PATTERNED ACTIVITY OF CO-ORDINATED MOTOR UNITS, STUDIED IN FLYING LOCUSTS

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INTRODUCTION

One goal of students of behavioural physiology is to analyse animal movements in terms of the individual nerve cell and motor unit events which contribute to the integrated activity. At present it seems a reasonable possibility to accomplish such a detailed description in only two categories of activity: very brief responses such as the startle reactions mediated by giant fibres, and neatly repetitive cyclic responses such as those affecting circulation, ventilation, and some kinds of locomotion. The startle responses do not provide a good model for understanding other reactions because they are too simple in regard to behavioural variability and are rather deficient in graded sensory control. Rhythmic activities, either very simple ones such as the song production of cicadas (Hagiwara & Watanabe, 1956) or moderately complex ones such as the control of the lobster heart (Bullock & Terzuolo, 1957), have been analysed at the single unit level. The latter shows some of the main characteristics that one can expect in control systems for more complicated behaviour: central automaticity and pattern formation, and effects of sensation on output pattern. It would be more convincing, however, if an activity involving more than a small part of an animal could be treated similarly.

Locomotion in continuous media (swimming and flying) often involves rhythms of limb movements with rather constant frequency and stroke pattern. The regularly repeated cycles of activity can be measured precisely and sampled with confidence. Nervous or muscular activity can be correlated both with the instantaneous posture of the animal and with the integrated resulting forces. While vertebrates include flying and swimming forms, they are not suitable for the reason that their nervous organization is too complex even in cases of simple behaviour. Arthropods with their economy in numbers of nervous and muscular units and their external skeletons which facilitate electrode placement are better. Even here most locomotion involves several limbs, each with several joints, each with several muscles. In addition the pattern of limb movement may be rather variable so that recognition of patterns of activity of individual units is difficult (Hoyle, 1957, 1962). The special case of insect flight is useful because an even more limited number of units act upon a small number of moving parts. By reason of its mechanical construction the flight system is able to carry out a complicated and highly controlled pattern of movements with these few units.

Behaviourally speaking, the flight of a locust is just as complex as the walking of a dog, but it is accomplished with many fewer parts. The flight control system contains

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motor neurons which may be parts of other systems and which may be influenced in several ways (by sensation, higher nervous command, and interaction with other flight neurons). They each have the possibility of independent action but during flight are coupled into a pattern with only a low order of lability necessary for control manœuvring. The flight control system is in other words not based just on relay principles but may be organized and function in a way similar to the much more complex systems in vertebrates. In the complex vertebrate systems one must analyse populations of units and design models which behave in an analogous way and this approach might lead to a large number of possible solutions, all of which fit the observations. In the case of the insect flight system we may obtain information about the general nature of complex systems on the basis of a direct empirical analysis.

An analysis of this kind divides easily into several parts; studies of sensory input, central patterning, motor output, and cyclic or reflex influences on each of these. In this paper we wish to present the method and results of analyses of the motor output pattern during normal locust flight. In the discussion we will relate this to previous work and to some preliminary observations on other aspects of the whole problem. This paper will thus provide a preview and background for future work.

STRUCTURE AND FUNCTIONS OF THE FLIGHT SYSTEM
(INCLUDING DEFINITIONS)

Wind-tunnel investigations on flying desert locusts have provided detailed information about the cyclical movements of the two pairs of wings, the variation of the aerodynamic forces during the wingstroke, and some information about major control mechanisms. Since, moreover, the mechanical and electrical properties of the flight muscles are well understood and since some basic properties of the central nervous system and of the sensory input during flight have come to light recently, the situation seems ripe for an analysis of the nervous co-ordination of the working thorax. This presupposes a precise and manageable description of the individual performances as well as knowledge of the morphology and function of the main members of the flight system. It is the purpose of this section to bring together relevant information for this and related studies.

(a) Flight and wing movements

Size and gross performance

In cage-bred desert locusts the size varies considerably but the ratio between the length of the elytra, E, and the length of the hind femur, F, is rather constant. In locusts from moderately crowded cages $E/F = 2\cdot16$, S.D. $0\cdot06$. Such animals, whether males or females, turn out to be geometrically similar with respect to wings, thorax, flight muscles and probably many other systems. The influence of size on a given performance can therefore be estimated by means of simple size indices (Weis-Fogh, 1952): length index $l = (EF)^{\frac{1}{2}}$, S.D. 2%; surface index $s = EF$, S.D. 4%; volume index $v = (EF)^{\frac{3}{2}}$, S.D. 6%.

In an average-sized adult, $l = 3\cdot78$ cm., $s = 14\cdot3$ cm.^{2} and $v = 54\cdot1$ cm.^{3} When fully grown but prior to sexual maturation, i.e. 2 or 3 weeks after the final moult, such a *standard* locust weighs $1\cdot98$ g. after about 1 hr. of flight. The corresponding *basic weight w* of an individual with volume index v is therefore $w = v\ 1\cdot98/54\cdot1$ g., S.D. 6%.

As with an aeroplane, the actual weight of an individual changes with load (food, fat, eggs) while the external dimensions remain almost constant. In free, level flight the main result of the wing movements is an average lift which just counteracts the actual weight of the locust. However, a suspended locust cannot perceive whether it would climb, descend or fly level if freed. It is therefore relevant to use the lift expressed in per cent of the basic weight, i.e. the *relative lift* $L_r = 100 \times$ actual lift/w. An immature female would then have to lift only 70 % of w in order to fly horizontally while she may have to lift 140 % some weeks later when loaded with eggs. In this way,
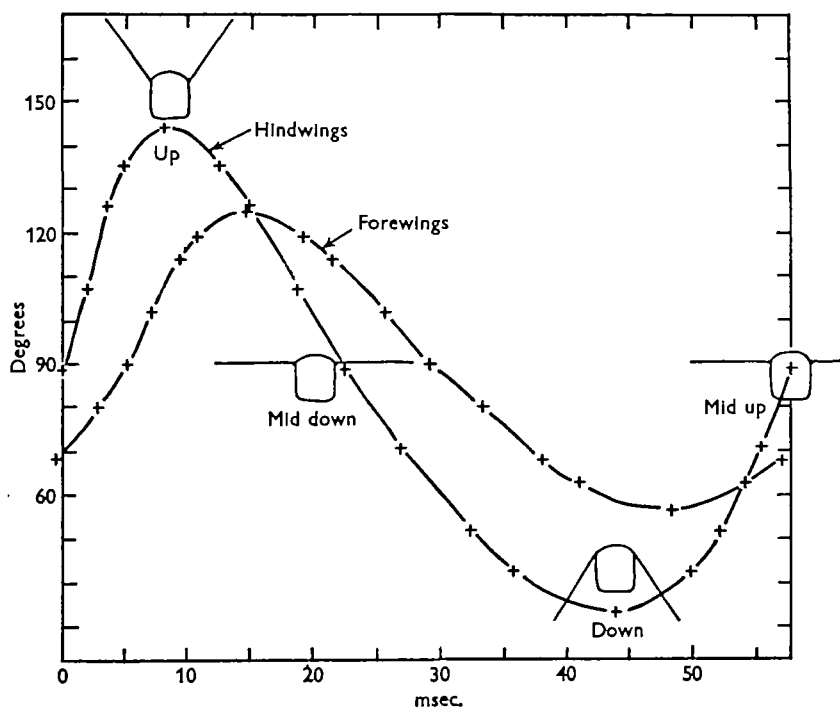

Fig. 1. Angular movements of the long wing-axes in the stroke planes during steady-state flight of an average-sized desert locust. The period corresponds to 100 % lift (standard flight). Redrawn from Weis-Fogh (1956a).

and because of the geometrical similarity between desert locusts, the performances of individuals can be compared with those of full migrants in nature. The other flight parameters can be treated in a similar manner.

The thrust is not measured as such but expressed in terms of the horizontal air speed or *flying speed* at which the extra-to-wing drag balances the average thrust. The drag depends on the posture and increases if the legs are not drawn up or the abdomen not kept straight. In complete *flight posture* (Fig. 2c), the speed is independent of size and sex and, according to Weis-Fogh (1956a, b), it depends only on L_r and on the *body angle*, i.e. the angle between the horizontal wind and the plane underside of the pterothorax. The body angle corresponds to the angle of pitch of a fixed-wing aeroplane but the functional relationship between angle and performance is different, hence the different name.

Wings relative to body. It simplifies analysis that the wing movements of steadily flying desert locusts are independent of variations in ambient temperature from 25° to 35°C. in spite of the fact that the muscle temperature varies by 10°C. The two pairs of wings both participate and are coupled but out of phase due to an interseg- mental *delay* which normally amounts to about 7 msec. at UP positions and about 4 msec. at DOWN positions, the hindwings being the leading pair (Fig. 1).

The coupled wings oscillate with the common period t. This period is surprisingly constant, which in part must be due to the strong elastic construction of the ptero- thorax (Weis-Fogh, 1959, 1961). During steady-state flight in complete flight posture the period depends on size and lift (Weis-Fogh, 1956a):

$$t = \frac{6 \times 10^4 \, l^{2/3}}{3 \cdot 30 L_r + 2190} \text{ msec., s.d. } 4 \cdot 5 \%.$$

If, for instance, a locust of average size lifts 70 % of its basic weight $t = 60$ msec. (s.d. 3 msec.) and at 140 % of lift $t = 55$ msec. (s.d. 3 msec.). This is but a small variation for a complex biological system. During non-steady performances, on the other hand, the period may vary from 50 to 75 msec.

The wings do not oscillate in a plane but the deviations (cf. broken curves in Fig. 2) are too small to be aerodynamically meaningful (Martin Jensen, 1956) so that a stroke plane, inclined about 30° to the vertical, can be defined in both pairs of wings. The stroke-plane angle varies with the body angle and is therefore not an independent parameter. In all essentials we are dealing with a two-dimensional movement of the long axis of the wings. During steady-state flight the angular movements of this axis in the stroke plane follow an almost constant pattern which is independent of tem- perature, lift, size, etc., as is seen from Fig. 1. The arms of the markings denote standard errors of the mean from 21 steady-state flights in which the volume indices ranged from 33 to 86 cm.[3] and the relative lift from 65 to 150 %. Again, non-steady performances are characterized by increased scatter particularly in the forewings while the hindwings are moved in almost the same manner throughout. The co- ordination seems more fixed and rigid than ordinarily found in animals both within a segment and when the two segments are compared. The major part of this co- ordination must have a neurological basis although there is some mechanical coupling between the segments (Weis-Fogh, unpublished).

Wing twisting. Each wing acts as an aerofoil. The wind forces are consistent with steady-state aerodynamics throughout the stroke cycle (Martin Jensen, 1956). Accord- ing to this the prerequisite for flapping flight is a sequence of wing twisting so that each cross-section of the wing hits the air almost edgewise during the entire cycle and so that the *angle of attack* is small and positive during the downstroke and almost zero during the upstroke (Fig. 2). This is accomplished by controlled twistings, the wing being *pronated* (leading edge held downwards) during the downstroke and *supinated* during the upstroke (leading edge held upwards). The directions and magnitudes of the resulting force are indicated on the figure. It is seen that lift and thrust are produced mainly during the downstroke, being maximal at MID DOWN, and that less lift and a negative thrust prevail during the upstroke. In fact, it was found that a locust in steady flight adjusts the wind forces to its demands mainly by adjusting the twisting, which determines the angles of attack, and not by altering frequency, stro

angles or stroke-plane angles to any appreciable extent (Weis-Fogh, 1956a). This simplifies the analysis greatly.

Fig. 2 also shows that the twisting of the slightly cambered wing is not entirely simple. At MID DOWN of the forewing, for instance, a rear flap is lowered, and the same flap is bent upwards during the major part of the upstroke so that the profile assumes the shape of the letter Z; this reduces lift *and* drag (Martin Jensen, 1956). In the hindwings the flap is present as the big vannal area which is also moulded directly by the wind. In both wing pairs, however, the operation of the rear part seems to be automatic and not under direct muscular control. Similarly, the supination during the
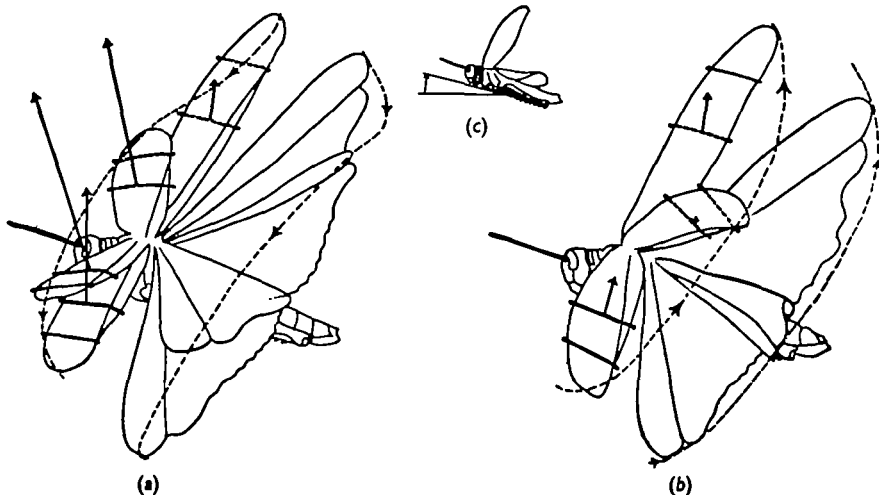

Fig. 2. Four wing positions during the downstroke (a) and three during the upstroke (b) of a steadily flying desert locust. The markings on the forewings show the pronation in (a) and the supination in (b). The broken curves illustrate the paths of the wing tips and the heavy arrows indicate the total wind forces acting on the forewings. (c) Complete flight posture with drawn-up legs; the body angle is indicated. From stroboscopic slow motion film.

upstroke is caused by passive-elastic forces. The upstroke muscles therefore act as *simple elevators* with no supination control. The pronation, however, is controlled by three muscles: the two basalar muscles which act partly against passive-elastic forces and partly against the supinating subalar muscle. All three muscles are also powerful downstroke muscles and constitute the *controller-depressors* of the wing. The large dorsal longitudinal muscle has no effect upon twisting and is a *simple depressor*. The main adjustment between wing and air therefore resides in only three muscles, one of which is probably of little effect (see later), leaving only three motor units per wing in charge of the main control of flight (Table 1).

As to timing, the supination always starts at DOWN and the pronation of the fore-wings at UP, but pronation of the hindwings may be somewhat delayed. At normal lift it does not become distinct until 8–10 msec. after UP, at low lift 10–12 msec. and at high lift about 5 msec. after top position (from unpublished slow motion films).

Control of lift. During prolonged steady-state flights a forced change of body angle (pitch) within the range 0°–15° was found not to influence the lift which was kept constant by the animal. An indirect analysis showed that this must be due to an

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active control of the twist during the downstroke so that a forced change in angles of attack is counteracted by a compensatory change in wing twisting (Weis-Fogh, 1956*b*). It was assumed that both pairs of wings took part in this *constant-lift reaction* but no direct proof was offered. By means of the present technique we could directly observe and photograph such compensatory changes in twisting of the forewings but, so far, we have no similar evidence for the hindwings (Pl. 1, fig. 3).

The constant-lift reaction and the small number of motor units involved offer an opportunity to study the neurological basis of the major control system in flying locusts, but the task is difficult since the animals must fly steadily, undisturbed, and in complete flight posture, for extended periods of time.

Table 1. *The principal flight muscles*

			Anatomical numbering in thoracic segments II and III according to			
			Snodgrass (1929)		Misra (1950)	
Name of muscle	Action on wing	Number of motor units	II;	III	II;	III
First basalar	Depressor and major pronator	1	97;	127	91;	118+119 I
Second basalar	Depressor and auxiliary pronator	2	98;	128	92;	119 II
Subalar	Depressor and supinator	2	99;	129	93;	120
Dorsal longitudinal	Simple depressor	5	81;	112	89;	117
(Mesial dorso-ventral group)	(Simple elevators)	(Unknown but small)	—		—	

(*b*) *Evaluation of performance*

By means of the statistical description of steady-state flight (Weis-Fogh, 1956*a*), it is possible to characterize any performance of an individual relative to a steady-state performance in complete flight posture (normal flight). The 'independent' parameters are the volume index, the body angle and the relative lift chosen by the locust; the normal values of speed, period (frequency), stroke angles, etc., then follow uniquely. If a figure falls within the range given by the standard deviation it is called 'normal', if it differs by between one and two times the standard deviations it is called 'high' or 'low' and if the deviation from the normal exceeds the standard deviation more than two times, it is 'very high' or 'very low'.

If, for instance, the period is found to be 10 % larger than the normal for a locust of that size and lift (S.D. 4·6 %) and the stroke angle of the hindwings is 123° instead of the normal 110° (S.D. 6 %), the period and the angle are both 'very high' in spite of the fact that the deviations are small according to ordinary standards. If the spectrum of flight parameters is normal and the lift equals 100 %, we have *standard flight.*

(*c*) *Flight muscles*

Anatomy and motor units

The numbered muscles in Fig. 4 are all concerned with flight in *Schistocerca gregaria* although some of them have other functions as well. They are numbered according to the study by Snodgrass (1929) on *Dissosteira carolina* with the exceptio
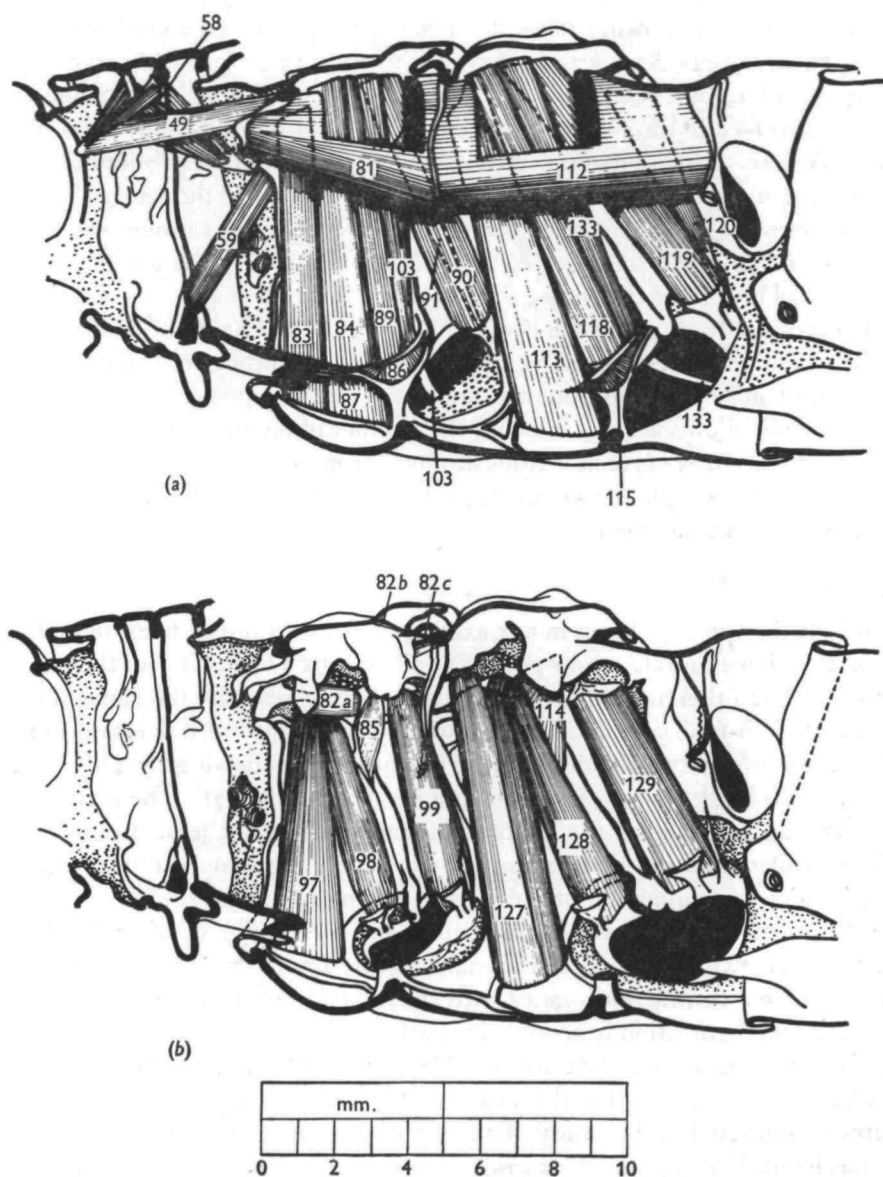
Fig. 4. Dissection of wing muscles and other pterothoracic muscles of importance for flight in *Schistocerca gregaria*, right half of bisected average-sized female, numbered according to Snodgrass (1929) with modifications as to muscle 82a, b and c (see text). (a) Mesial group consisting of dorsal longitudinal depressors (81 and 112) and the dorso-ventral elevators; the pleurosternal muscles (86 and 115) and the muscles moving prothorax relative to pterothorax are also shown. (b) Lateral group of large dorso-ventral controller-depressors, i.e. the pronating basalars (97, 98, 127, 128) and the supinating subalars (99, 129). The tergopleural muscle (82a) and the pleuro-alary muscle (85, 114) can be considered as auxiliary flight muscles while the function of the small 82b and 82c is unknown. Muscles 86, 115 and 82a influence thoracic elasticity and 85 and 114 assist in folding the wings.

that Snodgrass mentions only one small muscle no. 82 whereas Misra's (1950) and our own studies agree in showing three distinct muscles, here numbered 82 a, 82 b and 82 c. The small muscles 82 a, b and c, 85, 114, 86 and 115 are probably all of the slow, tonic type and have not been subjected to electrophysiological studies. Some of them seem to be involved in the control of the elastic recoil of the wings but not to play any decisive role in co-ordination of the movements. Apart from some prothoracic muscles, the remaining numbered muscles are the principal movers of the wings. The dorso-ventral muscles in Fig. 4 a are the elevators which are treated as a group; each morphologically distinct muscle seems to contain as few motor units as are present in the other principal movers of the wings, the longitudinal simple depressors and the dorso-ventral depressors (Fig. 4 b) which control the wing twist. The number of motor units reported in Table 1 was estimated by graded stimulation of the nerve and simultaneous observation of muscle action-potential and mechanical response. In the case of the dorsal longitudinal muscles, 81 and 112, the number of motor axons was also counted on cross-sections of the nerve at various distances from the ganglia (Neville, 1963). No deviation from the simple arrangement in Table 1 and Fig. 24 has been observed in any of the muscles concerned.

Mode of action

A single action-potential in a motor axon to an isolated dorsal longitudinal muscle gives rise to a single muscle action-potential followed by a fast twitch of the innervated motor unit. The other main flight muscles appear to react in the same way. This elementary twitch-type activity is often found during flight but it is also common for individual motor units to fire doubly, the second firing following by 4–8 msec. after the first, as seen in Pl. 1, fig. 5, from the first basalar muscle (97). The second muscle action-potential falls within the relative refractory period (at least 20 msec.) and is therefore smaller than the first by an amount depending upon the interval. There is no facilitation or summation of the muscle action-potentials.

The double firing was shown to result in an increase in degree of contraction over that of the single twitch, that is, there is mechanical summation. The magnitude of the doubly stimulated contractions varies with the interval between the action-potentials so that continuous gradation is possible in single units during very brief contractions.

The following quantitive data are provided by Neville & Weis-Fogh (1963). The contraction starts 1 msec. after the peak of the action-potential at all thoracic temperatures encountered in this study. Under the same conditions, the duration of the entire mechanical change is 27–35 msec. in singly fired contractions. When two or three nerve and muscle action-potentials follow closely after each other as in flight the total mechanical response is prolonged by the time interval between the first and last firing. Under these conditions the mechanical response resembles a smooth twitch, the peak tension of which is about 50 % larger than in singly fired twitches. Hence the double firing results in greater power but without greatly prolonging the contraction into the antagonistic phase of the wingstroke under the present conditions for steady-state flight. It is characteristic that prolonged repetitive stimulation of the nerve at wingstroke frequency results in trains of identical muscle action-potentials and identical well-separated contractions whether or not the stimulation takes the form of single stimuli or of doublets or triplets having the temporal characteristics of those identified in flight.

Locusts

Adult *Schistocerca gregaria*, Forskål, *phasis gregaria* were bred at the Anti-Locust Research Centre, London, sent by plane to Copenhagen and used 2–4 weeks after the final moult when skeleton and muscles are fully developed but the animals are barely sexually mature. They were fed on wheat sprouts and bran and kept at 30°–35° C. during daytime and 25° C. during the night (cf. Hunter-Jones, 1961). One day before the experiment the animal was induced to autotomize its hind legs in order to facilitate arrangement of the electrodes.

Operation

A brief blast of CO_2 immobilized the locust for about 1 min., during which the mesothoracic legs were removed near to the proximal end of the femur and the wounds sealed with wax (a mixture in the proportion of 10 g. beeswax + 4·5 g. resin). It appeared fully recovered after 5 min. and was not subjected to further anaesthesia. After the animal had been affixed to the suspension rod, wax was placed at appropriate places of the cuticle, small holes were pierced by a cold thin needle, electrodes were inserted without bleeding and firmly fixed by the wax which also sealed the wounds.

Electrodes

Monopolar extracellular intramuscular electrodes of 0·1 mm. diameter platinum or platinum-iridium (10%) were soldered to 10 cm. long 0·05 mm. lacquer-insulated copper wire and insulated by cellulose lacquer. Just before insertion the tips were cut to break insulation. Up to four 'hot' electrodes were inserted as centrally into the appropriate muscles as possible (*post mortem* checks were made) and a common neutral electrode was placed ventro-laterally in the anterior part of the abdomen parallel to the nerve cord. The latter electrode was always silent at the gains used here; the spike potentials of the muscles range from one to a few millivolts.

Apparatus

Figs. 6 and 7 and legends illustrate the main techniques. The animal was suspended from an aerodynamic balance (Weis-Fogh, 1956a) in a dark room with controlled temperature (28° C.) and humidity (55%). During steady flight its thoracic temperature would then vary between 32° (low lift), 34°–35° (normal lift) and up to 40° C. (very high lift).

The electrical activity was amplified (Tektronix Type 122 preamplifiers, with low and high filters set for half-amplitude attenuation at 80 and 1000 cycles respectively) and displayed on a Tektronix 502 double-beam oscilloscope. The unblanking pulse was inverted and fed to a General Radio Strobotac by way of a variable delay circuit. The intensity of the stroboscope flashes could be increased for photography by means of a General Radio Strobolume. By this method any selected action-potential could trigger the oscilloscope and after a predetermined delay trigger the flash so that the electrical activity could be accurately correlated with any wing movements.

The locust wings were also illuminated from behind by constant green light in ▶der to photograph the wing-tip path with the flash picture superimposed. The wing

twisting makes it possible from a single photograph to determine where in the stroke
the flash occurred (and therefore the action-potential). In some experiments, the
manually controlled stroboscope triggered the oscilloscope for the purpose of similar
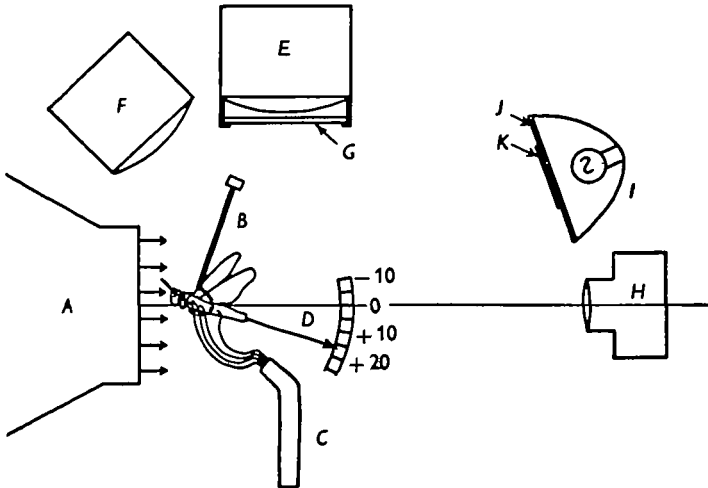observation.

Fig. 6. The locust is suspended in front of the open-jet wind tunnel (A) from a streamlined
rod (B) fastened to the aerodynamic balance. The thin flexible electrode wires lead to a
shielded stand (C) and from there to the preamplifiers. (D) measures the body angle. (E) is a
low-intensity stroboscope with high-intensity extension lamp (F) and a red filter (G). (H) is a
camera for flash exposures and wing-tip excursions illuminated by the paraboloid projector (I)
with green filter ($\mathcal{J}$) and a dark central mask (K).
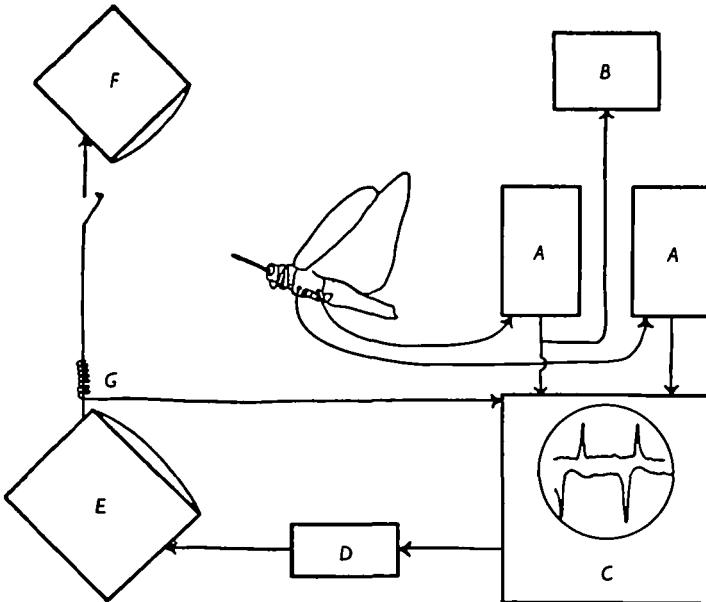
Fig. 7. Block diagram of recording and illumination arrangement. (A) preamplifiers, (B) loud-
speaker amplifier, (C) cathode-ray oscillograph, (D) variable delay circuit, (E) stroboscope,
(F) high-intensity flash lamp, and (G) connector for flash lamp artifact.

Since two pairs of legs were removed and therefore the flight posture could not be checked, it was particularly important to evaluate the performance in terms of the normal spectrum of stroke parameters.

RESULTS

(a) Analytical procedure

The primary information on the timing of activity of the various muscles with respect to the mechanical cycle was gathered from records of the type shown in Pl. 1, figs. 8, 9 and 10. In Fig. 8 the light flash which illuminated the animal occurred at the beginning of the oscilloscope sweep and activity at the electrodes during the next few cycles is recorded on superimposed sweeps. The aerodynamic and mechanical parameters measured show this to be almost standard flight. The second basalar muscle of the hindwings fires a single time just after the top of the stroke. It cannot begin the pronation of the wing. The subalar muscle of the same wing fires singly, or more often doubly, beginning its electrical activity just before the top of the stroke. It does not produce the supination during the upstroke.

The activity of the mesothoracic dorsal longitudinal muscle (forewing) is compared to that of the metathoracic subalar muscle (hindwing) in Fig. 9. The muscle action-potential of the latter triggers the oscilloscope sweep and the photographic flash lamp. The full stroke of the wings is indicated by exposing the picture of the animal for 10–20 sec. in dim light just prior to the flash and electronic recording. Small spots of white paint emphasize the wing tips. The performance of the animal is unusually powerful, that is, if the animal were in free flight it would climb. However, the wing-stroke amplitudes are not greater than usual even though the frequency is 'very high'. This can be attributed to the fact that powerful downstroke muscles are firing during the late part of the upstroke and therefore braking that movement and reversing the direction of the wings. The elevators may act similarly during downstroke. The result is normal stroke angles but a higher than usual frequency (or reduced period). The hindwing subalar muscle fires twice regularly, beginning a few milliseconds before the top of the stroke. The size of its action-potential is quite constant, indicating no changes in number or relative timing of the active units. The mesothoracic dorsal longitudinal muscle also fires twice and very early compared to the position of its wing. Its mechanical action must occur during the last third of the upstroke as well as during downstroke. The amplitude of the action-potential from this multiunit muscle is not constant. There is either a change in number of active units or changing degree of synchrony between them.

Fig. 10 shows increased stroke angles at low performance. The frequency is low and presumably the muscles are not actively braking the wings. Even at this low level of performance the mesothoracic first basalar muscle fires doubly. Two flashes are timed just before and just during the small potentials occurring midway between the large ones. These small potentials are interpreted as representing the elevator muscles which are then firing just before the bottom of the wingstroke. Similar potentials show up in many of the records. When the electrode placement is accurate within a downstroke muscle and the insulation good the elevator potentials have only a small fraction of the amplitude of the main potentials at that electrode.

Even with electrodes known to be placed within the bodies of specific muscles having known numbers of units there is some difficulty in interpreting how many units are firing and how often. Long continuous records illustrate such points better, and though they do not give information about the timing of electrical activity relative to the mechanical cycle we will present them for all other purposes. Figs. 11, 12 and 13 are chosen to demonstrate how we interpret the records as to numbers of units and repetitive firings.

Fig. 11. Second basalar muscle of forewing firing twice per wing beat (double firing).

Fig. 12. The two units of the subalar muscle of the forewing. (a) Each firing once per cycle. (b) One unit firing once or twice, the other sporadic. Numbering of units and of firings can be estimated with certainty.

Fig. 11 shows the second basalar muscle of the mesothorax firing once (single firing) or twice (double firing) per wing cycle. Only one of the two units was active. The size of the first spike is fairly steady but the second firing varies greatly although it always occurs less than 10 msec. after the first. The size of the second potential is a function of the interval between first and second, the greater the interval the larger the second response, as in Fig. 5.

Fig. 12a shows a muscle, the subalar muscle of the forewings, in which both of its two units were active, each unit firing a single time. The sizes of the individual spikes do not depend upon their relative timing. The two summate when they overlap in time rather than show the refractoriness of a second firing of a single unit.

Two units with one firing doubly can be seen in Fig. 12b, which is also from the mesothoracic subalar muscle. The largest spike is very labile and its amplitude does not depend upon its timing. The smaller regular unit fires once or twice and the second firing is always smaller than the first.

Records from the dorsal longitudinal muscles may show amplitudes changing in many steps (Fig. 13a, b). The largest potentials must represent at least three units, but an exact count is impossible. Differences in activity can be estimated only in a qualitative way and if the other muscles of the flight system had comparably large numbers of units the analysis would be impracticable.

The preceding indicates that it should be possible to give an almost complete description of the kind we want. To date we have completed about 30 experiments documented by hundreds of individual records, mostly of the kind that give timing data. The bulk of the available data is on the downstroke muscles, and especially the wing-twist controlling muscles. In the next sections we present an outline of how these muscles are used during normal flight and during high- and low-lift performance, and give the first direct information on how the degree of twist of the forewing is controlled.
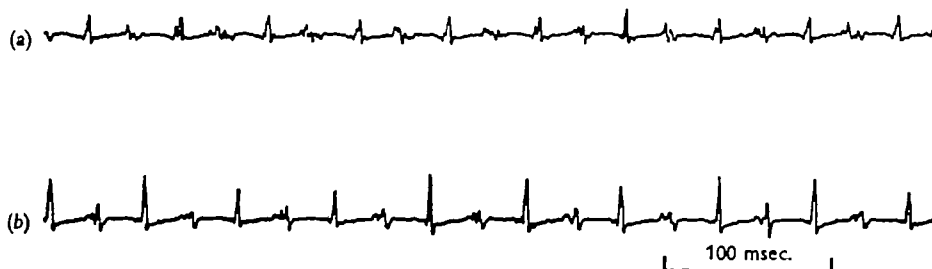
Fig. 13. Record from the 5-unit dorsal longitudinal muscle of the hindwing. Number of active units cannot be estimated accurately from such records. (*a*) and (*b*) are two samples from the same experiment.

(*b*) Metathorax; hindwings

It is convenient to begin the description with the hindwing muscles because the variability in the pattern of their use during flight is very small (cf. Fig. 24). The pattern in the homologous set in the mesothorax is basically similar but slightly later in time and more variable in details.

The metathoracic subalar muscle has been used as a common reference for several comparisons because it is the most constantly active muscle and the easiest muscle from which to get a noiseless electrical record. It is just under the cuticle so the electrode does not pass through other muscles, and positioning within the body of the muscle is not difficult. Only rarely is this muscle silent during wing flapping, and then only when the performance is below the ordinary range. During standard flight it usually fires so that the peak potential occurs about 2 msec. before the wings are UP and the muscle therefore assists in braking this movement. Both units are ordinarily active; only as flight stops can they be separated.

Activities in metathoracic dorsal longitudinal and subalar muscles during periods of normal lift are shown in Fig. 14*b*. Both muscles undergo single twitches. Elevator activity is rather spread in time. At high lift (Fig. 14*a*) there is greater activity in the dorsal longitudinal muscle and it sometimes fires doubly, and the subalar muscle always fires doubly. The elevator activity is also increased (arrows). At low lift (Fig. 14*c*) fewer units fire, there is no double firing and the subalar muscle misses on some cycles. The two muscles start almost synchronously at normal and high lifts but the dorsal longitudinal lags somewhat as its activity declines at low lift.

The first basalar and subalar muscles of the metathorax are often synchronous under a variety of flight conditions (Fig. 15) although the delayed pronation of the hindwings indicates that the basalar muscle may lag by several milliseconds. At very high lift
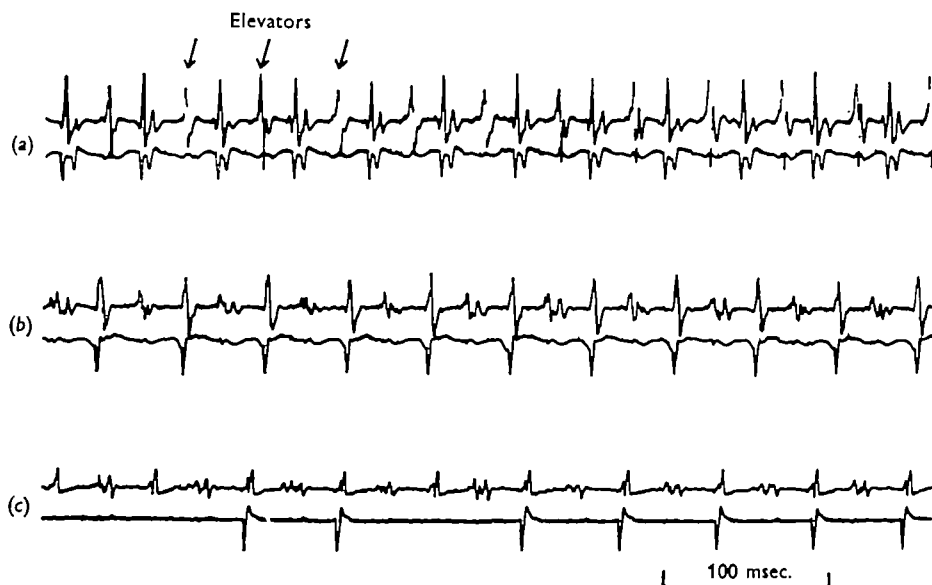
Fig. 14. The main downstroke power-muscles of the hindwings during strong, normal, and weak flights. Upper trace represents dorsal longitudinal muscle (and some elevators, indicated by arrows). Lower trace is from subalar muscle. (a) Relative lift = 141 %, frequency is 'very high', velocity is 'high'. (b) Relative lift = 93 %, frequency is 'very high', velocity is 'high'. (c) Relative lift = 66 %, frequency and velocity are 'normal'. For definition of 'very high', 'high' and 'normal' see p. 648.
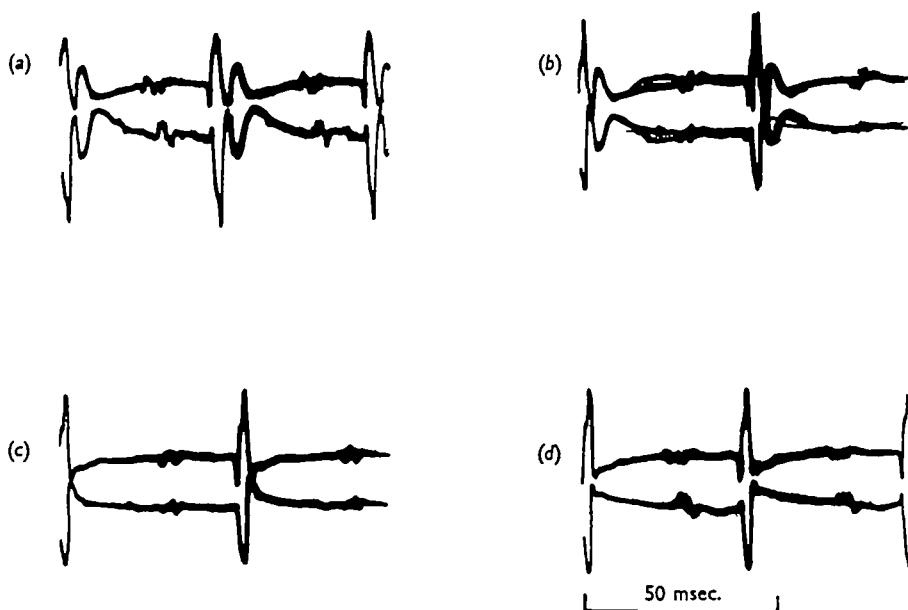

Fig. 15. Activities of the metathoracic first basalar and subalar muscles vary together with changes in lift but do not seem to vary with changes in body angle. Upper traces are from first basalar muscle, lower from subalar muscle. (a) Relative lift = 189 %, body angle = 5°. (b) Relative lift = 154 %, body angle = 5°. (c) Relative lift = 104 %, body angle = 5°. (d) Relative lift = 100 %, body angle = 15°.

both muscles are activated twice per cycle (Fig. 15*a*). At moderately high lift the second firing sometimes misses (Fig. 15*b*). At normal lift both muscles fire a single time both at low body angle (Fig. 15*c*) and at high body angle (Fig. 15*d*). The elevators underlying these two muscles are not synchronous but show a temporal spread of several milliseconds. The hindwing first basalar and subalar muscles seem to go together and do not show a nervously controlled antagonism which might adjust the wing twist when the body angle is changed. Changes in their activity correlate rather with changes in power output and the two muscles behave almost similarly. More work is needed to clarify this point. The metathoracic second basalar muscle likewise fires doubly at very high lift (Fig. 16*a*) and singly at moderate lift (Fig. 16*b*, *c*). It is slightly later than the subalar muscle. In Fig. 16*b* both units can be identified.
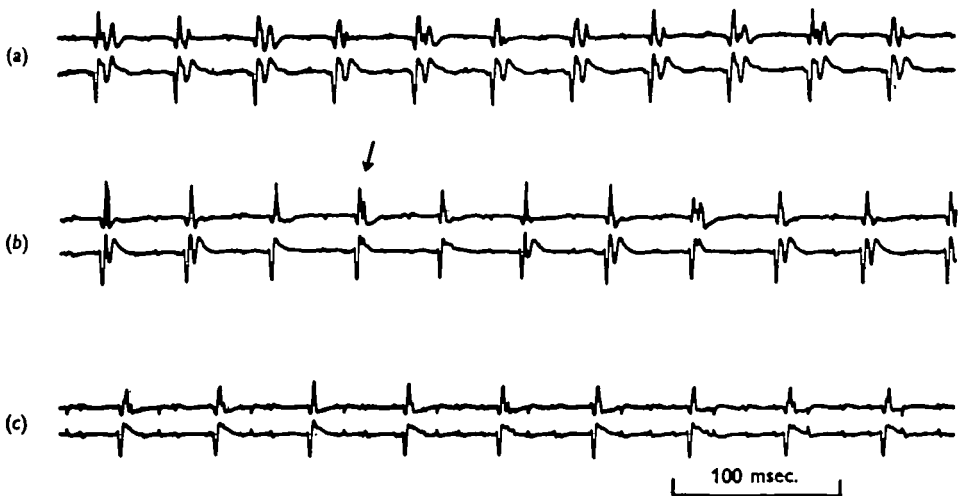

Fig. 16. Activity of the metathoracic second basalar muscle also varies with total flight power. Lower trace shows activity in metathoracic subalar muscle. (*a*) Relative lift = 219 %. (*b*) Relative lift = 117 %, both units discernible (arrow). (*c*) Relative lift = 96 %. Frequency and velocity 'normal' throughout.

They become asynchronous at medium and low lifts. Activity in this muscle also varies with power production of the whole flight system but not noticeably with changes in the body angle at constant lift.

In summary the metathoracic flight muscles operate in a quite constant pattern in which the main variable is that of total power output, which is correlated with the number of units operating and the number of times that each is active during each cycle. This fits with the observation that the movements of the hindwings vary little except for the changes in frequency. Within each period the onset of activity of the various downstroke muscles follows an almost constant pattern. The number of active units in each muscle and the amount of repetitive firing increase with lift in the same way in all the muscles. During standard flight the muscles are fired mostly once per cycle, but may be near the threshold for repetitive action (cf. Fig. 24). The first basalar and the subalar muscle are nearly always active. Normal wing movements probably could not occur otherwise. The first basalar muscle is necessary for a substantial pronation. The subalar, in addition to producing downstroke power, probably is

needed to mould the vannal area of the wing into the proper contour. The dorsal longitudinal muscle and the second basalar muscle may be inactive at very low levels of performance. All of the downstroke muscles can become mechanically active before the top of the wingstroke during powerful flight when the period of the wing-beat cycle is short. Under these conditions the muscles do negative work in braking the movement by absorbing kinetic energy and some of the muscles always do this at normal lift. The two basalar muscles and the subalar muscle do not seem to show an antagonism which could explain the constant-lift reaction. It may therefore not have a neurological basis in this segment.

(c) Mesothorax; forewings

The gross pattern of motor output to the flight muscles of the forewings resembles that of the hindwings except that most homologous parts begin activity 5–10 msec. later.

This latency corresponds to the phase difference between the two pairs of wings. However, this does not apply to the dorsal longitudinal muscle (see p. 660).

The two subalar muscles of one side are compared in Fig. 17. At an ordinary lift value and near to the preferred body angle the mesothoracic subalar muscle fires a single time 2–8 msec. after UP (cf. Fig. 24). Under similar conditions the mesothoracic first basalar muscle fires twice (Fig. 18) and starts 1–2 msec. before UP. In fact the majority of records show that this single-unit muscle always fires close to UP and is generally activated twice per cycle even during moderate performance. In contrast to the metathorax, the subalar muscle of the forewings is very labile, as would be expected from a twist-controlling muscle.

The second basalar muscle of the mesothorax is also a labile muscle which, though it does cause some pronation, does not seem to be primarily involved in the control of wing twist. On the other hand, it is more or less active at any one body angle and lift, depending mainly on the wingstroke frequency. At high frequencies it fires twice and at low frequencies may be totally silent (Fig. 19). The subalar muscle does not change with changing period (same figure). During some experiments the second basalar muscle did vary with body angle, but several other flight parameters changed as well; these were not steady-state flights.

As already mentioned, the first basalar muscle fires doubly under most conditions. It is compared in detail with the labile subalar muscle of the mesothorax in Fig. 20a, d. At moderate lift and low body angle one unit of the subalar fires once per cycle (a). At high angle it is silent (b). At somewhat higher lift and high body angle one unit fires once per cycle again (d). At the higher lift but low body angle the one unit often fires twice and a second unit is recruited (c). Within this normal range of flight performance the mesothoracic subalar muscle is more active at low body angles than high while the other muscles are affected little or not at all by changing body angle. The effect of its changing activity is to supinate the wing more (increase angle of attack) when body angle is decreased and thus counteract the decreased angle of attack which would occur if the wing had a fixed posture with respect to the body. This control of angle of attack while body angle is changed of course has limitations. One of these is illustrated in Fig. 21. As body angle is lowered excessively just before the forewings begin to flutter rather than flap and before the lift decreases markedly

the subalar muscle begins to fire erratically and all through the wingstroke. The second basalar muscle is here almost silent and the wing excursions must be produced by other muscles including the elevators. Since the frequency is 'high' the first basalar and dorsal longitudinal muscles are presumably fully active. This is clearly a situation
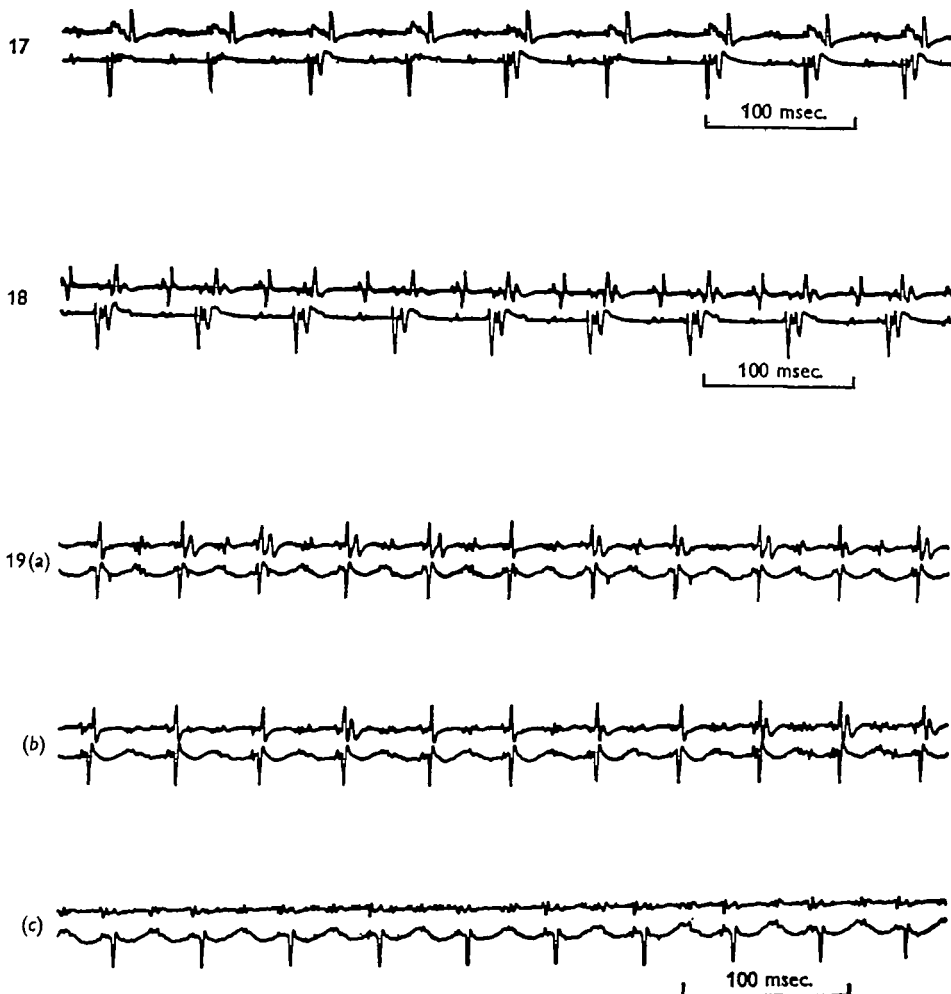

Fig. 17. Time difference between the subalar muscles of the two segments during standard flight. Upper trace mesothorax. Lower trace metathorax.

Fig. 18. First basalar muscle and an elevator muscle of mesothorax (upper trace) compared to the metathoracic subalar muscle. Standard flight except for 'large' forewing excursion.

Fig. 19. At constant lift (relative lift = 108%) activity of the mesothoracic second basalar muscle (upper traces) is correlated with wingstroke frequency. (a) Frequency is 'very high'. (b) Frequency is 'high'. (c) Frequency is 'normal'. Lower traces are from the mesothoracic subalar muscle which does not vary under these conditions.

on the limit of the ability to control. No further supination could be produced. The body angle at which this erratic firing of the subalar muscle occurs is the same as that below which flight normally ceases (Weis-Fogh, 1956a). The major part of the twist control therefore resides with the two motor units of the subalar muscle.

The dorsal longitudinal muscle of the forewings, although a simple downstroke power muscle, is also more variable in function than its posterior homologue. At very high lift all 5(?) units fire synchronously and doubly during each cycle and when the frequency is high, they fire very early during the wing upstroke (cf. Fig. 9). The action may begin at the same time as the metathoracic muscles (Fig. 22) and even contribute
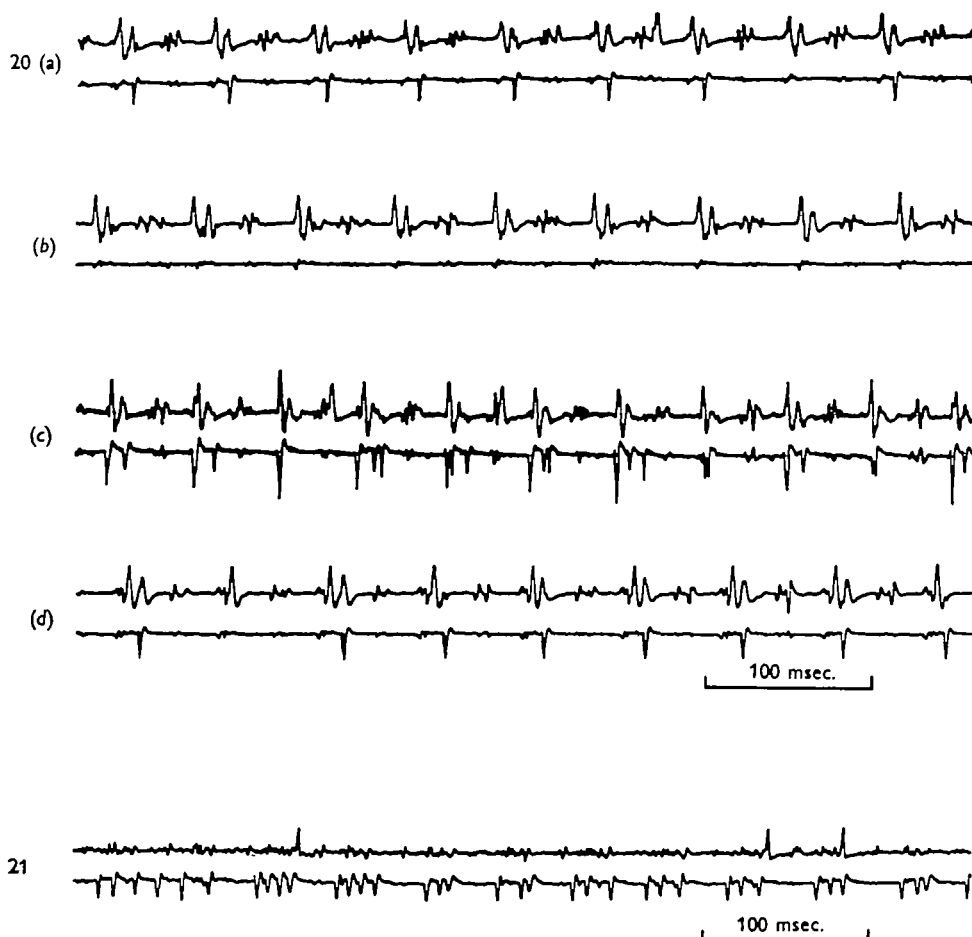

Fig. 20. Control of wing twist by the mesothoracic subalar muscle (lower traces). Upper traces show the first basalar muscle of the same segment. (a) Relative lift = 92 %, body angle = 4°; (b) relative lift = 96 %, body angle = 15°; (c) relative lift = 115 %, body angle = 0°; (d) relative lift = 115 %, body angle = 15°. In (a) and (b) the flight parameters are 'normal' except for 'large' wing excursions. In (c) frequency is 'very high'. In (d) frequency is 'low' and forewing stroke amplitude is 'very large'.

Fig. 21. Erratic firing of the mesothoracic subalar muscle (lower trace) at normal lift but just before flight stops due to low body angle. Upper trace is of the second mesothoracic basalar muscle. Relative lift = 117 %, body angle = 0°. Frequency is 'high' but forewing excursion is 'normal'.

to braking the hindwings by virtue of the mechanical coupling between the segmental nota. At medium lift the mesothoracic dorsal longitudinal muscle begins activity early but its units are not synchronous and without firing twice the muscle has effect over

longer time span than most others. A part of its action is to brake the wings but it continues to supply power during most of the downstroke (see Fig. 23 *a*). At low and normal lift the *main* activity of this muscle lags by the usual segmental time difference (Fig. 23 *b*) but some of its units are the earliest to become active in the mesothorax (Fig. 24).

In summary the mesothoracic flight muscles follow a pattern like that in the meta-thorax but with some detailed modifications which (1) limit and control the excursions of the forewings to a greater extent than is found in the hindwings, and (2) provide a neurological control of the wing twist. The first basalar muscle nearly always exhibits double firing. Each of the other units is not stimulated by more than a single impulse

22

100 msec.

23 (a)

(b)

100 msec.
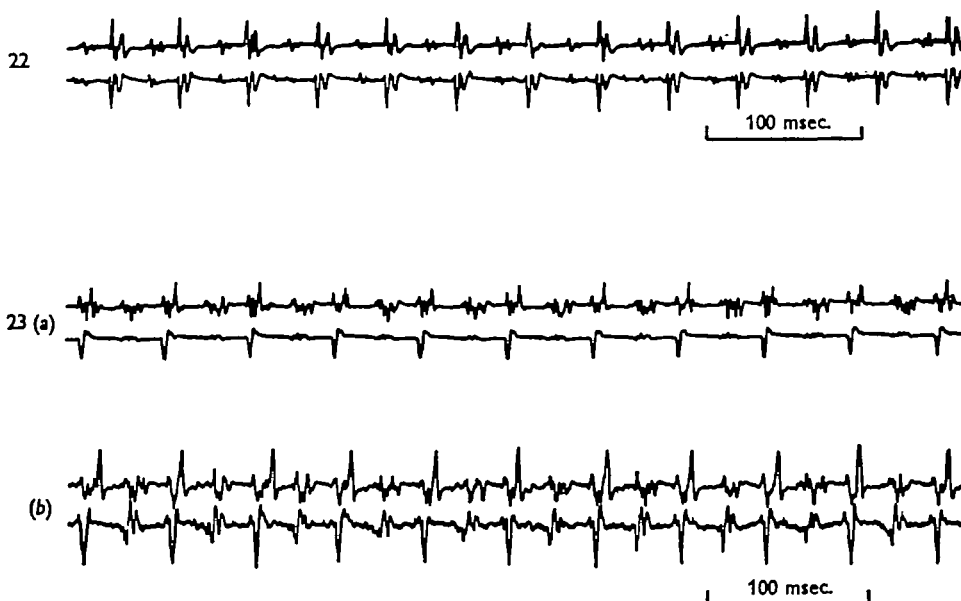
Fig. 22. At high relative lift (185 %) the mesothoracic dorsal longitudinal muscle (upper trace) fires at the same time as the metathoracic subalar muscle (lower trace). All of the units are nearly synchronous and there is double firing.

Fig. 23. At normal (*a*) and subnormal (*b*) lift the mesothoracic dorsal longitudinal muscle (upper traces) begins activity at the same time as the metathoracic ones (lower traces) but its units are not synchronous but are spread out in time. (*a*) and (*b*) are from different experiments. Relative lifts are respectively 100 and 86 %.

during moderate performances. The second basalar muscle is mainly a power muscle whose greatest activity occurs at high wingstroke frequencies. The dorsal longitudinal muscle has a rather wide temporal spread in activity due to either multiple firing or asynchrony of its units and it usually decreases the stroke angle by braking the wings during the last third of the upstroke. The stroke angle is abnormally large when this muscle does not fire early.

The subalar muscle increases activity as body angle is diminished, thus effecting a control of the wing twist counteracting that imposed by change in body orientation. This explains at least part of the constant-lift reaction. Unlike the metathoracic ▶ubalar muscle the mesothoracic one usually has only one unit active and there is a

reserve available for recruitment when greater supination is needed. When this muscle does not vary with changes in body angle the lift changes in the direction expected for a fixed-wing system.

At very low lift and high body angle any of the mesothoracic downstroke muscles except the first basalar muscle may be inactive. The wing may return from elevation because of elastic forces, but an active pronation is necessary if the movements are going to result in flight.

(d) The elevator muscles

In addition to the information about the elevators gained as a by-product of recordings from the depressor muscles, a few observations have been made with electrodes placed carefully in the tergosternal muscles of the mesothorax. These muscles may fire doubly during each cycle during high-lift flight. They fire just before the bottom of the wingstroke. In general, the elevators behave like the power depressors but during their appropriate time in the cycle. They may stop the downward movement of the wings as well as produce the upstroke. Their combined activity is spread over several milliseconds even within one segment. There is greater or less total activity depending on whether the lift is great or small. Although the data on these muscles are quite limited there is reason to believe that the principles on which they operate are not different from those found for the depressor muscles.

DISCUSSION

The activity of the motor neurons directly involved in the wing movements takes the form of a distinct pattern. In each segment it can be compared with a musical theme in which each note corresponds to a single action-potential and each potential is located within a definite phase of the movement. In the two segments of the locust the two themes resemble each other but are not identical so that, due to the phase difference, the combined pattern can be compared with a fugue. During standard flight the timing of individual potentials varies but little relative to each other or to the wing movements (Fig. 24), the only labile group being the two units of the subalar muscle of the forewings. This muscle controls the wing twist and thereby the lift. Such a control is essential even in level flight because of changes in body angle and, on the output side, one cannot imagine that it could be accomplished in a more simple way.

The main result of the analysis is the demonstration that the complex locomotory rhythm is based upon a complex but distinct, analysable and slightly variable pattern of single action-potentials. The establishment of the fundamental theme in the central nervous system, the control mechanisms which determine its rate of repetition (frequency), and the sensory inflow which modifies details, should now be open to direct analysis in the future. A few points, however, can be discussed on the basis of present evidence.

(a) Graduation of action

The flight is powered by rather few motor units of the fast type, that is, the muscle action-potentials are non-facilitating and non-summating but show a relative refractoriness lasting about 20 msec. at flight temperatures. There are some slow muscles involved in flight, for example the tergopleural and sternopleural muscles which he

to determine the elasticity of the thoracic box. It is possible that there are as yet undetected slow fibres innervating some of the main flight muscles as well. But the control measures we have sought to elucidate can be explained without postulating any unknown sources of innervation. With a few all-or-nothing elements the locust can produce a finely and continuously graduated control of its wing movements both in regard to the total power output and the amount of wing twisting at different body angles. Since the muscles which control the wing twist are also important depressors
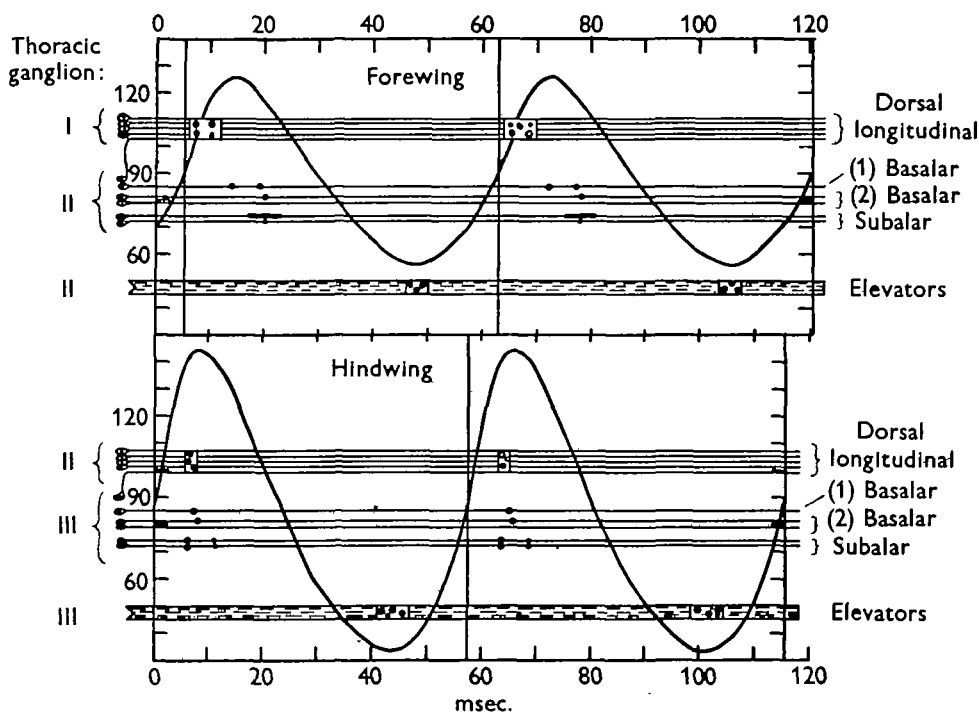
Fig. 24. Angular movements of wings (ordinate in degrees, cf. Fig. 1) in relation to the regularly patterned firing of the motor units during steady-state flight at about 100% of lift and thoracic temperature about 34° C. (standard flight). Each known motor unit is shown by a horizontal line and with its appertaining neuron and thoracic ganglion at the left-hand side (some data from Neville, 1963). ● The peak of the muscle action-potential always occurs within 2–3 msec. of the indicated time (abscissa). ● The potential may or may not be present. The heavy bar indicates that the single firing of the first subalar unit of the forewing fires at some time within this interval. A box with dots indicates firing of some units. The muscle names are given at the right-hand side. Mechanical activity starts 1 msec. after the peak of muscle action-potential.

of the wings, efficiency of operation demands that they exert tension only during certain parts of the cycle, that is for 20–30 msec. at a time, and not over long periods as they would if they were slow-type muscles.

The graduation is achieved in the following ways. A set of units always fires once per wingstroke but a few others may be recruited for extra work. Units of the dorsal longitudinal muscles, the second basalar muscles and the mesothoracic subalar muscles show this phenomenon. It appears also that any individual motor neuron may be more or less excited and therefore reach threshold slightly earlier or later in the cycle and,

if sufficiently excited, it may fire doubly. The second discharge of a motor neuron within one cycle falls within the relatively refractory period of the muscle membrane. Depending upon the interval between the two muscle action-potentials the resulting contraction may vary from a tension value equal to that of the single twitch up to 1·5 or 1·8 times this amount with all possible intermediate values (Neville & Weis-Fogh, 1963). In most cases the second firing was timed so as to give maximum extra work or tension, i.e. 5–7 msec. after the first.

(b) Control of frequency, twist and lift

During high-lift flight (climbing) although greater power is delivered to the wings the amplitude of their movements is no larger than usual. The muscles become active relatively early in the mechanical cycle and damp the wing excursions. The effect of this is to decrease the period (or increase frequency). During part of the stroke the wings, being elastically mounted, have a natural period and operation at the corresponding frequency should be maximally efficient (Weis-Fogh, 1961). An increase in frequency above the value set by the elastic forces can be accomplished only at the expense of greater muscular output, part of which is timed so that it reverses the direction of wing movement before the elastic components (in cuticle, elastic ligaments, and muscles) have absorbed the kinetic energy of the wings. This braking action involves activating the muscles while they are being stretched and work is done upon the muscle (the muscle does negative work). While the negative work may cost little metabolically, the same muscles must do an extra amount of positive work when the wing movement reverses corresponding to the increased frequency and kinetic energy. The total work therefore increases (for discussion see Weis-Fogh, 1961).

The twisting of the wing is accomplished by the combined action of pronating and supinating muscles during the downstroke. In both pairs of wings the supinated position during upstroke is passive, due to the mechanical structure of the system and not to the action of muscles. Pronation is produced primarily by the first basalar muscles. They pull the wing away from the supinated elastic equilibrium position. Since the first basalar muscles have a rather constant activity the amount of pronation would not vary much if no other factors were involved. The subalar muscles counteract the pronating effect of the basalars. Because of their timing they do not produce the upstroke supination but only decrease downstroke pronation. Like the first basalar muscles the subalar muscles of the *hindwings* are also rather constant in activity and may therefore not be effective controllers of the wing twist but mainly provide downstroke power. We have failed to demonstrate a nervous regulation of wing twist in the hindwings during periods when the animal exhibits the constant-lift reaction.

In contrast to this the subalar muscles of the *forewings* are far from constant in action but vary with body angle in a way that decreases pronation when the body angle is low, that is, when the angle of attack of the wing would be low if the wing angle followed the body angle. Within limits this mechanism can hold constant the angle of attack of the wings, and therefore lift, in spite of changing body angle (Fig. 3). We have not determined whether the forewings compensate sufficiently to make up for the apparent lack of compensation of the hindwings, or whether the lack of compensation of the hindwings produces a torque tending to restore the body angle to the normal

value, or whether there might be other compensating mechanisms in the hindwings. These questions will be investigated further.

(c) *Nature of co-ordination*

The fact that one or more muscles act differently depending upon changing aerodynamic conditions such as those associated with changes in body angle implies that sensory information has some reflex effect on the flight motor system. Even animals without supra-oesophageal ganglia can make these adjustments (Weis-Fogh, 1956*b*) and some of the important inflow is probably from the wings and wing hinge. Input from the wings also sets the frequency of the whole wingbeat oscillation (Wilson, 1961) and the main sensory component from frequency setting is probably a single-unit stretch receptor at each wing hinge (Gettrup, 1962). A low-frequency motor output can be elicited by unpatterned input to the thoracic ganglia even when the normal reflex loops have been broken by cutting away all wing sensory structures, but when the wing sense organs are intact they must discharge in a properly phasic way or the motor command pattern deteriorates (Wilson, 1961, and unpublished). They appear to provide not only a general tonic excitatory input but also some definite timing information. The flight system may be thought of in two parts: (1) a central oscillatory pattern with a rather long inherent period in which some of the delays between units may be rather fixed, and (2) a mechanical elastic system with shorter natural period. These two are coupled by nervous reflexes which assure operation at a frequency and according to a detailed pattern appropriate to the load. The need for the central oscillation itself during established flight is not clear, but may be necessary during flight initiation and during adverse external conditions in order that a fully patterned motor command can take place even when there is no ordinary patterned return.

The motor neurons which are part of the flight system fire in an orderly manner with only small changes in timing during flight, and the extremes of variation in flight do not involve really different patterns. However, the same motor neurons may act independently or according to some other pattern than the flight pattern. Several of the muscles attach not only to the wings but also to the legs, and they are sometimes used as leg muscles (see Wilson, 1962). Muscles which are synergists for the wings are antagonists for the legs and vice versa so any couplings which exist between the motor neurons themselves must be quite labile, and not fixed connexions. Still, it is likely that such connexions, or ones between antecedent cells not far removed in a chain of command or hierarchy, are important for establishing the flight pattern. It has been shown already that there is no single *centre* which regulates the firing of the motor neurons but that if pacing centres exist at all there must be many of them (Wilson, 1961). Taken together the results suggest that each motor neuron is itself an integrating cell. Together they are capable of co-ordinated activity because of connexions within the central nervous system but the co-ordination is not obligate. Comparisons between the pattern in the isolated central nervous system and in the intact system may throw light upon the functional organization of the oscillatory system. Co-ordination may be reinforced or modified by reflex effects.

As a model for the study of nervous regulation of locomotion the locust flight system may be the nearest approach to an ideal one. The number of parts makes it relatively

simple to analyse and the mechanisms involved do not appear to be too simple to provide a possible hypothesis about more compound systems nor to deviate in principle from such systems. It is an interesting case in which to investigate the relationship between central and peripheral control of locomotion and a synthetic view of these two seems the likely product. Finally, we can hope to find how numerous potentially independent nerve cells become co-ordinated into a unique repeating pattern of activity.

SUMMARY

1. A brief survey of the locust flight system is presented as background for this and future studies. Included are descriptions of the wing movements, the aerodynamic parameters and the pertinent muscle anatomy and physiology.

2. A procedure has been designed which makes it possible to study a complex locomotory pattern in terms of the activities of single nervous and muscular units, in this case during normal flight of locusts.

3. We have found a detailed repetitive pattern which is precisely correlated with the wing movements. Fig. 24 shows the pattern during normal flight. Variations in the details of the pattern are also correlated with significant variation in the movements.

4. During average flight most of the flight motor units fire a single time per wing stroke. In low-powered flight numerous units are inactive. With increase in power additional units are recruited and active ones may fire twice or more during a specific phase of a single wingstroke.

5. Increase in wingstroke frequency is correlated with increase in number of active units and with earlier onset of activity so that the wing movements are braked at top and bottom by muscular activity as well as by other restoring forces.

6. Lift is controlled by changes in wing twisting which are mainly due to changes in activity of a single two-unit muscle for each wing, the subalar muscle.

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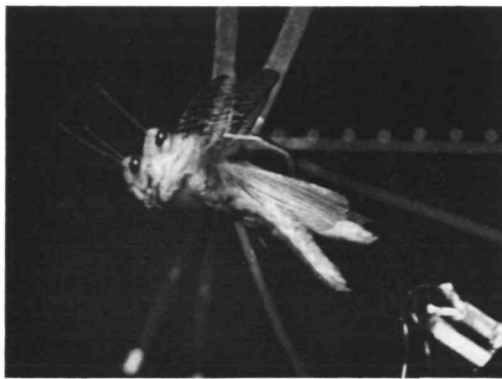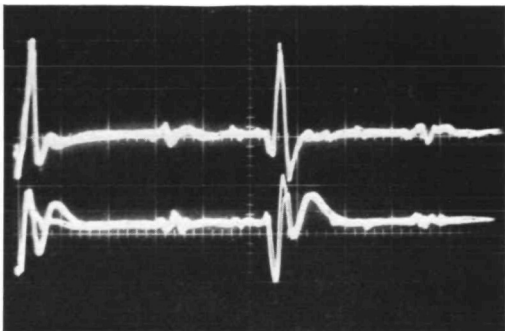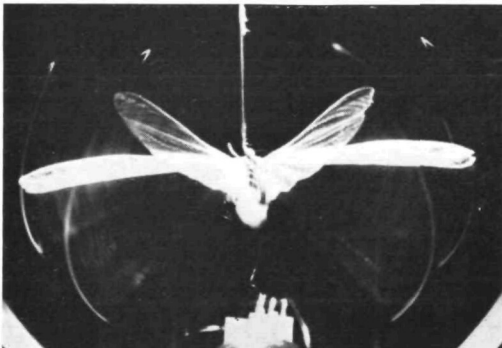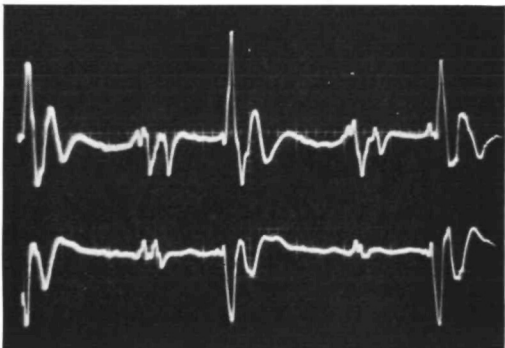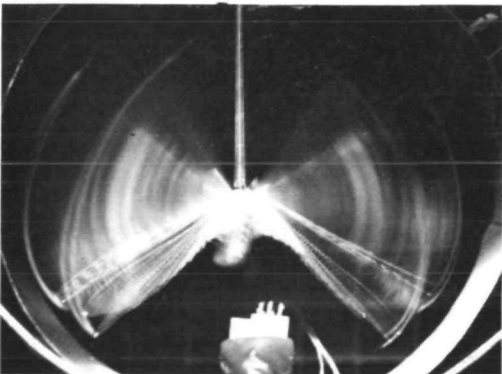
3

5

8 (a)
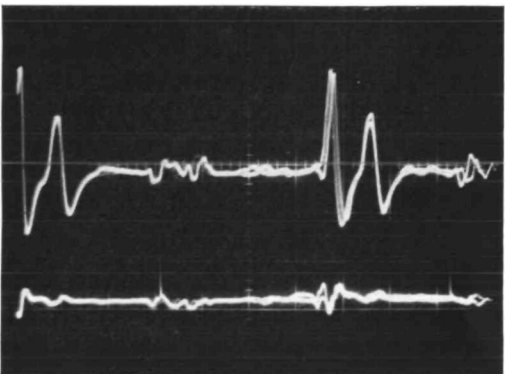

8 (b)

9 (a)

9 (b)

10 (a)

10 (b)

D. M. WILSON AND T. WEIS-FOGH
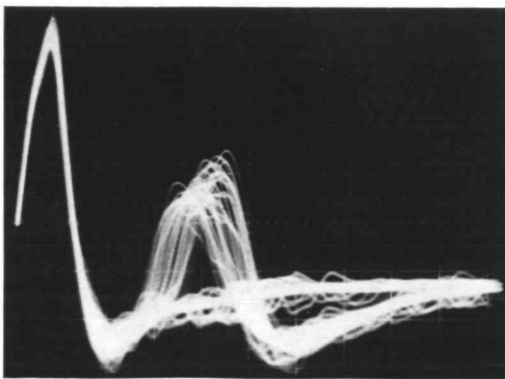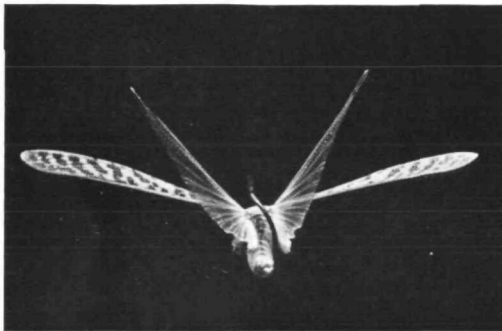
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EXPLANATION OF PLATE

Fig. 3. Steadily flying locust exhibiting constant-lift reactions. A muscle action-potential triggered a delay circuit which was timed so as to elicit a light flash when the downgoing forewings approached horizontal. A change in body angle of 18° hardly altered the setting of the forewing relative to wind.

Fig. 5. Double firing of first basalar muscle of the forewing during flapping in wind at different body angles. Several superimposed sweeps are triggered by the first firing. Note that the size of the second firing increases with increasing latency. Large horizontal grid markings equal 2 msec.

Fig. 8. Muscle action-potentials (*b*) correlated with wing position (*a*). The stroboscope flash occurred at the beginning of the first of two oscilloscope sweeps. Upper trace shows the left second basalar muscle of the hindwings firing once per cycle. Lower trace shows the left hindwing subalar muscle firing once or twice per cycle. Relative lift = 104%. Period and velocity were 'normal'. Large horizontal grid markings equal 10 msec.

Fig. 9. Wing position and magnitude of excursion (*a*) correlated with muscle activity (*b*). Both pairs of wings are moving upwards. Downstroke muscles are seen to fire before the end of the upstroke. Upper trace is a forewing dorsal longitudinal muscle. Lower trace is a hindwing subalar muscle. Relative lift = 153%. Wing excursions are 'normal'. Frequency is 'very high'. Large horizontal grid markings equal 10 msec.

Fig. 10. Large wing excursions (*a*) are associated with low-frequency, low-powered performance. Forewing first basalar muscle fires twice even here ((*b*), upper trace). Stroboscope artifact superimposed on lower trace for subalar muscle demonstrates that the small potentials occur just before the bottom of the stroke. Relative lift = 65%. Large horizontal grid markings equal 10 msec.