Biology and Physics of Locust Flight. IV. Notes on Sensory Mechanisms in Locust Flight

T. Weis-Fogh

Phil. Trans. R. Soc. Lond. B 1956 **239**, 553-584
doi: 10.1098/rstb.1956.0010

BIOLOGY AND PHYSICS OF LOCUST FLIGHT

IV. NOTES ON SENSORY MECHANISMS IN LOCUST FLIGHT

By T. WEIS-FOGH*
Professor August Krogh's Laboratory, Søbredden 24, Gentofte, Denmark,
and The Institute of Neurophysiology, The University of Copenhagen

(*Communicated by J. W. S. Pringle, F.R.S.—Received* 16 *July* 1955).

CONTENTS

The wing stroke of locusts is remarkably constant and independent of external conditions. Is this rigid rhythmicity due to a rhythmicity of the central nervous system or is it determined by peripheral factors? The flight behaviour of the desert locust (*Schistocerca gregaria*) was studied under various experimental conditions in order to find which external factors can initiate, maintain or alter the wing movements, excluding reactions which depend upon higher nervous centres. The 'tarsal reflex' and the response seen when the aerodynamic sense organ on the head is stimulated (Weis-Fogh 1949, 1950) were reinvestigated in order to relate them to two hitherto unknown reactions: the

---

* Now at The Department of Zoology, Cambridge.

maintenance of flapping when the wings are exposed to wind and the regulation of the lift when the body angle (= angle of pitch) is changed during forward flight. Both depend on receptors whose nature is still unknown.

Inhibition. As in most other insects, the flight of a locust cannot be started when the legs, or only part of one leg, have contact with a rigid body; flight stops when such contact is regained. Amputation of the legs abolishes these reactions, showing that some leg proprioceptors inhibit flight.

Initiation. A suspended locust can be induced to fly in three ways. (1) By application of a sufficiently strong stimulus which normally provokes escape reactions; the flight lasts only a few seconds. Adaptation is generally quick. (2) By sudden removal of the support for the legs ('tarsal reflex' although not confined to the tarsi). The flight lasts 5 s on average, corresponding to one hundred wing strokes. There is practically no adaptation. (3) By blowing upon the wind-sensitive hairs on the head. The wind must exceed 2 m/s, but its direction is of little importance. Since the static bending has no effect, the adequate stimulus seems to be minute vibrations of the hairs. The flight lasts as long as the wind blows and the hairs are therefore also involved in the maintenance of flight.

When the locust has stopped, the legs begin to flutter, and eventually remain still, but normally flight is not resumed unless one of the above stimuli is applied.

Maintenance. Two receptor systems are involved. (1) The wind-sensitive hairs on the head. In a wind they emit impulses irrespectively of whether the locust has any chance of flapping its wings or not. 'Wind on the head' is therefore an extrinsic flight stimulus. The flight posture is never complete. (2) A hitherto unknown receptor system in the pterothorax which was studied in insects whose supra-oesophageal ganglia were cauterized ('decerebrate'). It maintains the movements when the wings *oscillate in a wind* but cannot initiate them; the adequate stimulus is the rhythmically changing wind pressure on the wings. 'Wind on the wings' is therefore an intrinsic flight stimulus. When the average lift exceeds half the body weight, flight continues in complete flight posture but stops when the lift approaches zero. The experiments indicate that the stimulation ceases when the lift becomes negative during the *upstroke*. The receptors are unknown; it is suggested that they are situated at the wing hinge.

The locust does not adapt to either of these stimuli and invariably stops a few seconds after they have ceased.

Control of lift. The locust tends to keep the lift constant during a given performance. This observation, together with the constancy of most stroke parameters, made it possible to investigate the mechanism involved. The method was to make the insect fly steadily against a horizontal wind and then alter the inclination to the wind (= the body angle) at regular intervals. The data permitted an estimate of the mean change in wing twisting $\Delta\theta$. $\Delta\theta$ increased (wings pronated) by $15 \pm 3°$ when the body angle was increased from 0 to 15°. This is the main factor in the control of lift. The discussion shows that this presupposes a system of lift-sensitive receptors (probably campaniform sensilla at the wing hinge). If present in other insects, the homoeostatic character of the wing stroke of *Drosophila* (Chadwick 1953) may therefore be caused by a nervous mechanism and need not be a consequence of the energetics of flight.

Central rhythm. It is concluded that the central nervous system (*a*) does not initiate flight rhythm *de novo*; (*b*) does neither determine the stroke frequency nor the strength of the contractions of the controller-depressor muscles; (*c*) may control the phasing of the contractions, although a simpler hypothesis is advanced; (*d*) may control the indirect flight muscles but only as far as to produce stimuli of *constant* (maximum?) strength.

1. Introduction

The initiation, the maintenance and the control of locust flight depend upon the stimulation of a large number of different receptors whose nature is unknown or little understood. It is characteristic of locusts that in whatever way flight is induced and under nearly all conditions, the fundamental wing movements are similar in frequency, stroke angles, time relationships, and the details of the wing twisting. In fact, the pterothorax produces the most strikingly constant, complex locomotor rhythm known in higher animals (cf. part II). It can be triggered to function by various peripheral stimuli, but the effect sometimes lasts longer than the stimulation itself. Does the rhythmicity of the pterothorax originate in the central nervous system or is there another explanation?

The purpose of this paper is to analyze the peripheral stimuli and sense organs which are responsible for the initiation, maintenance and control of the wing movements. Such knowledge is essential for a discussion on the flight rhythm and can, furthermore, contribute to our understanding of the flight as a whole.

Only the most specific responses were studied and none which seem to depend on higher nervous centres. All results derive from observations on the *behaviour* of the locust and provide working hypotheses for further electro-physiological work.

The existence of two hitherto unknown flight reflexes is strongly indicated. The one assists in keeping the wings in motion when they are exposed to a wind of suitable speed and direction; the other is responsible for the control of the lift mentioned in part II.

2. Definitions

As in part II the *lift* L is the average vertical force with which the wings act upon the body. Its direction is opposite to the pull of gravity. When it is given as a percentage of the basic weight of the individual in question (see part II) it is denoted L_r (relative lift). The body angle B is the angle between the horizontal wind and the longitudinal body axis of the insect. Under normal conditions for flight it seldom exceeds 20°. In some of the experiments reported here, however, it was considerably larger as shown in figure IV, 3, where B was increased from 20° at the left-hand side of the diagram to 150° at the right-hand side, the direction of the wind being indicated by horizontal arrows at the upper left corner. When B was less than 20°, the average aerodynamic force with which the wings pull the wing base in the ventro-dorsal direction, here called the *aerodynamic pull* Λ, could maximally be 6 % greater than the vertical lift L and the two quantities need not be distinguished. When B exceeded 20°, however, Λ was measured instead of L. Λ is either given in grams or as a percentage of the basic weight.

The following qualities have all been defined in part II, §3, together with methods of measurement: the *flying speed* v; the *wing-stroke frequency* N; the *stroke angles* ϕ_1 and ϕ_2; the inclination of the stroke planes to the vertical, i.e. the *stroke-plane angles* b_1 and b_2; the instantaneous angular position of the long axis of the wings in the stroke plane, i.e. the *positional angles* γ'_1 and γ'_2. The subscripts 1 and 2 refer to forewings and hindwings respectively.

3. Material and methods

Only cage-bred, full-grown adults of the desert locust (*Schistocerca gregaria* Forskål) were used. The morphological data have been published (Weis-Fogh 1952, and part II).

(*a*) *Small wind tunnel*

In order to study the stimulatory effect of a smooth and uniform wind blowing past the head of a locust, a small free-jet wind tunnel was constructed. The circular entrance is only 15 mm in diameter. Air from a compressor gradually expands in the cylindrical horizontal middle section, 76 mm internal diameter; it then passes through two transverse tightly fitting nets set 50 mm apart. These nets offer a relatively large resistance and smooth air flow. The air travels for another 225 mm before the bore gradually narrows and becomes elliptic, the horizontal, small diameter of the orifice being 19 mm and the larger, vertical diameter 27 mm. The tunnel delivers a uniform horizontal jet of air of small turbulence at the working section situated 10 to 20 mm in front of the orifice. The wind speed is measured by means of a small pitot static tube.

The locust was suspended from the pterothorax (suspension type (2) in part II) so that its plane of symmetry coincided with the vertical plane of symmetry of the tunnel. The suspending bar was fixed to a circular metal ring which could be turned about a horizontal axis perpendicular to the centre line of the tunnel. Since the head of the locust was placed in the centre of the ring, it remained exposed to the full air stream at any angular setting of the ring, i.e. at any body angle. The wings, however, received practically no wind.

(*b*) *Decerebration*

The *supra-oesophageal* ganglia were cauterized under CO_2 narcosis; a nearly red-hot, blunt needle (1 mm diameter) was quickly pressed across the head capsule from the one compound eye to the other, completely destroying the brain and the optic ganglia (cf. figure IV, 2). The wound was immediately filled up with wax to prevent bleeding and the locust was allowed to recover for 24 to 48 h before the experiment. The effect of the operation was controlled by mapping the areas insensitive to minute tactile stimuli. The vertex, the frons, the upper two-thirds of the genae, the labrum and the clypeus were anaesthetic but no other parts. The few specimens which showed asymmetric tonus were rejected. The mortality after the operation was negligible, but at 30° C and 50 % r.h. the starving animals died 5 to 7 days after the treatment, apparently from desiccation.

Decerebrate locusts could not be induced to beat their wings until some time after the operation; during the initial period peculiar reactions could sometimes be seen. For instance, three of the thirty operated individuals lay motionless on the floor with all legs in complete flight posture about 12 h after the operation. The reaction was very strong and they resumed the posture after being ‘woken’. The postural reflexes must therefore to a certain extent be independent of the wing movements in spite of the fact that complete posture is not normally seen unless the locust is flying in a wind under such conditions that lift is produced (p. 564). One day after the operation the three individuals were found standing like the other operated locusts and wing movements could now be induced. Although the decerebrate locusts could ‘fly’ in the wind tunnel when suspended to the flight balance described in part II, they were unable to control the flight so that they always fell to the ground when thrown into the air.

(*c*) *Lift indicator*

In order to study the correlation between the induction of wing movements and the aerodynamic pull at various high body angles ($B > 20°$) the lift indicator shown in figure IV, 1 was constructed. Locusts can be induced to move the wings at any inclination to the vertical. In order to avoid the complication of the pull of gravity when B was altered, the insect was therefore suspended with its plane of symmetry horizontal and coinciding with the horizontal plane of symmetry of the big wind tunnel (see parts II and III). The outlet of the tunnel and the direction of the wind are indicated in figure IV, 1.

A decerebrate locust (*a*) was suspended in the middle of a horizontal ring (*b*). The ring rested upon a drum (*c*) which could be revolved about the vertical axis (*d*). The locust was fixed to a horizontal twin-spring consisting of two cantilevers (*e*) interconnected by a bar (*f*). The average dorso-ventral force Λ acting upon the locust body (= the lifting force L at normal body angles) was estimated by connecting (*f*) to a small Marey's capsule (*g*) fixed to the ring (*b*). The deflexions of spring plus capsule were directly recorded on the supporting drum by means of a small water-filled spirometer of 0·38 ml. maximum capacity (*h*). The narrow rubber tubing connecting (*g*) and (*h*) was long enough to enable the drum to be revolved 360° without interfering with the spirometer which remained fixed to a stand. An oil-filled dash pot (*i*) damped the rapid dorso-ventral oscillation, but the twin-spring was sufficiently stiff to prevent twisting oscillations. The extra-to-wing drag was reduced to insignificance by means of a shelter band (*j*); it did not in any way influence the wing movements of decerebrate locusts because the wings remained freely

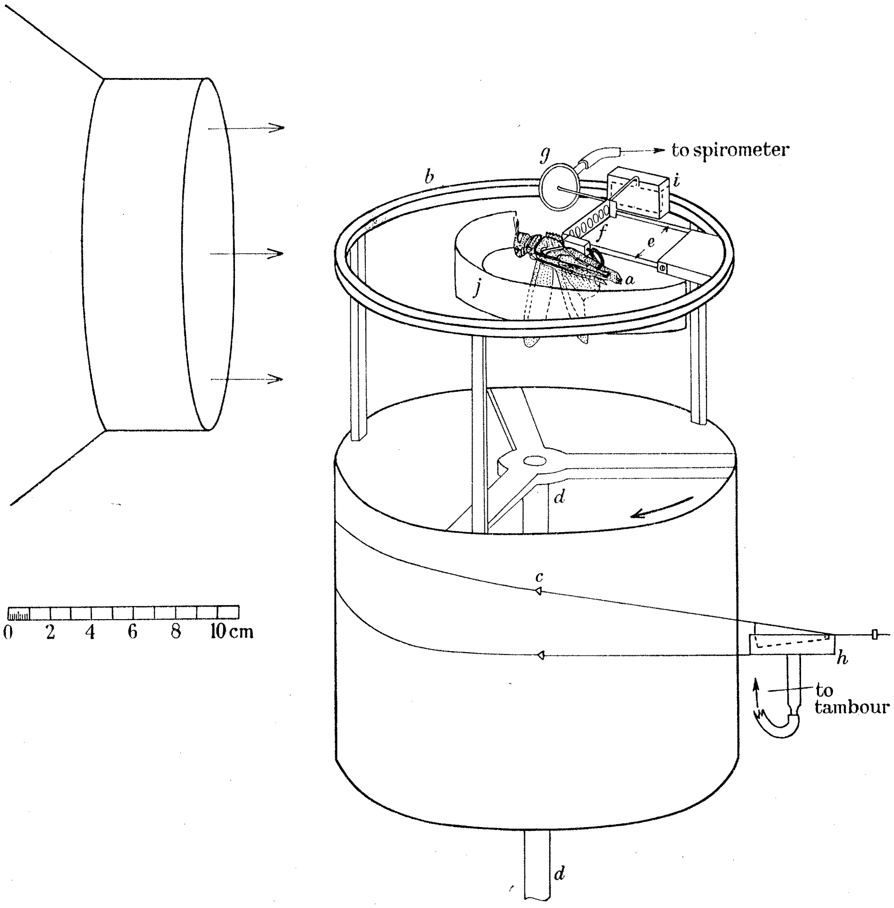

FIGURE IV, 1. Lift indicator. The decerebrate locust *a* (dotted) is fixed with its plane of symmetry horizontal to the twin-spring *e*, the sternum being fixed (wax) to the two curved steel bars (black) which pass along each side of the animal. The body, but not the wings, is thoroughly sheltered from the wind by means of the shelter band *j*. In order to make visible the spring *e* and the Marey's capsule *g*, the left wings have been removed.

exposed. The apparatus was placed in front of the wind tunnel, the locust was started by removing a platform on which the legs rested and the drum was slowly revolved in the direction of the arrow. The spirometer pointer drew a curve on smoked paper which directly showed the relationship between B and Λ. The flight posture as well as the wing-beat frequency were followed continuously and the alterations marked upon the curves. All experiments were run at $28 \pm 0{\cdot}1^\circ$ C and at 60 % r.h. The wind speed was kept *constant* at 3·3 m/s. Λ was estimated with an accuracy of 5 %.

(*d*) *Normal flight*

The regulation of the lift was studied in healthy individuals which were suspended from a flight balance and flew at their preferred speed against wind from a wind tunnel. The technique is described in part II; this performance will be referred to as *normal flight*. The methods of observation are given in part II. Some of the results from part III are used in the analysis. The air temperature was $30 \pm 1^\circ$ C, and the relative humidity was 65 %. The illumination was subdued red light to which the insects did not react.

4. Flight-inducing stimuli

(figures IV, 2 and IV, 3; tables IV, 1 and IV, 2)

A variety of external stimuli can release wing movements in a suspended locust, but only a few can maintain them. In most cases the movements are co-ordinated and their sequence and frequency are similar to those during normal flight.

(*a*) *Removal of support*

In *Drosophila* (Chadwick 1939) and in many other suspended insects (Fraenkel 1932; Davis & Fraenkel 1940) flapping in 'still' air can be maintained during prolonged periods of time when the legs have no contact with rigid bodies. This is not the case in locusts where the flapping soon stops (Weis-Fogh 1949, 1950). The loss-of-contact reaction was reinvestigated in order to see how it was related to the other specific responses.

When the legs touched a platform or a small ball of paper, for instance, all other stimuli generally failed to induce wing movements. Similarly, the flight stopped as soon as only one leg obtained contact. This applied equally well to decerebrate and normal individuals. Loss of contact is therefore a *necessary* condition both for release and for maintenance of wing movements. When the support was removed from a suspended locust, flight was immediately induced. In 'still' air the flapping generally lasted 3 to 10 s, corresponding to one or two hundred wing beats. The effect of the removal thus lasts an appreciable time, in rare cases up to 90 s. The average duration was identical in normal locusts, locusts with destroyed cephalic hair beds and/or with eyes blinded, and in decerebrate individuals. Loss of contact can therefore *not* be a *sufficient* stimulus for the *maintenance* of flight. This is furthermore indicated by the posture of the legs: during the first few seconds the forelegs were generally bent up but they very soon began to flutter; none of the other legs took up flight posture.

When a suspended locust stopped spontaneously, all legs began to flutter. It then often happened that it succeeded in 'standing' on its own forewings or that it pressed the tarsi against each other, providing sufficient inhibition to resist the flight-inducing effect of the wind. However, both in normal and in decerebrate locusts the legs often hang freely for extended periods of time without any renewal of flight, showing that a state of inactivity can be induced in the absence of contact stimuli from the legs. Similar reaction is seen in the spinal dogfish whose rhythmic swimming movements can be stopped by pressing a glass plate against the ventral skin; if the plate is gently removed the animal remains motionless (Lissmann 1946*a*).

(*b*) *Wind on the head*

Many suspended insects start to beat the wings when exposed to wind (Fraenkel 1932, in Orthoptera and Odonata; Hollick 1940, in Diptera). In Acrididae the upper part of the head was found to be sensitive to a small jet of air (Boyd & Ewer 1949; Weis-Fogh 1949, 1950). When the hairs on the frons and the vertex are covered with cellulose paint the flight response is absent but it returns upon removal of the paint. In this way the five pairs of wind-sensitive hair beds shown in figure IV, 2 were detected. Stimulation by means of a small air jet of other parts of the insect failed to elicit any flight response.

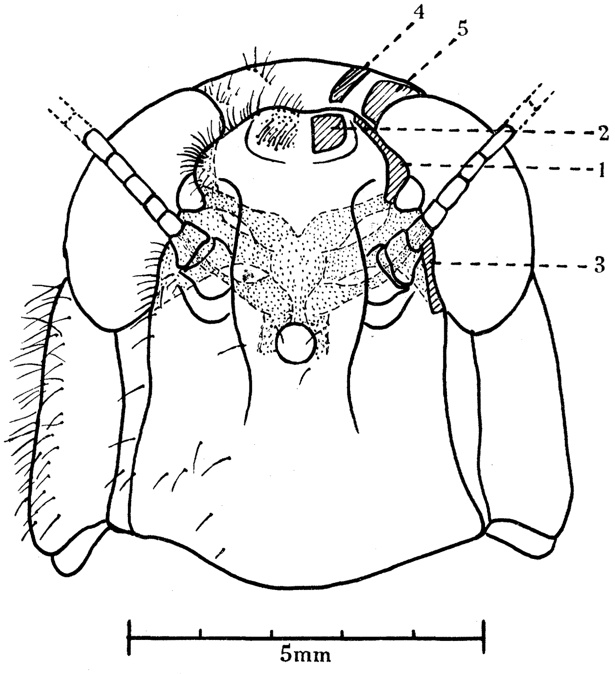

FIGURE IV, 2. The five pairs of wind-sensitive hair beds on the forehead of *Schistocerca gregaria*. Frontal view. The supra-oesophageal ganglia and the large cephalic nerves are dotted. The mouthparts are not shown.

All the sensitive hair beds appeared to be innervated by branches from the paired cerebral nerve, *Nervus tegumentarius* (Hanström 1928), called the dorso-tegumentary nerve of the tritocerebrum (Albrecht's figure 108, 1953). It is homologous to the nerve which innervates Eltringham's organ in neuropteroid insects (Ehnbom 1948). In *Schistocerca* it only seemed to innervate the wind-sensitive areas, but the central connexions are unknown (Weis-Fogh 1950). It is not unlikely that it is connected with the giant fibre system observed in the pterothoracic nerve chord (Cook 1951). According to Jawlowsky (1936) the nerve does not give off branches in the tritocerebrum of Coleoptera but runs directly to the oesophageal connectives.

In 'still' air, asymmetric stimulation induced wing movements which gave rise to asymmetric wind forces on the two sides, and it has therefore been suggested that this receptor system assists in controlling the yawing during free flight (Weis-Fogh 1950). This might be the case, but in the following we will confine ourselves to the effect of release and maintenance of the fundamental wing movements.

Response

As soon as the head was exposed to wind the forelegs were bent up, the wings started to flap and continued until the flow stopped. The two other pairs of legs, however, did not take up the normal flight posture. The stroke angle and the wing-tip curve of the forewings varied much when the body angle B was changed; sometimes the variations were systematic but they could not with certainty be interpreted as compensatory movements. The movements of the hindwings remained fairly constant. The wing-stroke frequency was generally 5 to 10 % lower than during normal flight.

The adaptation to wind is so slight that the 'flying' may continue for more than 1 h under completely unnatural aerodynamic conditions (for instance, when the locusts were etthered in a small jar (Krogh & Weis-Fogh 1951)). So far, wind is the only known mechanical stimulus which has this effect; neither bending of small groups of hairs (thin needles) nor faint touching of larger areas (camel-hair brush, loading with small particles, etc.) elicit wing movements. The impulses emitted from the hair beds upon wind stimulation must be very potent flight inducers; it was sometimes observed that individuals which were tied firmly to the table by means of Plasticine started to contract the flight muscles rhythmically both in spite of being prevented from actual flapping and in spite of the touch stimuli which the legs must have received.

Necessary conditions

(1) Normally, the legs must be free. (2) The sensitive hairs must be exposed to wind, but only a fraction of one bed is sufficient to give the full response. (3) The wind speed must exceed 2·0 to 2·5 m/s, i.e. the lower threshold is smaller than the natural flying speed (part II). (4) The direction of the wind in the sagittal plane is not critical provided it is within the wide range corresponding to $B=-45°$ (s.d. $=5°$) over zero to $B=+125°$ (s.d. $=15°$); beyond that range the response ceased.

In normal flight B ranged from 0 to 15° so that the hairs will be stimulated during all ordinary flight performances. When $B>125°$, all hair beds were in the sheltered zone and the lack of response is easily understandable. But this was certainly not the case when $B<-45°$; hair beds nos. 3, 4 and 5 in figure IV, 2 were then exposed to a greater or lesser degree. However, the problem was not analyzed further because its solution depends upon knowledge of the three-dimensional flow pattern about the head.

Probable mechanism

The wind-sensitive hairs are trichoid and provided with a large flexible basal plate. Under the microscope it was easy to see that wind bends the hairs at their base. Equally long trichoid hairs on the head and body often vibrated when exposed to a wind of similar strength but, when viewed under the binocular microscope, the wind-sensitive hairs appeared to be still (Weis-Fogh 1949). However, it is in fact most likely that very *quick* and *small* alterations of the wind pressure near to the head capsule are the effective stimulus, the wind not only deflecting the hairs but in addition causing them to vibrate at a high frequency and with a small amplitude. Otherwise it is difficult to understand why wind but not a static deflexion could induce the flight response. The problem needs further investigation.

Relation to other systems

Wind stimulation of the sensory areas of the head was *sufficient* both for the triggering and for the maintenance of the wing movements. But it was *not necessary* for either processes as could easily be shown by the following simple experiment: the hair beds were completely covered with paint and yet the locust was able to fly when it was thrown into the air. In this case the loss of contact is responsible for the start but certainly not for the maintenance, indicating the existence of a third factor. Furthermore, complete flight posture was never observed when the wind was restricted to the head.

(*c*) *Wind on the moving wings*

The following experiments demonstrate the existence of a hitherto unknown receptor system which can maintain the wing movements. It is sensitive to the wind pressure on the oscillating wings. These experiments were made with decerebrate locusts.

Evidence and response

In the wind tunnel a normal locust generally stops flying when the head is sheltered from the wind. If the sensitive hairs were destroyed (by heat) or covered with paint and the wing movements initiated by removal of a platform, it sometimes happened that the flight continued until the tunnel was stopped. When *decerebrate* locusts were used the insects always continued to fly and, in addition, a few seconds after the start, they always arranged their legs in complete flight posture. They stopped as soon as the wind was discontinued, and the wind could *not* then start them again even if the wings remained unfolded. At the beginning, the stroke frequency, the stroke angles, the speed and the lift were all normal (e.g. lift was close to the body weight), but the performance gradually declined and the flying stopped spontaneously 1 to 3 h after the start. It was then difficult to induce flight anew. During the entire period of flight the wing movements were exceedingly regular and the legs remained in complete flight posture. Obviously, a receptor system must exist which is sensitive to wind and which can (1) stimulate the animal to maintain normal, well co-ordinated wing movements and (2) bring the legs into flight posture. The movements must, however, have been initiated by other means than wind.

Localization

The body, the head and the legs could be covered with paint or be completely sheltered from wind without affecting the flight response. The receptors must therefore be situated either on the wings themselves or at some more proximal part of the flight motor. The first possibility was tested by destroying the nervous connexions between the wings and their attachment to the thorax. In decerebrate locusts a narrow transverse zone just distal to the median wing sclerites was heated by means of a thin, hot needle so that the fluid inside the veins was actually seen to boil. After the operation all parts distal to this zone were found to be completely anaesthetic. Nevertheless, in five out of ten cases the wind could still stimulate the animal to fly, but the performances were of course hampered by the decreased mobility of the wing sclerites. The wind forces must therefore be perceived at the wing hinge or in the pterothorax. The further localization within this complicated structure is so far unknown.

Necessary conditions

(1) The wings must be started by means of the loss-of-contact reactions or by a non-specific shock reaction, for instance by pinching the abdomen. (2) The *oscillating* wings must be exposed to wind speeds of the same order of magnitude as the natural flying speed (2 to 5 m/s). (3) The inclination of the body to the wind, i.e. the body angle B must be within the range -10 to $+120$ or $+150°$. Within this enormous range of inclinations the wind over the wings could maintain the oscillations. The response at high and at low body angles deserves special mention.

Small body angles

In the compound flight balance the flying invariably stopped when the body angle was decreased from a positive value to a negative value, the minimum being about $-10°$. This occurred both in normal locusts, in locusts with covered or destroyed cephalic hair beds, and in decerebrate individuals. In all these cases diminution of B to below zero was correlated with a rapid decrease in lift. The body angle at which flight ceased ranged from 0 to $-10°$ according to the individual, i.e. the scatter was as large as the range within which an effect upon the lift could be observed. A quantitative investigation of the relationship between body angle, lift and flight performance could therefore be performed with greater accuracy at large than at small body angles.

Large body angles

The effect of increasing B was studied in *decerebrate* locusts fixed to the lift indicator as seen in figure IV, 1. The wind speed was kept constant at 3·3 m/s. The locust was started at $B = 20°$, and when it had flown for some seconds in complete flight posture B was slowly increased by turning the drum. The posture, the angle at which the legs began to flutter, and the angle at which the movements ceased altogether were noted on the curve. In five experiments the wing-stroke frequency was also read at each 20° increase of B.

Each locust (three females and five males) was flown three to seven times in succession so that the results could be averaged for each individual, the average curves thus obtained being fairly smooth. The mean curve from the eight animals is seen in figure IV, 3, where the standard error of the mean is indicated. The variation of the aerodynamic pull Λ is shown by the solid points. By means of equation (II, 5), (part II), the probable normal stroke frequency of each individual could be calculated for all observed values of Λ. The frequencies *measured* in the present experiments were expressed as percentages of these calculated values in order to compare them with normal flight. The average results are marked as crosses in figure IV, 3. The drawings of the locust above the curve indicate its inclination to the horizontal wind (the arrows in the upper left corner). They are placed correctly on the abscissa, the reference point being the anterior margin of the pterosternum. The double line represents the stroke plane and the arrow heads indicate the wing movement during the downstroke. The broken arrow originating from the wing base shows the direction of the measured aerodynamic pull Λ.

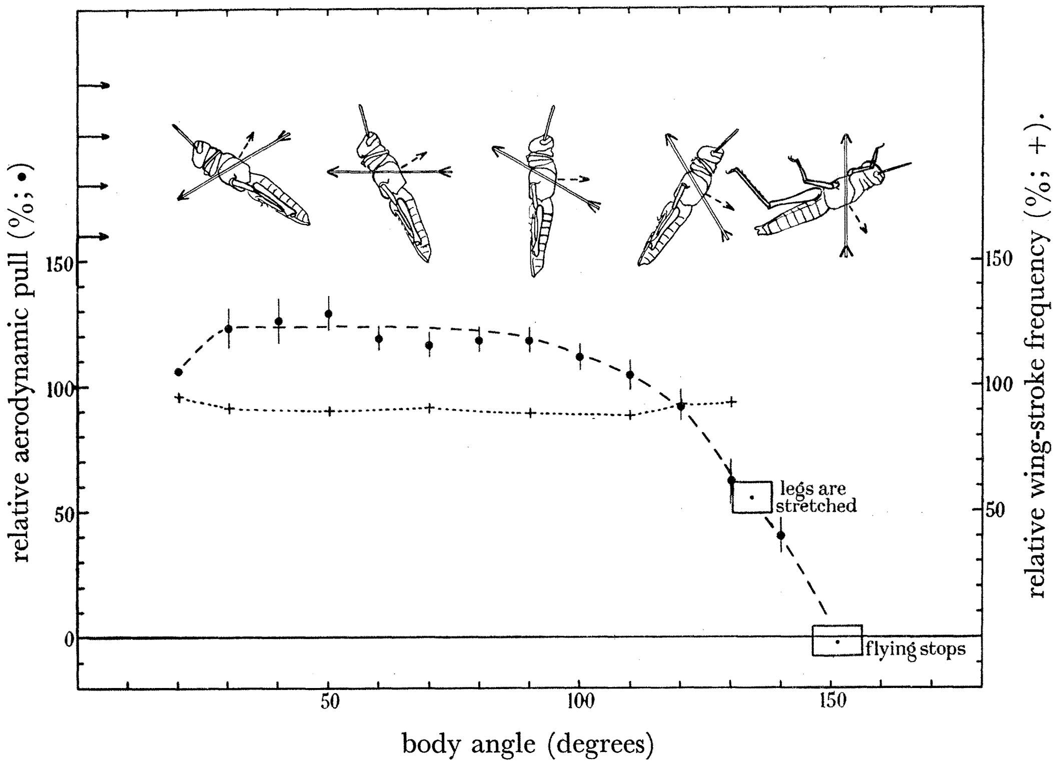

FIGURE IV, 3. The *relative* aerodynamic pull Λ (•) and the *relative* stroke frequency (+) in eight decerebrate desert locusts whose body angle was increased from 20° and until flying stopped in the lift indicator (figure IV, 1). The locusts drawn above the curves show how the body and the stroke plane (double line) are inclined relative to the horizontal wind blowing from the left-hand side.

The experiments revealed several interesting features. At the beginning $B=20°$, and the average aerodynamic pull was very near to the normal relative lift of 100%. In spite of the body angle being increased while the wind was kept constant, Λ remained nearly constant (110 to 130%) until B reached about 90°; it then began to decrease whereas the flight posture remained complete until $\Lambda=55\pm6\%$ (s.d. $=18\%$), corresponding to $B=134\pm4°$ (s.d. $=10°$). At this inclination all legs began to flutter, but somewhat irregular wing oscillations continued until the locust suddenly stopped when Λ had reached $-2\pm6\%$ (s.d. $=17\%$) and $B=151\pm5°$ (s.d. $=15°$). If the sense of revolving was reversed before the 'flight' ceased, the sequence could be reversed.

The dotted curve shows that the stroke frequency was very constant throughout the experiment and ranged from 90 to 100% of the values in normal flight. It tended to increase when Λ decreased, i.e. the relationship between the wing-beat frequency and the 'aerodynamic loading' had been reversed in decerebrate locusts compared with the normal (part II); it now resembled the type of relationship found during the initial flapping of tethered *Drosophila* spp. (Chadwick & Williams 1949; Chadwick 1953).

In this type of experiment, therefore, the following relationships are apparent. (1) The aerodynamic pull Λ is constant over a very large range of body angles. (2) The stroke frequency N does not vary by more than 10 % and is close to the normal. (3) The legs are held in complete flight posture as long as Λ exceeds half the normal body weight. (4) The wing oscillations cease altogether when Λ approaches zero; the same occurs in the flight balance when the body angle *decreases* from a positive to a small negative value. (5) At the highest body angles in the lift indicator the direction of the wind was reversed compared with the normal so that the anterior wing margin (towards the head) had become the trailing edge in relation to the wind. The overall force experienced by the wings must therefore be the decisive factor rather than the direction of the flow.

Regulation of Λ: *Stroboscopic observations*

When the body angle of a decerebrate locust was increased beyond its normal range (0 to 20°), the insect thus maintained the aerodynamic pull at a constant level but, in contrast to normal flight, this regulation was brought about mainly by decreasing the stroke angles. The wing twisting which is most important during a normal performance (part III) was hardly altered during the stroke, so that the wing plane remained nearly perpendicular to the stroke plane at all phases of the stroke. These observations were made in stroboscopic light and confirmed in all individuals used.

Aerodynamic forces and maintenance of flight

Unfortunately, neither the stroke angles nor the wing twisting could be accurately measured by the methods used, but the following rough estimates indicate the magnitude and the direction of the aerodynamic forces which the locust experienced in the lift indicator.

When $B = 20°$, the flight was near to the normal in respect of Λ ($\simeq L$), stroke angles, stroke frequency and wing twistings (direct observation). When B had increased to 60°, the stroke plane was parallel to the wind and, due to the very small wing twisting, the wings functioned as paddles the planes of which were approximately perpendicular to the direction of flow. At the given wind speed (3·3 m/s) and with an average stroke angle estimated at between 50 and 60°, the aerodynamic pull of a standard *Schistocerca* could be calculated from the wing areas (Weis-Fogh 1952), the stroke frequency, and from the angular movements of the wings (part II). The average dynamic wind pressure ($\frac{1}{2}\rho v^2$) was found by graphical integration and the resistance coefficient was estimated at 1·2 (rectangular plate with side ratio 1:4 set perpendicular to the stream). During the *downstroke* (wings moving against the wind) the average aerodynamic pull Λ was then +3·1 g, and during the *upstroke* (wings moving with the wind) it was +1·0 g, i.e. it remained positive throughout. Taking the relative duration of the upstroke and downstroke into consideration, the average Λ during an entire stroke became $3{\cdot}1 \times 0{\cdot}6 + 1{\cdot}0 \times 0{\cdot}4 = 2{\cdot}3$ g, or 115 % of the basic weight. The maximum pull was 4·2 g, while the minimum was 0·5 g. This means that, owing to the decreased stroke angles, the wings experienced aerodynamic forces of roughly the same magnitude and time course as during normal flight (part III).

During the *downstroke* the aerodynamic pull possibly remained positive until $B \simeq 150°$, but in the *upstroke* the wings would stand nearly edgewise to the relative wind when B reached 130°. In other words, during the upstroke the aerodynamic pull remained positive until $B = 130°$ and then it became negative, while, during the downstroke, Λ remained positive until B reached about 150°. These estimates are of course very rough, but they indicate that the flight movements deteriorated only when the wind forces began to resist the ascent of the wings.

Flash photographs and stroboscopic observations of locusts which were stimulated to fly in '*still*' air (part VII) showed that a positive pull must be produced during the downstroke and a negative pull during the upstroke. Under these conditions sustained flapping flight could be elicited only by stimulation of the cephalic hair beds. Thus, the results obtained with the lift indicator and the direct photographic recordings of tethered flapping both tend to show that the stimulus necessary for maintaining wing movements in a decerebrate locust is a positive aerodynamic pull during the upstroke; a direct proof of this is, however, still lacking.

(*d*) *Conclusions*

In the desert locust the highly co-ordinated wing oscillations can be *initiated* in two ways: by eliminating touch stimuli from the legs or by directing a jet of air against the wind-sensitive hairs on the forehead. When started, the movements can be *maintained* either by continuous wind stimulation of these hairs or by exposing the oscillating wings to wind pressure under such conditions that they produce a positive aerodynamic pull. In the latter case the adequate stimulus is the total wind force upon the wing as perceived at the wing hinge or at a more proximal part of the pterothorax. All flight movements stop when the legs obtain contact with a rigid body.

The sense hairs react to the relative movement between the head and the surrounding air and switch on the flight reflexes provided the air speed is above 2 m/s. This response is of course independent of whether the locust is actually flying or not. The thoracic system, on the other hand, only provides maintenance stimuli when the wings oscillate and experience wind forces of a certain magnitude and direction. The wind speed must not be less than 2 m/s. There were indications that the stimulation ceases when the wings work *against* wind forces during the upstroke (negative aerodynamic pull); during normal flight the lift is positive during all phases of the stroke.

In normal flight both types of maintenance stimuli ('wind on the head' and 'wind over the wings') are of such strength and direction that the receptors must be stimulated.

The primitive nature of the thoracic maintenance system as compared with the sense hairs manifests itself in several ways. (1) It gives rise to exceedingly regular wing movements which, at low body angles (0 to 20°), may serve in detail as a paradigm of the normal movements. In contrast to this, stimulation of the cephalic hairs results in very variable oscillations, indicating that they are also involved in the control of flight. (2) Its function depends upon the thoracic ganglia being intact but not upon the higher nervous centres. (3) Provided the aerodynamic pull exceeds half the body weight the decerebrate locust *always* adopts complete flight posture.

The main observations are summarized in table IV, 1. At present no electro-physiological evidence is available, but some sensory mechanisms are tentatively suggested in table IV, 2.

TABLE IV, 1. OBSERVED REACTIONS

stimulus	can stimulus initiate flight?	can stimulus maintain flight?	are legs in flight posture?	maintenance: is stimulus sufficient?	maintenance: is stimulus necessary?
loss of contact	yes	no	no	no	yes
wind on head	yes	yes	forelegs	yes	no
wind on wings	no	yes	all legs	yes	not known

TABLE IV, 2. SUGGESTED SENSORY MECHANISMS

gross stimulus:	adequate stimulus:	receptive areas:
loss of contact	release of stress from mechanoreceptors of legs	all parts of the legs?
wind on head	bending and minute vibration of sense hairs in wind	on forehead only
wind on wings	wind pressure transmitted to wing hinge	at wing hinge or inside pterothorax

In designing *suspension devices* for normal, flying locusts one must be aware of two fundamental requirements if steady and sustained performances are to be obtained in the laboratory: the head must be exposed to wind of not less than 2 to 2·5 m/s, and the wings must be exposed to wind whose direction corresponds to a body angle between 0 and 20° and whose speed is within 2·5 and 5 m/s.

5. REGULATION OF THE LIFT

(figure IV, 6; tables IV, 3 to IV, 6)

With very few exceptions, a *normal* locust flying in the compound flight balance kept the lift constant for extended periods of time even when the body angle was forcibly changed from 0 to 15°. This phenomenon was studied in detail in seven desert locusts (one female and six males), all of which were healthy and flew steadily.

(*a*) *Experimental results*

When a locust had flown for some time with all legs in flight posture, the body angle was changed every 3 min to any of the values 0, 5, 10 or 15°. At each angle a set of flight parameters was read, giving the following simultaneous quantities (see part II): the relative lift L_r, the flying speed v, the body angle B, the stroke frequency N, the stroke-plane angles b_1 and b_2, and the stroke angles ϕ_1 and ϕ_2. An experiment lasted 20 to 40 min, so that at least two and often four readings could be averaged at each body angle.

In wind-tunnel experiments the preferred relative lift varies from individual to individual and from one flying to the next with the same locust (part II). But in the course of a given performance, the lift is kept constant. The present data, for example, derived from seventeen experiments corresponding to seventeen different 'choices' of lift, and it consisted of 118 sets of observations. Nevertheless, none of the deviations from the chosen average lift of an individual during an experiment exceeded ±10%. In fact, the deviation was less than $\pm 5\,\%$ in 113 of the 118 cases. This clearly shows that some mechanism must be present which regulates the resultant aerodynamic forces.

The observations are summarized in table IV, 3. The preferred relative lift of the individuals varied from 55 to 150 % of their basic weight, but the mean lift ($L \bumpeq \Lambda$) of the total material was about 100 %. It tended to decrease somewhat when B was increased above a certain limit; at $B = 15^\circ$, L_r was thus 94 %, corresponding to $\Lambda = 97\,\%$. The stroke frequency remained constant but the flying speed decreased significantly by $0{\cdot}4 \pm 0{\cdot}2$ m/s for each 5° increase in B. The inclination of the stroke planes to the vertical, b_1 and b_2, increased when B increased but to a somewhat smaller extent. The stroke angle of the hindwings ϕ_2 remained constant, but ϕ_1 increased significantly from 65 to 80°.

Table IV, 3. The observed effect of altering the body angle in steadily flying locusts

Mean results from seventeen experiments comprising 118 sets of observations on seven individuals. Quantities marked * differed considerably from individual to individual according to the preferred flight intensity (lift) or to the size (frequency), so that only the mean values, but not the mean scatter, are of significance. In each individual they remained constant during the experiment.

	body angle, B (degrees)			
	0°	5°	10°	15°
no. of experiments	12	14	15	9
mean relative lift* (%)	102	105	102	94
mean stroke frequency* (min^{-1})	1080	1080	1080	1090
mean flying speed (m/s)	$3{\cdot}8 \pm 0{\cdot}1$	$3{\cdot}4 \pm 0{\cdot}1$	$3{\cdot}0 \pm 0{\cdot}1$	$2{\cdot}6 \pm 0{\cdot}1$
mean stroke-plane angles (degrees): b_1	31 ± 2	34 ± 1	36 ± 1	42 ± 2
b_2	29 ± 1	31 ± 1	33 ± 1	36 ± 1
mean stroke angles (degrees): ϕ_1	65 ± 3	69 ± 2	71 ± 2	80 ± 4
ϕ_2	110 ± 1	110 ± 1	111 ± 1	113 ± 2

Some important stroke parameters were not measured, namely, the sequence of the wing twistings and changes of the wing profiles. For two reasons the last factor cannot be of decisive importance in the present context. First, in locusts the only possibility for an active change of the profile is a more or less distinct lowering of the rear flap of the forewings (parts III and VII). But the forewings are only responsible for one-third of the lift and the flaps can maximally alter this amount by 30 % (part III). Secondly, the passive deformations due to wind forces can also be considered as small because of the constant lift. The main unknowns are therefore the changes in wing twisting.

(*b*) *Wing twisting*

Figure IV, 4 is an idealized diagram of the wing movements of an insect which flies horizontally through the air from left to right. The body angle B is also indicated. In this context the wing can be considered as a plate which is twisted along its long axis a; the dorsal surface (dotted) is provided with the three markings b (base), m (middle), t (tip), and whose anterior points (i.e. of the leading edge) are indicated by a circle. The markings run perpendicular to a; b corresponds to the axis of pivoting, i.e. to the fulcrum. In flight the points of intersection between the markings and the wing axis move through the air from left to right along the three drawn curves. The movements of b correspond to the rectilinear movement of the body, while m and t move in a complicated way on the surface of a cylinder whose centre line coincides with *b*. The movements of an insect wing are generally more complicated than this, partly because the stroke plane deviates from the vertical and partly because the wings *also* oscillate about a vertical axis. The true movements of the locust wings are described in detail in part III, but figure IV, 4 gives an impression of the main principle.

At any instant the direction of movement is opposite to the direction of the relative wind which is indicated by the arrow heads on the curves. The angle between the relative wind and a wing marking is the angle of attack of the wing element in question. It is seen that, according to the results in part III, the angles of attack are of moderate magnitude (0 to 15°) at all distances from the wing base and during the entire stroke. This is important because the flow stalls if the wings are inclined more than 20 to 25° to the wind. The angles of attack are biggest during the downstroke where the main lift and thrust is produced and smallest (often zero) during the upstroke. The only value which remains constant is the one at the fulcrum (*b*) which is determined by the body angle. In order to produce this result the locust twists its wings about the long axis, as indicated. The wing is so constructed that when the anterior part of the wing hinge is slightly raised above the plane of the paper (figure IV, 4, top) the whole leading edge will turn upwards and *t* will be lifted more than *m*. This movement is called a *supination* and it prevails during the upstroke. Conversely, when the proximal part of the leading edge is depressed a little below the plane of the paper the dots on *m* and *t* will move downwards and the other ends upwards, the migrations being again biggest at the wing tip. This movement prevails during the downstroke and is called a *pronation*. The difference in angle between *b* and *t*, for instance, is a measure of the wing twisting θ.

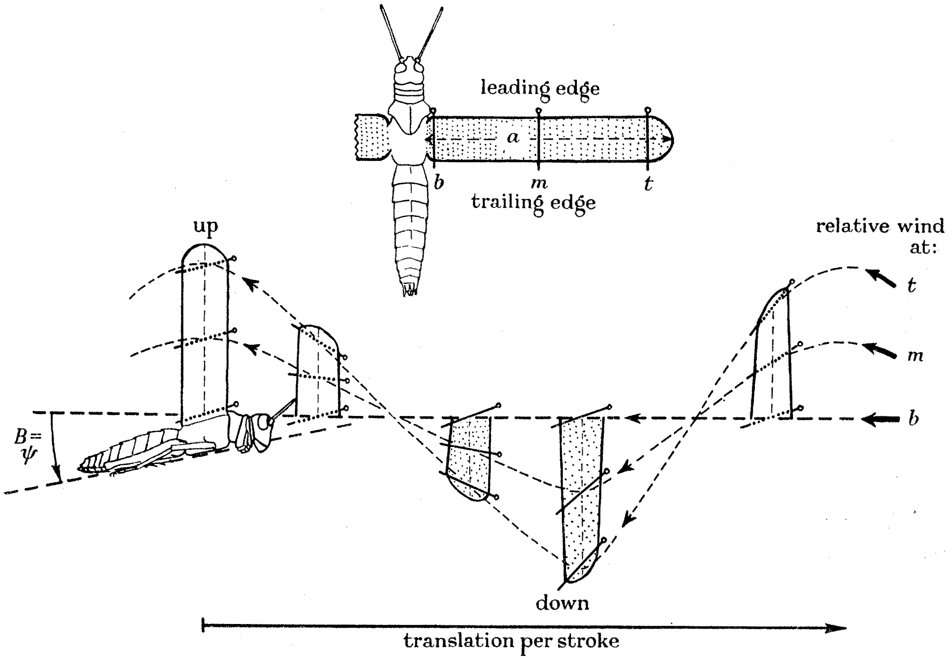

FIGURE IV, 4. Diagram of the wing twistings of an insect in forward horizontal flight. The direction of the relative wind is indicated.

Evidently, an estimate of the angle of attack at a given wing element requires knowledge both of the movements of the element and of the twisting. In the experiments just described a number of kinematic parameters was altered when B was changed. A direct measurement of the wing twisting would therefore, if it could be done, be of little use in itself. On the other hand, since the angles of attack did not vary much from tip to base during most of the stroke (part III), one could estimate the *mean angle of attack* from: (1) the aerodynamic forces produced; and (2) the actual distribution of the dynamic wind pressure. One could furthermore calculate (3) the mean inclination of the relative wind and thus estimate the mean wing twisting. However, instead of dealing with the absolute wing twisting in the different flyings to be examined the problem could be somewhat simplified by estimating only the *changes in mean wing twisting* $\Delta\theta$ which would tell us whether an active control had taken place or not.

(*c*) *Relative wind and angles of attack*

It might be thought that the constant lift was a passive consequence of the mechanical construction of the wing system so that it did not involve any active change of the stroke parameters. However, the stroke-plane angles changed systematically, although only to a small extent. In order to solve the problem the attempt was made to estimate the angle of attack and the inclination of the relative wind during some representative phase of the stroke. When the changes of these two quantities are known, the changes in the wing twisting can be estimated.

Presuppositions

The method was based upon the detailed studies of normal flight in parts II and III. First, the angular movements in the stroke plane of the long axis of the wings are extremely regular and can, for the present purpose, be expressed in simple mathematical terms (part II). Secondly, the aerodynamic characteristics of the wings have been measured in a wind field much resembling the field to which they are exposed during normal flight (part III). Thirdly, the variation during the stroke of the lift produced by each pair of wings has been analyzed in two individuals whose average lift in both cases was near to 100 %; the deviations between the experimental results were small and the found variation with time was rather simple. Moreover, the same *relative changes* in the lift were found in two other experiments in which L_r was 70 and 162 % respectively. It was therefore possible to estimate the lift produced by each pair of wings at some characteristic phase of the stroke.

Middle part of downstroke

This phase is the most important part of the stroke and, moreover, the calculations are simple. (1) The angular velocity ω of the long axis of the wing is maximum and could be calculated as $(\mathrm{d}\gamma'/\mathrm{d}t)_{\max.}$ from equations (II, 9) and (II, 10) in part II. (2) The lift contributions L_1 and L_2 produced respectively by forewings and hindwings are also maximum and could be estimated from figures III, 16 and III, 17 in part III. When the average lift of the whole insect is $\bar{L}$, each pair of wings will contribute by $L_1 = 0{\cdot}5\bar{L}$ and $L_2 = 1{\cdot}4\bar{L}$. These coefficients seem to be independent of the relative lift. (3) The flying velocity of the insect through the air, $-v_f$, and the velocity of a point on the wing in relation to the wing base, $-v_{ry}$, are both included in a vertical plane parallel to the direction of flight. Moreover, the wing axis is nearly perpendicular to the long body axis in both pairs of wings. (4) The positive aerodynamic work done by the wings during the middle third of the downstroke amounts to one-half of the work done in a complete wing stroke (part III).

Relative wind

Figure IV, 5*a* shows the relative wind v_{ry} during the middle part of the downstroke at a point on the long wing axis in the distance y from the fulcrum. The locust flies horizontally from right to left with the air velocity $-v_f$. v_f is therefore the horizontal component of v_{ry} due to the forward movement through the air. v_y is the wind velocity due to the flapping movements and amounts to

$$v_y = y\,\omega_{\text{max.}},$$

so that

$$v_{ry}^2 = v_f^2 + v_y^2 + 2v_f v_y \cos{(90-b)},$$

where b is the stroke-plane angle of the wing in question.

In the distance y from the wing base the inclination of the relative wind to the horizon is β_y so that

$$\tan\beta_y = \frac{v_y \cos b}{v_y \sin b + v_f}.$$

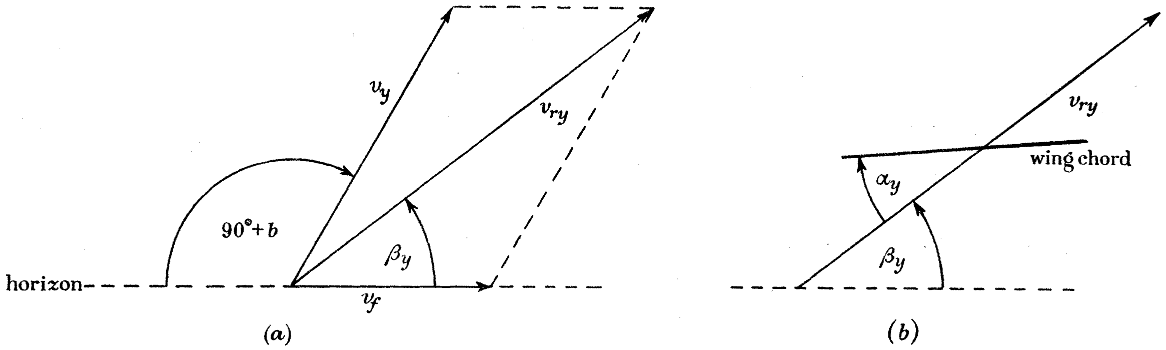

FIGURE IV, 5.

The dynamic wind pressure per unit area is $P_y = \frac{1}{2}\rho v_{ry}^2$. The mean pressure for the total wing P could therefore be estimated by graphical integration from the fulcrum to the wing tip. The mean inclination of the relative wind β could also be estimated by graphical integration.

Angle of attack

Since the lift contributions L_1 and L_2 were known together with the mean dynamic wind pressure and the average wing dimensions, the lift coefficient C_L of the forewing and the unit lift L_u* of the hindwings could be calculated. By means of these figures the mean

---

* The unit lift L_u is the lift in grams of one hindwing of standard size exposed to a dynamic wind pressure of 1 mm H_2O ($=1$ kg/m^2). C_L is not defined in the hindwings (part III).

angles of attack α_1 and α_2 could be found from the polar diagrams in figures III, 12 and III, 14 (part III). In figure IV, 5*b* the angle of attack at the distance y from the fulcrum α_y is seen to be the acute angle between the relative wind and the wing chord at that distance. In the hindwings the chord only refers to the rigid remigium (see part III). The small systematic error introduced by disregarding the mutual effect of the wings on the circulation Γ is of no importance here *inter alia* because the lift remained constant.

(*d*) *Mechanism of lift regulation*

Angle of attack

By using the flight data in table IV, 3, the *mean* coefficient of lift C_L (forewings) and the *mean* unit lift L_u (hindwings) were calculated together with the corresponding *mean* inclinations of the relative wind, β_1 and β_2. Table IV, 4 shows these calculated quantities together with the mean angles of attack α_1 and α_2 (to nearest half of a degree) during the middle part of the downstroke. In the right-hand column the figures in brackets show the order of magnitude provided Λ had remained constant instead of having decreased from 102 % ($B=0°$) to 97 % ($B=15°$).

TABLE IV, 4. CALCULATED MEAN VALUES OF C_L, L_u, α, AND β DURING THE MIDDLE PART OF THE DOWNSTROKE

The figures in brackets in the right-hand column show the result if the relative lift had not decreased from 102 to 94 % when B was increased from 10 to 15°. Same experiments as in table IV, 3.

	body angles, B (degrees)				
	0	5	10	15	
mean relative lift (%)	102	105	102	94	(99)
		forewings			
coefficient of lift, C_L	0·66	0·73	0·89	0·79	(0·85)
angle of attack, α_1	6°	$7\frac{1}{2}$°	11°	9°	(10°)
inclination of wind, β_1	$14\frac{1}{2}$°	16°	$16\frac{1}{2}$°	18°	
		hindwings			
unit lift (g/mm H_2O) L_u	0·70	0·81	0·95	0·84	(0·91)
angle of attack, α_2	$7\frac{1}{2}$°	10°	15°	12°	(14°)
inclination of wind, β_2	22°	$23\frac{1}{2}$°	$24\frac{1}{2}$°	25°	

TABLE IV, 5. LIFT/DRAG RATIO OF LOCUST WINGS

From measurements in graded wind field (Martin Jensen, part III).

	lift/drag	
α	forewings	hindwings
0°	6	4
5°	11	8
10°	11	8
15°	7	7
20°	4	6
25°	stalls	4, stalling begins

According to part III, the locust wings resemble ordinary airfoils, but the stalling limit is less clearly pronounced, especially in the hindwings. The optimum range of operation is characterized by the highest ratio between lift and drag (table IV, 5). When the figures in table IV, 5 are compared with table IV, 4 it is seen that, in both pairs of wings, the estimated angles of attack fell within the optimum range. A rough estimate suffices to show that this would not have been the case in a 'rigid' mechanical system. When, in the experiments, B was increased from 0 to 15°, the stroke parameters and the flying speed changed, increasing β_1 and β_2 by 3 to 4°; in a non-regulated system this means that the angles of attack would be increased by 18 to 19°. At the high body angle, α_1 and α_2 would therefore amount to 24 and 26° respectively. The forewings would then be stalling, the hindwings would have reached the stalling limit and, just before stalling, the lift would have been 40% higher than actually found. Thus, there can be little doubt that the locust changed the wing twisting when the body angle was altered by the observer.

Wing twisting

It is now possible more accurately to estimate the *mean change* in wing twisting $\Delta\theta$ which accompanied a change in body angle. Consider that B increased from 0 to the positive value ψ. At the same time β would change from β_0 to β_ψ due to the new flying speed, stroke angle, etc. Let α_y and β_y in figure IV, 5*b* represent the mean values of α and β. It is then evident that α would increase by $\psi+(\beta_\psi-\beta_0)=\Delta a$ provided that no change in wing twisting took place at all. Now the corresponding true change of α was $\Delta\alpha=\alpha_\psi-\alpha_0$. The difference between these two quantities gives the change in wing twisting looked for:

$$\Delta\theta=\Delta a-\Delta\alpha.$$

The results are seen in table IV, 6 and in figure IV, 6. They show that when the body angle was changed the wing twisting of both pairs of wings also changed. With the sense chosen, an increased body angle was met by an increased average wing twisting, the changes being of nearly the same magnitude.

Accuracy

It is difficult to estimate the accuracy of the calculations. However, since they concern the changes and not the absolute magnitudes of the twisting, and since all figures derived from the *same* locusts producing the *same* lift at all body angles, the errors would tend to be small. Provided that the high values of $\Delta\theta$ at $B=15°$ in table IV, 6 (16 and 14°) were an artifact, the total error in estimating $\bar{L}$, L_1 and L_2 would be about 40% (see above). But at each value of B, $\bar{L}$ was the mean value of about thirty single weighings each performed with an accuracy of ±2%. The error of the mean is therefore small. This also applies to the flying speed and to the stroke parameters and thus to β. In such homogeneous material $\Delta a=\psi+(\beta_\psi-\beta_0)$ could therefore not be charged with any big relative error, at least not compared with $\Delta\alpha=\alpha_\psi-\alpha_0$. The estimation of the angles of attack essentially depended upon $L_1=0{\cdot}5\bar{L}$ and $L_2=1{\cdot}4\bar{L}$. These coefficients derived from only two experiments with two individuals, but these flights were carefully selected to correspond very closely to a standard performance (part III). The same coefficients were also found in two other experiments characterized by a high lift (162%) and by a low lift (70%) respectively. Moreover, the two sets of results at normal lift differed but little, and L_1 and L_2 were estimated to within ±10% of their true values. This error being adopted here, the relationship between α_1 and C_L as well as between α_2 and L_u allowed the angle of attack to be estimated within ±2° in both pairs of wings. The total probable error in estimating $\Delta\alpha$ was therefore ±3° and, this being the dominating error, also in determining $\Delta\theta$.

Table IV, 6. Calculated mean change in the angle of twist, $\Delta\theta$, when B was altered

All figures refer to the middle part of the downstroke. Figures in brackets, see legend to table IV, 4. Same experiments as in table IV, 3.

	body angle increased from 0° to			
	5°	10°	15°	
forewings: Δa (degrees)	6·5	12	18·5	(18·5)
$\Delta\alpha$ (degrees)	1·5	5	3	(4)
$\Delta\theta = \Delta a - \Delta\alpha$	5	7	16	(15)
hindwings: Δa (degrees)	6·5	12·5	18	(18)
$\Delta\alpha$ (degrees)	2·5	7·5	4·5	(6·5)
$\Delta\theta = \Delta a - \Delta\alpha$	4	5	14	(12)

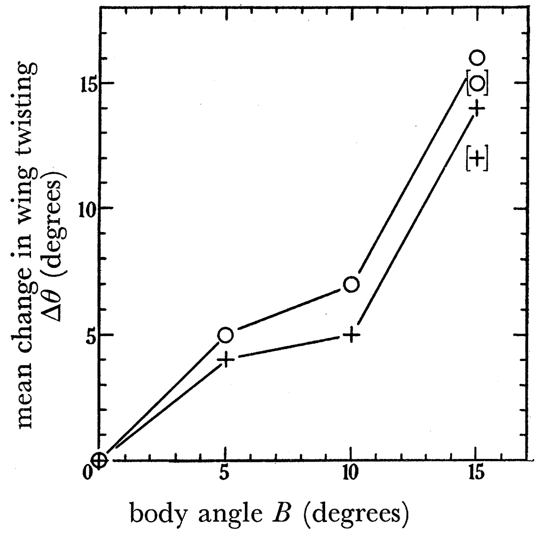

Figure IV, 6. The calculated mean change in wing twisting when the body angle of steadily flying desert locusts was changed within 0 and 15°. ○ forewings, + hindwings. Markings in brackets, see legend to table IV, 4. An increase of $\Delta\theta$ is equivalent to an increased pronation during the middle part of the downstroke.

(e) *Conclusions*

The desert locust is provided with a mechanism which keeps the lift constant and independent of the body angle when this angle varies between 0 and 15°.

The slight decrease in lift already observed at $B = 15°$ and the further decrease generally seen when B was increased to 20° indicates that the normal regulation is limited to body angles between 0 and 15°. This is in accordance with the fact that both pairs of wings are attached to the thorax by means of a broad hinge almost parallel to the sternum. When $B = 15°$, the angle of attack at the proximal part of the wings must also be near to 15°, and a further increase will cause stalling in this region.

The aerodynamic means by which the lift is regulated concerns also the stroke-plane angles (both pairs of wings) and the stroke angle of the forewings. The *major mechanism*, however, is an adjustment of the twisting of the wings. According to the sense used here, the twisting is increased when the wing plane is *pronated* and decreased when it is *supinated*. When B was increased from 0 to 15°, the mean wing twisting during the downstroke was increased by 16° in the forewings and by 14° in the hindwings, the error being about ±3°.

In a later paper (part VI) it will be shown that the wing twisting is determined both by elastic forces and by muscular pull. The elastic equilibrium position is the maximally supinated one. The delicately adjusted pronation during the downstroke must therefore be caused by the resultant pull of the supinator and pronator muscles, acting against elastic and aerodynamic forces. It cannot be a passive consequence of the mechanical arrangement of the skeleton. In this sense the lift regulation is active. It may be caused by two alternative mechanisms. (1) It may be a simple consequence of the mechanical properties of muscle receiving a constant amount of stimulation per stroke, the amount being determined only by the central nervous system. (2) It may be caused by the interaction of a lift-sensitive receptor system which controls the motor impulses. These alternatives are discussed on p. 577; the latter was found to be the most probable.

6. Discussion

The complicated wing movements in locusts are to a large extent determined by the mechanical suspension of the wings which offers little degree of freedom; this aspect of co-ordination will be further discussed in parts VI and VII.

No indication has been found of a myogenic rhythm like that of the flight muscles in higher insects (Pringle 1949; Roeder 1951) and of the tymbal muscle of Cicadas (Pringle 1954). On the contrary, in locust flight muscle each motor impulse results in an action potential followed by a distinct twitch (Ewer & Ripley 1953; Hagiwara 1953; Hagiwara & Watanabe 1954). At 28° C Ewer & Ripley (1953) found that the indirect flight muscles of *Locusta migratoria* could contract *in situ* without fusion of contraction at a frequency comparable to the normal wing-stroke frequency of the animal. This is in agreement with experiments on the *isolated* dorsal longitudinal muscle of *Schistocerca gregaria*; at 30° C the duration of the mechanical change in an isometric twitch corresponded to that of a normal wing-stroke cycle (Buchthal, Weis-Fogh & Rosenfalck, unpublished). If, therefore, a slow-fibre system is present, one must assume that it plays a subordinate role in flight.

Ordinary neuro-physiological principles can therefore be applied to locust flight. Unfortunately, the anatomy of the nervous system is little known. It has been reviewed by Albrecht (1953). La Greca (1949) and Ewer (1953) have studied the nerves to the flight muscles of *Anacridium aegypticum* and *Acanthacris ruficornis* respectively. The distribution of afferent and efferent nerve fibres to the flight system as well as their central connexions are virtually unknown, however. Nevertheless, we shall attempt to discuss the nervous mechanisms in locust flight on the basis of the present scattered observations in order to arrive at a working hypothesis for future investigations. The presence or absence of a centrally induced locomotor rhythm is decisive for the interpretation of the results.

(*a*) *Reactions found in locusts* (figure IV, 7)

Figure IV, 7 is a diagram of the systems concerned. The central nervous system (*CNS*) is considered as the connecting link between the receptor systems (*S*) and the effector muscles (*M*). S_h is the wind-sensitive hairs on the head; S_l is mechano-receptors on the legs; S_t is the supposed system which is sensitive to wind and which regulates the wing twisting, i.e. the lift; finally, S_m is the other wind-sensitive system in the pterothorax; it is responsible for the maintenance of flight movements in decerebrate locusts. S_t and S_m may be part of the same complex or may be completely separated, as is indicated in the figure. M_u is the elevator muscles of the wings (upstroke) and is antagonistic to the dorsal longitudinal depressors M_d (downstroke), but it is not clear how the stimulation of these muscles is brought about; in figures IV, 9 and IV, 10, the arrows therefore stop before reaching the 'box' $M_u + M_d$. M_t is the controller-depressors which depress the wings and adjust their twist; there are no muscles which can control the twist during the upstroke. M_t is supposed to be connected in some way with the receptors S_t (see p. 577). The other muscle groups are very heterogeneous. M_a brings the antennae and the forelegs into flight posture (anterior group), while M_p has the same function in the remaining legs and in the abdomen (posterior group). When both M_a and M_p function the posture is said to be complete. It must be emphasized that the *arrows* connecting the systems *do not represent nervous pathways*; they only symbolize the relationships which have been observed between the units.

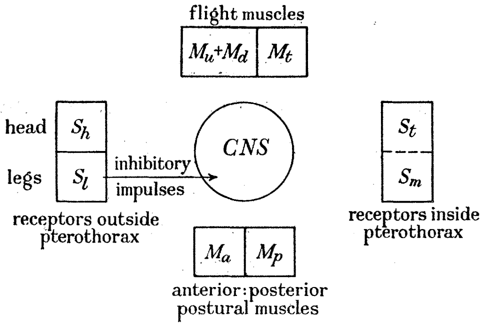

FIGURE IV, 7. Diagram of the receptor systems (*S*) and the effector systems (*M*) studied in this paper. Here and in figures IV, 9 and IV, 10, the arrows to and from the central nervous system (*CNS*) symbolize observed relationships but must *not* be taken for established nervous pathways. When the legs have contact, S_l elicits impulses which inhibit flight (see p. 579).

(*b*) *Centrally induced 'rhythm'?* (figure IV, 8)

Rhythmic wing movements sometimes occur in a normal locust suspended in still air, but such 'spontaneous' flapping only lasts a short time; it depends upon processes in the supra-oesophageal ganglia, being absent in decerebrate animals. When a locust is suspended and no wind is applied, both a normal and a decerebrate individual produces a short burst of flight when the support is removed ('tarsal reflex'), but it soon stops, flutters its legs, and eventually remains still. There is therefore no indication of the *CNS* being able to *initiate* the wing movements in the absence of peripheral stimuli.

The fact that the 'flight' only lasts a few seconds when neither the head nor the wings are exposed to wind shows that the *CNS* alone is incapable of *maintaining* the locomotor activity. It might be argued that the wind blocks some inhibitory stimuli, but this is certainly not the case as far as the wind-sensitive hairs are concerned; the normal locust remains still when they are covered or destroyed.

These observations do not of course exclude that parts of the rhythm are controlled independently by the *CNS* while other parts are under peripheral control. In attempting to analyze this problem it is convenient to distinguish between three different features of what is generally called 'rhythm': (*a*) the *frequency* of the recurring cycle of motor impulses; (*b*) the magnitude or *strength* of each impulse or train of impulses; and (*c*) the relative sequence of the impulses, i.e. the *phasing*.

Frequency

The observations reported in part II clearly demonstrate that the wing-stroke frequency depends on the size of the locust and on the aerodynamic work but is independent of the temperature of the pterothorax. The duration of a twitch and the speed of contraction of the isolated muscle, however, were found to depend upon temperature (Buchthal *et al.* unpublished). There can be little doubt that this also applies to the activity within the *CNS*. As to frequency, therefore, the *CNS* does not show any sign of an independent rhythm.

Strength of motor impulses

It has repeatedly been pointed out by Gray (1950) that the refined environmental adjustments of the ambulatory contractions in a freely moving animal indicate that peripheral sense organs play a dominating role. In locusts, however, this need not concern all muscle groups. M_u and M_d, for instance, drive the fundamental up and down movements which were found to be constant and independent of the aero-dynamic performance (part II). It is therefore compatible with the observed facts to suggest that both M_u and M_d receive an ungraded stimulus once during each cycle, for instance, a maximum one. It must be stressed that this does not imply that their energy requirements become independent of the aerodynamic performance because the controller-depressor muscles M_t may modify the mechanical conditions under which they work. If M_u and M_d normally give an all-or-none response, the *CNS* functions merely as a 'trigger' as far as these muscles are concerned.

The controller-depressor muscles M_t are illustrated in figure IV, 8, which should be compared with figure IV, 4. *p* is the *pronator*-depressors and *s* the *supinator*-depressors. In a later paper (part VII) it will be shown that there are no other muscles present in the locust pterothorax which are able to influence the wing twisting. When *p* contracts, it twists the wing along the long axis as indicated by the circle on the figure (pronation). Conversely, *s* supinates the wing but, because of the vannal fold *v*, *p* and *s* are not simple antagonists. This makes a detailed analysis difficult but does not invalidate the following considerations. *p* and *s* are of course synergists as far as the main wing movement (downstroke) is concerned. It will be shown that M_t mainly works against aerodynamic forces (part IX).

Consider a locust which flies at a low body angle, $B = 0°$. When B is increased to 15°, we saw that the lift and most of the wing parameters remain constant, apart from the wing twisting; the pronation during the downstroke is increased by about 15°. The first indication of a pronation occurs at the top position initiating the downstroke and disappears at the bottom position. The movements of the wing axis (*a*) relative to the body are not influenced by *B*, so that, at the extreme positions, the muscles *p* and *s* must be in the same situation at all values of *B*. The 15° increase in pronation following the alteration of the body angle must therefore be caused by an increased shortening velocity of *p*. This can be realized in two different ways: (1) the excitation remains constant (controlled by the *CNS*), but the load upon *p* is decreased; (2) the excitation is adjusted by means of a receptor system.

Let us discuss (1). Since the lift as well as the kinematics remain constant, a decrease of the force set up by *p* must be compensated by a corresponding increase of the force produced by *s*. One may, for instance, think of a backwards migration of the centre of pressure when *B* is increased, moving part of the load from *p* to *s*. However, under constant kinematic conditions the force produced by *s* can only be increased by increasing the strength of stimulation. We must then assume that *s* is under sensory control. In this context, it does not of course make any difference whether we regard *p* as independent of and *s* as dependent on peripheral sense organs. The point is that we must assume the lift to be controlled by means of a receptor system, here called S_t.

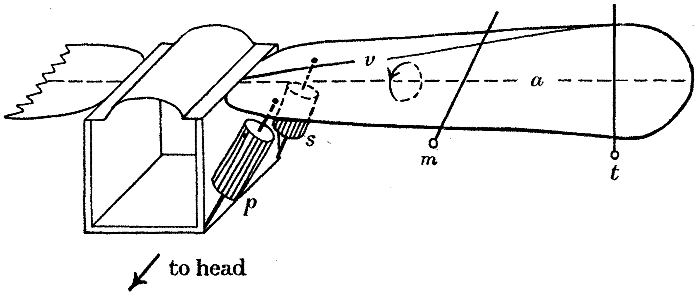

FIGURE IV, 8. Diagram of the controller-depressor muscles M_t. *p* is the two pronators, *s* the supinator, *v* the vannal fold, and *a* is the long wing axis. The transverse markings at the middle section (*m*) and at the tip (*t*; see figure IV, 4) show that the wing is in the pronated state, the leading edge of the tip section being vertically below the trailing edge.

As a working hypothesis it is concluded that the pattern of excitation of M_u and M_d is constant (maximal?) while that of M_t is controlled by S_t.

Phasing

The co-ordination of the limb movements in Amphibia has been discussed in great detail by Gray & Lissmann (1946*b*); they concluded that 'the individual proprioceptor limb responses integrate to form an adequate picture of the co-ordinated limb movements seen when an intact toad ceases to swim and begins to walk on land'. Gray (1950) further attempted to describe the function of the spinal cord in the simplest possible terms of proprioceptive reflexes, assuming that each limb is driven by two antagonistic motor centres which mutually inhibit each other, and that the proprioceptor impulses arising in one limb will affect the excitatory balance in other limbs. 'In this way it is not difficult to reconstruct at least some of the main features of normal ambulation.' This approach is a very fertile one, but we are still left in ignorance about *how* the integration within the

CNS comes about because the above system presupposes a high order of functional organization within the spinal cord, a feature which one might well *describe* as definitely patterned 'scores' constituting the motor repertory (Weiss 1950). Furthermore, some important observations on lower vertebrates at the same time demonstrate the necessity of proprioceptors and the surprising extent to which they can be omitted. In the spinal dogfish (Lissmann 1946*b*) as well as in Amphibia (Gray & Lissmann 1946*a*), co-ordinated swimming and walking movements, respectively, could be elicited in individuals which had all but one sensory nerve root cut, whereas total deafferentation abolished the rhythmicity altogether. Gray & Lissmann (1946*a*) found that a toad could walk even when that nerve (unilateral) did not innervate any part of the limbs. A very remarkable quantitative reduction in the normal amount of afferent impulses can thus be tolerated before the co-ordination breaks down. It is difficult to imagine that such a large *security factor* could exist unless one assumes that the *CNS* elicits a 'preformed' cycle of locomotory impulses when it is triggered by some peripheral sense organ, whether this receptor is a proprioceptor or of another nature. In lower vertebrates the phasing of the locomotor impulses therefore seems to be determined by the spinal cord, but in order to have the rhythm set up at all the *CNS* must receive an adequate 'entrance' signal; this afferent impulse must originate in some intact segment which need not be of any direct importance for the normal locomotion.

So far, co-ordination in insects has never been analyzed in such detail as in vertebrates, *inter alia* because of the less favourable anatomy of their nervous system. It is therefore impossible to make any suggestions based upon experimental evidence about the nervous mechanisms responsible for the 'rigid' phasing of the wing stroke of a locust. Is it possible to imagine that this phasing originates in the *CNS*? If this were the case one should, because of the constant frequency, expect the phasing to change with temperature, which is in contradiction to the experiments in part II; but the question cannot be satisfactorily answered as yet. On the other hand, the following hypothesis seems simpler and, in addition, explains why the wing-stroke frequency is so constant. Let us assume that a given contraction is part of an ordinary reflex mechanism, the proprioceptor of which starts firing when certain parts of the cuticle are bent. The pterothorax of locusts is a very strong elastic box, as will be described in part VI, so that a given wing position corresponds to a given state of deformation. It is therefore perfectly probable that one synergic muscle group can stimulate another group to contract at the right *relative* instant. As to the absolute timing, the upstroke is little influenced by aerodynamic forces (part III), while the kinetic energy of the wings reaches a maximum (part VI). The work done by a twitch of a flight muscle was found to be independent of temperature; it only depends upon the degree of shortening, i.e. on the geometry of the pterothorax (Buchthal *et al.*, unpublished). The duration of a considerable part of the upstroke *may* therefore be determined by physical factors which remain nearly constant under all conditions. One can imagine a system where this characteristic is used as a 'clock'.

Conclusions

The *CNS* does not appear to possess a rhythm which can initiate and maintain the flight movements. On the contrary, they depend upon specific peripheral stimuli. In fact, only the relative phasing of the contractions may be controlled by the *CNS*, but a simpler hypothesis based upon proprioceptive reflexes is equally probable.

(*c*) *Inhibition of flight* (figure IV, 7)

The flight movements of most insects stop when the tarsi or, in general, the legs obtain contact with a rigid body (see Chadwick 1953). This can be thought of as the result of two alternative mechanisms. (*a*) When the legs are free from support the mechano-receptors may emit impulses (off-responses) which stimulate the locust to fly, implying that these impulses stop, and thereby the flight movements, when contact is again obtained. Amputation of the legs should therefore prevent flying. However, both in locusts and in most other insects (Fraenkel 1932) flight continues when the legs are cut. We must therefore assume that (*b*) the leg receptors S_l emit impulses which *inhibit* the flight movements.

(*d*) *Initiation of flight* (figure IV, 9)

Flight can be initiated in three ways as illustrated in figure IV, 9: (1) By a *sudden* removal of the support for the legs (S_l). (2) By pinching, strong light, etc. (shock). (3) By means of a jet of air directed against S_h. When none of these stimuli is supplied, a suspended locust remains still. When S_l and S_h are destroyed or removed, flight can only be induced by an unspecific shock. S_l and S_h therefore emit excitatory impulses. In all cases the forelegs and the antennae take up flight posture, i.e. M_a is stimulated, but there is no absolute coupling between flight movements and M_a; sometimes the wings flap without the forelegs being folded and vice versa (see also next section).

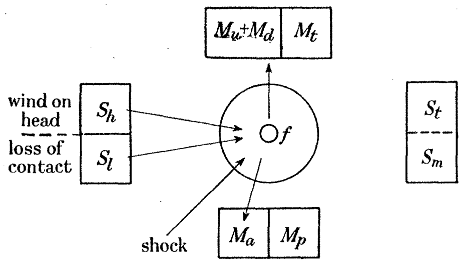

FIGURE IV, 9. Observed specific and unspecific (shock) stimuli which can *initiate* the flight, possible impulses originating in the cerebral ganglia being disregarded. The experiments indicate the existence of a common flight centre *f* within the *CNS*.

The simplest hypothesis is that the excitatory impulses reach a common flight centre *f* within the *CNS*. M_p never functions in 'still' air and depends upon impulses from other sense organs (S_m).

(*e*) *Maintenance* (figure IV, 10)

S_h adapts little or not at all and can therefore maintain the flight. It has not yet been possible to localize the wind-sensitive system in the wing apparatus S_m. The following arguments indicate that S_m, like S_h, produces excitatory impulses. Let us assume that it emits inhibitory stimuli and that the normal wind forces on the wings cancel this inhibition. The maintenance stimuli for movements in a wind must then derive either (*a*) from the *CNS* in contradiction to the foregoing conclusions, or (*b*) from other sense organs of which

S_h is the only one known to be able to do so. But S_h could be put out of action without preventing the wing movements. The experiments showed that the stimuli for S_h and S_m are both above the threshold during normal forward flight.

Since the impulses from the general body surface (shock), from the legs (S_l) or from the wind-sensitive hairs (S_h) have no direct relation to the wing movements, they can be considered as *extrinsic* flight impulses. Those from S_m, on the other hand, are strictly coupled to the wing movements themselves and are therefore *intrinsic* maintenance impulses and need not pass the hypothetical flight centre *f*. The same applies to the motor impulses to M_p. The observations mentioned on p. 556 indicate that neither M_a nor M_p are coupled directly to the sense organs; the complete flight posture sometimes occurs in motionless locusts some hours after they have been decerebrated.

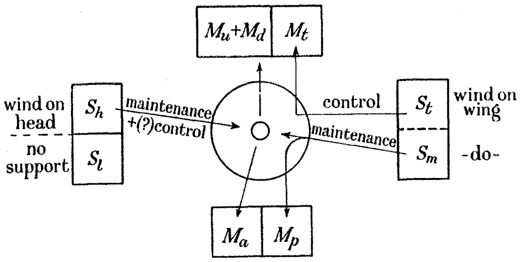

FIGURE IV, 10. Observed stimuli which can *maintain* and *control* the flight; those from S_h are extrinsic flight stimuli in contrast to the intrinsic stimuli from the working pterothorax.

It has been suggested that the modified wings of Strepsiptera and Diptera, the halteres, have a 'stimulatory' function (Buddenbrock 1919; Melin 1941) besides being stabilizing organs (Fraenkel & Pringle 1938; Pringle 1948; Schneider 1953). For *flight* such a stimulatory function has never been unambiguously demonstrated. The suggestion is interesting from the point of view of insect evolution: the greater the manoeuvrability becomes the less reliable will be maintenance systems whose signals, like those of S_h and S_m in locusts, depend upon the forward speed or on the wind forces experienced by the wings; a perfect device must be independent of the aerodynamic effect of the wing movements. Are some of the sensilla at the halteres homologous to S_m?

(*f*) *Control mechanisms* (figure IV, 10)

Smith (1952) has briefly discussed the evolution of control mechanisms in natural flapping flight as compared with those of aeroplanes, without paying much attention to the fact that one should consider the air speed of the *wings* rather than that of the body. As to manoeuvres, he rightly stressed the superiority of an unstable construction over an 'aeroplane' which is automatically stable, i.e. which is endowed with *structural* stability. In the case of birds, bats and many higher insects we must assume that stable flight is achieved by means of quick and accurate adjustments of the wing movements so that the supposed instability of these animals is compensated by a refined sensory system, the integrated effect of which is *functional* stability.

Rotations

When a fly is rotated about its vertical axis (yawing), the oscillating halteres act as gyroscopic organs in which the shearing forces set up in the base of the haltere stalks are sufficiently big to be perceived by a refined system of campaniform sensilla (Pringle 1948). The fly then responds with compensatory movements (cf. Faust & Buddenbrock 1951); there is some indication that the compensation results from a mechanical coupling between the halteres and the effector system (Schneider 1953). Anyhow, in insects with no oscillating parts which are sheltered off from the wind, the control of the yawing must take place by other means. In suspended locusts whose head was exposed to a jet of air, previous experiments have indicated that the wind-sensitive hairs S_h stabilize yawing movements in addition to their function as stimulatory organs (Weis-Fogh 1949, 1950). But it has not been possible so far to design a wind-tunnel experiment which could actually prove this suggestion. Hollick's (1940) experiments tend to show that the pitching of flies is influenced by the wind pressure on the antennae (Johnson's organ). Practically nothing is known about the control of rolling.

Control of lift

The altimeter of an aircraft tells the pilot whether he is climbing or descending but, within the biosphere, such a device would be of little use. It is, however, essential for insects or birds to be able to estimate the lift when visual or auditory stimuli fail to give information on vertical movements. A system which adjusts the average vertical force and assists in keeping it constant for some length of time would obviously be an advantage for the stabilization of flight. The present experiments have shown that such a mechanism exists in locusts. It was concluded that the regulation is active and depends upon special sense organs, labelled S_l. What can be suggested about their nature? The lift of a flapping animal changes rhythmically. If, therefore, the 'signals' from S_l should be representative of the *average lift*, the relative changes in the aerodynamic forces must be rather constant during a stroke. In fact, this was found to be the case in *Schistocerca*, especially during the middle part of the downstroke (see p. 569 and part III). Also for other reasons, this phase would be especially suited for an 'estimate' of the lift: the aerodynamic force reaches its maximum and is nearly vertical; the force due to the acceleration of the wing mass is small or zero and the centripetal force, although maximal, is normal to the lifting force.

It seems therefore profitable to look for a receptor system which could respond to the integrated lifting force during the downstroke; two suggestions concerning its nature are worth considering. (*a*) The bending of the inner part of the wing may be perceived without much interference with other forces, for example, by a system of campaniform sensilla (Pringle 1938) which are known to be abundant at the base of wings and halteres in many insects (cf. Guenther 1901; Pflugstaedt 1912; Ulrich 1930; Pringle 1948). The centripetal force would tend to stretch the veins but would maximally amount to 0·2 g in one forewing and 0·35 g in one hindwing, i.e. 0·3 times the simultaneous lifting force (p. 569). During the upstroke the corresponding figures are 0·65 and 1·5 g respectively, or considerably more than the aerodynamic bending force. (*b*) The integrated aerodynamic pull may be perceived by means of stretch sensilla inside or attached to the main wing hinge. Actually, before reaching the hinge, a small thin nerve branches off from the big sensory nerve supplying each wing. This branch has not been described by La Greca (1949) and Ewer (1953); it could be traced to the membranes enclosing the main ligaments of the fulcrum. Furthermore, in some cases the endings were found to be simple elongated cells reminiscent in form of the primitive stretch receptors mentioned by Snodgrass (1935, p. 504) as sensory neurones of type II.

It is reasonable to suggest that the elaborate system of sensilla at the wing base of many insects is concerned with the quick, quantitative control of the aerodynamic forces (S_t), while the sensilla attached to the wing hinge proper are responsible for the qualitative maintenance response (S_m). The described innervation provides the anatomical basis for testing these hypotheses.

Apart from the importance of a system controlling the size of the main force resultant in insect flight, the control of the lift has another aspect. The theoretical calculations in part I indicate that the power used by insects to produce sufficient lift constitutes a considerable part of the metabolic rate, and this result has been confirmed in experiments to be described in part VIII. A control of the lift can therefore be regarded as an indirect control of the power in flight. Considered in that way, it is tempting to suggest that the homoeostatic mechanism which has been postulated in the flight system of *Drosophila* (Chadwick 1953) is but the result of a similar receptor system being present in flies. It need not be a consequence of the energetics of flight. Such a sense organ also makes it difficult to interpret experiments on the effect of altering the moment of inertia of the wing mass (Sotavalta 1952).

The lift-sensitive system in locusts has no direct counterpart in aircraft. In principle it would correspond to a *servo-mechanism* whose sensitive part is a strain gauge the output from which controls the elevators (conventional aeroplane) or the pitch of the rotor blades in a helicopter. In the first case one might place the gauge at the transition between wings and fuselage so that its signals become proportional to the moment between these units. In a helicopter one might measure the tension in the vertical carriage for the rotor.

I am grateful to Professor F. Buchthal for laboratory facilities, and to Mrs and Mr B. Muus for assistance. The work has been supported by the Anti-Locust Research Centre, London, the Carlsberg Foundation, Copenhagen, and the Scandinavian Insulin Foundation, Copenhagen. The MS. was prepared during my tenure as a fellow of the Rockefeller Foundation. I am indebted to Dr H. W. Lissmann, F.R.S., and Dr J. W. S. Pringle, F.R.S., for comments and criticism.

REFERENCES

References to other Parts of this study are given as part I, part II, etc. The following Parts are printed in this volume:

Part I. Weis-Fogh, T. & Jensen, Martin. Basic principles in insect flight. A critical review.
Part II. Weis-Fogh, T. Flight performance of the desert locust (*Schistocerca gregaria*).
Part III. Jensen, Martin. The aerodynamics of locust flight.

The following Parts are being prepared:

Part V. Jensen, Martin. Strength and elasticity of locust cuticle.
Part VI. Weis-Fogh, T. Wing movements and elastic deformations in flying locusts.
Part VII. Weis-Fogh, T. Functional anatomy of the wing system of the desert locust (*Schistocerca gregaria*), including the tracheal system.
Part VIII. Weis-Fogh, T. Lift and metabolic rate of flying locusts.

Part IX. Jensen, Martin & Weis-Fogh, T. The energetics of locust flight.
Part X. Jensen, Martin & Weis-Fogh, T. General discussion of locust flight.

Albrecht, F. O. 1953 *The anatomy of the migratory locust*. London: The Athlone Press.

Boyd, K. & Ewer, D. W. 1949 Flight responses in grasshoppers. *S. Afr. Sci.* **2**, 168–169.

Buchthal, F., Weis-Fogh, T. & Rosenfalck, P. (Unpublished).

Buddenbrock, W. v. 1919 Die vermutliche Lösung der Halterenfrage. *Pflüg. Arch. ges. Physiol.* **175**, 125–164.

Chadwick, L. E. 1939 Some factors which affect the rate of movement of the wings in *Drosophila*. *Physiol. Zoöl.* **12**, 151–160.

Chadwick, L. E. 1953 In Roeder, K. D. [ed.]. *Insect physiology*. New York: John Wiley and Sons, Inc.; London: Chapman and Hall Ltd.

Chadwick, L. E. & Williams, C. M. 1949 The effects of atmospheric pressure and composition on the flight of *Drosophila*. *Biol. Bull., Woods Hole*, **97**, 115–137.

Cook, P. M. 1951 Observations on giant fibres of the nervous system of *Locusta migratoria*. *Quart. J. Micr. Sci.* **92**, 297–305.

Davis, R. A. & Fraenkel, G. 1940 The oxygen consumption of flies during flight. *J. Exp. Biol.* **17**, 402–407.

Ehnbom, K. 1948 Studies on the central and sympathetic nervous system and some sense organs in the head of neuropteroid insects. *Opusc. ent.* Suppl. 8.

Ewer, D. W. 1953 The anatomy of the nervous system of the tree locust, *Acanthacris ruficornis* (Fal.). I. The adult metathorax. *Ann. Natal Mus.* **12**, 367–381.

Ewer, D. W. & Ripley, S. H. 1953 On certain properties of the flight muscles of the Orthoptera. *J. Exp. Biol.* **30**, 170–177.

Faust, R. & Buddenbrock, W. v. 1951 Die Regulierung des Gleichgewichtes der höheren Dipteren durch die Halteren. *Experientia*, **7**, 265–266.

Fraenkel, G. 1932 Untersuchungen über die Koordination von Reflexen und automatisch-nervösen Rhythmen bei Insekten. I. Die Flugreflexe der Insekten und ihre Koordination. *Z. vergl. Physiol.* **16**, 371–393.

Fraenkel, G. & Pringle, J. W. S. 1938 Halteres of flies as gyroscopic organs of equilibrium. *Nature, Lond.*, **141**, 919–920.

Gray, J. 1950 The role of peripheral sense organs during locomotion in the vertebrates. *Symp. Soc. Exp. Biol.* no. 4, pp. 112–126.

Gray, J. & Lissmann, H. W. 1946*a* Further observations on the effect of de-afferentation on the locomotory activity of amphibian limbs. *J. Exp. Biol.* **23**, 121–132.

Gray, J. & Lissmann, H. W. 1946*b* The co-ordination of limb movements in the amphibia. *J. Exp. Biol.* **23**, 133–142.

Guenther, K. 1901 *Ueber Nervenendigungen auf dem Schmetterlingsflügel*. (Thesis.) Jena: Fischer.

Hagiwara, S. 1953. Neuro-muscular transmission in insects. *Jap. J. Physiol.* **3**, 284–296.

Hagiwara, S. & Watanabe, A. 1954 Action potential of insect muscle examined with intra-cellular electrode. *Jap. J. Physiol.* **4**, 65–78.

Hanström, B. 1928 *Vergleichende Anatomie des Nervensystems der wirbellosen Tiere unter Berücksichtigung seiner Funktion*. Berlin: Julius Springer.

Hollick, F. S. J. 1940 The flight of the dipterous fly *Muscina stabulans* Fallén. *Phil. Trans.* B, **230**, 357–390.

Jawlowsky, H. 1936 Über den Gehirnbau der Käfer. *Z. Morph. Ökol. Tiere*, **32**, 67–91.

Krogh, A. & Weis-Fogh, T. 1951 The respiratory exchange of the desert locust (*Schistocerca gregaria*) before, during, and after flight. *J. Exp. Biol.* **28**, 344–357.

La Greca, M. 1949 I nervi motori e sensori degli organi di volo degli Acrididi. *R. C. Accad. Napoli*, **15**, (1948), 121–130.

Lissmann, H. W. 1946*a* The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula*, *Acanthias vulgaris*). I. Reflex behaviour. *J. Exp. Biol.* **23**, 143–161.

Lissmann, H. W. 1946*b* The neurological basis of the locomotory rhythm in the spinal dogfish (*Scyllium canicula*, *Acanthias vulgaris*). II. The effect of de-afferentation. *J. Exp. Biol.* **23**, 162–176.

Melin, D. 1941 Contributions to the knowledge of the flight of insects. *Uppsala Univ. Årsskr.* no. 4.

Pflugstaedt, H. 1912 Die Halteren der Dipteren. *Z. wiss. Zool.* **100**, 1–59.

Pringle, J. W. S. 1938 Proprioception in insects. II. The action of the campaniform sensilla on the legs. *J. Exp. Biol.* **15**, 114–131.

Pringle, J. W. S. 1948 The gyroscopic mechanism of the halteres of Diptera. *Phil. Trans.* B, **233**, 347–384.

Pringle, J. W. S. 1949 The excitation and contraction of the flight muscles of insects. *J. Physiol.* **108**, 226–232.

Pringle, J. W. S. 1954 The mechanism of the myogenic rhythm of certain insect striated muscles. *J. Physiol.* **124**, 269–291.

Roeder, K. D. 1951 Movements of the thorax and potential changes in the thoracic muscles of insects during flight. *Biol. Bull., Woods Hole*, **100**, 95–106.

Schneider, G. 1953 Die Halteren der Schmeissfliege (*Calliphora*) als Sinnesorgane und als mechanische Flugstabilisatoren. *Z. vergl. Physiol.* **35**, 416–458.

Smith, J. M. 1952 The importance of the nervous system in the evolution of animal flight. *Evolution*, **6**, 127–129.

Snodgrass, R. E. 1935 *Principles of insect morphology.* New York and London: McGraw-Hill Book Company, Inc.

Sotavalta, O. 1952 The essential factor regulating the wing-stroke frequency of insects in wing mutilation and loading experiments and in experiments at subatmospheric pressure. *Ann. (bot.-zool.) Soc. zool.-bot fenn. Vanamo* (Zool.), **15**, 1–67.

Ulrich, W. 1930 Die Strepsipteren-Männchen als Insekten mit Halteren an Stelle der Vorderflügel. *Z. Morph. Ökol. Tiere*, **17**, 552–624.

Weis-Fogh, T. 1949 An aerodynamic sense organ stimulating and regulating flight in locusts. *Nature, Lond.*, **164**, 873–874.

Weis-Fogh, T. 1950 An aerodynamic sense organ in locusts. *8th Int. Congr. Ent.* 1948, pp. 584–588.

Weis-Fogh, T. 1952 Fat combustion and metabolic rate of flying desert locusts (*Schistocerca gregaria* Forskål). *Phil. Trans.* B, **237**, 1–36.

Weiss, P. 1950 Experimental analysis of co-ordination by disarrangement of central-peripheral relations. *Symp. Soc. Exp. Biol.* no. 4, pp. 92–111.