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THE GYROSCOPIC MECHANISM OF THE HALTERES OF DIPTERA

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[Plate 23]

CONTENTS

The paper gives a detailed anatomical, dynamical and physiological analysis of the gyroscopic mechanism of the halteres of the higher Diptera.

(1) A re-examination has been made of the structure of the articular region of the halteres of *Lucilia sericata*, *Calliphora erythrocephala* and *Eristalis tenax*. In these higher Diptera the organ as a whole is free to move only in one plane, by oscillation through an angle of approximately 150° about a horizontal hinge. A secondary articulation distal to the main hinge allows a slight, damped movement about an axis at right angles to the hinge in the plane of oscillation.

(2) The frequency of oscillation is determined by the mechanical resonance of the system. The single muscle produces, by its contraction, an upwards movement of the haltere and the downstroke results from the elasticity of the hinge.

(3) Stroboscopic observation of the haltere in the living fly shows that the cycle of oscillation consists of two phases of nearly constant angular velocity with rapid reversals at the ends of the stroke.

(4) Dynamical analysis of such a mechanical system shows that: (*a*) when the fly as a whole is not rotating, the secondary articulation ensures that the only forces acting on the basal region of the haltere are the 'primary' torques about the main hinge. (*b*) When the fly is rotating in any plane not that of the oscillation, gyroscopic torques are set up at the base of the haltere about an axis at right-angles to the haltere in the plane of oscillation. (*c*) The magnitude and periodicity of these torques are different for yawing rotations and for pitch or roll.

(5) Since pitching and rolling rotations can be distinguished only by a phase comparison between the gyroscopic torques in the halteres of opposite sides, and since it can be shown experimentally that flight is unimpaired under conditions when the two halteres are oscillating at different frequencies, it is evidently only in the yawing plane that unique indications are given to the fly by the haltere sense organs.

(6) A detailed re-examination of the structure of the sensilla groups on the haltere base in the light of recent advances in knowledge of the function of campaniform and chordotonal sensilla suggests a functional classification into three classes: (A) those sensitive to the vertical 'primary' forces (scapal plates, Hicks papillae and small chordotonal organ), (B) those sensitive to the lateral gyroscopic forces (basal plate, large chordotonal organ) and (C) those without selective sensitivity (undifferentiated papilla).

(7) A method is described of obtaining oscillograph records of impulses in the haltere nerve while the haltere is being oscillated by the pull of its own muscle.

(8) When there is no rotation of the body of the fly, the volleys of impulses recorded in the haltere nerve are of the type to be expected if the sensilla groups are being excited by the 'primary' forces.

(9) When the body of the fly is rotated in yaw or roll the pattern of impulses in the haltere nerve changes in the manner which is to be expected if certain sensilla groups are being excited by the gyroscopic forces.

(10) Detailed analysis of the waveform of the oscillograph records at the beginning and end of yawing and rolling rotations reveals differences between the two types of impulse pattern which are consistent with the dynamical analysis.

(11) Flash photographs of a haltere-less fly in free flight confirm that such an insect is in that state of spiral instability which is to be expected if there is inadequate stabilization in the yawing plane.

(12) A brief comparison of the distribution of sensilla on the bases of the halteres and wings, and a review of what is known of the nature and periodicity of the forces acting on the base of the wings during flight, suggest that it may be possible to trace the stages through which the gyroscopic mechanism of the haltere has evolved from the flight mechanism of the wing.

INTRODUCTION

The halteres of Diptera have attracted the attention of zoologists for a very long time, and probably no insect organ of comparable complexity has given rise to so much argument as to its true function. The original discovery that flies deprived of these organs are unable to maintain balance in flight is usually ascribed to Derham (1711), and since that date various workers in England, France and Germany have put forward hypotheses to account for the phenomenon. From these earlier papers (see Fraenkel (1939) for a recent review) two main ideas have emerged: that favoured by the German workers, following v. Buddenbrock (1919), that the halteres are 'stimulationsorgane', contributing by their activity to the 'energy' of muscular movements; and the earlier view, restated by Fraenkel & Pringle (1938), that the halteres are specific sense organs of equilibrium. These two suggestions have equally failed to progress or to satisfy subsequent workers owing to the lack of any explanation of the mode of action of the organ in terms of sensory physiology. It is the object of this paper to provide such an explanation.

Fraenkel & Pringle (1938) were led to revise the earlier 'balancer' theory against the evidence of v. Buddenbrock and his co-workers by two observations, made independently by the two authors. It was discovered, on the one hand, that the effect of haltere extirpation in certain muscid flies could be compensated by the attachment of a thread to the tip of the abdomen; and it was noticed that the anatomical arrangement of certain groups of sensilla at the base of the haltere was consistent with the idea that the organ was functioning as an organ of equilibrium by virtue of its gyroscopic properties. Fraenkel (1939) published details of his experiments on Muscidae at about the same time as Braun (1939) produced a comprehensive comparative account of the morphology and results of extirpation in Brachycera, the two authors drawing different conclusions about the function of the halteres. It is clear, therefore, that no agreement has yet been reached.

The suggestion (Fraenkel & Pringle 1938) that it is the gyroscopic properties of a moving mass that provide the haltere with its special features as a sense organ was derived from a study of the detailed anatomy of the organ, and has been confirmed by experiments. Since there is, so far as is known, no other structure anywhere in the animal kingdom (except possibly the similar organ in Strepsiptera (Ulrich 1930); see also Wigglesworth 1946) in which this particular physical property is employed, it has been necessary to include a treatment of the dynamics involved. The fact that the moving mass of the haltere oscillates rather than rotates makes even the physical problem a novel one, and no reference could be found in mathematical literature to any treatment of the theory of such a system; this has therefore been worked out from first principles (see appendix II). It is necessary to have a clear picture of the dynamics of the haltere in order to appreciate the validity of the experiments described later in the paper.

The hypothesis that the halteres of Diptera are gyroscopic organs of equilibrium applies generally to the whole group. Differences in structure between different flies make it difficult to judge of the effectiveness of the organ in some families, and the descriptions and discussion in this paper refer particularly to the higher muscid flies, on which most of the new investigations have been made. Braun (1939) established clearly the correlation between the degree of development of the halteres and the power of flight, and it may be that in some of the dipterous families where flight is poor the full capabilities of the organ are not realized.

THE STRUCTURE OF THE HALTERE

The general structure of the halteres is well known (figure 1, plate 23). In all winged members of the group Diptera in place of the hind wings is found a pair of dumbbell-shaped organs, which are oscillated rapidly in the vertical plane during flight. The curvature of the thorax usually results in the halteres being inclined backwards from the transverse axis of the fly by an angle of about 30°. In the more primitive members of the group (e.g. Tipulidae) the halteres are relatively long and exposed; in the more specialized families they are very short (0·7 mm. long in *Calliphora*), and in the calyptrate Diptera are covered by a flap of the wing, the squama, so that they oscillate in a space enclosed between the thorax and abdomen, and must be almost unaffected by the air-flow over the body. The halteres of Syrphidae are remarkable in that the stalk of the organ is not straight but curved backwards round the front end of the abdomen. In many of these higher families the shape of the haltere appears to be related to the shape of the narrow space in which it oscillates; the clearance between it and the sides of the thorax and abdomen is often less than the diameter of the end-knob.

The sensilla of the haltere and the distribution within it of the two branches of the haltere nerve have been investigated with great thoroughness by Pflugstaedt (1912). Unfortunately, this author did not pay close attention to the articulation nor to the exact shape of the cuticular folds of the basal region. Reinvestigation of the structure of this part of the haltere in *Lucilia* and *Calliphora* has failed to reveal any differences from Pflugstaedt's account of the sense organs, but it has been necessary to extend his description of the cuticular anatomy of the base of the organ and of certain features of the campaniform sensilla.

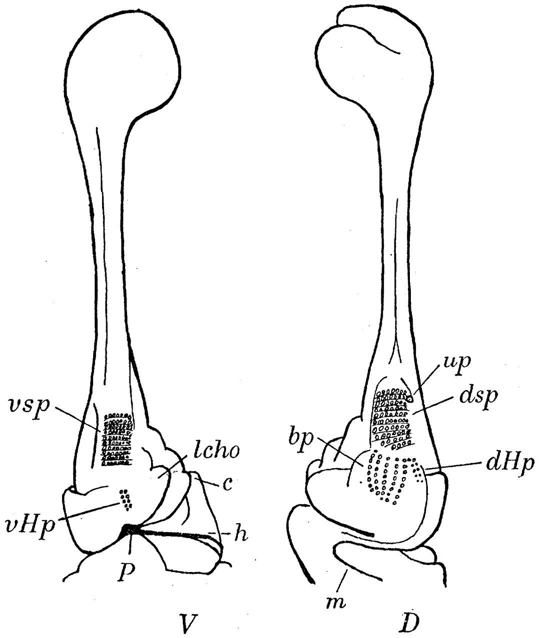


FIGURE 5. Ventral (*V*) and dorsal (*D*) sides of the left haltere of *Lucilia sericata*. *c*, condyle of secondary articulation; *h*, main hinge line; *m*, point of attachment of muscle; *P*, strong point in the articulation at the intersection of the main hinge and the secondary fold; *bp*, basal plate; *dsp*, dorsal scapal plate; *dHp*, dorsal Hicks papillae; *lcho*, large chordotonal organ; *up*, undifferentiated papilla; *vsp*, ventral scapal plate; *vHp*, ventral Hicks papillae. (Magn. × 100.)

The folding of the cuticle near the articulation of the haltere with the metathorax is exceedingly complicated. Stereoscopic photomicrographs of the upper and lower surfaces of the haltere of *Lucilia sericata* (figures 2 and 3, plate 23) give a general picture of the shape of the organ, and the photographs of a model (figure 4, plate 23) show the salient features of the basal region.

The main articulation of the haltere is about a horizontal hinge (*h*, figure 5) formed by the close approximation of the cuticle of the upper and lower surfaces. The opening from the body cavity into the haltere is thus a narrow slit through which pass the two branches of the haltere nerve and the tracheal supply. The cuticle at this hinge line is curved and thickened in such a way that the haltere tends to take up a position of ventral flexion.

A single small muscle attaches by an apodeme to the dorsal side of the cuticle of the metathorax *m* near the hinge. Tension on this apodeme moves the haltere dorsally by distortion of the cuticle of the hinge, and on release of the tension it returns to its ventrally flexed position by virtue of the elasticity of the cuticle.

Distal to the main hinge line the haltere is a rigid structure apart from one further point. Viewed from the ventral surface, a depressed fold of cuticle may be seen running from the front end of the main hinge *P*, diagonally outwards to a point on the rear surface of the basal swelling where a proximal peg-like fold of cuticle fits between two distal folds to make a condylic articulation *c*. This fold gives a slight freedom of movement to the whole of the rest of the haltere by rotation about the point of intersection of the main hinge and the depressed fold, the rotation being accompanied by a sliding of the peg between the two distal folds. The point on the main hinge *P* about which this movement takes place is the point at which the cuticle of the hinge is thickest, and is the strongest part of the attachment of the haltere to the metathorax.

The rest of the haltere has no clear lines of bending. The description now follows Pflugstaedt (1912). The cuticle of the ventral surface of the basal swelling has two important specialized regions: the ventral scapal plate, a semi-cylindrical thickened region continuous with the 'scape' or stalk, folded in a characteristic manner and bearing numerous transverse rows of campaniform sensilla; and a domed and thickened region bearing beneath it, but invisible from the surface, the attachments for the large chordotonal organ. The cuticle of the dorsal surface also has two specialized regions: the dorsal scapal plate, similar to the ventral, and, like it, semi-cylindrical and characteristically folded; and the basal plate, much thickened and domed and bearing large numbers of a different type of campaniform sensillum. The structure of these plates will be discussed in more detail later. The basal swollen portion of the haltere contains four other sensory structures of importance in this discussion: a small chordotonal organ stretching vertically from a point on the dorsal surface just distal to the basal plate to a point on the ventral surface just proximal to the ventral scapal plate; two groups of 'Hicks papillae' (campaniform sensilla), one row on the dorsal surface to the front of the basal plate and the other opposite it on the ventral surface; and a small group (one only in *Lucilia* and *Calliphora*) of 'undifferentiated papillae' on the dorsal surface just to the front of the dorsal scapal plate. A full description of the histology of these sensilla is given by Pflugstaedt (1912); each group retains its position, orientation and structure with remarkable accuracy in individuals of the same species, differs little in these respects from the corresponding group in related species, and is represented in the halteres of nearly all families of Diptera (Braun 1939).

The scape or stalk of the haltere continues the structure of the scapal region of the basal swelling. It is oval in cross-section, the major axis being horizontal, with a partial cuticular division down the centre suggesting its origin in the fusion of two wing veins. It may be straight or curved. A fine nerve trunk passes up it, the fibres being distributed, according to Pflugstaedt (1912), to the large hair sensilla on the end-knob. There is also a tracheal trunk.

The end-knob is again a specialized structure. It has a thin cuticle in contrast to the thickened cuticle of the stalk, and a fold in this cuticle adds still further to its distensibility. Nearly the whole of it is filled with highly vacuolar cells which maintain a turgor pressure keeping the cuticle of the end-knob distended. Injury to the cuticle involving loss of fluid can be compensated to some extent by a fresh development of turgor in these cells, but leads finally to collapse of the knob due to evaporation of its liquid contents. In the intact condition the centre of gravity of the distended end-knob is consistently to the rear of the axis of the haltere stalk.

THE DYNAMICS OF THE HALTERE

The haltere may be considered, from a mechanical point of view, as a system as shown in figure 6. This diagram includes all the articulations of the organ in a way which makes it easier to understand their action. The main horizontal articulation is represented by the bearings *AA*; the secondary freedom of movement given by the depressed fold and the condylic peg by a rotation about the pin *P*, whose axis lies at right angles to the paper. This movement is damped by the fluid contents of the basal swelling, the damping being represented by the dash-pot *H*. Owing to the fact that the centre of gravity *C* of the end-knob lies to the rear of the axis of the haltere stalk, the line joining this to the articulation point *P* makes an angle of less than 90° with the main hinge *AA* when the haltere is at rest. The elasticity of the main hinge is represented by the spring *S*, whose ends are inserted respectively in the axle and the bearing, and the arm *M* represents the attachment of the haltere muscle, whose pull must be taken as coming in a direction at right angles to the plane of the paper.

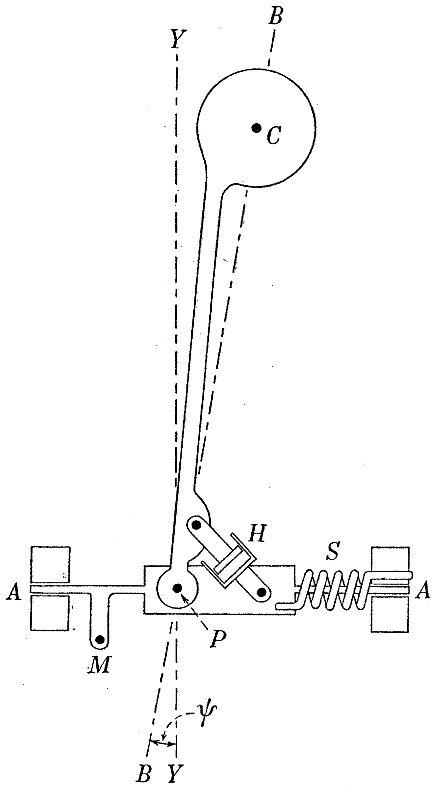


FIGURE 6. Diagram to illustrate the mechanics of the haltere articulations.

The first point to note about such a system, which can be rotated about *AA* in one direction only by the pull of the muscle, being restored by an elastic force, is that the frequency of oscillation must be very nearly the natural period of the system. Successive contractions of the muscle must occur at a frequency related accurately to the mechanical resonance of the system, and to achieve a build-up of amplitude the phasing of these contractions must be adjusted to the natural period of oscillation of the haltere, which in turn is determined by the mass of the system and the elasticity of the hinge. The physiological corollaries of this are discussed later.

The next feature to be considered is the effect of the secondary articulation at *P*. When the haltere oscillates about the axis *AA* the mass of the moving portion, considered as located at the centre of gravity *C*, moves round the circumference of a circle. Since the line *BB* through *P* and *C* makes an angle of less than 90° with the axis *AA*, there will be a torque tending to rotate the line *BB* into the position *YY* at right angles to *AA* (see appendix I). This torque is discontinuous, but it is always in the direction tending to rotate the line *BB* into the position *YY*; it fluctuates at a frequency twice that of the oscillation of the haltere. Provided the articulation at *P* is sufficiently free and the damping produced by the fluid contents of the haltere is sufficient to average out this fluctuating torque, the slight secondary freedom of movement will therefore ensure that the centre of gravity of the moving portion of the haltere always moves in a plane through *P* at right angles to the axis *AA*, i.e. a vertical plane if *AA* is horizontal. Curvatures and irregularities in the stalk are therefore unimportant, and when the haltere is oscillating with the insect at rest the forces acting on the basal region just distal to the secondary articulation will always be in the vertical plane.

Now consider the effect on the dynamics of the haltere of angular rotations of the entire fly. The angular momentum of the oscillating mass, being rotated out of its own plane of oscillation, will produce gyroscopic torques in the same way as if the mass were continuously rotating, except that these torques will not be constant in magnitude or direction. In order to obtain a satisfactory theoretical treatment of the problem of an oscillating gyroscope it is necessary to make three approximations, each of which will be examined later: (*a*) that the oscillating system distal to the articulations already described is rigid, (*b*) that the mass of the system is concentrated at a point, and (*c*) that the oscillation is a simple harmonic motion. With this simplification the properties of the system may be analyzed by the methods of dynamics (see appendix II). The analysis shows that, apart from the primary torques inherent in the oscillatory motion and present when the fly is stationary, angular rotations of the whole fly set up a torque at the base of the haltere acting about an axis at right angles to the moving stalk in the plane of oscillation; and, further, that whatever the plane of rotation of the fly this is the only new torque set up. The magnitude and periodicity of the torques at the base of the haltere differ for different planes of rotation in the manner shown in figure 7.

Certain interesting deductions may be made from the analysis (expressions 3 to 10 of appendix II):

(1) There is no qualitative difference between the torques generated during rolling and pitching rotations. On the other hand, the primary torque due to the oscillation and the gyroscopic torque for yaw differ qualitatively from each other and from that for pitch or roll, in that the maxima occur at different instants in the cycle of oscillation. Furthermore, the torque for yaw oscillates at twice the frequency of the other torques.

(2) The maximum values of these qualitatively different torques change disproportionately as the frequency and amplitude of the oscillation are changed. Thus, with

increased frequency of oscillation, the primary torque becomes relatively larger than the other two, while with increased amplitude the gyroscopic torque for yaw shows a relative increase. In comparing the halteres of different families of Diptera, between which there are considerable differences in frequency and amplitude of oscillation, these relative differences must be kept in mind.

(3) It has already been seen that when the fly is stationary or has zero angular rotation, what has been called the secondary articulation of the haltere ensures that all forces acting on the base of the organ are in the vertical plane. The gyroscopic torques, acting about an axis at right angles to the stalk in the plane of oscillation, are therefore qualitatively different from anything present when the insect is not turning.

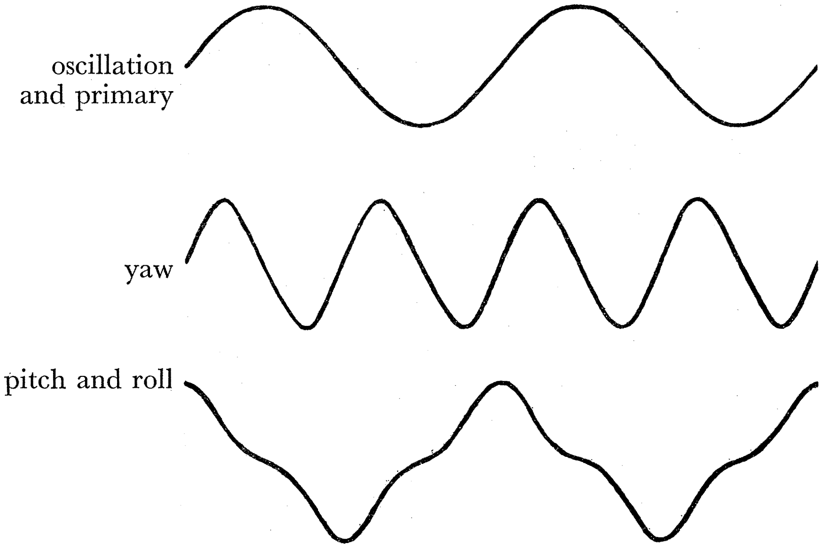


Figure 7. Graphical representation of the expressions derived in appendix II for the torques generated at the base of a haltere oscillating with simple harmonic motion. Note the relative positions of the maxima of the three curves.

(4) The gyroscopic torques act about an axis which moves with the haltere. Any sense organs sensitive to these torques must therefore be situated on the moving portion of the haltere.

(5) The gyroscopic torques during rotation of the whole fly act about the same axis as the torque mentioned above which ensures that with the fly at rest the centre of gravity of the moving portion oscillates in a plane at right angles to the main hinge line. Unlike that torque, however, the mean value of the gyroscopic torques is zero, and they cannot therefore affect the mean lateral position of the moving portion. The same fluid viscosity which smoothes out the pulsating forces keeping the haltere on the arc of maximum radius (*YY*, figure 6) ensures that the secondary articulation does not give it freedom to follow the rapidly oscillating gyroscopic torques, and the full stresses will therefore be developed in the cuticle at the base of the moving portion of the organ.

(6) The fact that the gyroscopic torques during pitching and rolling movements differ only by a constant depending on the sweep-back of the halteres from the transverse axis of the fly necessarily implies that the fly could only distinguish between these two planes of rotation by a comparison of the phasing of the torques from the halteres on the two

sides of the body, the two torques being in phase during pitching movements and in anti-phase during rolling movements. The experiments quoted by Fraenkel (1939) showing the slight effect of unilateral haltere extirpation suggest that such a phase comparison is not an important part of the nervous mechanism associated with the haltere, a conclusion which is supported by the fact that under certain circumstances it is possible to make the two halteres of a fly oscillate at different frequencies (Sellke 1936; see also p. 357). This treatment, which does not affect the ability of the insect to fly, would completely upset any nervous mechanism dependent on phase comparisons between the two sides.

(7) It was pointed out above that in order to produce a simple theoretical treatment of the dynamics of the haltere it is necessary to assume that the moving portion is a rigid structure. If one examines more precisely the effect on the dynamics of the system of departures from rigidity, it becomes apparent that flexibility in a lateral direction is much more serious than flexibility in a vertical direction. The full torque of any gyroscopic system is only developed if the system is restrained. Two features of the structure of the haltere suggest that it is, in fact, much more resistant to lateral than to vertical bending. These are (*a*) the oval section of the stalk, the major axis of the oval being horizontal, and (*b*) the peculiar corrugations of the dorsal and ventral scapal plates found in the higher Diptera (see p. 362).

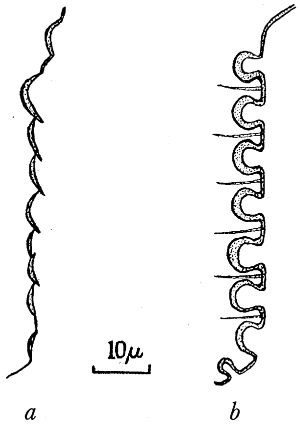


FIGURE 8. Longitudinal sections through the dorsal scapal plate of *a*, *Tipula*; *b*, *Calliphora*; showing the different degree of corrugation of the cuticle.

It is quite consistent with the working of the haltere as an alternating 'restrained' gyroscope that there should be considerable flexibility in the vertical plane. This selective flexibility may, indeed, be demanded, when the frequency of oscillation is high, by the relatively enormous difference between the maximum values of the gyroscopic torques and the torque due to the primary oscillation. Figure 8 shows the extent to which the corrugations of the scapal plates are developed in the Tipulidae and Muscidae which are at opposite ends of the frequency range (*Tipula* 9 per sec.; *Calliphora* 90 to 150 per sec.).

EXPERIMENTS

It will be as well to describe next certain experiments undertaken to check the validity of the dynamical analysis given above and the conclusions derived from it.

(1) *The action of the secondary articulation*

If a fully mature specimen of *Calliphora* or *Lucilia* is lightly anaesthetized and held in an inverted position by means of a wire fixed with wax to the top of the thorax (as described by Hollick 1940), the halteres can be observed under a binocular microscope without dissection. When the effect of the anaesthetic has passed off it is possible to induce normal movements of the wings and halteres. Observation of the haltere is rendered easier if the legs of the fly are allowed to come into contact with a solid object (such as ball of cotton wool), since this inhibits wing movements (Fraenkel 1932).

When the halteres of these particular flies are oscillating the movement of the white end-knob produces the appearance of an arc of a circle. The position of this arc in relation to the sides of the thorax and abdomen is appreciably farther forward (i.e. nearer the thorax) than the position of the end-knob when the haltere is at rest. Particularly in *Calliphora*, which has the habit of oscillating its halteres in short bursts alternating with periods of rest, the movement backwards of the end-knob at the cessation of oscillation can be seen clearly. The existence of a measure of damping of the articulation producing this movement is proved by the delay of the haltere in assuming its resting position as it comes to rest after a burst of oscillation. This delay is of the order of ½ sec., which represents a considerable degree of damping of a torque pulsating at about 300 c./sec.

(2) *The mechanical resonance of the haltere*

Since the ventral movement of the haltere on relaxation of its muscle is produced by the elasticity of the main hinge, dynamical considerations demand that the frequency of oscillation be determined by the mechanical resonance of the system. Physiologically, this implies either (*a*) the existence of a reflex mechanism linking the excitation of the muscle with sense organs sensitive to the movement of the haltere, or (*b*) that the haltere muscle contracts spontaneously when stretched. In either case, alteration to the mass of the end-knob, by altering the mechanical resonance of the system, should alter the frequency of oscillation.

If an anaesthetized fly is mounted, as before, on a wire waxed to the top of the thorax, and the wire is held in the needle-holder of a piezo-electric gramophone pick-up connected through an amplifier to headphones, any movement of the fly becomes audible. On recovery from the anaesthetic, the oscillation of the halteres can be heard clearly as a musical note superimposed on a background of noises caused by leg movements. The pitch of this note, which is a measure of the frequency of oscillation of the halteres, can be estimated roughly by comparison with a tuning fork or determined accurately by means of an oscillograph. If the fly executes movements of flight the vibration caused by the wing muscles is sufficiently large to drown the sound of the haltere movements, but since the halteres frequently show bursts of oscillation without movements of the wings, opportunity is provided for studying these alone.

Measurements have been made of the frequency of oscillation of the left haltere of two individual specimens of *Calliphora* before and after crushing of the end-knob, the right haltere being removed. The results were as follows:

sex	normal	end-knob crushed	after recovery
female	105–120	125–140	105–120
male	160–185	185–200	160–185

During each of the bursts of activity which are typical for this fly the frequency falls over the range indicated, the amplitude of oscillation remaining apparently unchanged, but then the oscillation ceases abruptly. This variation in frequency shows that the system is not sharply tuned, and that the damping due to the muscle or the resistance of the air must be considerable. On the other hand, when the end-knob is crushed, thus reducing the oscillating mass and increasing the natural period of the system, the range of frequencies is significantly higher than before. Provided the cuticle of the end-knob is not severely damaged it regains its former shape in about 30 sec., and the frequency of oscillation then returns to its former value. Since nothing has been changed except the mass of the end-knob, it is clear from this experiment that there must exist a mechanism linking the excitation of the haltere muscle to the natural period of oscillation.

If, instead of removing the other haltere, both are left intact and only one has its end-knob crushed, the note in the headphones is clearly audible as a musical chord, usually about a minor third (frequency ratio 6:5), which reverts to a single note as the knob recovers its original size. This asynchronism between the two halteres was described by Sellke (1936) in *Tipula maxima* after additional loading of the stalk of one organ. Loading would be expected to slow the treated haltere in the same way as lessening the mass of the end-knob accelerates it. In either case the haltere of the other side continues at its normal frequency.

Another type of experiment may be performed to confirm the inherent mechanical resonance of the haltere. If fine platinum wire electrodes are inserted into the top and bottom of the hind region of the thorax of a decapitated fly, the haltere may sometimes be caused to oscillate by the application of high-frequency shocks from a neon-lamp stimulator (type used by Pantin 1934). If the frequency of the oscillation is measured by means of a stroboflash lamp at the same time as the frequency of stimulation is varied over a range from 40 to 400 shocks per sec. (amplitude just adequate to produce oscillation), the haltere frequency is found to be nearly constant and unrelated to the frequency of stimulation. Evidently the stimuli are not producing synchronous contractions of the haltere muscle, but are somehow bringing into a state of excitation a neuromuscular system whose frequency of activity is determined by other means. The nature of this neuromuscular mechanism will not be discussed in this paper, which is concerned mainly with the mechanics of the haltere system, but the experiment provides additional confirmation of the existence of a mechanical resonance.

(3) *Correlation between wing and haltere frequencies*

v. Buddenbrock (1919) was the first author to point out the error of previous statements that there is a rigid correlation between the frequencies of oscillation of the wings and halteres. He showed, in *Tipula*, that if the area of the wings is reduced by section of the tips, the wing-beat frequency is raised but that of the halteres is unchanged. Sellke (1936) performed the complementary experiment of reducing the haltere frequency by loading the stalk while leaving the wing-beat frequency unchanged. On the other hand, the statement made by both Braun (1939) and Sellke (1936) that the movements of flight have no effect on the haltere is not strictly true. Some explanation is required of the undoubted fact that in the normal fly the two frequencies are identical.

In Diptera, as in most insects, the main movement of the wings is produced by distortion of the whole of the skeleton of the thorax by vertical and longitudinal indirect muscles. That this has an effect on the halteres is shown by the following experiments on *Calliphora*:

(*a*) The same depression of the wings as is caused by contraction of the indirect vertical muscles may be produced by laying an anaesthetized fly on its back and pressing on the sternum with the point of a blunt needle. This simultaneously raises the haltere.

(*b*) If a normal fly supported on a wire waxed to the top of the thorax is observed with a stroboflash lamp, it can be seen that the wings and halteres move in anti-phase.

(*c*) If the synchronism between the wings and halteres is upset by cutting the wings (raising the wing-beat frequency), there is a clear indication in the movements of the haltere of an interaction between the two frequencies, the amplitude of the haltere movement varying at the beat frequency of the two oscillations.

These experiments, considered together with the fact that the haltere is a mechanically resonant system, suggest that in the normal fly the frequency of the haltere oscillation is 'locked' to that of the wing-beat by a mechanical interaction between the two systems, that this 'locking' is effective only when the natural frequencies of the two systems are nearly the same, and that the two can function independently when either is upset. To this must be added also the inherent independence of the halteres on the two sides of the body; the wings are necessarily coupled through their common motivating mechanisms.

(4) *The absolute magnitude of the forces involved*

An approximate estimate can be made of the absolute magnitude of the various torques present at the base of the haltere. The average fresh weights of the halteres of *C. erythrocephala* are as follows:

sex	average weight of fly (g.)	average weight of haltere (g.)
male	$2{\cdot}3 \times 10^{-2}$	$9{\cdot}5 \times 10^{-6}$
female	$3{\cdot}7 \times 10^{-2}$	$13{\cdot}1 \times 10^{-6}$

This gives a ratio of haltere to body weight of 0·00041 and 0·00035 respectively for males and females. Clearly the oscillation of the haltere can have little mechanical reaction on the fly as a whole (as believed by Weinland 1891).

The above figures are the weights of the whole of the moving portion of the haltere, at least half of which is concentrated in the basal swelling. For the purpose of estimating the torques generated in the region of the sensilla groups it will be more accurate to take one-half of these values which will be the approximate weight of the stalk and end-knob. For a male *Calliphora* this gives the following approximate values (in c.g.s. units) for the symbols used in formulae (7) to (10) of appendix II:

mass	$4{\cdot}75 \times 10^{-6}$
length	0·07
half-amplitude of oscillation	$75° = 1{\cdot}3$ radians
frequency of oscillation	150
angle of sweep-back	30°

Assuming a harmonic oscillation, the maximum values of the various torques (in dyne-cm.) are therefore

primary torque		$2{\cdot}7 \times 10^{-2}$
gyroscopic torques:	yaw	$3{\cdot}7 \times 10^{-5}\,\omega_3$
	pitch	$4{\cdot}9 \times 10^{-5}\,\omega_2$
	roll	$2{\cdot}8 \times 10^{-5}\,\omega_1$

where ω_1, ω_2 and ω_3 are the angular velocities of the fly about its three axes.

Two points are clear from the above evaluations:

(i) The absolute magnitude of the gyroscopic torques is not significantly different for any of the three planes of rotation.

(ii) With a rotational velocity of the whole fly of one rotation (about 6 radians) per sec., the gyroscopic torques are about $\frac{1}{100}$th of those due to the primary oscillation.

(5) *The actual form of the haltere oscillation*

Throughout this paper so far it has been assumed that the oscillation of the haltere is a simple harmonic motion. This is not strictly correct. The main hinge of the haltere is a flexible structure requiring only a small force to produce full movement of the organ between its two limiting positions. The stalk, on the other hand, though flexible in the vertical plane, is relatively rigid.

If the oscillating haltere is observed with a stroboflash lamp not quite synchronized to its natural frequency the angular velocity of the organ during its up-and-down movements is seen to be nearly constant, with a rapid reversal of direction at the ends of the stroke. This type of movement alters slightly the magnitude and variation of the resulting torques, and instead of figure 7 we must substitute the curves given in figure 9. Since the formulae for the instantaneous values of the gyroscopic torques are generalized expressions which hold good for any type of oscillation (see appendix II), the lower curves of figure 9 may be derived by graphical methods from the approximate curve for the oscillation.

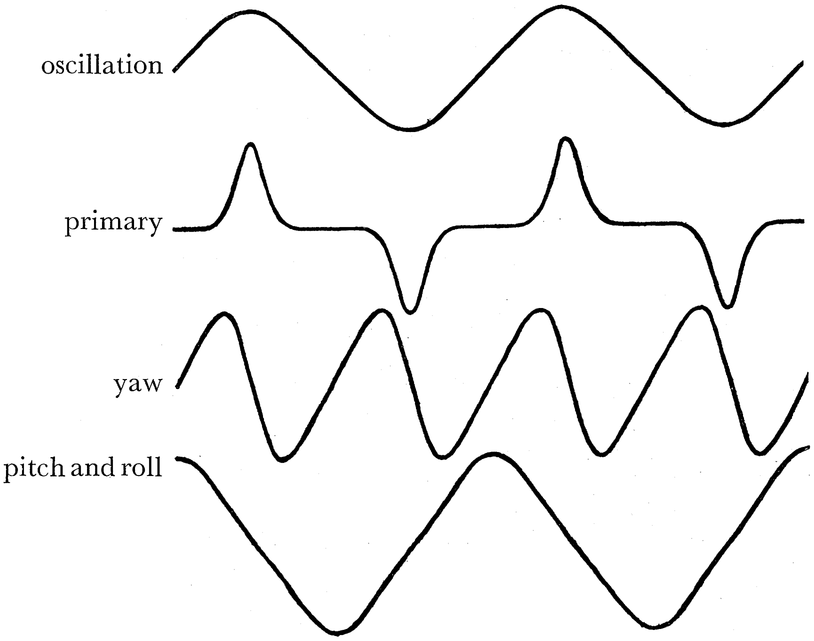


FIGURE 9. Calculated curves for the torques present at the base of a haltere oscillating with linear angular velocity for half of each cycle. The relative amplitude of the three derived curves has no significance.

It is also sometimes apparent when observing the haltere stroboscopically that there is a greater delay at the bottom of the stroke than at the top, particularly when the frequency of the oscillation is slightly lower than normal. This type of movement would result if the haltere muscle did not contract again immediately the organ reached its most ventral position. The effect has not been shown in the curves in figure 9, as it is not always present.

These departures from simple harmonic motion have two effects. The maximum values and rates of change of the primary forces and the gyroscopic torque for yaw are increased, whereas those for pitch and roll are reduced. If the delay at the bottom of the stroke is present there is also introduced an asymmetry in the curve for the primary forces whose possible significance will be discussed later.

Summary of anatomical and experimental observations on the dynamics of the haltere

It may be helpful at this point to summarize the features of the dynamics of the haltere so far described.

(1) Each haltere, with its hinge mechanism, is a mechanically resonant structure which can be set in oscillation by contractions of the single muscle attached to the cuticle at its base. The two halteres are fundamentally independent of each other and of the wing-muscle system, but there is sufficient mechanical interaction between them to produce synchronized oscillation when the resonant frequencies are suitably matched, as they are in the intact fly.

(2) The haltere itself (i.e. the oscillating portion of the system) shows some flexibility in the plane of oscillation, but, apart from one secondary articulation allowing damped movement at right angles to this, it is laterally rigid.

(3) When the whole fly is rotating about any axis not that of the main hinge, an oscillating torque is set up in the base of the moving portion which is unique in the sense that it cannot be produced in any other way in the normal fly.

(4) The gyroscopic torques set up by yawing movements of the fly differ from those set up by pitching and rolling movements in that they oscillate at twice the frequency of the primary oscillation. The torques set up by rolling and pitching movements differ only in magnitude, and, since a phase comparison mechanism is evidently not present, these two planes of rotation cannot be distinguished by the haltere sensory system.

(5) The primary torque maintaining the oscillation and the two types of gyroscopic torque produced respectively by pitching (or rolling) and yawing movements of the fly have their maxima at different instants in the cycle of oscillation.

(6) For the particular case of *Calliphora* rotating at one revolution per sec., the maximum values of the gyroscopic torques are approximately the same for each of the planes of rotation, and are about $\frac{1}{100}$th of the maximum value of the primary torque.

(7) The actual form of the haltere oscillation is not a simple harmonic motion but comprises two phases of approximately constant angular velocity during the movement of the organ on its hinge, together with two elastic phases at the ends of the stroke during which there is a rapid reversal of angular velocity. This has the effect of increasing above the calculated values the primary torque and the gyroscopic torque for yawing rotations, and decreasing the gyroscopic torques for pitch and roll.

The sense organs of the haltere base

The above consideration of the dynamics of the haltere directs attention to the base of the moving portion, where is situated the remarkable concentration of sensilla which has always been the chief attraction for investigators of these organs. Pflugstaedt (1912) gives a most valuable detailed description of the sense organs of this region, and no differences from his account have been discovered in the course of this work. The sensilla are grouped as follows (figure 5):

Campaniform sensilla:	(1) Dorsal scapal plate.
	(2) Ventral scapal plate.
	(3) Basal plate.
	(4) Dorsal Hicks papillae.
	(5) Ventral Hicks papillae.
	(6) Undifferentiated papillae.
Chordotonal organs:	(7) Large chordotonal organ.
	(8) Small chordotonal organ.

Innervated hair sensilla, which are not numerous on the haltere, do not appear to play any part in its functioning as an organ of equilibrium, and they will not be described. But it is instructive to consider whether a particular role may be ascribed to any of the other sensilla groups consistent with the dynamical analysis given above.

Number of sensilla and sensory nerve fibres

The number of sensilla in the different groups has been studied by Weinland (1891) and Pflugstaedt (1912). From their results it is clear that the sensilla of the dorsal and ventral scapal plates, the basal plate and the large chordotonal organ are much more numerous than those of the other groups. In *Calliphora* each of these four groups has about 100 sensilla, whereas the dorsal and ventral Hicks papillae number 17 and 10 respectively, the small chordotonal organ 7, and there is only 1 undifferentiated papilla. A count of the number of fibres in the haltere nerve of *Calliphora* from a section stained with osmic acid gives a figure of 418. It therefore seems reasonable to assume that there is no appreciable fusion of nerve fibres from these sensilla, and that the four groups mentioned above are the main contributors of fibres to the haltere nerve.

Campaniform sensilla

(1) *and* (2) *Dorsal and ventral scapal plates* (figures 5, *dsp*, *vsp*, and 10)

These two groups are similar in structure and may be considered together. The sensilla are situated on the dorsal and ventral sides of the base of the stalk where it joins the expanded basal portion of the haltere. In these regions the cuticle is folded in the peculiar corrugated manner shown in figure 8, the sensilla being arranged in rows in the cuticle of the transverse corrugations.

The sensilla themselves have the typical features of campaniform sensilla in that each has a single sense cell whose distal process is inserted on the underside of the thinned region of the cuticle by a fan-shaped chromophilic lamella (cp. Pringle 1938*b*, pp. 120–121). In these two groups the orientation of the fan-shaped lamella which, as always, is constant throughout the group, is nearly parallel to the longitudinal axis of the haltere, i.e. at right angles to the transverse corrugations. More accurate examination of a number of different species of flies, especially Syrphidae where the stalk is curved, shows that the lamellae are, in fact, orientated parallel to a line joining the intersection of the main and secondary basal articulations (*P*, figure 5) to the centre of the end-knob. This is significant in the light of the dynamical considerations outlined above.

From a mechanical point of view, a hollow structure with corrugations on the dorsal and ventral surfaces and unfolded cuticle on the sides has differential flexibility in the two planes. It is much more flexible to dorsoventral than to lateral bending. Here again, as in the oval section of the stalk, we have apparently a device giving flexibility in the plane of oscillation of the haltere, while preserving rigidity in the plane at right angles, i.e. the plane of the gyroscopic forces.

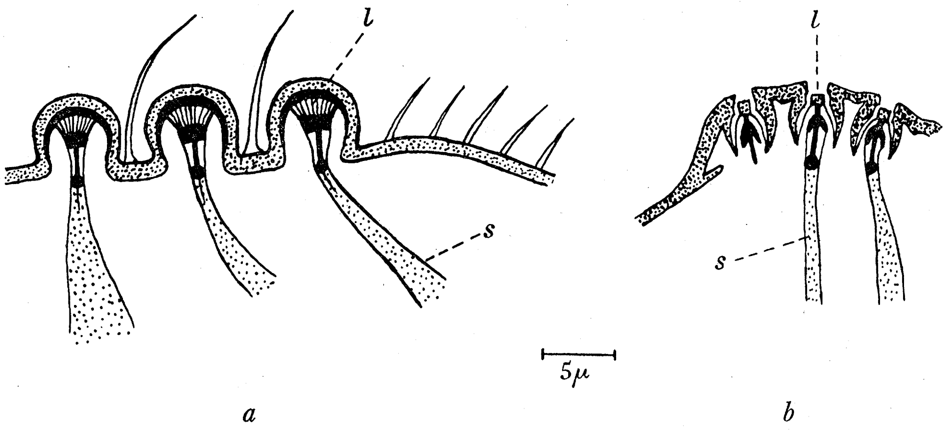


FIGURE 10. Sections of the dorsal scapal plate (*Sarcophaga*) cut (*a*) longitudinal to the axis of the haltere, (*b*) transverse to the haltere axis through one of the rows of sensilla. Note the orientation of the lamella *l* at the ending of the process of the sense cell *s*. (Redrawn from Pflugstaedt 1912.)

According to the explanation of the mode of action of campaniform sensilla given in Pringle (1938) as 'stress receptors' sensitive to those strains in the cuticle whose compression component lies parallel to the fan-shaped lamella, the sensilla of these two dorsal and ventral scapal plates will, owing to their orientation, respond to the strains set up by the primary oscillation of the haltere. Since there are two groups, one on the dorsal and one on the ventral surface, an indication should be given to the insect of both the upwards and downwards accelerations (cp. Demoll 1917, who reached a similar conclusion).

(3) *Basal plate* (figures 5, *bp*, and 11)

The basal plate lies on the dorsal surface of the haltere about in the centre of the basal swelling. It is a domed and thickened region of the cuticle bearing numerous campaniform sensilla which are arranged in rows running approximately longitudinally but converging at the base towards the point of intersection of the main and secondary articulations. The sensilla have a different structure from those of the scapal plates. They are raised above the cuticle instead of being sunk into it, and the fan-shaped lamella at the insertion of the distal process of the sense cell is orientated at an angle of about 30° to the line of the rows.

The significance of the structure of this group of sensilla was outlined briefly in the preliminary publication of the gyroscopic hypothesis of the action of the haltere (Fraenkel & Pringle 1938). It was there pointed out that the basal plate is so perforated by the sensilla (figure 12*a*) that its mechanical properties must resemble those of a trellis or piece of gauze (figure 12*b*), which is relatively strong or weak in shear according as the compression and extension components lie parallel to or diagonal to its component strips. The distribution of the lines of force in the cuticle at the base of the haltere cannot be ascertained directly owing to the complexity of shape of this part of the organ. One may, however, consider the structural properties of a cylindrical tube and argue from this to the haltere.

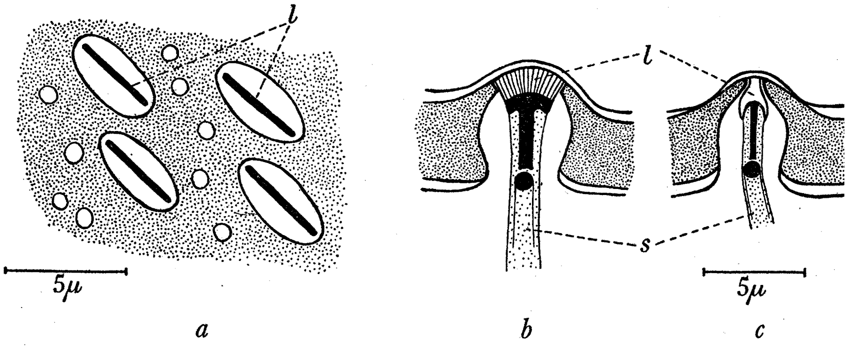


Figure 11. *a*, surface view; *b* and *c*, diagonal sections of the basal plate (*Calliphora*); *b* and *c* cut respectively parallel to and at right-angles to the lamellae of the basal sensilla. *l*, lamella; *s*, process of sense cell. (Redrawn from Pflugstaedt 1912.)

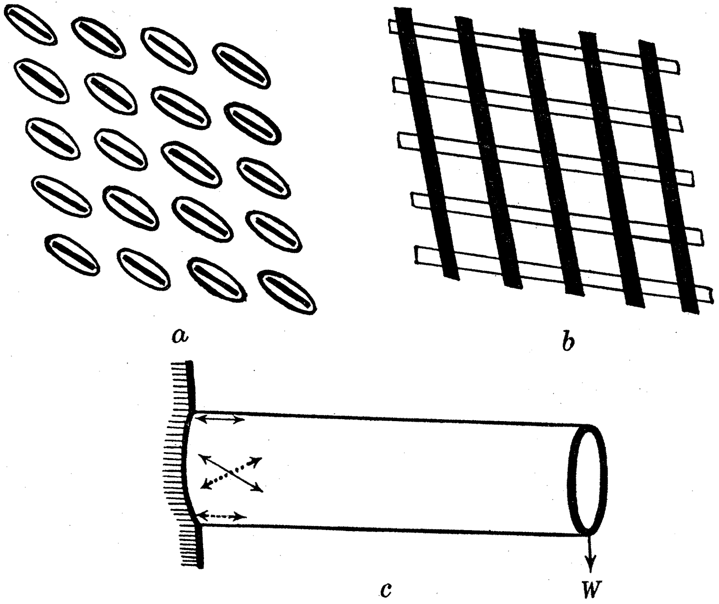


Figure 12. *a*, diagrammatic surface view of basal plate sensilla; *b*, trellis with similar mechanical properties; *c*, diagram of stresses at the base of a cylindrical tube subjected to a bending moment. Continuous arrows—extension; dotted arrows—compression.

A bending moment applied to the end of a cylindrical tube produces stresses as shown in figure 12*c*. If the applied force is vertical there are longitudinal compression and extension forces on the upper and lower surfaces and diagonal shearing stresses on the sides. In the case of the haltere the normal oscillation will produce vertical bending moments at the base and the gyroscopic torques the equivalent of lateral bending moments. It is clear from the approximately longitudinal arrangement of the rows of sensilla of the basal plate that this region of the dorsal surface is relatively strong for the forces produced by the vertical oscillation but relatively weak for those produced by lateral bending. The gyroscopic torques will thus produce the maximum of distortion. The convergence of the rows of sensilla towards the point of intersection of the main and secondary articulations probably represents the expected convergence of stresses towards the point of application of the applied force.

By a similar process of reasoning, and adopting the explanation that sensilla are sensitive to strains parallel to the orientation of their fan-shaped lamellae (Pringle 1938*b*), it is clear that the diagonally orientated sensilla of the basal plate are maximally sensitive to the strains produced by lateral bending, i.e. to the gyroscopic torques. There exists, then, in the basal group of sensilla, a sensory structure which should respond to the particular type of stimulation which can only be produced by angular rotations of the body of the fly while the halteres are in oscillation.

(4) *and* (5) *Dorsal and ventral Hicks papillae* (figures 5, *dHp*, *vHp*, and 13)

These two groups of sensilla are of similar structure. The dorsal group consists of two rows running diagonally to the longitudinal axis of the haltere on the forward side of the basal plate. The rows are close together and diverge proximally from the adjacent rows of basal sensilla. The ventral group also comprises two rows running slightly diagonally and is situated just proximal to the ventral scapal plate. The two groups are thus roughly opposite to each other on the dorsal and ventral sides of the haltere.

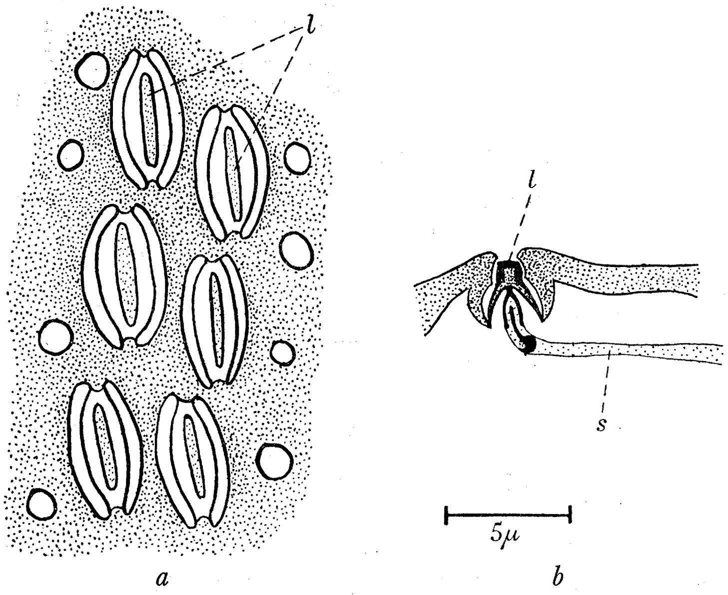


FIGURE 13. *a*, surface view; *b*, transverse section of dorsal Hicks papillae. *a*, *Lucilia*; *b*, *Syrphus*. *l*, lamella; *s*, process of sense cell. (*b* redrawn from Pflugstaedt 1912.)

The sensilla resemble, individually, the sensilla of the scapal plate, but the cuticle in the region of both groups is smooth and not folded into corrugations, so that the sensilla appear to be entirely below the surface. Unlike the scapal sensilla the orientation of the fan-shaped lamella in the Hicks papillae is diagonal to the direction of the rows, so that the lamellae come to lie, like those of the scapal sensilla, parallel to the longitudinal axis of the haltere. Figure 14 shows a drawing of a section cut tangentially through the cuticle of the dorsal surface in the region at the forward edge of the basal plate where the rows of basal and dorsal Hicks papillae approximate. One whole row of basal sensilla has been cut at various depths and the first five of the two rows of Hicks papillae. It is clear that the lamellae of these two groups are oriented in different directions at a relative angle of about 45°.

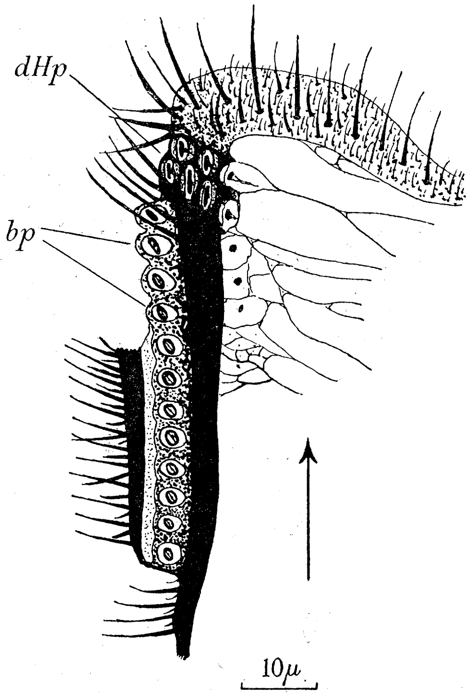


FIGURE 14. Tangential section through the distal region of the basal plate to show the different orientation of the lamellae of the basal sensilla (*bp*) and those of the dorsal Hicks papillae (*dHp*). The arrow indicates the axis of the haltere and points towards the end-knob.

Since the orientation of the lamellae of the Hicks papillae and their structure are similar to those of the scapal plates, it is reasonable to suppose that they are sensitive to the same strains, i.e. those produced by the vertical oscillation of the haltere. Whether there is any qualitative or quantitative difference between the adequate stimuli for these two pairs of groups it is impossible to say. The arrangement of the Hicks papillae in rows increases their sensitivity and selectivity in the same way as does the regular arrangement of the sensilla of the basal plate, and their position nearer to the hinge line implies that the stresses here will be larger. More than this cannot safely be deduced from anatomical considerations.

(6) *Undifferentiated papillae* (figures 5, *up*, and 15)

This type is represented in the high Muscidae by a single sensillum situated just to the front of the dorsal scapal plate at the level of the second row of scapal sensilla. It is a relatively large circular structure with heavily thickened lips, and where the nerve ending reaches the cuticle there is a circular instead of a fan-shaped chromophilic button. According to Braun (1939) the halteres of some brachycerous flies have more than one such sensillum, in some cases even one on the terminal portion of the haltere. Since there is no oriented structure present one would expect it to be equally sensitive to any strains in the cuticle. Its function is not clear.

Chordotonal organs

Chordotonal organs differ from other insect sensilla in having no external cuticular structures. They have a complicated arrangement of internal chromophilic rods, and their sensory cell terminations are usually stretched internally between two points on the cuticle, apodemes or tracheae. They are commonly supposed to be mechano-receptors, sensitive to changes in length between their two points of attachment.

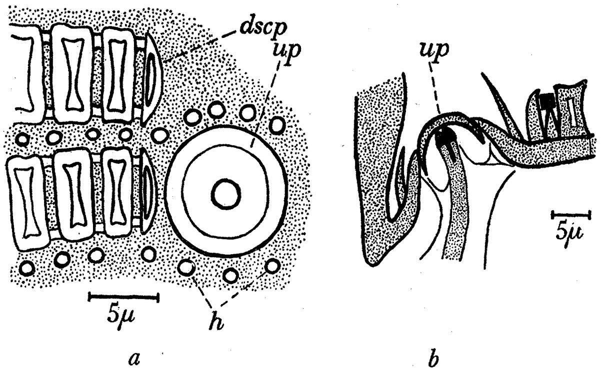


FIGURE 15. *a*, surface view; *b*, transverse section of the undifferentiated papilla. *a*, *Calliphora*; *b*, *Sarcophaga*. *dscp*, dorsal scapal plate; *h*, hair sensilla; *up*, undifferentiated papilla. (Redrawn from Pflugstaedt 1912.)

(7) *Large chordotonal organ* (figure 5, *lcho*)

This organ, which consists, according to Pflugstaedt (1912), of a large number of sensilla of typical structure, lies under a well-marked protuberance of the cuticle on the ventral side of the basal region of the haltere posterior to and proximal to the scapal plate. The two points of attachment of the sensilla are so situated that a line joining them makes an angle of about 45° to the longitudinal axis of the haltere, sloping distally towards the rear.

If we assume that this chordotonal organ responds in a typical manner to changes in length between its two points of attachment, the analysis of strains given above in the discussion on the basal plate indicates that its maximal stimuli will be produced by the gyroscopic torques in the haltere base when the whole fly undergoes angular rotations. The orientation of the organ is parallel to that of the fan-shaped lamellae of the sensilla of the basal plate, and since it is situated on approximately the opposite side of the haltere to the basal plate, it should respond to the same types of stimuli. Here, then, is another organ which may be expected to be selectively sensitive to the gyroscopic torques.

(8) *Small chordotonal organ*

Pflugstaedt (1912) describes this organ as stretching across the haltere in a vertical direction from a point on the dorsal surface at the distal margin of the basal plate to a point on the ventral surface behind the proximal end of the scapal plate. In different Diptera it may slope to a varying extent proximally and distally, but it is always vertical. The shape of the basal region of the haltere is so complicated that it is not possible to deduce with any degree of reliability what applied forces will produce a change in length between the two points of attachment of the organ, but the fact that it is consistently oriented in the vertical plane suggests that it responds to distortions produced by the vertical oscillation of the haltere.

Summary of deductions from the structure of the sensilla

Of the eight groups of sensilla described by Pflugstaedt (1912) and confirmed in the present work, the foregoing discussion suggests a functional grouping as follows:

A. Sensitive to the strains produced by the vertical oscillation of the haltere:

Dorsal scapal plate,	Ventral Hicks papillae,
Ventral scapal plate,	Small chordotonal organ.
Dorsal Hicks papillae,	

B. Sensitive to the strains produced by the gyroscopic torques:

Basal plate, Large chordotonal organ.

C. Sensitive to all strains in the cuticle of the haltere base:

Undifferentiated papilla.

Of these eight groups four are numerically considerably more important than the others, namely, the dorsal and ventral scapal plates, the basal plate and the large chordotonal organ. These four will be discussed later in the paper.

One further deduction may be made from the structure of these four groups. It has been found in a study of campaniform sensilla from a large number of situations in insects that they are always oriented so that it is the *compression* component of shear that is the adequate stimulus (see Pringle 1938*b* p. 128). On the other hand, for chordotonal organs it seems highly probable from anatomical considerations that it is *extension* between the two points of attachment that excites these sensilla. On this basis the stimuli necessary to excite the haltere sensilla groups may be defined still further. The dorsal and ventral scapal plates should be excited by downwards and upwards angular accelerations respectively, i.e. they should each be excited once per cycle of oscillation in antiphase of each other. The orientation of the fan-shaped lamellae of the basal plate sensilla is such that they should be excited by forces bending the haltere forwards, while the large chordotonal organ should be excited by forces bending the haltere backwards. These deductions cannot be verified directly, but they are the logical conclusions to be drawn from the anatomical features described.

The physiology of the haltere

Review of previous work

There are many accounts in the literature of experiments on the physiology of the haltere in which the behaviour of the entire fly has been used as a criterion from which to deduce the function of the organs. Among these, only one attempt has been made to distinguish between the different sensilla groups.

Sellke (1936), working with *Tipula maxima*, claimed to have eliminated in turn the scapal and basal sensilla groups by cautery with a fine wire 0·1 mm. in diameter. His results were as follows:

(1) Cautery of the basal plate sensilla reduced considerably the frequency and amplitude of haltere oscillation; the insect did not fly and crawled only sluggishly. It died within 8 hr.

(2) Cautery of either of the scapal plates left the haltere oscillation normal. Crawling appeared to be normal, and the upset to flight was only that the insect could not maintain height. The flies survived well, but became 'apathetic'.

(3) Cautery to the stalk or end-knob, even when the contents of the latter were completely coagulated, appeared to be without effect on the behaviour of the insect.

These results are consistent with the roles suggested for the various groups on p. 367. The basal plate is essential for the gyroscopic mechanism, but the function of the scapal plates might be carried out to some extent by the Hicks papillae, which should be undamaged in experiment 2. Since the end-knob is merely an inert mass as far as the gyroscopic mechanism is concerned, coagulation of its contents should have little effect. On the other hand, the short life of Sellke's insects from which the basal plate had been cauterized suggests that the treatment is too drastic to allow conclusive deductions to be drawn.

The results of previous workers on the effects of extirpation of the halteres may be summarized as follows:

(i) Bilateral extirpation eliminates or reduces the power of flight and other muscular activities of the insect, including crawling and copulation (v. Buddenbrock 1919, *et al.*).

(ii) A similar effect is produced by removal at the end-knob, or by immobilization (Weinland 1891, *et al.*).

(iii) Unilateral extirpation produces a variable result. In the case of one Asilid (Braun 1939) the fly stands asymmetrically ('tonuswirkung'); in Muscidae there is little upset to co-ordinated flight (Pflugstaedt 1912, *et al.*).

(iv) To some extent the reduction in muscle power after haltere removal is a temporary effect. If such a fly is examined 24 hr. later it is 'perfectly able to take to flight and to fly for long periods when suspended in mid-air', but 'equilibrium during flight is upset, and as a consequence of this the fly cannot keep in the air' (Fraenkel 1939).

(v) 'The effects of the removal of the halteres are almost eliminated by fixing a piece of cotton to the tip of the abdomen' (Fraenkel 1939; confirmed 'to a certain extent' by Braun 1939).

Neurophysiological experiments

Methods

The most direct and unequivocal method of studying the physiology of a sense organ is to record impulses in the nerve supplying it. In the case of the haltere the technical difficulties of applying this method are considerable owing to the small size of the flies available in this country and the fact that the organ does not function at all unless it is oscillating. When the fly has been dissected sufficiently to allow the haltere nerve to be picked up on electrodes, the haltere muscle is usually found to be inexcitable.

To overcome this difficulty several different methods were tried of causing the haltere to oscillate artificially. These included attaching a small iron filing to the end-knob and moving it in an alternating electromagnetic field, touching the cuticle near the hinge with the point of a vibrating needle, and the application of an intermittent tension to the cut peripheral end of the haltere muscle. Although a large discharge of impulses in the nerve can be produced by each of these methods, only the last of them simulates the natural conditions in which energy is supplied to the haltere through the apodeme of its muscle. Finally, a method was found which, in a few preparations, preserved the natural contractions of the haltere muscle, and these constitute the most conclusive experiments.

The apparatus used is shown in figure 16. A lightly etherized fly (*Calliphora*, *Lucilia* and *Eristalis* have been used—mainly *Calliphora*) is accurately bisected dorsoventrally with a sharp safety-razor blade. Both halves may be used. The wing, squama, head, abdomen and legs are removed and the half-thorax is secured by pins on a wax block, cut surface upwards. The longitudinal indirect flight muscles are dissected off to expose the haltere nerve and muscle, the preparation being kept moist with insect Ringer solution (formula in Pringle 1938*a*). If the thoracic ganglion has been accurately bisected by the razor cut, a few preparations then show a tendency for the haltere to oscillate when it is flicked with the point of a needle. If the ganglion is not cut accurately no method of electrical stimulation has been found which will induce contractions of the haltere muscle and the oscillation has to be produced artificially. In that case, after the cut peripheral end of the haltere nerve has been picked up on fine platinum wire electrodes held in one micro-manipulator, the cut peripheral end of the muscle is picked up on another fine platinum wire mounted on the diaphragm of a small moving-coil oscillograph unit held in a second micro-manipulator. By feeding the correct frequency of alternating current to the moving-coil unit the vibration of the wire on the diaphragm is transmitted to the muscle and produces oscillation of the haltere up to full amplitude. The whole rigid assembly is mounted on trunnions so that it can be rotated about a horizontal axis; by adjusting the position of the half-thorax on the wax block the conditions of rotation in yaw and roll may thus be reproduced.

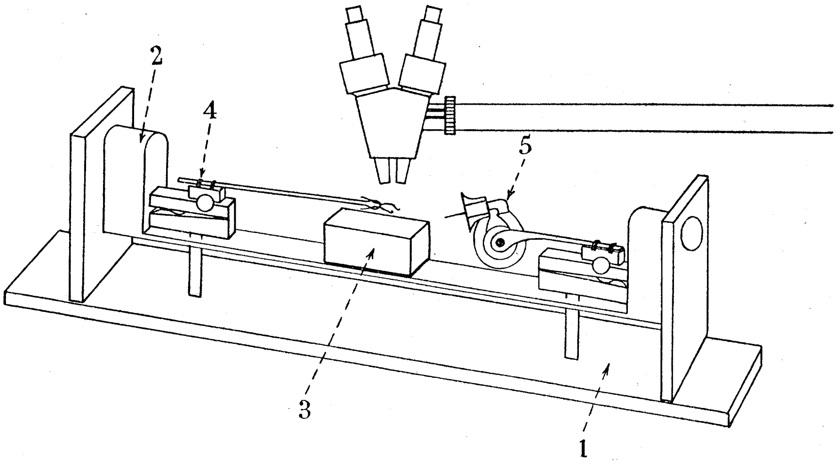


FIGURE 16. Arrangement of apparatus for experiments on the effect of rotation. 1, solid base; 2, frame carried on ball bearings; 3, wax block; 4, micromanipulator carrying glass rod to which are fixed the platinum wire electrodes; 5, moving coil unit, supported on a second micromanipulator, and having a fine platinum wire fixed to the centre of its diaphragm.

Results

Experiment 1

With the electrodes connected through a condenser-coupled amplifier to headphones and oscilloscope in the usual manner, a discharge of impulses may be detected in the nerve when the stationary haltere is touched with a needle. Since there are at least 400 fibres in the nerve, analysis of these records is unprofitable, but certain features may be noted. There is a much greater discharge of impulses if the haltere is bent laterally than if it is bent dorsally or ventrally; most of the endings adapt rapidly, and only a few impulses are present with constant pressure on the stalk.

Experiment 2

A similar effect is observed if an iron filing on the tip of the haltere is moved by an alternating magnetic field whose orientation can be adjusted. Although the maximum amplitude of oscillation is produced when the field is parallel to the natural plane of oscillation of the haltere, the maximum discharge is produced when the field is approximately at right angles to this.

Experiment 3

Using the technique described above with a moving-coil unit attached to the haltere muscle, one can again observe the relative insensitivity of the sensilla to movement in the natural plane of oscillation. As the amplitude of the applied vibration is increased, the haltere may oscillate through a whole angle of about 90° without any discharge being apparent in the nerve. Only as the oscillation approaches full amplitude are synchronous bursts of impulses generated.

Experiment 4

With full oscillation the records obtained (figures 17*a*, *b*) are similar whether the haltere is oscillating normally by contraction of its muscle or is being driven at its resonant frequency by the moving-coil unit attached to the muscle. Volleys of impulses occur twice per cycle of oscillation, with periods of comparative quiet in between. There is considerable asymmetry between alternate volleys, which appears to be due to an unsymmetrical oscillation of the haltere about its natural mean position, as it can be controlled by adjusting the mean tension on the muscle by means of the micromanipulator. Even with the natural oscillation this asymmetry is often present on the records and it is evidently a normal phenomenon.

Very often, with full amplitude of oscillation, the nerve discharge is not a series of exactly synchronous volleys at each half-cycle but shows a varying degree of breaking up of the volleys into separate groups of impulses (figure 17*b*). The volleys may thus last for up to a quarter of a cycle, but the discrete nature of the separate bursts of impulses is always clearly indicated.

Experiment 5

If the whole assembly is rotated by hand so as to simulate yawing rotations of the fly, a different type of record is obtained (figure 17*c*, *d*). With a rate of rotation equal to about 1 revolution per sec., the interval between the volleys becomes completely filled in with impulses whose size is comparable to that of the regular volleys. This effect is present only during rotation and is similar with either direction of rotation; it has been observed both with natural and artificial oscillation of the haltere. It is not easy to give a quantitative measurement of this effect, which consists essentially of a break-up of the volleys into a series of separate asynchronous impulses. One method of showing it numerically is to count the number of individual spikes visible on the records. This gives the following figures:

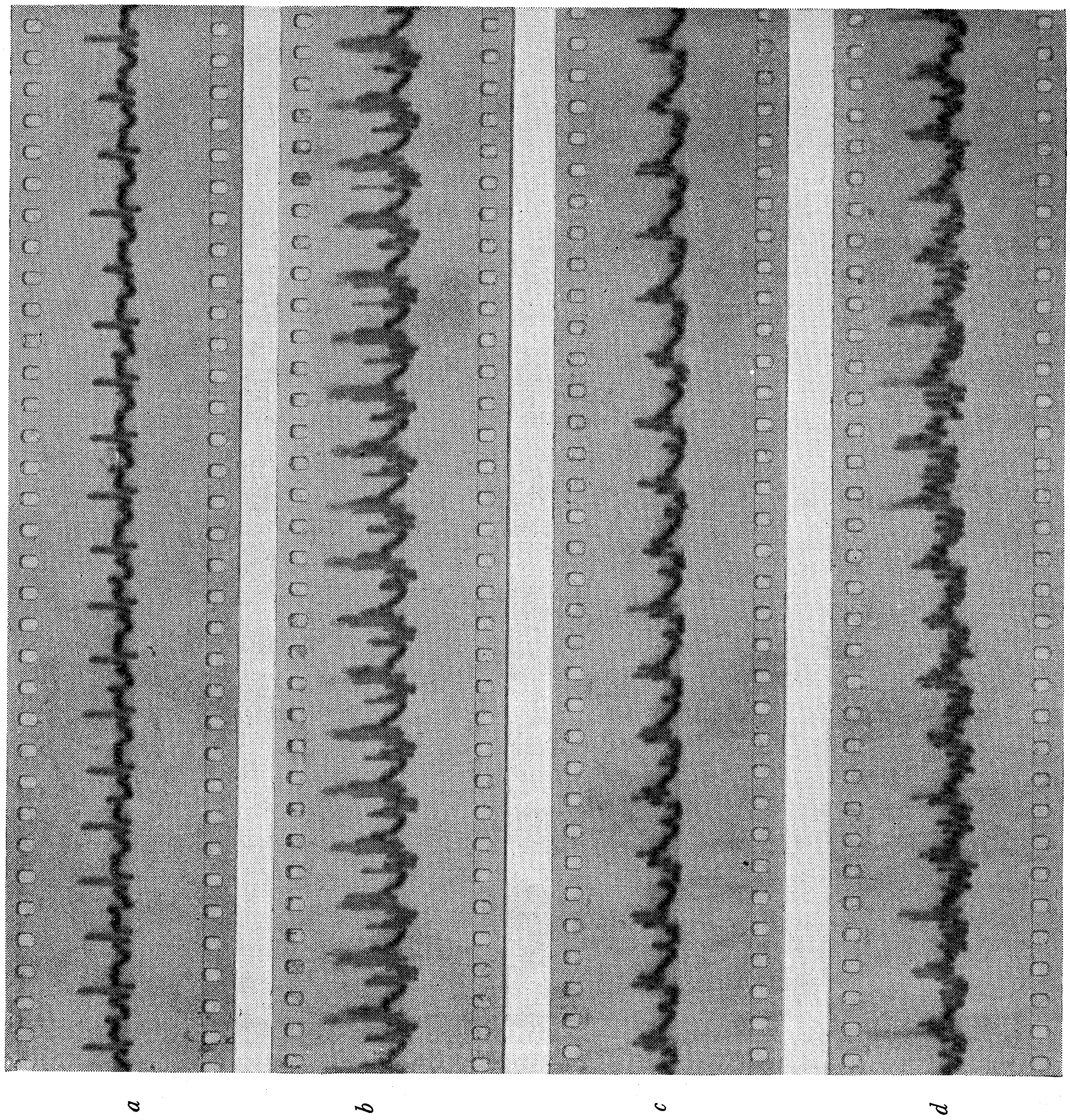
		fly stationary		fly rotating in yaw	
number of spikes in 4 cycles of oscillation	exp. A	47	average 41	65	average 65
		36		66	
		39		63	
	exp. B	45		60	

The break-up of the volleys into asynchronous spikes is usually accompanied by a reduction in the amplitude of the maxima on the record. This suggests that the endings which, during rotation, are being excited at other instants in the cycle are also excited when the fly is stationary, and that the large size of these volleys is due to the additive effect of a large number of approximately synchronous impulses. Further evidence for this is provided at the beginning and end of the rotation. Figure 17*e* shows a portion of a record covering the period as the rotation was starting. The mechanical movement of the haltere and the escape of the alternating current driving the moving-coil unit attached to the muscle combine at this high amplification to give a sinusoidal background which makes interpretation of a short length difficult. It is apparent, however, that the single volleys at the start of this portion (no rotation) divide into two main spikes whose relative separation becomes greater as the rate of rotation increases. By measurement of the record of which figure 17*e* is a portion it is possible to make a reconstruction (figure 18) which shows the changes in timing relative to the haltere oscillation of the spikes corresponding to volleys of impulses in the nerve. Each of the spikes is diphasic, the downward deflexion giving the clearer picture.

At line 0 (no rotation) there is a large (saturating) spike A once per cycle with a smaller spike B about half-way between the A spikes. These are similar to those shown in figure 17*a*. As rotation starts, a spike C appears before the A spikes and grows in size until it is comparable in size to A; at the same time it moves forward until it is one quarter of a cycle ahead of the point originally occupied by A. The A spike itself breaks up (line 2) and the major part of it lags in phase until, with the full rate of rotation (line 3), it is about one-eighth of a cycle behind its original position. The B spike is not so easy to follow owing to its smaller size, but it appears in line 3 to have split up in a similar manner and to comprise three spikes of which only the middle small one occupies the same position as it did originally. The final result is a record with a jumble of spikes whose individual identity becomes difficult to follow as rotation continues.

Experiment 6

If the preparation is mounted so that rotation on the trunnions simulates roll instead of yaw, a different type of nerve discharge is obtained (figure 17*f*). Once again there is the sinusoidal background, which is clear enough in this record to serve as a reference time scale. The individual cycles have been numbered. This fragment shows the end of a rotation. Considering it backwards, from cycles 26 to 21 there is the usual regular volley just before the peak of the sine-wave, and a much smaller spike just before the trough. Preceding the main spike is a smaller spike which was always faintly visible in the stationary record from this preparation. From cycle 17 to 11 this grows until it is equal in size to the main spike. At cycle 13 a fourth spike begins to be visible before the spike in the trough and by cycle 9 has passed it in size. At the beginning of the record, which corresponds to full rotation, four spikes are present, spaced almost evenly through each cycle; throughout the record there is no change in the timing of the spikes relative to the oscillation, and there is not the confused jumble of spikes typical of the record during yawing rotations.



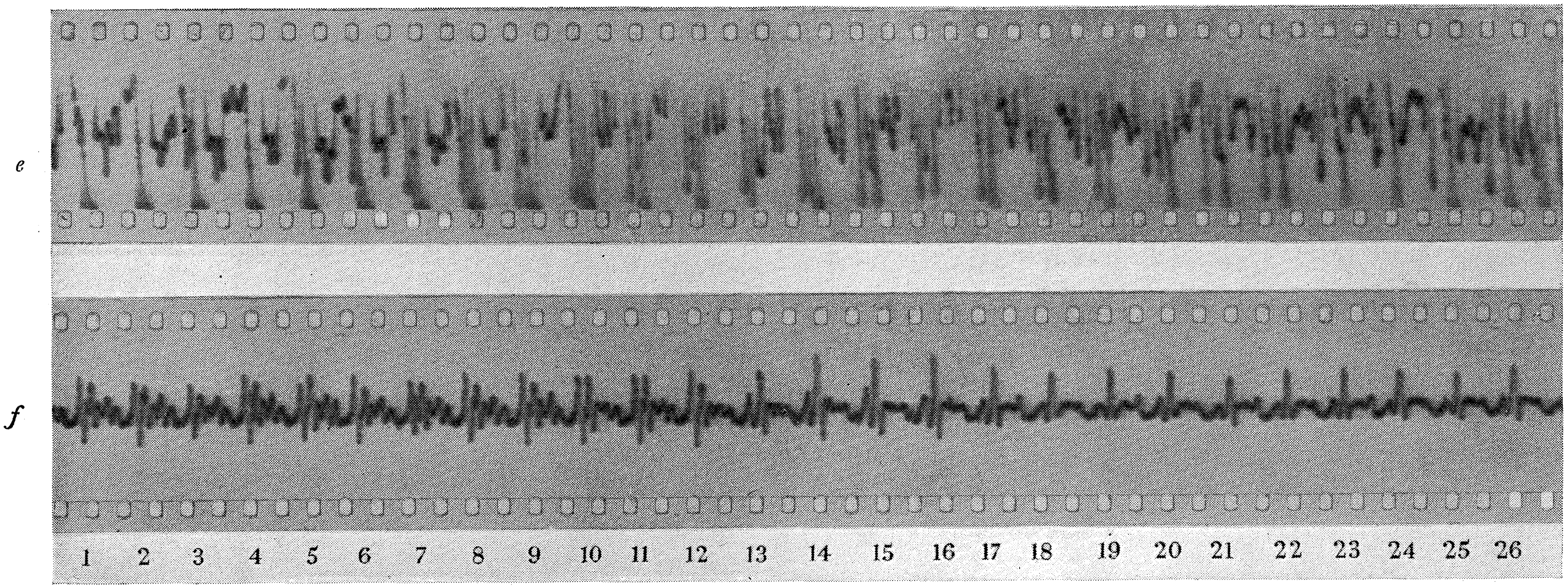


FIGURE 17. Oscillograph records from the haltere nerve of *Calliphora*. Time scale 175 perforations per second.

a, haltere driven at 99 oscillations per sec. by means of moving-coil unit. No rotation of frame.

b, haltere oscillating at 96 c./sec. with active contractions of its own muscle. No rotation of frame.

c, *d*, haltere oscillating with active contractions of its muscle. *c*, no rotation; *d*, rotation in the yawing plane at about 1 revolution per sec.; the two pieces are cut from a single strip of film.

e, haltere driven by moving-coil unit. Record at higher amplification to show the change in the nerve discharge at the beginning of rotation in yaw.

f, haltere driven by moving-coil unit; preparation mounted on wax block so that rotation of frame simulates rolling movements of fly. Portion of record showing the stopping of rotation.

Discussion

The explanation of the above results is to be found in the dynamics of the oscillating haltere as summarized on p. 360 and in figure 9, and in the range of sensitivities of the sensilla groups deduced from their anatomy and summarized on p. 367.

Experiment 1 demonstrates that the rate of adaptation of most of the sensilla is rapid. A rapidly adapting sensory ending gives a response proportional to some combination of the intensity of the stimulus and the rate of change of the intensity. This must be borne in mind when considering the stimulating effect of the various torques developed. The existence of a slight persistent discharge to constant stimulation indicates, however, that there is some variation in the rates of adaptation of the various types of sensilla.

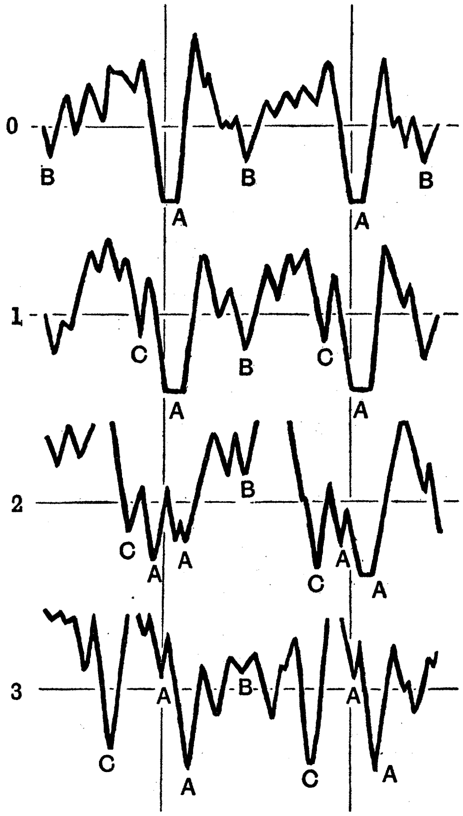


Figure 18. Four portions of the record shown in figure 17*e*, each comprising two cycles of haltere oscillation, superimposed to show the changes in the wave-form of the nerve discharge as the whole preparation is rotated.

Experiments 1 and 2 both demonstrate that there are a large number of endings present which are selectively sensitive to lateral forces in the haltere. These laterally sensitive sensilla have a much higher sensitivity than those which respond to forces in the plane of oscillation.

Experiment 3 shows that, in the plane of oscillation, the sensitivity of the sensilla is low. If, as suggested on p. 367, the scapal plate sensilla are responsible for this discharge in the nerve, it seems that these are only excited when the oscillation reaches full amplitude. The possibility arises that the function of these groups is to indicate when the amplitude of the oscillation has reached its maximum. The haltere is oscillating in a very restricted space, and its function is disturbed if it touches the sides of the thorax or abdomen. Some means of limiting its amplitude of oscillation is therefore demanded.

Experiment 4 shows that some of the sensilla are excited at two instants in the cycle, and it seems probable that these are at the moments of greatest angular acceleration, i.e. at the ends of the stroke. The asymmetry of the spikes, even with normal oscillation, can be explained if the reversal at the top of the stroke is more rapid than at the bottom; this is consistent with the form of the haltere oscillation sometimes observed. The fact that at full amplitude the volleys consist of a number of spikes suggests that more than one group of sensilla is being excited, and possibly that the laterally sensitive groups (basal plate and large chordotonal organ) are also being excited by the large forces produced by the rapid angular accelerations. To be completely insensitive to these 'primary' forces while retaining sensitivity to the gyroscopic forces which are about $\frac{1}{100}$th of the magnitude, the orientation of the basal plate sensilla would have to be correct to better than 1° relative to the position of the centre of gravity of the moving portion of the haltere, and if this were an essential feature of the mechanism it is unlikely that it would function correctly, as it does, after complete heat coagulation of the contents of the end-knob (Sellke 1936).

Experiment 5 gives the results of rotation in yaw. At the beginning and end of rotation the lateral gyroscopic forces are increasing or decreasing, while the component of the vertical forces to which the laterally sensitive sensilla are responding remains constant. The total stimulating effect on the laterally sensitive sensilla will change as shown in figure 19. The heavy curve represents the vertical forces (on a much reduced scale) and the curves 1, 2 and 3, the resultant from the addition to this curve of increasing proportions of the theoretical curve for the gyroscopic force for yawing rotation taken from figure 9. The horizontal dotted lines are arbitrarily chosen threshold values for the response of the sensilla groups.

Below the curves are shown the theoretical instants in the cycle at which the various sensilla groups should respond. For simplicity it is assumed that the scapal groups respond to the vertical forces at the same instant as the laterally sensitive groups respond to the component of the vertical force in the absence of rotation. This gives a single synchronous volley when there is no rotation.

It was deduced on p. 367, from anatomical considerations, that the basal plate sensilla and those of the large chordotonal organ should respond to opposite directions of lateral force. If this is so, the spikes on the record from the haltere nerve should change in the manner shown at 1, 2 and 3 (figure 19) as the rotation increases in the two directions. A preparation in which the component of the vertical forces in the absence of rotation excites the basal plate sensilla should also excite the sensilla of the large chordotonal organ at the opposite swing of the haltere, and there is therefore an asymmetry in the theoretical pattern of spikes at alternate half-cycles of the oscillation. At which phase the record may be expected to show one or the other pattern of spikes for a given direction of rotation depends on the exact position of the centre of gravity of the moving portion of the haltere in relation to the directions of maximum sensitivity of the basal and large chordotonal sensilla.

The theoretical pattern of spikes shown in figure 19 may be compared with the observed pattern shown in figure 18 for the beginning of a yawing rotation. The resemblance between the observed and the theoretical pattern for what has arbitrarily been called right-handed rotation in figure 19 is close. Whereas the largest spike derived from spike A of figure 18 lags slightly as rotation increases, spike C advances considerably. The virtual disappearance of the original spike in line 3 of figure 18 suggests that, of the single volley in the absence of rotation, the major part is composed of impulses from the basal and large chordotonal sensilla responding to the large vertical forces and that in this experiment the scapal sensilla were only just being excited. The two large spikes, C and A, in line 3 of figure 18 are therefore interpreted as being derived from the large chordotonal organ and basal plate respectively, and the smaller spike marked A as representing the remaining excitation of the scapal plate.

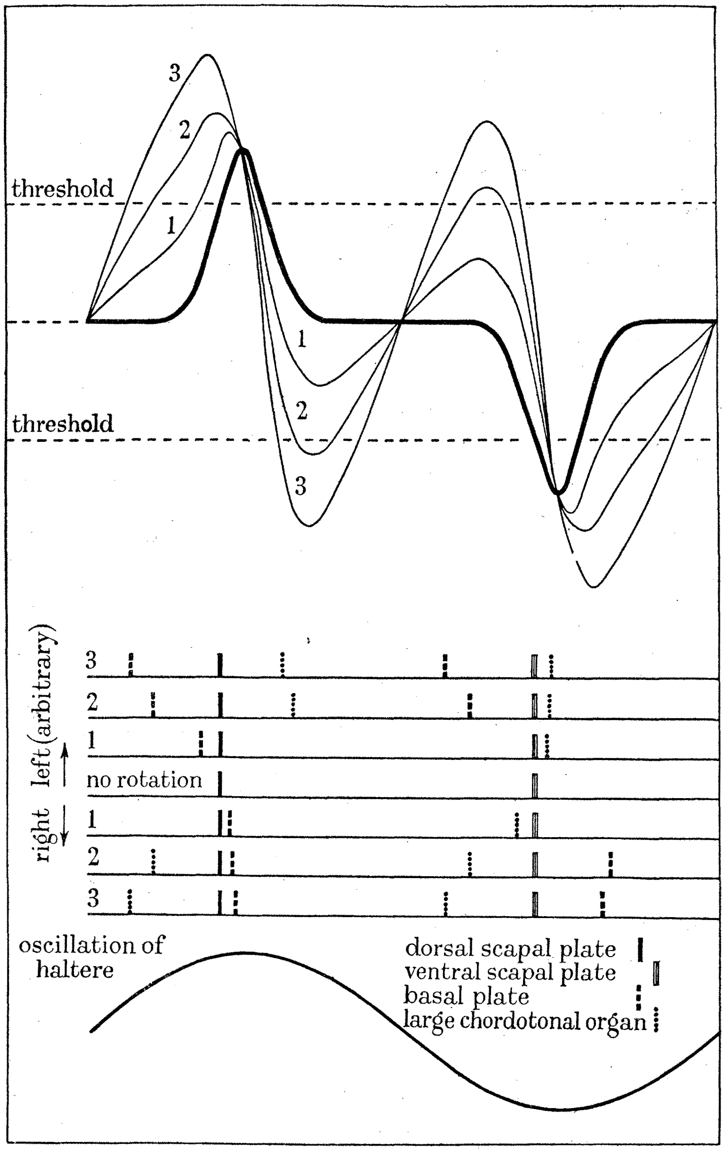


FIGURE 19. Upper: calculated change in the adequate stimulus to the laterally sensitive sensilla of the haltere base at the start of rotation in yaw. Thick curve, no rotation; curves 1, 2 and 3, increasing angular velocities of rotation. Lower: diagram to show the instant in the cycle when the various sensilla groups should respond to the stimulus, assuming an arbitrary threshold.

Experiment 5, giving the result of rotation in roll, may be explained on similar lines. The spikes present at the end of the record in figure 17*f* do not break up into several spikes during rotation but remain more or less unchanged, and in this preparation they would appear to be due to excitation of the scapal plate sensilla only. Figure 9 shows that the gyroscopic forces for rolling rotations have their maxima half-way between the peaks of the primary forces, and the position of the extra spikes on figure 17*f* during rotation is therefore in accordance with theory. Of these extra spikes one in each cycle should arise from the basal plate sensilla and one from the large chordotonal organ; the frequency of excitation of each of these is therefore only half of that produced by yawing rotations. Furthermore, their timing relative to each other is different, the interval between them being always approximately half a cycle.

Summary of conclusions from neurophysiological experiments

In spite of the difficulty in analyzing oscilloscope records from a haltere nerve containing a large number of nerve fibres, the experimental results show a definite effect of rotations in yaw and roll at a rate of about 1 revolution per sec., and these effects are in accordance with the theoretical expectations. The identity of the spikes on the records with volleys from particular groups of sensilla could only be verified from experiments with single nerve fibres, and these have not proved possible with a nerve consisting of a mass of non-medullated fibres enclosed overall in a tough sheath. The following facts, however, are established:

(1) In the absence of rotation the nerve discharge consists of single or closely grouped volleys of impulses occurring twice per cycle of oscillation. Alternate volleys may be unequal in size.

(2) During rotations in the yawing plane, these volleys break up into three main spikes whose temporal separation increases as the rotation speeds up, producing finally a confused jumble of spikes.

(3) During rolling rotations the original volleys remain distinct, and two new volleys arise at points corresponding approximately to one-quarter and three-quarters of a cycle of oscillation.

On the basis of the dynamical and anatomical analysis, the original volleys are ascribed largely to the dorsal and ventral scapal plate sensilla respectively, with some contribution from the other groups, and the new volleys during rotation to the basal plate sensilla and those of the large chordotonal organ.

Statement of hypothesis

A hypothesis to explain the function of the halteres may now be stated:

(1) *The halteres of Diptera are organs of special sense giving an indication to the fly of rotations in the yawing plane.*

(2) *The discharge of impulses in the haltere nerve is interpreted as indicating a turn to the left or to the right according as the impulses from the basal plate sensilla precede or follow those from the large chordotonal organ.*

(3) *The impulses from the dorsal and ventral scapal plate sensilla serve to measure the amplitude of the haltere oscillation and, by reflexly inhibiting the contractions of the haltere muscle, preserve a constant amplitude of oscillation.*

(4) *The rate of rotation in yaw is indicated by the relative timing of the impulses from the basal plate sensilla and those from the large chordotonal organ, and also by their intensity* (*i.e. number of sensilla excited*). *If there is no separation in time, a simultaneous increase in intensity of both will have no effect. Slight maladjustment of the organ so that both groups are excited in the absence of rotation will therefore not be interpreted as a turn.*

(5) *For a given direction of rotation the two halteres will be oppositely excited; the indications must therefore be interpreted in opposite sense.*

(6) *Pitching and rolling rotations are not interpreted as turns owing to differences in the timing of the impulses. Since the haltere system is fundamentally incapable of distinguishing between pitching and rolling rotations, it is difficult to see how it can give useful indications in these planes.*

THE INFLUENCE OF THE HALTERES ON THE MECHANISM OF FLIGHT

Having stated a reasoned hypothesis to account for the functioning of the halteres as organs of special sense, we may now proceed to consider experiments with the entire fly. The first step is to examine the type of instability shown by the haltere-less fly. Figure 20 shows tracings from a series of flash photographs in free flight of an *Eristalis tenax* whose halteres had their end-knobs removed about two hours previously. The photographs were taken by releasing the fly in front of a moving film camera in the beam of an 'arditron' lamp giving 2 μsec. flashes 8 times per sec. In spite of the fact that the wings were beating apparently normally, the fly was unstable in yaw and during the 1 sec. covered by the photographs executed one complete turn about the vertical axis. The insect, in fact, fell to the ground and was unable to maintain itself in the air.

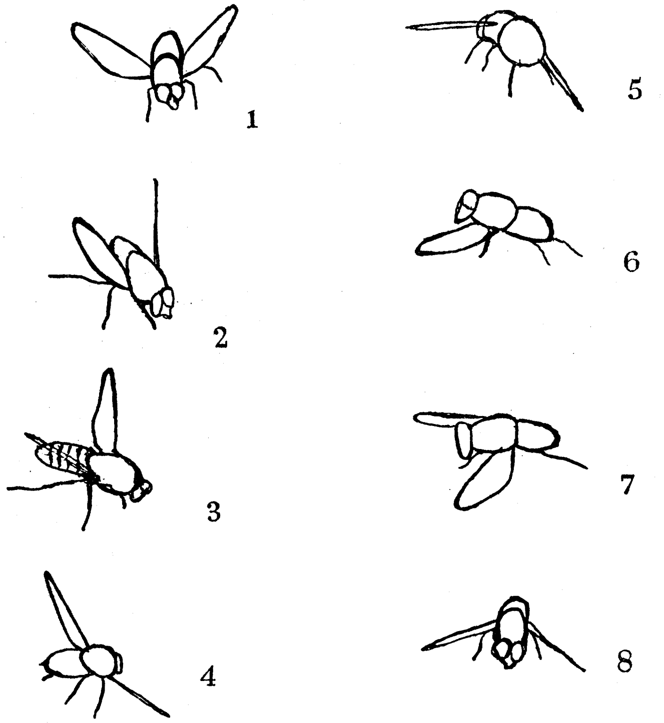


FIGURE 20. Outline tracings from instantaneous flash photographs of an *Eristalis tenax* in free flight, the halteres having been removed 2 hr. previously. Interval between exposures $\frac{1}{8}$ sec.

Not all haltere-less flies launched into the air fall vertically to the ground. Some progress for a short distance horizontally with an oscillating motion before losing control, and sometimes the spin is checked before the ground is reached, to be followed by a short period of level flight before it starts again. Only when a powerful orienting stimulus such as a source of light is present, do the flies make any progress in one direction. These experiments confirm the hypothesis that it is in the yawing plane that the dipterous insect requires reflex stabilisation.

The aerodynamics of dipterous flight have been studied most recently by Hollick (1940). The data given in his paper for *Muscina stabulans* show that the position of the mean resultant of the forces produced by the wings during flight moves in such a way, as the inclination of the body to the horizontal changes, that the insect will be inherently stable in pitch; i.e. alterations of attitude will be corrected automatically by a change in the amplitude of the wing-beat without any physiological response on the part of the insect. Hollick states that the form of a wing-beat also alters, so as to produce a pitching moment, as the result of excitation of the antennal sensory system by the forward movement of the fly through the air, but he distinguishes between this reflex response and the aerodynamic equilibrium conferred by changes in amplitude. The arguments he uses would also suggest that there may be some inherent stability in the rolling plane, but there is nothing to indicate stability in yaw; his measurements of the position of the centre of pressure of the body of the fly show that it coincides with that of the centre of gravity, so that no stability is conferred by the body; and the position of the resultant of the wing forces precludes the possibility of yawing stability from the wings. Hollick's data therefore suggest an absence of inherent stability in yaw which would account for the observed movements of the haltere-less fly.

In general aerodynamical terms, the fly probably shows what is known as 'spiral instability'. Any slight inequality in the force produced by the wings of opposite sides will generate a rolling and yawing moment which, if not immediately corrected by some reflex mechanism, will lead to a spin. The phenomenon is one commonly encountered in the design of fixed-wing aircraft and is usually corrected by the addition of a fixed tail-fin. Fraenkel's (1939) experiments, in which the stability of a haltere-less fly was restored by the addition of a piece of cotton to the tip of the abdomen, are directly comparable.

THE EVOLUTION OF THE HALTERE

A mechanism as unusual and complicated as that of the haltere can hardly have come into existence suddenly in the course of evolution of the Diptera. The zoologist is often faced with insuperable difficulties in attempting to find an answer to this aspect of the morphology or physiology of a particular organ. Fortunately in the case of the haltere it is possible to see how the gyroscopic mechanism of the organ probably came to be developed.

It is generally accepted that the halteres are modified hind wings; their position, shape and type of movement all support this conclusion. In various other orders of insects, and on the wings of Diptera, groups of sensilla have been described which bear a close resemblance to those found in the haltere (Erhardt 1916; Vogel 1911, 1912). For example, Erhardt (1916) describes the sense organs of the wing of *Chrysopa* as consisting of three groups of campaniform sensilla situated on the bases of the wing veins, and two sets of chordotonal organs, one set oriented vertically between the top and bottom surface of the wing and the other diagonally between two veins at the base. She does not describe the orientation of the campaniform sensilla so that the function of the various groups cannot be worked out, but the resemblance to the haltere is obvious.

A superficial examination has been made of the sensilla on the wings of a number of Diptera. Figure 21 shows the arrangement of sensilla on the radial vein of the wing of *Eristalis tenax*. The sensilla fall into two groups, a compact row at the base on the anterior side (anterior series) with a few extending out along the vein, and a long row starting on the posterior side at the base and curving over the top of the vein round the posterior edge (posterior series). The sensilla of the anterior series are more deeply sunk below the surface than are those of the posterior series. A longitudinal lamella is visible in the sensilla of the posterior series, and this shows a constant orientation in a direction inclined at about the same angle to the length of the vein as the line of the row of sensilla, but in the opposite sense. Thus in the right wing the row of sensilla is arranged in an anti-clockwise spiral from base to tip, while the orientation of the fan-shaped lamellae is a clockwise spiral.

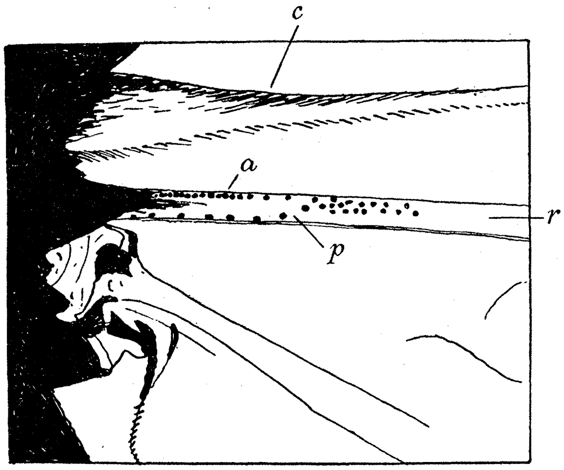


FIGURE 21. Tracing from photomicrograph of whole mount of the wing of *Eristalis* to show the position of the campaniform sensilla on the radial vein. *c*, costa; *a*, anterior row; *p*, posterior row of campaniform sensilla; *r*, radial vein.

By the same type of reasoning as that used on pp. 362 to 364 to deduce the function of the basal plate sensilla on the haltere, the structure of the posterior series of sensilla on the wing suggests that they should respond to the twisting forces in the radial vein. Rather less conclusively the anterior series may be identified as receptors for the vertical bending forces in the vein, and the large chordotonal organ as a receptor for horizontal drag forces. All the types of force produced by the movements of the wing through the air could be registered by such a system of sense organs.

During the cycle of wing-beat a regular succession of lift, drag and twisting forces must be produced at the wing base. Although nothing definite is known about these, the observed figure-of-eight form of the wing beat (Hollick 1940) suggests that they may vary in a manner in general similar to the forces acting at the base of the haltere, with the horizontal forces changing at twice the frequency of the wing beat. One can imagine an evolutionary process, involving a gradual reduction of the wing area and increase of the wing mass, in which the effect of the inertia forces gradually became more important than the aerodynamic forces. A pattern of reflexes presumably exists connecting the sensory impulses from the wing sense organs with the contractions of the muscles controlling flight; as the inertia forces became more important in the hind wings these reflexes would be already present to link them with the steering mechanisms. Clearly a much more detailed study of the forces acting on the wings is necessary before final conclusions can be drawn, but some guidance as to the type of forces to be looked for may be obtained from the knowledge that they have evolved into the gyroscopic system of the halteres. During the evolutionary process some instability might be expected, and it is interesting to note that the lower Diptera, almost without exception, have long thin abdomens, which must increase their inherent stability in pitch and yaw. Inherent stability, however, is a definite hindrance to the making of rapid turns; this may account for the gradual reduction in length of the abdomen in the group as the haltere efficiency increases. The final culmination is perhaps seen in the hover flies, whose control of movement in the air is unsurpassed in the animal kingdom.

I wish to acknowledge assistance received from many people during the course of this work, and particularly from Mr R. Lubbock (appendix II), Mr S. Smith (weighing halteres), Dr R. H. J. Brown ('arditron' apparatus), Mr J. Richardson (construction of model illustrated in figure 4), and my assistant Mr C. H. Moore (construction of electrical apparatus). During the long interval when the work was interrupted I benefited from conversations with many people unconnected with zoological research, especially with Mr F. W. Meredith, of Smith's Aircraft Instruments Ltd. To all of these I express my sincere gratitude.

APPENDIX I

Forces acting at the secondary articulation of the haltere

In the mechanical system of figure 6, let m = the mass of the moving portion acting at C, l = the distance PC, ψ = the angle BPY, ω = the maximum angular velocity about AA.

If the rod PC oscillates about AA with simple harmonic motion at frequency n, then the instantaneous torque about an axis through P at right angles to the plane APC is given by

$$|\, ml^2\omega \sin\psi \cos 2\pi nt\,|.$$

$$\text{Mean value of torque} = 2n\int_{-\frac{1}{4n}}^{+\frac{1}{4n}} ml^2\omega \sin\psi \cos 2\pi nt\, dt$$

$$= \frac{ml^2\omega}{\pi}\sin\psi.$$

APPENDIX II

The properties of an oscillating gyroscope

A mass m (figure 22), supported on a light arm of length l, oscillates in the plane zoa, the arm at any instant making an angle ϕ with the horizontal plane. The plane zoa is inclined at a constant angle θ to the transverse axis oy of the supporting object, the whole of which is subject to constant rotations about the axes x, y, z of magnitude $\omega_1\omega_2\omega_3$.

Let $\omega_a \omega_b$ be the components of rotation about the horizontal axes *oa*, *ob* respectively in and at right angles to the plane of oscillation. Then

$$\omega_a = \omega_1 \sin\theta + \omega_2 \cos\theta, \tag{1}$$

$$\omega_b = -\omega_1 \cos\theta + \omega_2 \sin\theta. \tag{2}$$

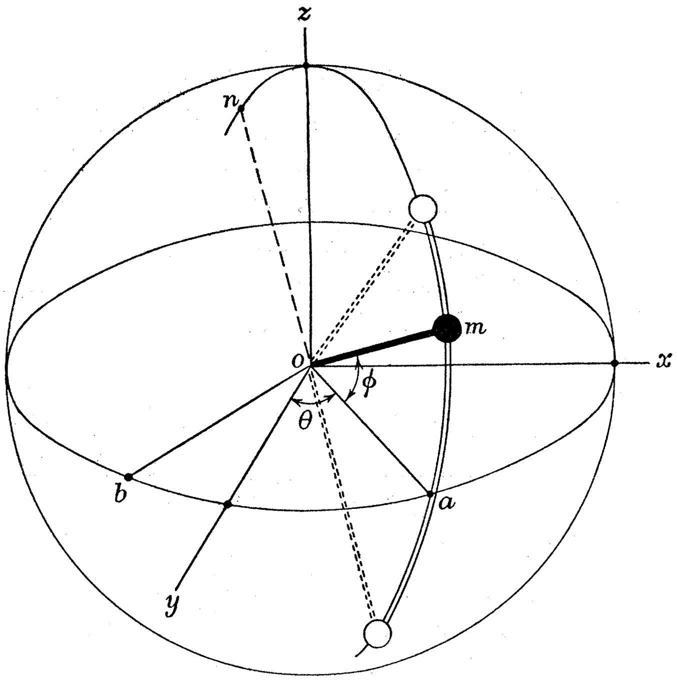


FIGURE 22

Let the component velocities of *m* in the directions of the axes *oa*, *ob*, *oz* be u, v, w, respectively. Then

$$u = l\sin\phi\,\omega_b - l\sin\phi\,d\phi/dt, \quad v = l\cos\phi\,\omega_3 - l\sin\phi\,\omega_a, \quad w = -l\cos\phi\,\omega_b + l\cos\phi\,d\phi/dt.$$

The acceleration of *m* in the direction *ob* is given by

$$\begin{aligned} &dv/dt + \omega_3 u - \omega_a w \\ &\quad = -l\sin\phi\,d\phi/dt\,\omega_3 - l\cos\phi\,d\phi/dt\,\omega_a + l\sin\phi\,\omega_b\omega_3 - l\sin\phi\,d\phi/dt\,\omega_3 - l\cos\phi\,\omega_b\omega_a - l\cos\phi\,d\phi/dt\,\omega_a \\ &\quad = -2l\sin\phi\,d\phi/dt\,\omega_3 - 2l\cos\phi\,d\phi/dt\,\omega_a + l\omega_b(\omega_3\sin\phi - \omega_a\cos\phi). \end{aligned}$$

Since the angular velocity of *om* is large compared with any of the velocities of the supporting object, terms not containing $d\phi/dt$ may be neglected. Hence, substituting for ω_a according to equation (1), the acceleration of *m* in the direction *ob* becomes

$$-2l\sin\phi\,d\phi/dt\,\omega_3 - 2l\cos\phi\,d\phi/dt\,\omega_1\sin\theta - 2l\cos\phi\,d\phi/dt\,\omega_2\cos\theta.$$

Referred to the origin this represents a torque about the axis *on* at right angles to *om* in the plane of oscillation. For the three planes of rotation of the support, the magnitude of this torque is

Yaw $\quad -2ml^2\omega_3\,d\phi/dt\sin\phi,$ (3)

Pitch $\quad -2ml^2\omega_2\,d\phi/dt\cos\phi\cos\theta,$ (4)

Roll $\quad -2ml^2\omega_1\,d\phi/dt\cos\phi\sin\theta.$ (5)

The acceleration of m in the direction oa and oz may be combined into a single acceleration perpendicular to om in the plane zoa, of magnitude

$$\sin\phi(du/dt-\omega_b w+\omega_3 v)-\cos\phi(dw/dt+\omega_a v-\omega_b u).$$

Again neglecting terms not containing $d\phi/dt$ this reduces to

$$-l\,d^2\phi/dt^2.$$

Referred to the origin this represents a torque about ob of magnitude

$$-ml^2d^2\phi/dt^2, \tag{6}$$

which is the primary torque maintaining the oscillation, and is virtually unaffected by rotations of the supporting object.

The torques about the axis on are therefore the only new torques introduced by rotation.

If the oscillation is harmonic $\phi=\phi_0\sin 2\pi nt$,

and the maximum values of these expressions are

Primary torque	$4ml^2\pi^2n^2\phi_0$,	(7)
Yaw	$2ml^2\pi n\phi_0^2.\omega_3$ (approx.),	(8)
Pitch	$4ml^2\pi n\phi_0\cos\theta.\omega_2$,	(9)
Roll	$4ml^2\pi n\phi_0\sin\theta.\omega_1$.	(10)

Expression (8) for the maximum value for yaw is approximate since it assumes that the amplitude of oscillation (ϕ) is small. The error is not significant at the amplitudes observed, and is less than that introduced by the departure of the actual oscillation from the harmonic form.

Figures 7 and 9 show the relative phasing of the various torques, respectively for a harmonic oscillation and for the form actually observed. It is to be noted that

(*a*) the maxima of the primary torque, the gyroscopic torque for yaw and the gyroscopic torques for pitch and roll occur at different instants in the cycle of oscillation,

(*b*) the gyroscopic torque for yaw oscillates at twice the frequency of the oscillation,

(*c*) since θ is constant, the gyroscopic torques for pitch and roll are qualitatively indistinguishable in a single haltere. The arrangement of the two organs on each side of the body of the fly (figure 1) provides a possible means of discriminating between these two planes, the two torques being in phase for pitch and in antiphase for roll. It is shown, however, on p. 354 that such a discriminating mechanism is not of physiological importance.

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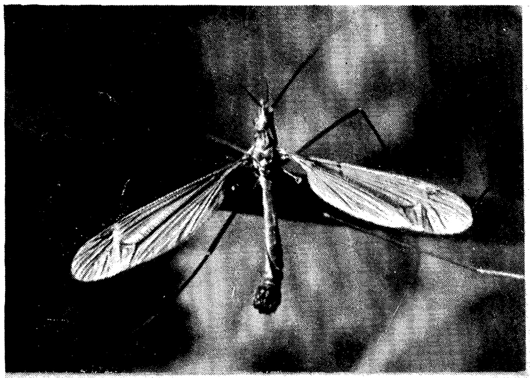
Description of Plate 23

Figure 1. *Tipula* sp. To show position of halteres. (Natural size.)

Figure 2. Left haltere of *Lucilia sericata*; stereoscopic photographs of dorsal side to show structure of basal region. (Magn. × 100.)

Figure 3. Left haltere of *Lucilia sericata*; stereoscopic photographs of ventral side to show structure of basal region. (Magn. × 100.)

Figure 4. *a*, ventral view; *b*, dorsal view of a model of the left haltere of *Lucilia sericata*. (Magn. × 200.)



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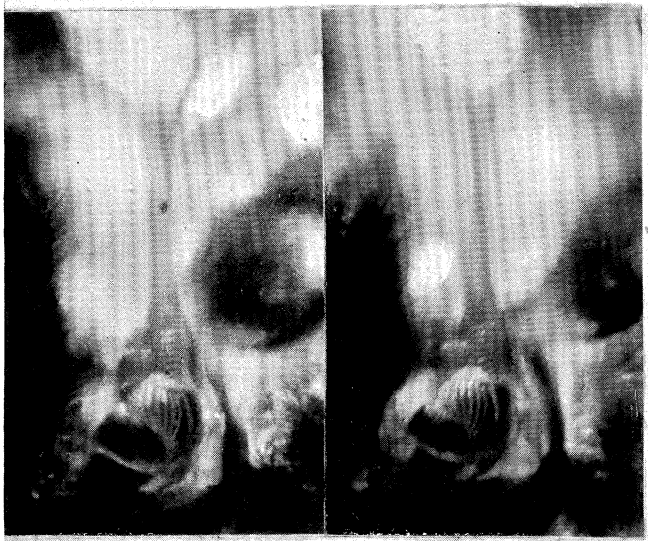

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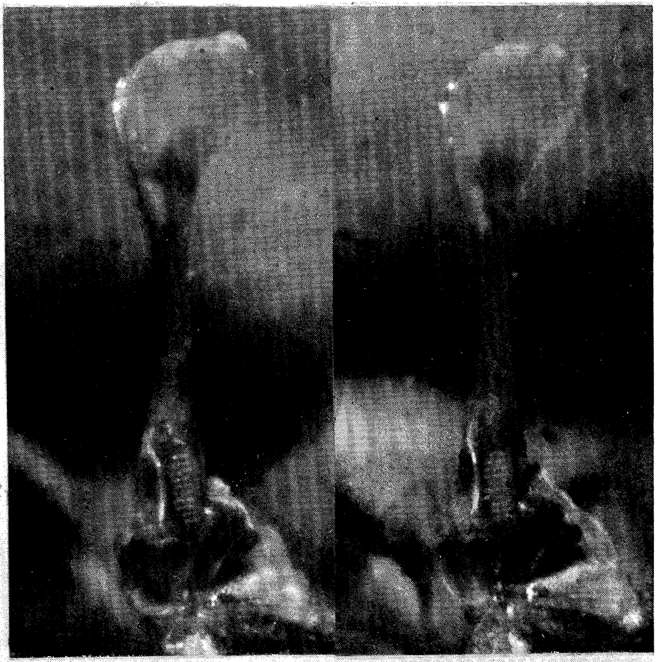

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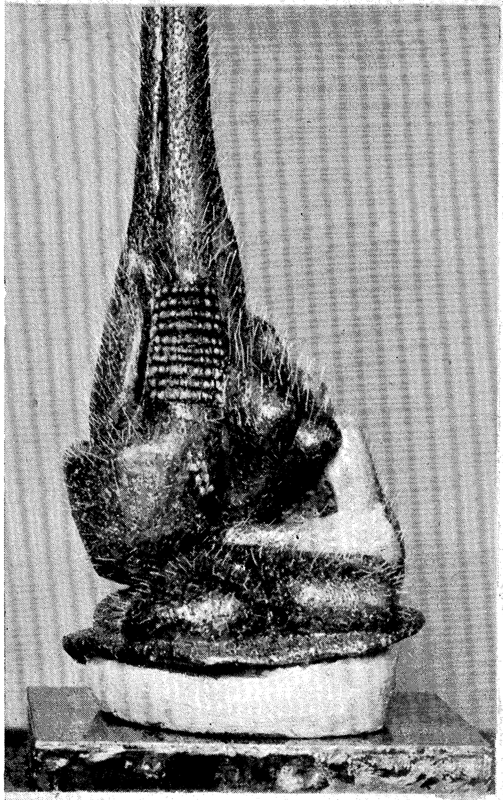

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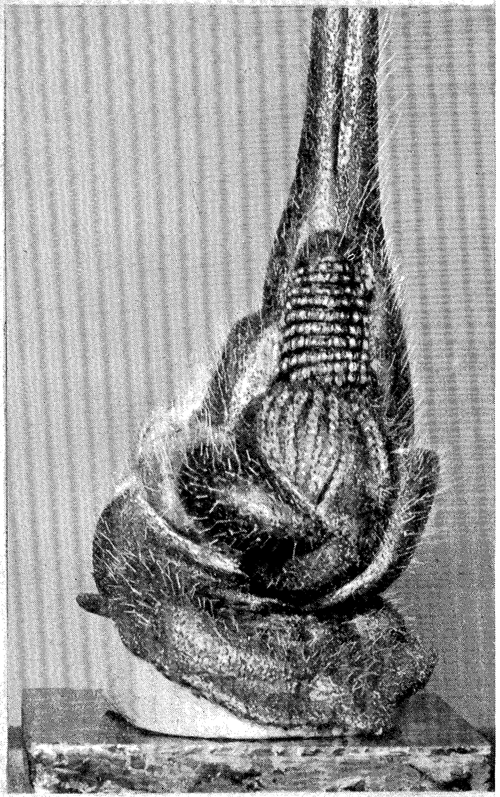

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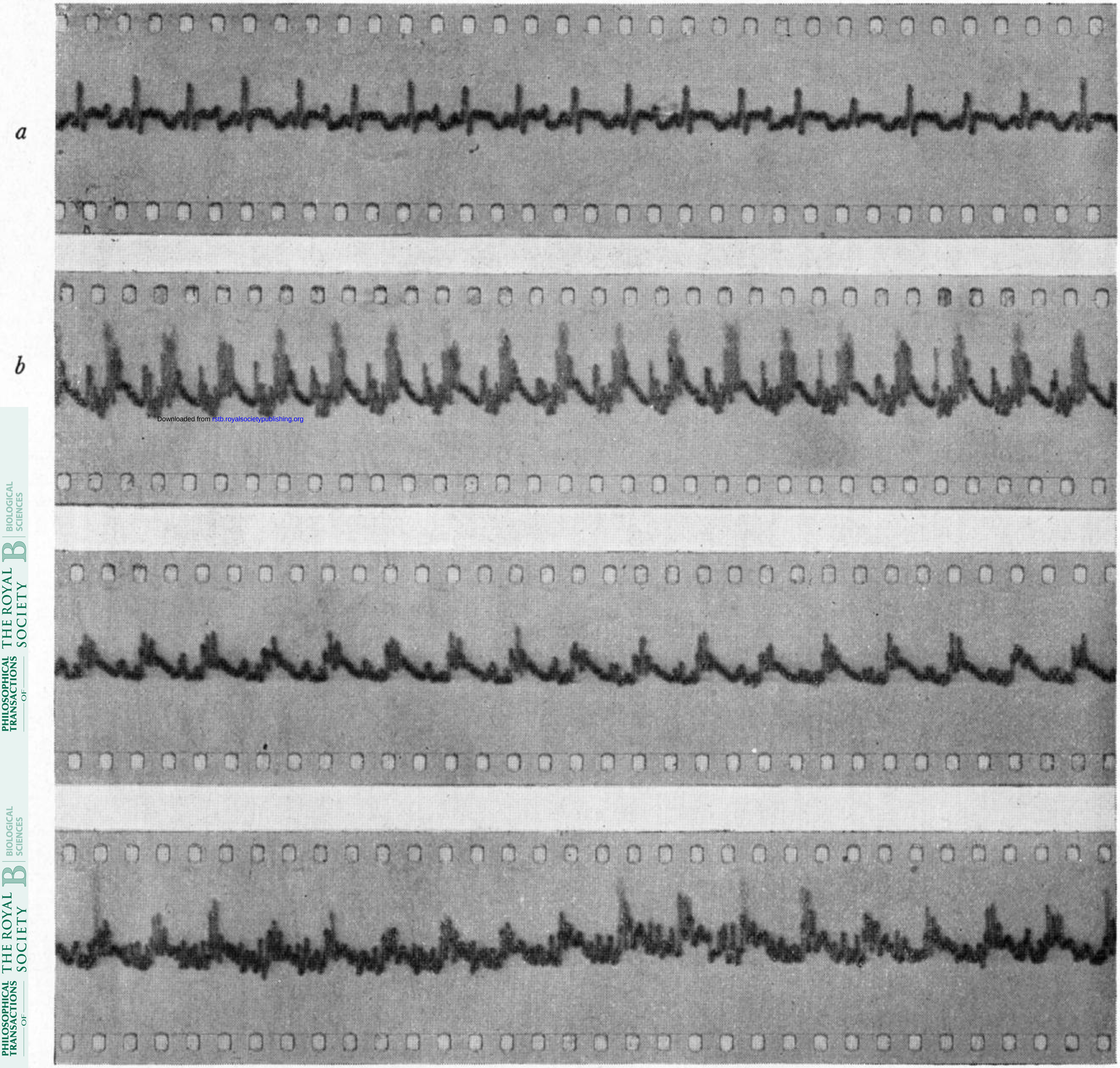

a
b

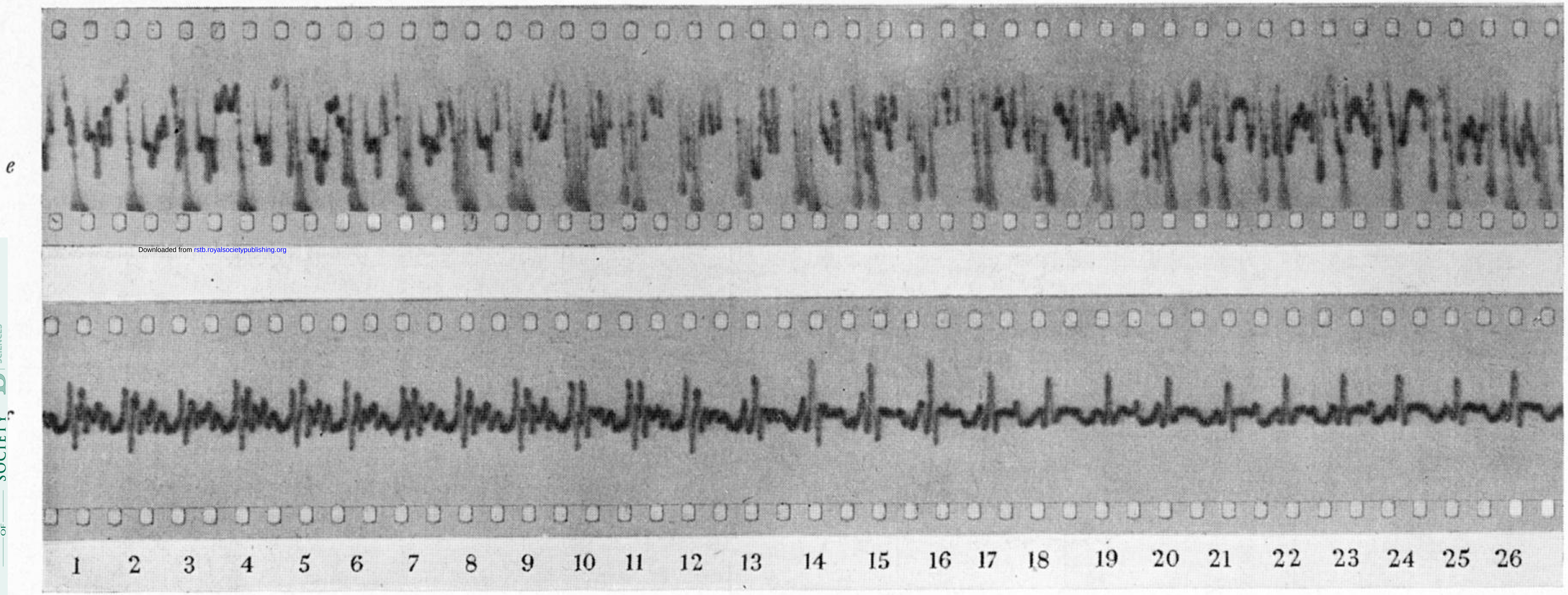


FIGURE 17. Oscillograph records from the haltere nerve of *Calliphora*. Time scale 175 perforations per second.

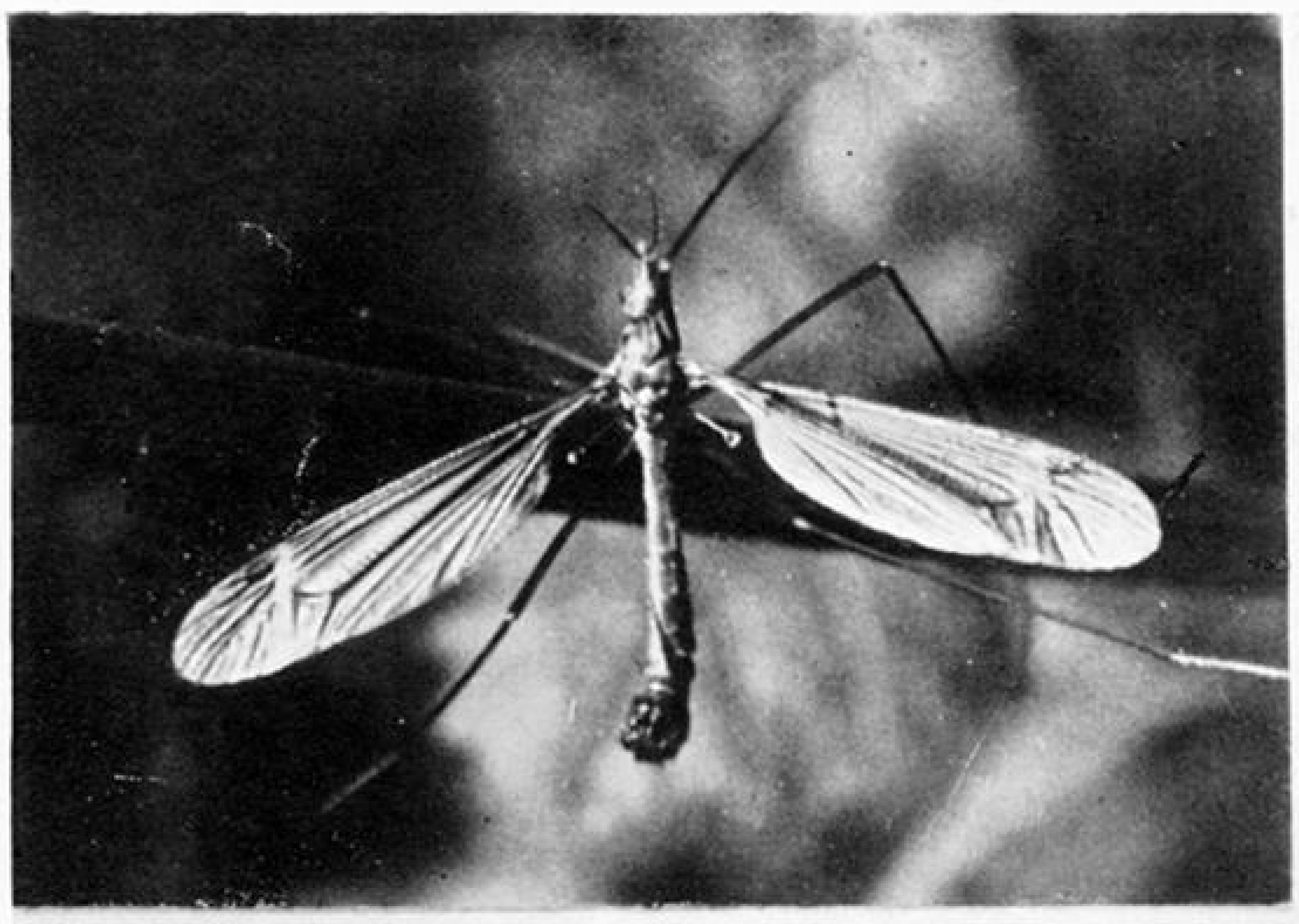
a, haltere driven at 99 oscillations per sec. by means of moving-coil unit. No rotation of frame.

b, haltere oscillating at 96 c./sec. with active contractions of its own muscle. No rotation of frame.

c, *d*, haltere oscillating with active contractions of its muscle. *c*, no rotation; *d*, rotation in the yawing plane at about 1 revolution per sec.; the two pieces are cut from a single strip of film.

e, haltere driven by moving-coil unit. Record at higher amplification to show the change in the nerve discharge at the beginning of rotation in yaw.

f, haltere driven by moving-coil unit; preparation mounted on wax block so that rotation of frame simulates rolling movements of fly. Portion of record showing the stopping of rotation.



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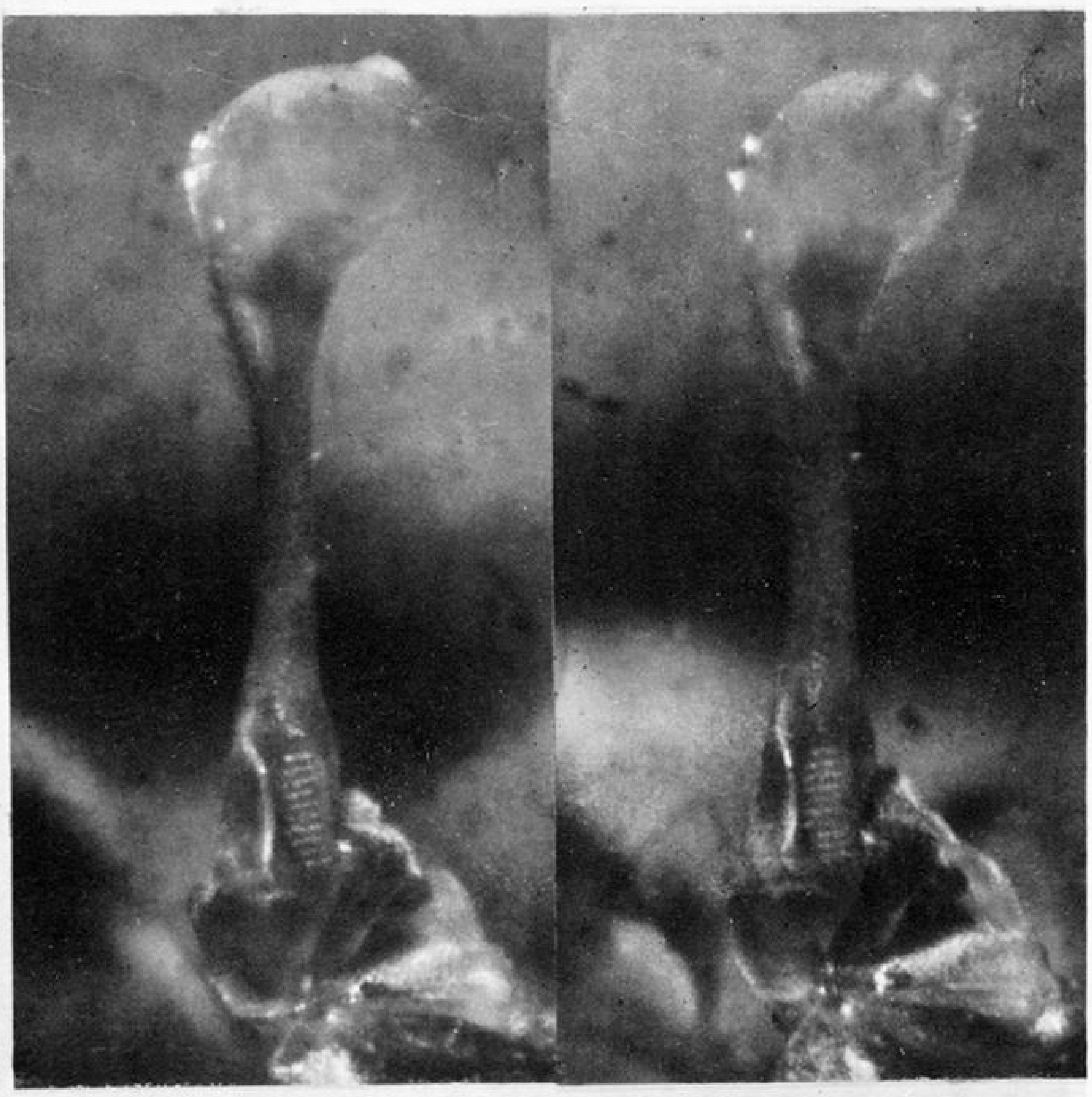

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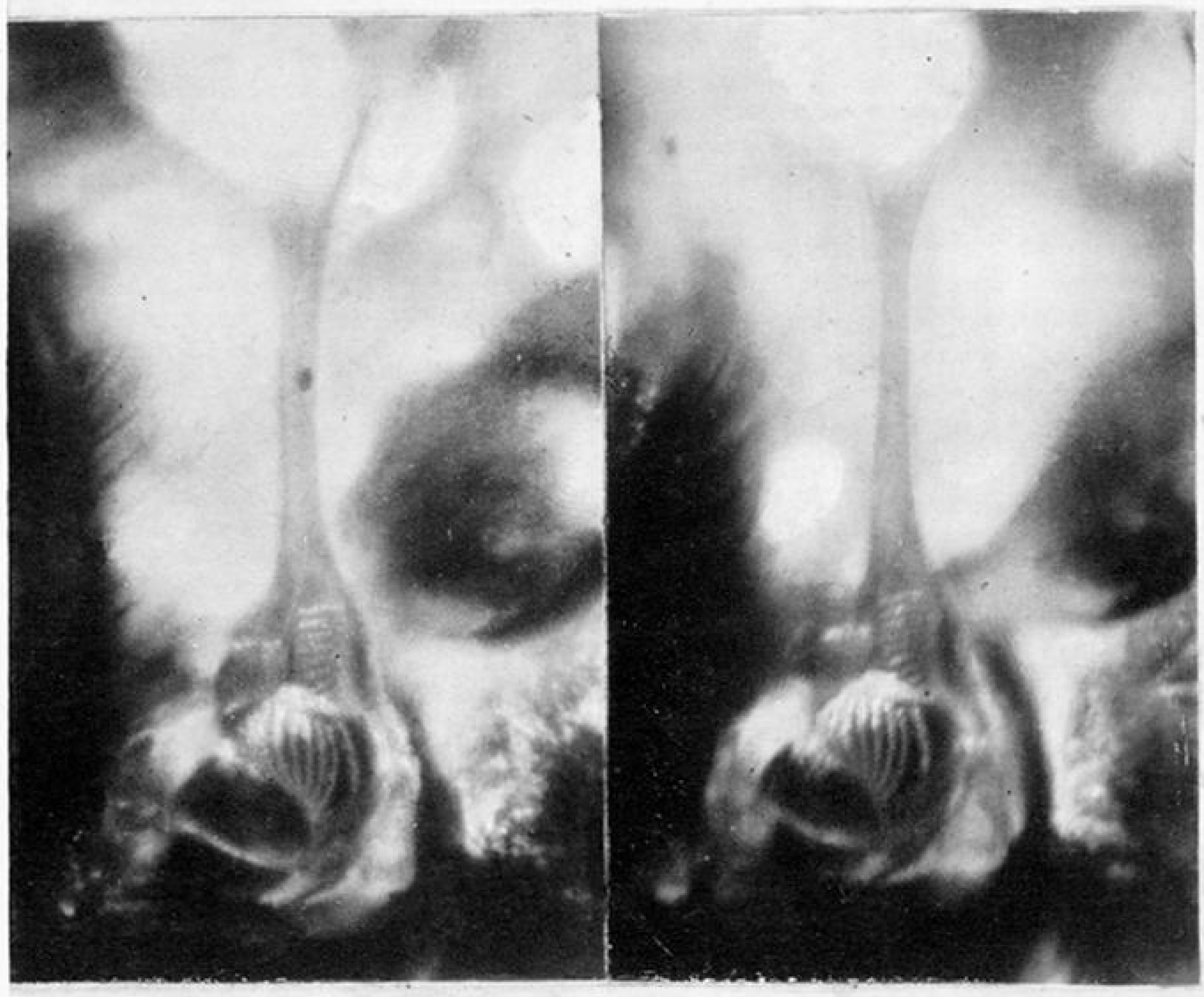

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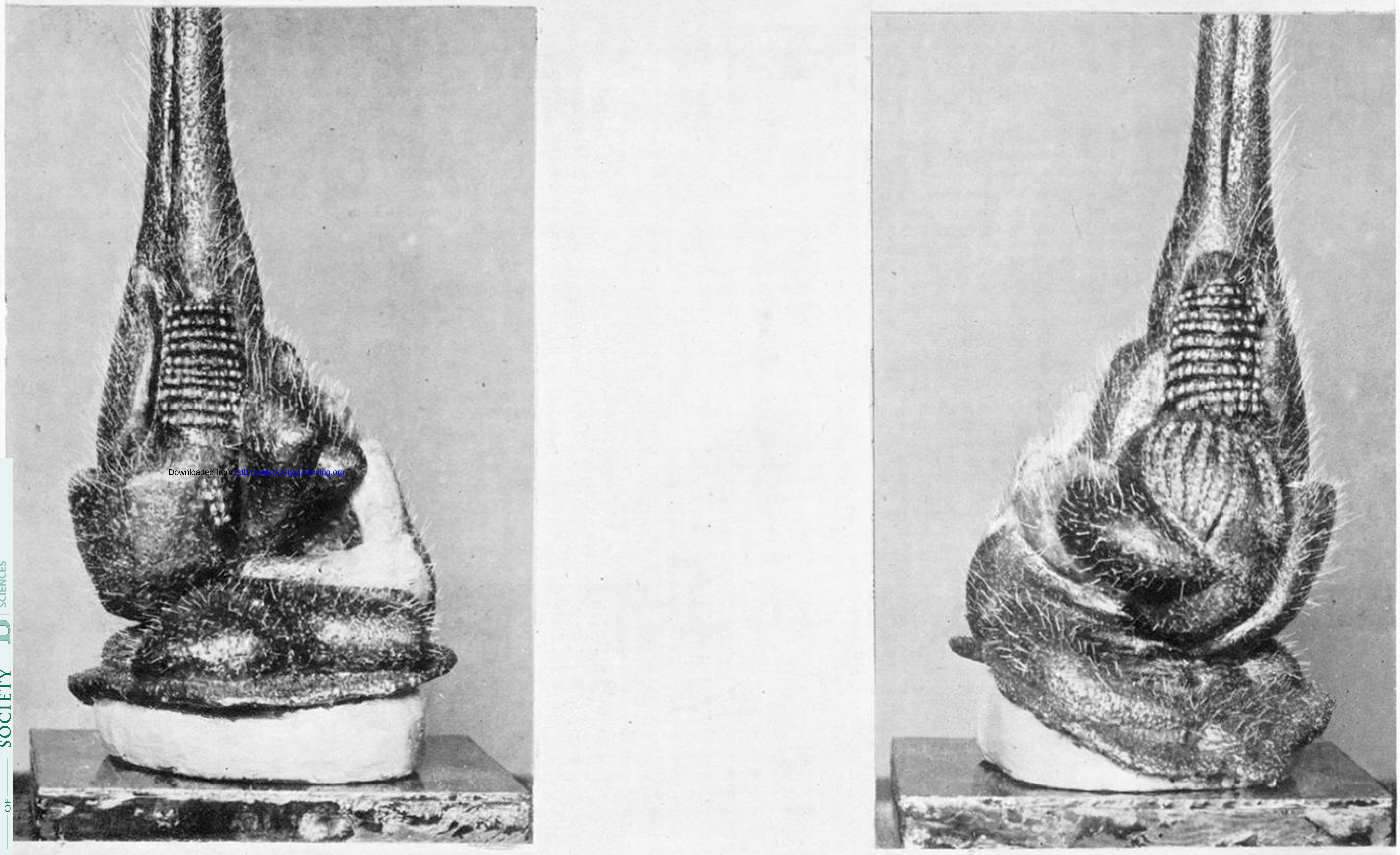

4*a*

4*b*

DESCRIPTION OF PLATE 23

FIGURE 1. *Tipula* sp. To show position of halteres. (Natural size.)

FIGURE 2. Left haltere of *Lucilia sericata*; stereoscopic photographs of dorsal side to show structure of basal region. (Magn. × 100.)

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