. It will be seen at once that there is a decrease in amplitude with increasing speeds of airflow and with increasing inclination of the body axis to the direction of flow, and that in general the amplitude is less in a stream of air than in 'still air', under conditions which are in other respects similar.

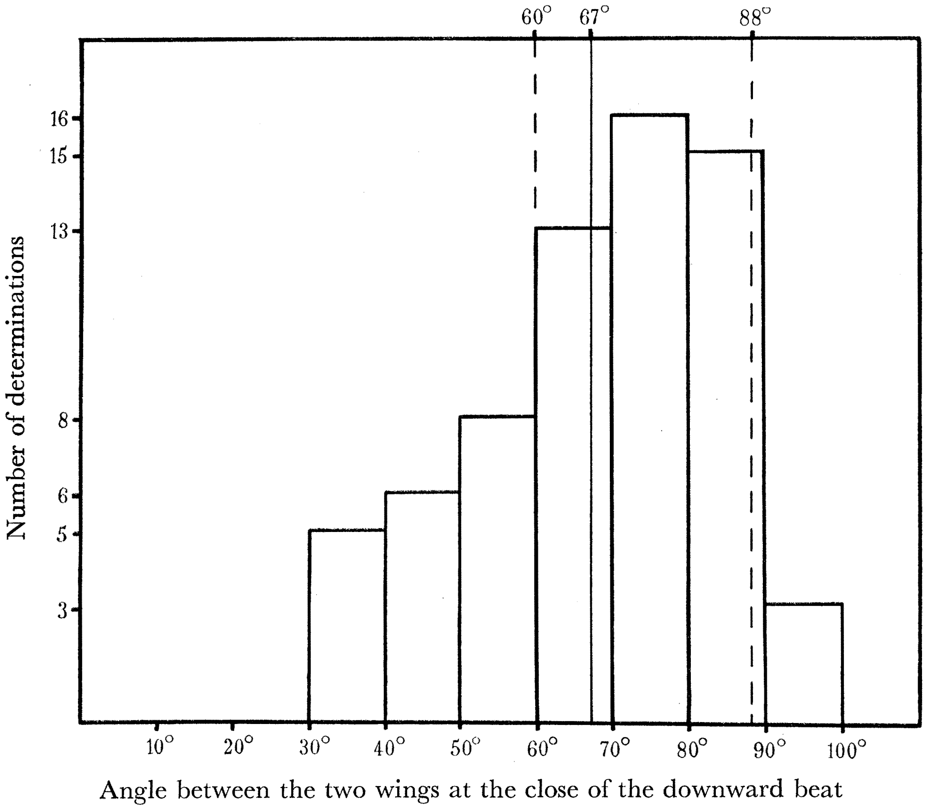

FIGURE 3. Histogram showing the range of behaviour in 'still air' observed in the ten individuals studied, expressed in terms of the angle between the two wings at the close of the downward beat, recorded in sixty-six determinations.

It may be noted that since an increase in amplitude may be expected to produce a forward displacement of the line of action of the resultant force generated, the system being constant in other respects, the increase in amplitude on reduction of inclination with constant airspeed, here recorded, may account for the greater magnitude of the forward displacement of the resultant shown by the figures in table 1, when the insect is exposed to a stream of air at smaller angles of inclination.

It is also of interest that the sense of these changes in amplitude with inclination is such that they will tend to confer longitudinal stability on the system.

It has already been shown: (*a*) that a reduction in amplitude in 'still air' is associated with a backward displacement of the line of action of the resultant force relative to the centre of gravity of the insect, and (*b*) that there is a forward displacement of the resultant in the reverse direction when the insect is exposed to a stream of air. Since it now emerges that there is a reduction in amplitude in a stream of air, some third factor must be involved which is of sufficient influence to produce a forward displacement of the resultant in spite of this reduction in amplitude. One such factor was detected in a study of changes in the path travelled by the wing tip relative to the insect.

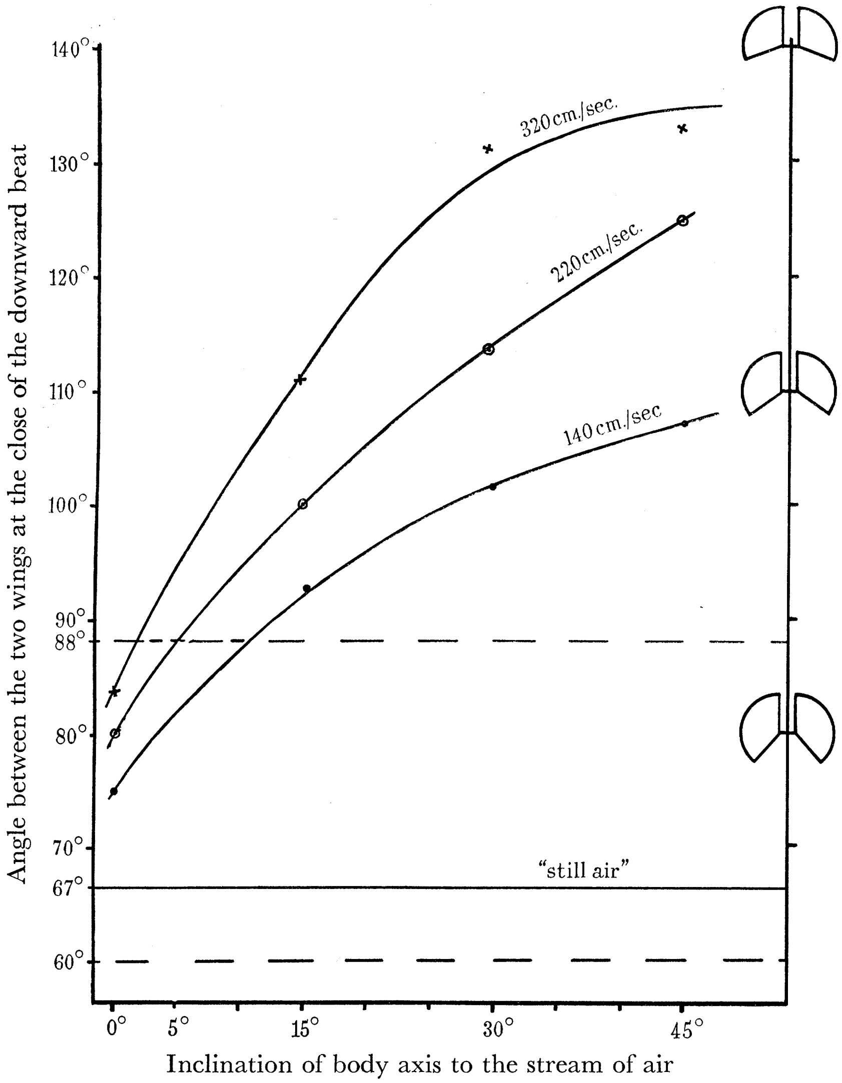

FIGURE 4. Graph giving the average values of the angle between the two wings at the close of their downward beat for different inclinations of the body axis in ten individuals under conditions of 'still air', and at three speeds of airflow.

(iii) *The path travelled by the wing tip relative to the insect*

A fragment of gold leaf was attached to the tip of the wings, and the path travelled by the wing tip, viewed with a microscope through a circular window, *C*, figure 9, in the side of the tunnel, was recorded with the aid of a camera lucida. The fly, mounted in the usual way, was supported opposite the window. The path travelled by the wing tip in 'still air', as seen from this viewpoint, is represented on the left of figure 5. It is a curved, somewhat elliptical path and quite different from the figure of '8' course recorded by Marey (1868), whose observation is repeatedly quoted by later writers. The direction of the wing beat along this path was determined by Marey's method. A glass hair, previously smoked, was held for a moment so that its tip lay in the path of the wing. Subsequent examination showed that the glass had been scraped clean at the tip, on the side that was facing the direction in which the wing had approached the hair in that particular part of its beat. In 'still air' the figure of '8' course was to be seen occasionally as a momentary excursion from the steady condition.

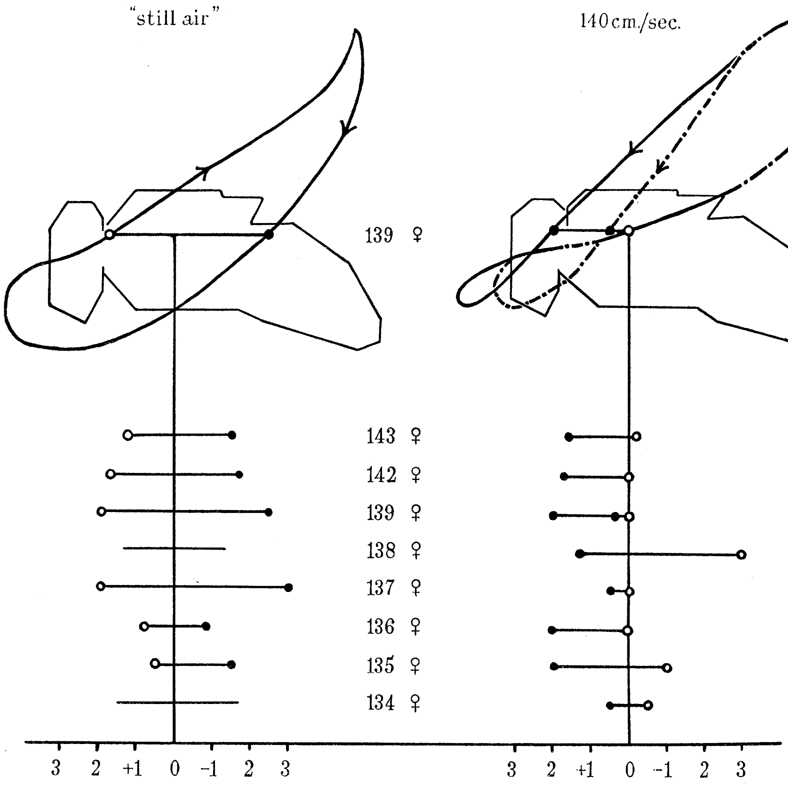

Figure 5. Diagram showing, above, the path travelled by the left wing tip and the relative positions of the wing tip on the downward, ●, and upward, ○, beats as the wing passed through the horizontal plane containing the wing bases, with the insect held stationary in 'still air' and in an airflow of 140 cm. per sec. These positions for eight individuals are expressed below in terms of their distance normal to a vertical plane passing through the wing bases at right angles to the body axis.

On exposing the insect to a stream of air (at 140 cm. per sec. for example) the path travelled by the wing during the downward stroke moved forwards so as to lie throughout the greater part of its length in advance of the path of the upward stroke and in crossing it produced a figure of '8' path, illustrated on the right of figure 5. This was true also of *Musca domestica*, as is shown in the upper part of figure 6. There was at the same time a backward displacement of the upward path. The magnitude of this fore and aft displacement of the wing path relative to the insect for eight individuals is represented in the lower part of figure 5, as explained in the legend to that figure. No change was observed at any time, however, in the inclination of the general plane of movement of the wings, comparable with that described by Stellwaag (1916) in the bee, *Apis mellifica*. Quite apart from any changes in the position of the centre of pressure relative to the wings—such as Demoll (1918) has suggested may play a part in giving stability in insect flight—or changes in the magnitude of the forces acting in different parts of the beat, this modification in the path travelled by the wing relative to the body would be expected to produce a considerable displacement of the resultant force, such as has been shown in fact to occur when the insect is exposed to a stream of air.

The path travelled by the wings under any set of conditions will be that in which there is equilibrium between the aerodynamic forces acting on the wing surface, and those forces, imposed upon the wing at its base, which result from the nature of the wing articulation and the applied forces of muscular origin. A change in path may be initiated by modifications in either of these. We must consider next whether the observed changes in path result primarily from the former, the aerodynamic side of the equilibrium, or from the latter, the physiological side.

Two types of change in wing movements with alteration of airspeed and inclination have been noted already and described respectively in terms of (*a*) the amplitude in the general plane of movement of the wings, and (*b*) the fore and aft displacement (along the body axis) of the path travelled by the wings on their upward and, more particularly, on their downward course—effects which it is recognized may be only conspicuous features of more complex phenomena. Although, mathematically speaking, any change in wing path can be defined in terms of these two components, and although a change in one of these usually involves to some extent a change in the other, biologically, these two appear to be separate phenomena controlled by distinct and separate mechanisms. In anaesthetized insects which did not respond to visual or tactile stimuli, changes in amplitude of beat still occurred, but there was no forward displacement of the downward beat, giving the figure of '8' course. The latter must, therefore, result primarily from changes on the physiological side of the equilibrium, and may involve a sensory inflow from peripheral sense organs. The changes in amplitude, on the other hand, may not necessarily be dependent on impulses of peripheral origin, and may result directly from changes in the aerodynamic side of the system: airflow + wing + articulation and associated musculature, while on the physiological side, one of the factors concerned in subsequently re-establishing equilibrium may be the loading of the muscles which vibrate the wings. Unlike *frequency*, the *amplitude* of either wing can be varied independently. In Diptera such as *Tipula*, *Laphria* and *Calliphora*, Roch (1922) has shown that the frequency is dependent upon the loading of the wing on the side on which the loading is the greater, an effect perhaps involving nervous co-ordination. In his experiments, the reduction in magnitude of the forces concerned (produced by shortening the wings) should operate throughout the whole beat; one suspects, however, that the period when the wing, towards the close of the downward beat, sweeps forwards before continuing on its upward course may be of special importance in respect of amplitude. The loading of the muscles will depend chiefly upon the component of the aerodynamic force acting on the wings, resolved parallel to the general plane in which the wings vibrate. On the downward beat the proportion of the aerodynamic force which can be resolved in this plane will become greatest at some stage during that phase at the bottom of the stroke, when the wing is rotated about its long axis. During the same phase, the wing also passes through an attitude when the chord—a line transverse to the long axis of the wing and joining the fore and hind borders—is at right angles to the stream of air to which the insect is exposed. It is likely, therefore, that the increase in loading of the muscles due to an increase in the speed of the airflow will be maximal during this phase of the beat. The exact position in which this occurs will depend on the inclination of the body axis to the direction of the airflow. At small angles of inclination it may occur after the wings have passed the lowest point in their path, at larger angles it may occur before this, and so lead to a greater reduction in amplitude. Here, then, is a tentative suggestion as to the mechanism involved in re-establishing equilibrium between the aerodynamic and physiological sides of the system; it entails a change in amplitude, while satisfying the condition that nervous impulses of peripheral origin are not involved, and is dependent on the speed of the stream of air relative to the insect and on the angle of inclination of the body axis. The forward displacement of the downward beat, on the other hand, follows primarily from the physiological side of the equilibrium and will be considered next.

(iv) *The role of the antennae in flight*

One physiological condition which, it is immediately apparent, is associated with the airflow of the system, is the tonus of the muscles that determine the attitude of the legs and abdomen in flight. When walking or standing, the attitudes of the legs of an insect, such as a cockroach, are influenced by stimuli from receptors situated at the leg joints. Among these are the campaniform sensilla which, as shown by Pringle (1938), respond to stress within the cuticle of the leg joint, associated with the support of the weight of the insect's body. When the insect is supported so that the legs are not in contact with the substratum, the conditions for the production of these stimuli no longer exist, and in *M. stabulans* the legs then hang limply down. As soon as the insect is exposed to a stream of air, the legs are pulled up, so that the femora and tibiae of the pro- and meso-thoracic legs are held against the sides of the thorax, their tarsi lying close under the head, while the meta-thoracic legs are extended. This attitude is shown in figure 1, C. A small jet of air was used to locate the proprioceptors concerned in this response. They were found to be situated in a small area of the head containing the antennae. The response was elicited under the following conditions:

(1) with the first joint of both antennae coated with wax and rigidly fixed to the head but with the second and third joints free;

(2) with the first and second joints coated and fixed in this way, and with the third joint free;

(3) with the arista coated and fixed to the third joint with wax, but with the antennae otherwise free.

There was either no response to a stream of air, or the legs were held in the flight attitude both with a stream of air and in 'still air' when

(1) the wax was extended from the second to the third antennal joints,

(2) the top of a small column of wax built up on the gena of each side of the head was attached just to the tip of the third antennal joint, thus holding the antenna of each side rigidly but not the arista.

Clearly the response is dependent upon movement of the third antennal joint relative to the second. The apex of the second joint is conical, and the base of the third joint fits over this, giving considerable freedom of movement, chiefly of a rotational character. The antennae, which project forwards and somewhat laterally, were observed through a microscope. They were held a little more erect when in a stream of air, and the air impinging on the third joint and its arista produced rotation relative to the second joint. The degree of rotation clearly varied with the direction and velocity of the stream of air, though no quantitative study of this has been made. At this joint is situated that elaborate sensory structure, Johnston's Organ, which occurs throughout this class of the Arthropoda. Eggers (1924) has already pointed out in *Calliphora vomitoria* that this organ would respond to passive movements of the antenna rather than to active movements by the antennal muscles, and has suggested that it may be concerned in responses to air movements. One is certainly tempted to connect the reactions described above with the function of Johnston's Organ in this species, and to connect with this also certain other responses to airflow, considered below, which form an integral part of normal flight.

The role of the antennae was further studied in this connexion by observing the flight movements with the insect in a wind tunnel, but with the antennae either removed or isolated from the flow in the surrounding air. The latter was effected by enclosing the insect's head in a small translucent half-capsule of celloidin. These were made in various sizes on the rounded ends of glass rods of different diameters. Since the arista of each side projects laterally, these were cut short, and a half-capsule of suitable size slipped over the head of the insect and held in position with a thin wire, attached by wax to the outside of the capsule in front, and behind to the wire supporting the insect. This thin wire was sufficiently flexible to allow a certain amount of movement. Thus without greatly modifying the shape presented to the air or interfering markedly with the illumination of the eyes, the antennae were left projecting freely into a small volume of still air, while the rest of the insect was exposed to the flow outside. With the antennae isolated in this way in seven individuals it was found that vigorous wing vibrations were maintained so long as the insect was just sufficiently anaesthetized to give no responses to tactile stimuli, such as touching the feet, which normally stopped the vibration of the wing immediately. The presence of the capsule did not, therefore, interfere with the mechanism of wing vibration. One hour later, however, when the insect was no longer anaesthetized, wing movements were not regularly maintained, either in 'still air' or in a stream of air in the wind tunnel. Fraenkel (1932) has noted that wing movements were maintained in certain of the Orthoptera and Odonata, when a stream of air was blown at them from directly in front. It is clear from the observations just described that the antennae play an important part in the similar reactions shown by *Muscina stabulans*. The reason why the insect, fitted with a capsule, does not continue to vibrate its wings in 'still air' is, possibly, that the antennae are isolated from the airflow, created by the wings themselves, which may normally influence them, when the insect is held stationary in nominally still air. Since the insects do not continue to vibrate their wings with the antennae isolated in this way, this made further study of their role in flight more difficult. Fortunately, however, material suitable for further analysis was found among individuals whose antennae had been removed.

In the following observations the procedure was to anaesthetize the insect, mount it on a wire in the usual way, and hold it dorsum downwards with the antennae resting against the edge of a microscope slide. Each antenna was then removed by a downward cut against the slide with a sharp knife. Although the method was standardized as far as possible, one respect in which individual operations differed was in the amount of antennal nerve that came away with each antenna. What effect, if any, this may have had on individual behaviour was not successfully determined. Individuals so treated were then released from their wire support, and kept isolated in numbered lamp-glasses standing in a shallow dish of water. Each glass was covered with muslin at the top and plugged with cotton wool at the bottom. Honey was provided, and in this way individuals were kept for repeated observations.

For some hours after this operation, the insect (mounted on its supporting wire) did not cease to vibrate its wings, and the legs were held as in flight. One day later this effect of the operation was no longer observed. Wing vibrations were initiated by breaking contact between the feet and substratum and the period during which the wings continued to beat was timed with a stop watch. Eleven individuals were selected at random from the stock cages; from six of these the antennae were removed, five were left intact as controls. The times of five successive determinations of the period during which the wings continued to beat, in 'still air', and with a flow of 140 cm. per sec., are given in table 2. These determinations were made one day after extirpation of the antennae, repeated three days later, and yet again 29 days after the operation in the cases of Nos. 113 ♀ and 115 ♀, which were then still alive and active. From this it will be seen first that without the antennae a stream of air had no marked effect on the duration of wing vibrations; secondly that the individuals fell into two groups, those, such as 114 ♀, 115 ♀ and 118 ♀, which tended to continue to vibrate their wings under all conditions, and those which did not. Individuals similar in behaviour to those of the former group made possible further analysis of the role of the antennae in flight. Although the physiological basis of the difference in behaviour between the individuals of the two groups is not understood, in the absence of more suitable material, deductions from observations of those flies which continued to vibrate their wings may perhaps be applied, though with reserve, to flight in normal individuals. In such individuals without antennae supported in a wind tunnel, the path travelled by the wing tip at airspeeds of 140 and 220 cm. per sec. was recorded as before, with the aid of a camera lucida and with a speck of gold leaf attached to the tip of the wing. In all cases the path was of the elliptical type similar to that of the wing movements in 'still air'. The figure of '8' course only occurred as an occasional excursion from this. In figure 6 are given the equivalent records for an individual of *Musca domestica* on which similar observations were made. The transition from the elliptical to the figure of '8' course when the insect is exposed

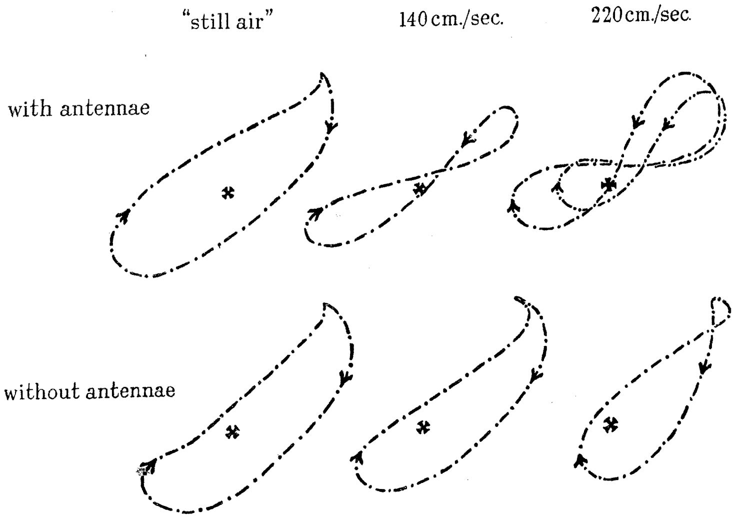

FIGURE 6. Camera lucida drawings of the path travelled relative to the wing base, X, as seen from the side, by the tip of the left wing of a housefly, *Musca domestica* ♀, held facing to the left with the body axis horizontal under three conditions of airflow: above, a normal intact insect and, below, the same individual 26 hours after removal of the antennae.

Table 2

	Flies with both antennae removed														Normal flies				
Reference no. of individuals	113 ♀			114 ♀		115 ♀			116 ♀		117 ♀		118 ♀		119 ♀	120 ♀	121 ♀	122 ♀	123 ♀
Number of days after operation	1	4	29	1	4	1	4	29	1	4	1	4	1	4	1	1	1	1	1
Five successive determinations of the time in seconds that wing vibrations were maintained in 'still air'	1·0	1·5	1·7	> 60	> 60	> 60	56·0	> 60	12·0	6·0	4·0	4·0	> 60	3·0	1·5	1·0	> 60	10·0	2·5
	0·7	1·0	0·5	> 60	> 60	> 60	1·0	25·0	5·0	> 60	6·5	9·0	> 60	> 60	2·0	2·0	> 60	14·0	1·5
	1·0	0·7	1·0	> 60	> 60	> 60	> 60	> 60	> 60	> 60	7·5	58·0	> 60	> 60	1·5	2·0	> 60	16·0	2·0
	0·7	0·5	2·0	> 60	> 60	> 60	11·0	6·0	22·0	> 60	21·0	4·0	> 60	> 60	1·0	2·5	> 60	2·5	5·0
	0·7	0·7	13·0	> 60	> 60	> 60	57·0	2·0	7·0	> 60	> 60	6·0	> 60	> 60	1·0	1·5	> 60	1·5	1·0
Average time	0·8	0·8	3·6	> 60	> 60	> 60	> 39	> 28	> 21	> 49	> 19	16·2	> 60	> 49	1·4	1·8	> 60	8·8	2·4
Five successive determinations of the time in seconds that wing vibrations were maintained in an airflow of 140 cm. per sec.	1·5	1·0	6·5	> 60	> 60	> 60	> 60	57·0	34·0	0·5	1·0	1·2	> 60	> 60	> 60	> 60	> 60	> 60	> 60
	0·7	1·5	29·0	> 60	> 60	> 60	36·0	> 60	3·5	1·0	0·5	7·0	3·0	> 60	> 60	> 60	> 60	> 60	> 60
	1·3	1·0	6·0	> 60	> 60	> 60	> 60	> 60	1·5	1·0	26·0	23·0	> 60	> 60	> 60	> 60	> 60	> 60	> 60
	0·7	1·0	40·0	> 60	> 60	> 60	> 60	> 60	3·0	1·2	1·3	> 60	3·0	> 60	> 60	> 60	> 60	> 60	> 60
	0·5	1·0	14·0	> 60	> 60	> 60	> 60	2·0	20·0	2·5	1·0	8·0	> 60	1·5	> 60	> 60	> 60	> 60	> 60
Average time	0·9	1·0	4·7	> 60	> 60	> 60	> 55	> 49	12·4	1·2	5·9	> 19	> 37	> 48	> 60	> 60	> 60	> 60	> 60

to a stream of air, and the attendant forward displacement of the resultant force involve, therefore, at least one initiating factor which is physiological rather than aerodynamic. The maintenance of this figure and the forward position of the resultant is associated with the effect of a stream of air in producing an angular deflection of the third antennal joint relative to the second.

In considering further how this change in wing path occurs, it will be recalled that in the Diptera two systems of muscles are concerned in flight. There are first the 'indirect muscles' acting on the thorax, which is thereby periodically deformed; this effect, transmitted through the articulation, produces vibration of the wings. The periodic action of these muscles appears to be self-maintained, in that if there are stimuli of peripheral origin concerned in maintenance of vibration these are not abolished by an anaesthetic sufficient to eliminate responses involving the eyes and tactile organs of the legs. Secondly there are the 'direct muscles', inserted at various points on the wing base; phylogenetically, certain of these are 'primarily leg muscles that have been given over to the service of the wings' (Snodgrass 1935). Stimulation of the antennal organs involved in the responses noted above clearly influences the tonus of the leg muscles. It seems likely that the modification of the wing path in a stream of air may result similarly from the influence of these sensilla on the 'direct muscles' of the flight system.

The importance of the antennae in flight demonstrated here may be summed up as follows:

1. The influence of airflow on the antennae is normally necessary for the maintenance of wing vibrations.
2. Responding to movement of the third relative to the second joints are sensilla (Johnston's Organ?) which are stimulated by the flow of air associated with forward flight.
3. The stimulation of these sensilla influences the tonus of the leg muscles, so that in flight the legs are held in the characteristic flight attitude.
4. This stimulation also influences the path travelled by the wing tip, possibly through an effect upon the 'direct muscles' of the flight system.

(v) *The influence of the halteres*

An anaesthetized individual flew stably so long as it was bilaterally symmetrical. If the tip of one wing was cut off, flight under anaesthesia was no longer stable, though the insect flew well enough later when the influence of the anaesthetic had passed off. This suggested that there are sense organs which are concerned in the maintenance of stable flight and that the responses of these as well as the visual and tactile faculties had been eliminated by the anaesthetic used. In three individuals of the series in which the wing path was recorded by the method previously described, the halteres were mutilated by cutting off the terminal knob from each. The operation was performed three days before the records were made. In a flow of 140 cm. per sec.

the path travelled was found to alternate between the figure of '8' course normally maintained when the insect was exposed to a stream of air, and the elliptical course characteristic of wing movements in 'still air', so that both tracks were visible to the eye simultaneously, while at the higher speed of 220 cm. per sec. a figure of '8' course was continuously maintained. Fraenkel and Pringle (1938) have called attention to the likelihood of the campaniform sensilla of the halteres being sensitive to the stresses produced by rotation of the flying insect in any plane except in the plane of vibration of the halteres themselves, and have demonstrated the loss of stability in various species of Diptera on cutting off these organs. The above observations show that associated with such mutilation are modifications of wing movements of a type that greatly influences the position of the resultant force and, hence, the magnitude of the integral concerned in longitudinal stability.

In considering longitudinal stability, it may be noted that, during the downward beat, only a forward displacement of the path of the wing is possible from the elliptical course associated with 'still air'. With the figure of '8' course it appears to be possible for this path to be displaced forwards or backwards, bringing into action a powerful positive or negative restoring integral. The possibility of this greater measure of control in normal flight arises from the influence of the antennae in maintaining conditions in which the downward path of the wing is somewhat forward relative to the path in 'still air', thus allowing displacement in either direction. The interaction of the sensory inflow from the antennae and halteres, upon which the path of the wing relative to the insect depends, is a subject for further study. It remains to be seen whether in this connexion the function of the antennae can best be described as 'kinetic', using the term as applied by Wigglesworth and Gillett (1934) to the antennae of the bug *Rhodnius*.

The physiologist is familiar with the difficulty of rightly assessing the function of an organ by observing mutilated or anaesthetized individuals. The difficulty arises not only because certain processes are modified or eliminated in such cases, but also because of the inevitable readjustment in activity throughout the remaining whole. A similar but more profound difficulty will have been noted in the present analysis, for it is not sufficient to regard the 'remaining whole' as merely the rest of the insect. Readjustment extends into the surrounding air which, as we have seen, forms an essential link in a closed circuit, which may be broken within the animal, by cutting off the antennae, or outside it, by interrupting the normal flow of air. The compass of this system is wide, since the air communicates the supporting forces to the limits of a circumscribed universe. For the purposes of calculation and analysis, it becomes a practical necessity to recognize the unitary character of the system, even though the appropriate boundaries can only be arbitrarily defined. This has dictated the method used in the present analysis, where a single force, representing the whole system and susceptible to changes in any part of it, has been the subject of special study.

My gratitude to Prof. J. Gray cannot adequately be expressed by formal acknowledgement. I should like to record here that this work was undertaken and has developed as a result of his initial interest and continued encouragement. My warmest thanks are due to him for his invaluable advice in all stages of this research. Among others I am especially indebted to Dr L. E. R. Picken who read through the manuscript of this paper and offered many helpful criticisms, to Dr A. D. Imms who has given every facility for rearing the living material, and to Dr C. G. Lamb for checking the identification of the species used.

This research has been carried out during the tenure of a Fellowship at St John's College, Cambridge.

5. Appendices

I. *The method of mounting living insects for experiments*

A small cautery was constructed by mounting two pins in an ebonite handle, soldering to their points a small loop of No. 34 Eureka wire and to the head of each a flex, completing the circuit with a 2 volt accumulator and 2 ohm rheostat in series. The rheostat was adjusted so that the wire loop was at a temperature just sufficient to melt 56° C embedding wax. A small drop of such wax was taken on to the loop as shown in figure 1, A. This was transferred to the tip of a 5 cm. length of similar Eureka wire having a diameter of about 0·2 mm. The wire was held inclined somewhat downwards and heated by pressing the cautery against it, whereupon the wax flowed to the tip as shown in figure 1, B. It was then allowed to cool. For convenience during mounting, the fly, lightly anaesthetized with ether, was placed in a closely fitting groove cut in a sheet of cork. The wire was held horizontally and symmetrically relative to the fly, so that the wax globule was in contact with the mesothorax, and the wire reached forwards as far as the transverse suture. The wax was then melted with a touch of the cautery and, flowing on to that region of the scutum devoid of macrochaetae, solidified there immediately. A fly thus attached with the legs in the attitude characteristic of free flight is shown in figure 1, C. A sharp puff of air from below and behind the insect usually blew the wings forwards and initiated their vibration. The wings frequently continued to vibrate even though the insect might not have recovered sufficiently from the anaesthetic to show any response to visual and tactile stimuli. Recovery was hastened when the wings were vibrating and half an hour later the behaviour did not appear to differ from that of an insect that had not been anaesthetized.

II. *The design, calibration and use of an aerodynamic balance*

The essential features of the balance are shown in figure 7. Its housing was a shallow trough made of brass and divided by the partition, *J*, figure 7, into two compartments, the larger of which contained condenser oil of suitable viscosity. The suspension consisted of a thin flexible rod of pyrex glass, *K*, cemented at one end into a brass ball, *F*, clamped in its socket by the screw, *G*. At the other end of the rod was a bow of glass, *N*, across which a glass fibre, *M*, was stretched. The glass rod, bow and fibre were all in one piece which extended horizontally from its point of attachment, as shown in the sectional elevation in the upper part of figure 7. The balance arm, Q_1Q_2ZV, which was also of glass and in one piece, was lightly constructed but with struts so placed as to make it sufficiently rigid. The chief features of its shape will be seen from the plan in figure 7. A bridge-like portion, *O*, connects the part in the oil bath with the long projecting arm, Q_2ZV, which lies in the same plane outside. The balance arm rests on the fibre and is cemented to it at two points, L_1 and L_2. It is loaded at Q_1 and Q_2 so that there is very nearly an even distribution of weight about these points of attachment, but the weight actually supported by the fibre is small, since four floats, *R*, are fixed to the balance arm. Each of these is a gelatine capsule, sealed with an aceto-cellulose varnish, the two component parts which form the capsule being fitted together in such a position that the requisite volume of oil is displaced. In the plan in figure 7 the balance arm is represented as resting on supports at the three points P_1, P_2, P_3, and on the block, *Y*. On removing the block and lowering the three supports by the arrestment lever, *E*, the whole system projects horizontally from its point of attachment at the base of the glass suspension rod and swings freely, though vibrations are effectively damped by the oil in the bath. Its movement may be resolved into three components: bending of the suspension rod in a vertical and in an horizontal plane, and rocking of the balance arm about its supporting torsion fibre. Three mirrors with a lamp and scale are so arranged that the deflection of the beam from each on the scale is determined by one of these movements and independent of the other two. Mirror *A* is tilted by movements of the suspension rod in a vertical plane, these being communicated by the lever, *S*. Mirror *B* is similarly tilted about an axis parallel to that of *A* by displacement of the rod in a horizontal plane. Mirror *C* is mounted directly on the balance arm.

The wire supporting the fly, *T*, attached in the manner described in Appendix I, fits into the end of the tubular balance arm, *V*. While sliding this into position with the left hand the tip of the balance arm is supported on the block and held firmly with the thumb of the right hand against the shaped metal angle-piece, *W*. This operation completed, the block is removed. When the arm is swinging freely the angular deflection from the zero of mirror *A* is proportional to the vertical component of the resultant force acting, that of mirror *B* to its horizontal component. The whole balance is mounted with its mirrors near the centre of a semicircular translucent scale 20 cm. in radius, as shown in figure 8, and when the mirrors are illuminated by the lamp, the beams reflected from mirrors *A* and *B* traverse 7 cm. of scale for each 10 mg. change in vertical or horizontal component respectively. The electromagnet of a small bell (figure 8) is mounted so that the clapper, *I*, figure 7, strikes the wall of the balance housing. The circuit being momentarily completed by depressing the key,

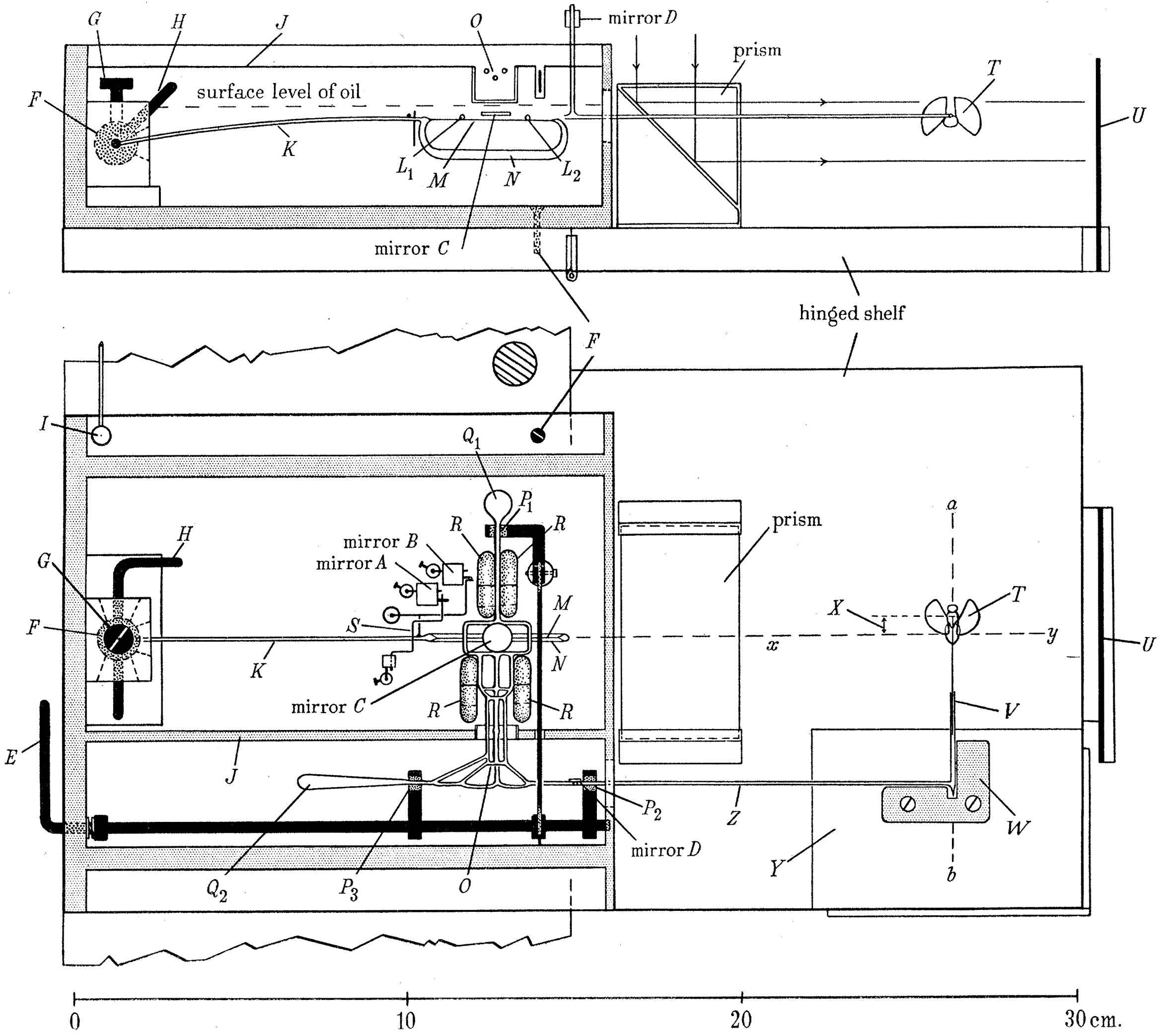

FIGURE 7. Plan and sectional elevation of the aerodynamic balance used to determine the magnitude and position of the resultant force acting on the insect performing regular wing movements in 'still air', or in the airflow of a wind tunnel. The mirrors *A*, *B* and *C* respond independently to vertical, horizontal and rotational movements of the balance arm, Q_1Q_2ZV, mounted on the glass suspension, *K*, which projects freely from its point of attachment, *F*. *E*, arrestment lever; *F*, ball clamped in its socket by the screw, *G*, and carrying the adjustment arm, *H*; *I*, clapper of bell; *J*, partition; *K*, flexible suspension rod; L_1 and L_2, points of attachment of the balance arm to the fibre, *M*, stretched across the bow, *N*; *O*, that part of the balance arm bridging the partition; P_1, P_2 and P_3, supports lowered by the arrestment lever; Q_1 and Q_2, loaded extremities of balance arm; *R*, floats; *S*, lever which tilts mirror *A*; *T*, fly; *U*, screen; *V*, tubular end of balance arm; *W*, metal angle-piece; *X*, horizontal distance between the transverse suture of the fly and the axis of rotation, *xy*, of the balance arm; *Y*, removable block; *Z*, projecting arm; *ab*, vertical plane containing the tip of the balance arm.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

this brings the system of mirrors and levers to their equilibrium positions before any readings are made.

After adjustment of the alignment and inclination of the suspension rod by means of the ball and socket joint, the balance was calibrated for its vertical and horizontal components by applying known vertical and horizontal forces to the tip of the balance arm. The adjustment of inclination of the suspension was facilitated by the use of a handle which fitted on to an arm, *H*, figure 7, allowing considerable delicacy of control. This adjustment was necessary at intervals, since the suspension rod showed a detectable sag after a few days' use; the calibration was periodically checked.

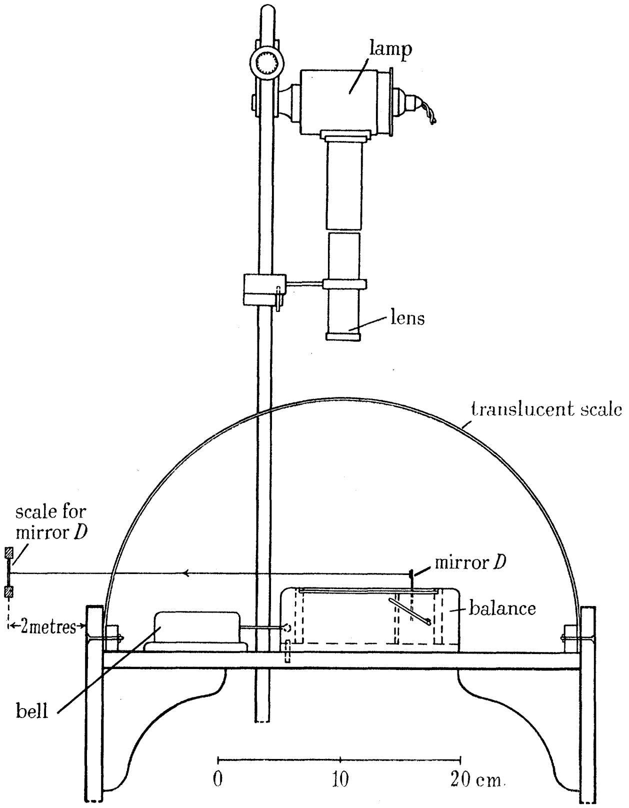

FIGURE 8. Elevation of the aerodynamic balance seen from the left in figure 7, showing the arrangement of the lamp illuminating the mirrors *A*, *B* and *C*, the translucent scale and the scale for mirror *D*.

Calibration to relate the torsion about the fibre with the couple acting is not necessary, as a null method is employed in determining the position of the resultant force. For this determination a lens is swung into position below the lamp, as shown in figure 8. This focuses an image of a cross-wire reflected from the mirror *C* on to a finely ruled region of the scale immediately above it. These readings are always made with the aid of a magnifier and can be determined to ±0·1 mm. A complete series of such readings covers a range of not more than 3 mm. on the scale, so that the change in inclination of the insect due to rotation of the balance arm is so small as to be neglected.

In all determinations of this sort the position of the fly relative to the axis of rotation of the balance arm must be known. For this, the position of the axis of rotation of the balance arm relative to a suitable fixed point on the arm is determined, when the apparatus is calibrated, and this is periodically checked, while in each individual case a quick and accurate method is used to record the position of the fly relative to this fixed point of reference. The latter procedure can best be appreciated by reference to figure 7. With the lens referred to above swung to one side, light from the lamp used to illuminate the mirrors falls on the prism and projects a silhouette of the fly and the tip of the balance arm on to a screen, *U*. This screen is graduated in millimetre squares, and the position on the screen of the tip of the wire supporting the fly, which lies immediately over the transverse suture, is in each case noted and easily recorded to within ±0·25 mm. With the balance arm in its arrestment position, the shadow of the tip of the balance arm lies at the zero of the graduations on the scale and is taken as the point of reference. The position of the axis of rotation relative to this was determined empirically. A horizontal wire was fitted into the tip of the arm and the deflections produced by hanging a weight at various positions on it were plotted against the distance of these from the point of reference. The point of intersection of a series of such curves for different weights gave the horizontal distance of the vertical line intersecting the axis of rotation from the point of reference. To determine the point of intersection of the axis with this vertical line, it was necessary to plot similar curves for the deflections produced by horizontal forces applied at different levels. A steel pin-head was mounted at different levels on a support coincident with the vertical line already determined. The horizontal forces were applied by an electromagnet, whose position was adjusted so as to give the desired horizontal force, determined from the scale reading of mirror *B*, and a zero vertical component, shown by mirror *A*.

In this and in all readings of the deflection of mirror *C*, a preliminary correction is necessary. The angular deflection of mirror *C* which it is desired to measure is that about the axis of rotation of the fibre. The corresponding scale reading is unaffected by rotation of mirror *C* about a *horizontal* axis at right angles to the axis of rotation, such as is caused by changes in the load on the balance arm. This reading is not, however, independent of rotation of mirror *C* about a *vertical* axis, such as is produced by applying a horizontal force to the balance arm. Before taking any reading it is, therefore, necessary to correct this by rotating the whole balance about the vertical axis, *F*, figure 7, until this rotation of mirror *C* is zero relative to the scale. For this purpose a fourth mirror, *D*, is mounted on a vertical support arising from the balance arm. A lamp and scale are placed as indicated in figure 8 (scale and reflected beam only being represented) and the above correction is easily effected by rotation of the balance until the spot on this scale returns to zero. By this method the point of intersection of the axis of rotation of the balance arm, *xy*, figure 7, with a vertical plane, *ab*, containing the tip of the balance arm, was found to lie within a circle 0·3 mm. in diameter for the range of vertical and downward, and horizontal and forward forces of 0 to 50 and 0 to 28 mg. respectively.

The position of the resultant force acting on the fly, under any set of conditions in which the system is bilaterally symmetrical, is defined in terms of the distance of the point of intersection between the line of action of the resultant and the long axis of the body from the centre of gravity. The long axis passes through the centre of gravity, the position of which, relative to the outline of the body, is shown in figure 2. If it is required to know the perpendicular distance of the resultant from the centre of gravity in order to calculate the magnitude of the couple tending to rotate the insect about its centre of gravity, this can readily be deduced from the figure giving the position of the line of action as defined here and from a knowledge of the magnitude of the angle between the line of action and the body axis. The way in which this distance was measured is best illustrated by following a determination of the position of the centre of gravity and of the distance from it of the resultant acting when a fly supported on the balance in 'still air' performs regular wing movements. The wire supporting the fly can be pushed into the tubular end of the balance arm so that the distance, *X*, figure 7, between the transverse suture of the fly and the axis of rotation of the balance arm, *xy*, may be varied. The deflections of mirror *C* are plotted against this distance for four different values of *X* with the fly motionless. These values thus plotted give a straight line. At the close of the determinations similar readings are taken for the wire support without the insect attached, giving a second line which cuts the first. With the supporting wire in the position denoted by this point of intersection, the angular deflection of the balance arm is the same, whether or not the insect is attached. In this position the weight of the insect must, therefore, act through the axis of rotation of the balance arm, whose position relative to the fly is known. The position of the centre of gravity of the fly on its body axis is thus obtained. Similarly, with the fly performing the flight movements it is desired to study, a third line is obtained which intersects that for the motionless insect. When the fly is situated in a position equivalent to this second point of intersection on the graph, the resultant force acting on the body of the fly passes through the axis of rotation of the system. In this way the position of the resultant is determined.

By this method the vertical and horizontal components of the force, and hence its magnitude and direction of action, as well as the position of its line of action in the system, could be measured with an adequate degree of accuracy.

III. *The wind tunnel with plate glass top and bottom*

The chief features of this wind tunnel, used for observing the behaviour of insects when exposed to a stream of air, and for recording the amplitude of their wing beats, are shown in the elevation in figure 9 and in the plan of the middle section, drawn to a larger scale, in figure 10. The tunnel itself, *I*, figure 9, is square in section with wooden sides and plate glass top and bottom. A part, *B* (figures 9 and 10), of the upper plate can be removed to allow the insect to be placed in position within the tunnel. The intake is shaped, and a honeycomb of straws, *H*, is fixed into the entrance. At the other end the tunnel clamps on to the tapering section *A*. The anemometer, *J*, shown in both figures, projects into the tunnel from the side. The chief feature of the design is the single supporting unit, which can be set at any angle about a horizontal axis, transverse to the tunnel, and which carries the insect, *T* (figure 10), within the tunnel, the recording camera, *E* (figure 9), above, and the mirror, *M* (figures 9 and 10), below, from which is reflected the beam, shown in figure 9, that illuminates the insect. By this means the insect can readily be set at any angle to the airflow, while the relative positions of insect, camera and apparent source of light remain the same. This support, *G*, is a rigid frame of angle iron, forming a rectangle about the tunnel, which passes through it. The support can be rotated about the axis, *D*, and held rigidly, when inclined at the desired angle, by a clamp, *K* (figure 9), gripping the sector of metal, *L*. The position of the insect, and the way in which it is held in the tunnel are best seen from the plan in figure 10. In this figure the supporting frame, *G*, is stippled as in figure 9, and the small unit, *S*, carrying the fly mounted on its supporting wire, is sprung into sockets, *U* and *V*, on the axis of rotation of the frame. The angle of the fly relative to the supporting frame is fixed, so that the photographic

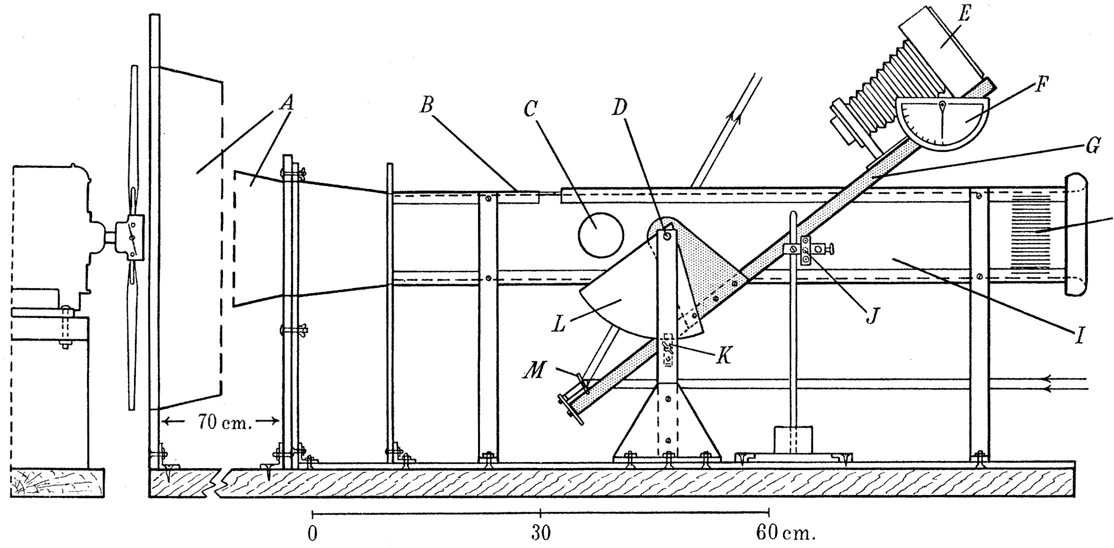

FIGURE 9. Elevation of the wind tunnel. *A*, tapering section; *B*, part of the upper glass plate which can be removed; *C*, observation window; *D*, axis of rotation of the frame; *E*, camera; *F*, scale giving the inclination of the fly to the stream of air; *G*, the frame of angle iron; *H*, honeycomb; *I*, main shaft of tunnel; *J*, anemometer; *K*, clamp, gripping the sector of metal, *L*; *M*, mirror.

plate and plane of movement of the wings are parallel, and a scale, *F* (figure 9), graduated in degrees, with a pointer hanging freely, is mounted on the frame, *G*, so that for any inclination of the frame the direct reading is the angle of inclination of the body axis of the fly to the direction of the stream of air. The camera is so placed that by using the transverse and vertical movements of the lens-mount sixteen separate exposures are made on one $3\frac{1}{2}\times 2\frac{1}{2}$ in. cut film. With exposures of $\frac{1}{25}$th of a second the sector travelled by the wings is clearly recorded, and the angles can be measured from enlarged projections of the negative.

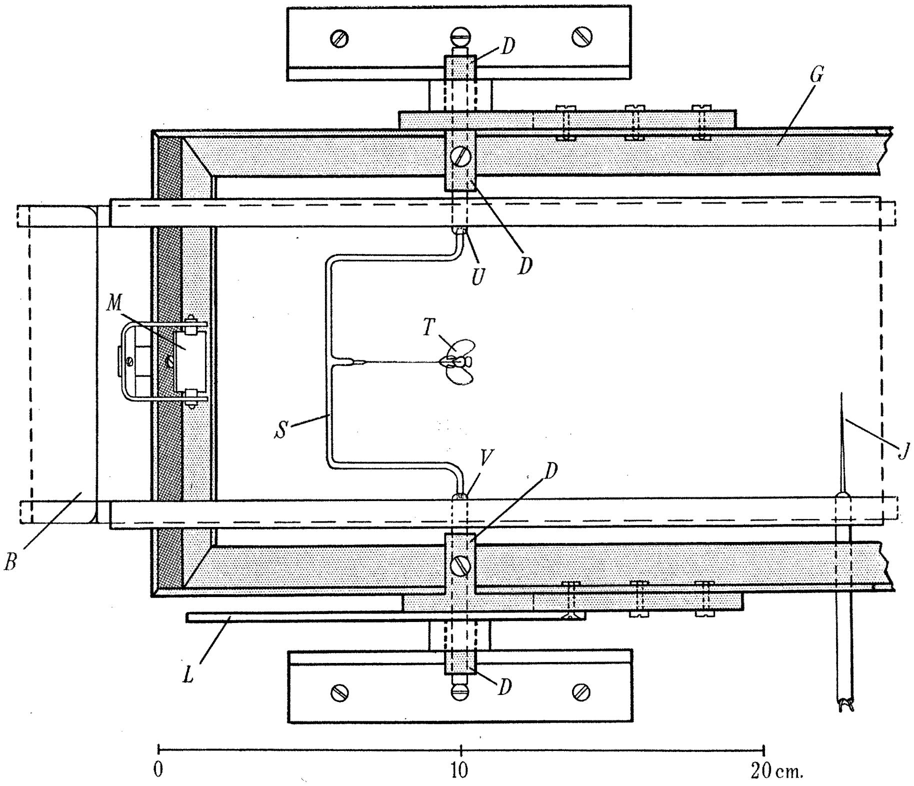

FIGURE 10. Plan of the middle region of the wind tunnel. *B*, part of the upper glass plate which can be removed; *D*, axis of rotation of the frame, *G*; *J*, anemometer; *L*, sector of metal by which the frame is clamped at the desired angle; *M*, mirror reflecting light on the fly; *S*, removable support, which carries the fly, *T*, and is sprung into the sockets *U* and *V*.

6. SUMMARY

1. Females of the dipterous fly *Muscina stabulans* Fallén were chosen for an investigation of flight. The most suitable method of mounting the living insects for experiment is discussed.

2. As a preliminary stage in a detailed study of flight in this species, a comparison was made between the flight system with the insect held stationary and in normal

free flight. The resultant of those forces which, by their action on the body of the insect, maintain or change its state of motion during flight, was selected as the basis for this comparison.

3. Values for this resultant were determined in thirty-two individuals performing regular wing movements when held stationary in 'still air'. In all except four of these the resultant force generated was equal to or greater than the weight of the insect. On an average, the line of action of the resultant was inclined forwards and upwards at 48° to the body axis of the insect. The line of action cut the body axis between 1·75 mm. in front to 3·25 mm. behind the centre of gravity, according to the amplitude of the wing beat. In the majority of cases the point of intersection was behind the centre of gravity in a position incompatible with stable free flight.

4. This last result was confirmed by observing the path travelled by insects performing these wing movements when suddenly liberated in 'still air'. It was found that if the insect is moved forwards at the speeds of normal flight, with the body axis inclined as in free flight, it continues in the same state of motion on liberation.

5. The effect of exposing the insect, held stationary, to a stream of air was investigated with the aid of a wind tunnel. It was found that in those cases where the resultant force passes behind the centre of gravity of the insect in 'still air', the resultant is displaced forwards and comes to pass close behind, through, or in front of the centre of gravity, depending on the velocity of the stream of air and the inclination of the body axis of the insect.

6. There are good grounds for believing that the living insect held stationary in an appropriate stream of air closely resembles in essentials the system in free flight and is therefore suitable for further study of flight.

7. In analysing further the forward displacement of the line of action of the resultant, it was found that the effect of the stream of air on the body of the fly was negligible in this connexion, as compared with that upon the wings.

8. By recording photographically the amplitude of wing beat for ten individuals inclined at 0, 15, 30 and 45° to airflows of 0, 140, 220 and 320 cm. per sec., it was shown that the amplitude decreased with increasing airspeed and inclination of the body axis—an effect which might be expected to produce a backward displacement of the resultant, that is, in a direction opposite to that observed.

9. A study of the path travelled by the wing relative to the insect revealed a factor that would tend to produce the observed forward displacement of the resultant. It was observed that when the insect is exposed to a stream of air the course of the downward beat is displaced forwards, so as to convert the elliptical track, characteristic of wing movements in 'still air', into the figure '8' path, commonly associated with insect flight.

10. This change in the path travelled by the wings was found to be dependent upon the movement or position of the third antennal joint relative to the second, resulting from the action of the stream of air on the third joint with its arista. The

characteristic flight attitude of the legs, and the continued maintenance of wing vibrations when air was blown upon the insect from in front, were also found to be dependent upon the integrity of this system.

11. The path travelled by the wing relative to the insect is also dependent on the interaction of the sensory inflow from the antennae and halteres, since after mutilation of the latter the wing movements associated with stimulation of the former were interrupted.

12. In the appendices are described: (I) the method of mounting living insects for experiment; (II) the design, calibration and use of an aerodynamic balance suitable for determining the magnitude of the vertical and horizontal components of the 'resultant' and the position of its line of action relative to the centre of gravity of the insect; and (III) a small wind tunnel, with plate glass top and bottom, for observing the behaviour of the insect when exposed to a stream of air, and for recording photographically the amplitude of wing beat.

REFERENCES

Bull, L. 1910 *C.R. Acad. Sci., Paris*, **150**, 129–131.
Demoll, R. 1918 *Der Flug der Insekten und der Vögel*. Jena.
Eggers, F. 1924 *Z. Morph. Ökol. Tiere*, **2**, 259–349.
Fraenkel, G. 1932 *Z. vergl. Physiol.* **16**, 371–393.
Fraenkel, G. and Pringle, J. W. S. 1938 *Nature, Lond.*, **141**, 919.
Magnan, A. 1934 *Le vol des insectes*. Paris.
Magnan, A. et Sainte-Laguë, A. 1933 *C.R. Acad. Sci., Paris*, **196**, 1171–1172.
Marey, E.-J. 1868 *C.R. Acad. Sci., Paris*, **67**, 1341–1345.
Pringle, J. W. S. 1938 *J. exp. Biol.* **15**, 114–131.
Roch, F. 1922 *Biol. Zbl.* **42**, 359–364.
Schmitt, O. H. 1938 *J. Sci. Instrum.* **15**, 303.
Snodgrass, R. E. 1935 *Principles of insect morphology*. New York.
Stellwaag, F. 1916 *Biol. Zbl.* **36**, 30–40.
Voss, F. 1914 *Verh. dtsch. zool. Ges.* **24**, 59–90.
Wigglesworth, V. B. and Gillett, J. D. 1934 *J. exp. Biol.* **11**, 120–139.