

A STRETCH REFLEX CONTROLLING WINGBEAT FREQUENCY IN GRASSHOPPERS

By DONALD MELVIN WILSON

*Zoophysiological Laboratory B, University of Copenhagen,
and Department of Zoology, University of California, Berkeley*

AND ERIK GETTRUP

Zoophysiological Laboratory B, University of Copenhagen

(Received 16 November 1962)

INTRODUCTION

There are now several known cases of centrally established nervous output patterns which control rhythmic animal movements, and their occurrence in different animal groups and for quite different functions suggests that central control is an important if not general phenomenon. On the other hand, proprioceptive reflexes seem to be common to the majority of animals, and these reflexes sometimes seem sufficient to explain a whole pattern of activity. In many systems it is probable that both central patterning and reflex feedback play a role. This is now known to be true in the case of the flight control system of the desert locust, *Schistocerca gregaria*, and other grasshoppers.

A fairly detailed analysis of the centrally inherent flight control pattern has already been presented (Wilson, 1961). We wish here to give an account of reflex effects upon that cyclic pattern, especially in regard to the control of the overall frequency.

Important in the frequency control is a proprioceptor situated in each wing hinge. Elimination of the input from these receptors results in a decrease in the wingstroke frequency to about one-half the normal value (Wilson, 1961; Gettrup, 1962). Gettrup (1962) has shown that the proprioceptor is a stretch receptor. Although it was suggested shortly after the discovery of the receptor that it might influence the flight frequency in a non-phasic way by increasing the general excitation of the flight control system (Wilson, 1961) we had little confidence in that idea and began this work with the opposite hypothesis, namely, that firing of the stretch receptor during a particular part of the wingstroke triggered the next event earlier than it would have occurred if the central oscillator ran alone, thus decreasing the whole period. This was suggested by the precision with which the motor output pattern is timed to the wing movements (Wilson & Weis-Fogh, 1962), a precision which seemed to us to require a triggering event. Indeed, from earlier indirect evidence Weis-Fogh (1956*b*) concluded that such a triggering must occur. We have now amassed considerable evidence against this point of view.

Since this is the first case of an analysis of this kind it is impossible to decide whether the results are of general importance or not. But there is no reason to think that other reflexes do not work in a similar way, that is by superimposing their effects tonically upon a background of cyclic activity having another principal cause.

ANATOMY

The main nervous structures dealt with in this paper are indicated in Fig. 1. The numbering of the nerves is that of Ewer (1953). The anterior wing nerve, *IA*, is sensory and innervates the tegula and the campaniform sensilla and other sensilla of the wing itself. Nerve *IB* has a motor branch, *IBa*, to the dorsal muscles, and a sensory branch, *IBb*, to the posterior region of the wing hinge where it innervates a single-unit stretch receptor and several units of a scolopoforous organ. The dorso-ventral flight muscles are innervated by nerve II. Each of the nerves probably contains small sensory fibres from other cuticular structures as well, but we have not studied these.

A recent description of the muscular anatomy may be found in the paper of Wilson & Weis-Fogh (1962). Only a few details are required here and these will be introduced as needed in the text.

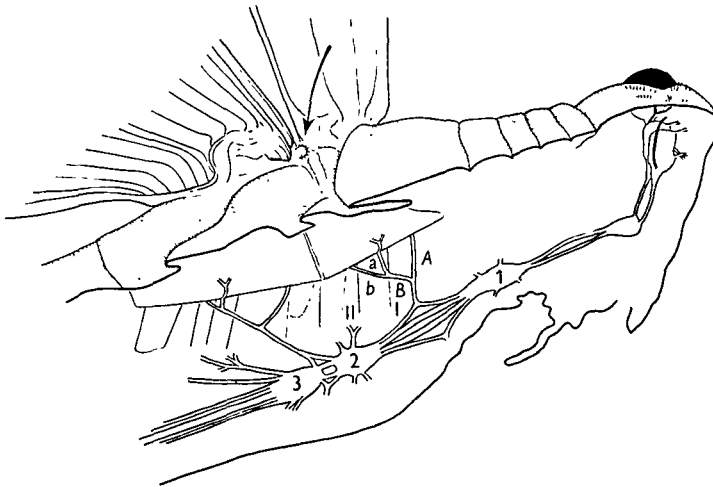


Fig. 1. Diagram of a dissection of a grasshopper or locust (After Wilson, 1961). Many structures not related to flight have been omitted. The arrow indicates the hindwing tegula. It is not possible to show the stretch receptors in this view. They lie behind the posterior end of the dorsal longitudinal muscles. (See Gettrup 1962.)

The main subject of this study, the stretch receptor, has been described in regards to anatomy by Gettrup (1962) who also made exploratory attempts to define its function. Some aspects of the cellular physiology have been analysed by Pabst & Schwartzkopf (1962).

We have identified the stretch receptor either by anatomical means or by physiological means or by both in numerous orthopterans including the grasshoppers *Schistocerca*, *Melanoplus*, *Romalea*, (Acrididae); the cricket *Gryllus* (Gryllidae); the katydid *Scudderia* (Tettigonidae). It may be present in all winged Orthoptera. It has not been found in the wingless mole cricket *Stenopelmatus* (Gryllotalpidae). Nor have we identified it in several species of cockroaches belonging to the genera *Periplaneta*, *Blatta* and *Blaberus*.

In the very large grasshopper, *Romalea*, it has been possible to record from the thoracic stretch receptor in the nymphal stages as early as the third instar. In such

Animals the wings are tiny pads having no articulation and the adequate stimulus for the receptor is elongation of the thorax which is not yet fused into the solid box-like structure of the adult. This finding is strongly suggestive that the thoracic proprioceptor is serially homologous with the better known abdominal stretch receptors (Finlayson & Lowenstein, 1958) and that, instead of losing this structure in the fused adult thorax as some insects do, the grasshoppers rearrange it to suit another function. Another suggestion of homology may be made with an adult insect organ in the case of the tympanum of noctuid moths. The posterior branch of nerve I of the moth meta-thorax carries not only the vibration-sensitive 'A' cells but also a large tonic proprioceptive 'B' cell (Treat & Roeder, 1959) whose function is unknown. It is possible that the 'B' cell corresponds to the stretch receptor and that the 'A' cells correspond to the scolopoforous organ of the locust.



Fig. 2. Firing of a mesothoracic stretch receptor during tethered flight. Upper trace of each pair is from the first basalar muscle, the lower is from nerve *IBb*. At the higher frequency there are fewer impulses per wing stroke cycle and the stretch receptor fires later with respect to the muscle.

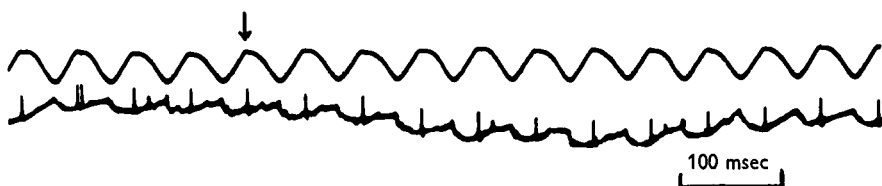


Fig. 3. Firing of the metathoracic stretch receptor (lower record) in relation to movements of the notum (scutellum). The arrow indicates the top of the wing stroke.

EXPERIMENTS

Timing of the stretch receptor

The first step in our attempt to find the behavioural role of the stretch receptor was a determination of the exact time of firing during the wingstroke cycle. We knew this already under the unnatural condition of tethered flight, that is with an animal held in a wind not necessarily of a velocity appropriate to its performance. Figure 2 shows the firing of the mesothoracic receptor in relation to potentials from a downstroke muscle. Figure 3 shows the firing of the metathoracic receptor in relation to movements of the notum. In tethered flight, interpretation of these records reveals that

the stretch receptor fires once or several times beginning near the time of the top of the upstroke of the wings. It may fire later than some of the downstroke muscles.

The similarity of response in the two segments, we felt, permitted us to concentrate our attention on the easier one for recording, that in the metathorax. In order to approach as nearly as possible the conditions of true flight we used the technique described at length by Wilson & Weis-Fogh (1962). In resumé: animals were flown suspended from a pendulum in front of a wind tunnel; a servo-mechanism adjusted the wind speed so that the pendulum was always vertical, that is, the animal was flying at the speed of the wind and was therefore experiencing normal wind forces; the pendulum was mounted on a balanced beam and the weight (or lift) of the animal could

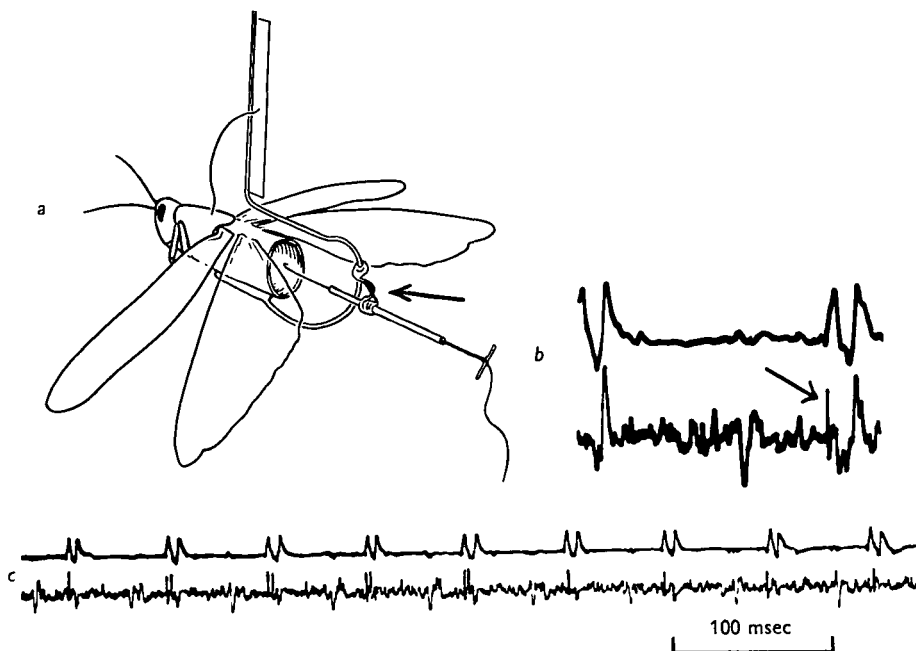


Fig. 4. (a) Sketch of the arrangement for recording from the metathoracic stretch receptor during flight in the aerodynamic balance. The joint indicated by the arrow is of soft wire which can be bent in any direction without elastic return. To it is attached a tube through which the insulated electrode wire is lightly friction-fitted. The combination allows all the necessary manipulations but is so light that it does not interfere with the aerodynamic measurements. (b) Firing of the stretch receptor (arrow) during flight when the locust is suspended in the flight balance. Length of trace about 75 msec. (c) under normal flight conditions the stretch receptor fires once or twice per cycle. The upper trace in (b) and (c) records activity of a downstroke muscle, the first basalar muscle of the metathorax.

be read. The preparation of the animal included advances over the earlier techniques. The soft cuticle between head and prothorax was cut dorsally and laterally and the head bent down to expose the gut. The abdomen was transected posteriorly freeing the gut which was then pulled through the forward wound and cut off. The head was set back in position. It should be stated that the animals treated in this way fly quite well when thrown in the air. The remainder of the abdomen was trimmed away and the eggs, fat body, and air sacs in the thorax removed. A ground electrode of platinum wire was inserted into the prothorax from the dorsal side. An electrode for muscle

Recording was set according to the means of Wilson & Weis-Fogh. The sensory response was recorded through a wire placed under the nerve *IBb* inside of the thorax and the posterior opening of the thorax was covered with petroleum jelly in order to keep the preparation from drying. The nerve was pulled away from the muscles into the air space left by removal of the thoracic structures.

Two special criteria were necessary for the success of the experiment. Holding the sensory nerve on the recording electrode during flight required a manipulator which could be fixed with respect to the animal, but the apparatus for the measurement of the aerodynamic parameters demanded some free movement of the animal and only very

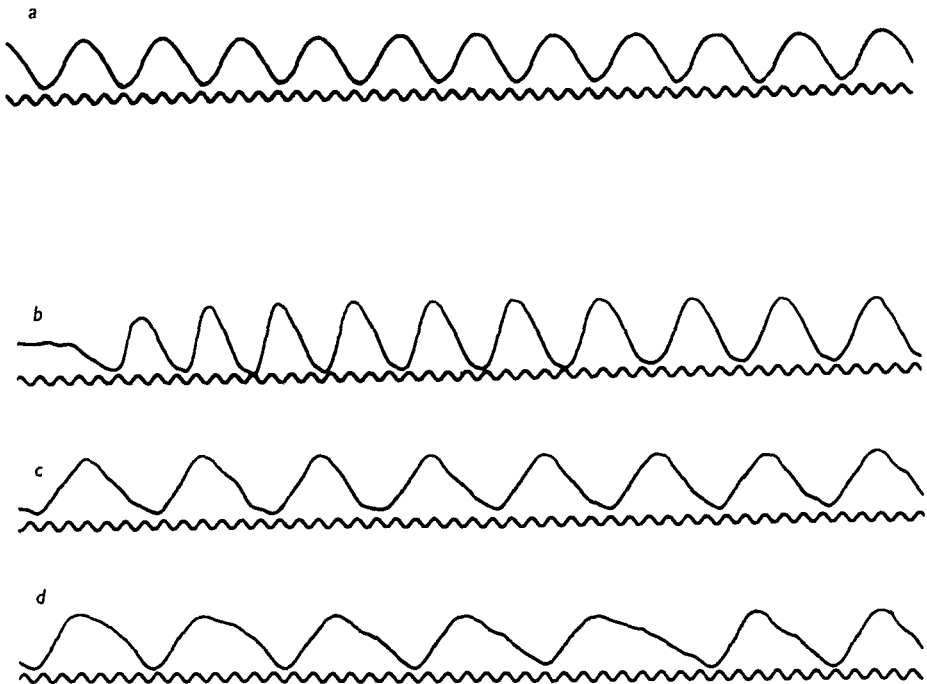


Fig. 5. Frequency of wing movement recorded from movements of the scutellum. The lower trace of each pair is a 50 c/s time signal. The first record (a) is from the middle of a normal flight. The last three records show the beginning of flight after damage to the four stretch receptors. About 15 cycles are deleted between (b) and (c) and between (c) and (d).

fine wires attaching to it. Both conditions were satisfied by constructing a very small manipulator on the bar which held the animal in the flight balance. Figure 4 includes a sketch of this arrangement.

Under these more perfect flight conditions the same result was obtained as in tethered flight, namely, the stretch receptor discharged so that the first impulse during each wingstroke cycle passed the recording electrode just as the wings reached the 'up' position. During an average performance it fired either once or twice per cycle (see Fig. 4). The result shows that it is quite impossible that the stretch-receptor impulse can be responsible for triggering the downstroke muscles during the same wingstroke cycle. It remained possible that it might trigger some later event.

Destruction of the stretch receptors

The stretch receptors may be removed by surgery or cautery without much dissection. As stated above, even extensive dissections do not necessarily preclude a good flight performance. The following results were obtained from animals flown under tethered conditions. Destroying two or more of the four wing-hinge receptors always

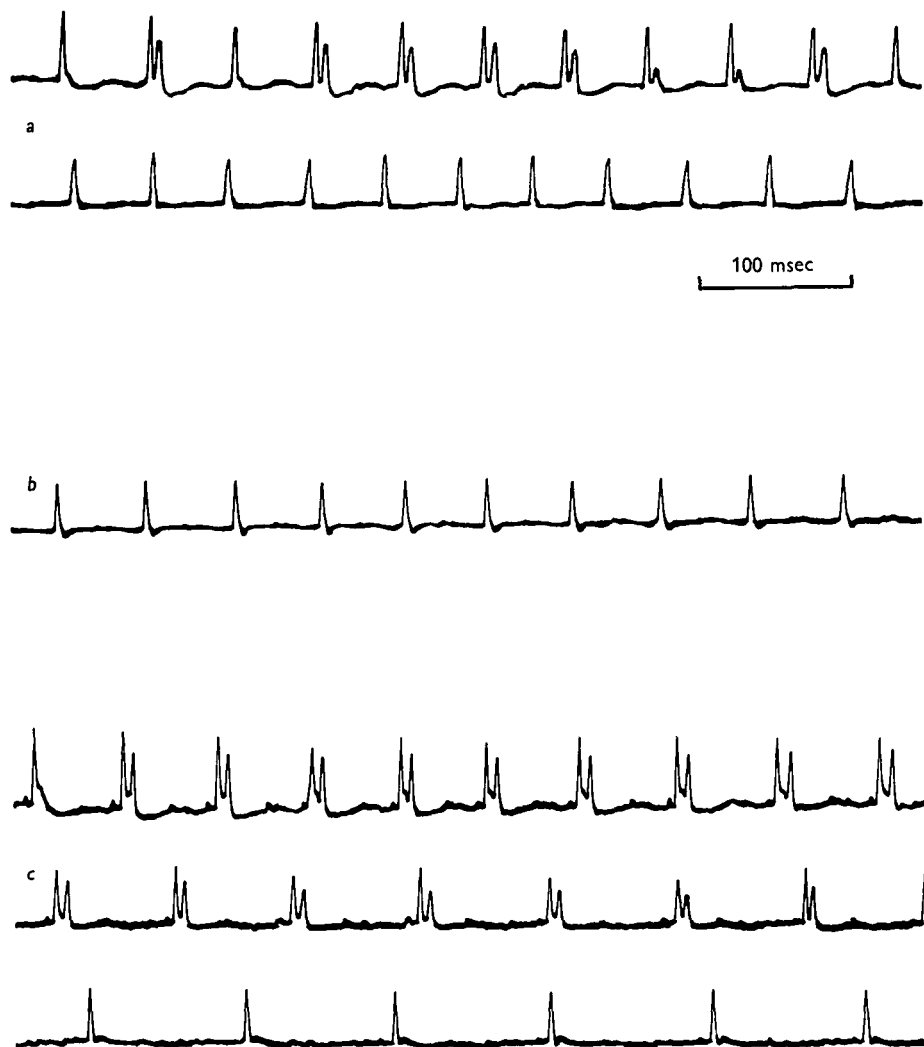


Fig. 6. Records from the metathoracic subalar muscle. (a) Start of a normal flight and mid-flight (65 cycles later). (b) Mid-flight after damage to the two metathoracic stretch receptors. (c) Start of a flight after damage to the two mesothoracic stretch receptors as well. About 10 cycles missing between traces.

results in a decrease in the stroke frequency. The metathoracic receptors could be inactivated by cutting their attachments to the soft cuticle below the subalar sclerite. There was no general damage to the animal. The mesothoracic receptors were burnt by running a hot needle along the lateral edge of the posterior phragma. There was usually

Some bleeding and sometimes damage to the tergo-coxal muscle. If the mesothoracic receptors were damaged first then otherwise undamaged animals gave a good symmetrical performance with only slightly lowered stroke frequency. Such animals were subjected to further tests.

Removal of any two of the stretch receptors (either segmental pairs or lateral pairs) resulted in a frequency decrease of only about 10 %. This result would disappear into the normal range of variation in frequency except that the difference always had the same sign. Removal of three gave a decrease to about three-quarters of normal and destruction of all four gave a drop to about one-half normal (see Figs. 5 and 6). This last



Fig. 7. (a) Upper trace, the metathoracic tergosternal muscle (a wing elevator) and lower trace, the metathoracic first basalar muscle (a wing depressor), during normal flight. (b) The same after ablation of the stretch receptors. The relative timing is about normal even at the reduced frequency. This record is somewhat atypical in showing especially well the multiple firing at low wingstroke frequency.

value approximates the frequency of operation of the inherent central pattern when not influenced by any proprioceptive feedback, and the dominant role of the stretch receptors in frequency control is thus established. It is significant that removal of any four receptors has about the same effect and that the effect is uniformly distributed over the whole flight system. There are no apparent differences in the way in which the wings are co-ordinated; the pairs remain synchronous and the two segments maintain their relative asynchrony. Whatever the effect of the stretch receptors is in the ganglia, it seems to be spread over the entire pterothorax irrespective of its anatomical source. After ablation of all four receptors the wing movements appear normal in shape and recordings from several different muscles do not indicate any specific effects on special muscles. Each muscle of course is affected along with the rest to operate at the reduced frequency. Muscles may still fire twice per wingstroke; in fact, at very low wingstroke frequencies they may fire several times, so the stretch receptors cannot be held responsible for causing the 'double firing' (Wilson & Weis-Fogh, 1962) which has significance in the control of normal flight (see Fig. 7).

Another view is obtained if one studies the beginnings of flights rather than the steady conditions of well established flight. In normal animals the frequency rises slightly during the first few cycles and then declines very slowly over many thousands of cycles. Animals having the four stretch receptors removed begin flight with a somewhat lower than normal frequency but during the first few cycles the period lengthens conspicuously on each cycle until after 5–20 cycles the frequency is about

one-half of normal. Figures 6, 8 and 9 illustrate this. If the frequencies in normal and operated animals are compared the impression is gained that at the beginning of flight the effect of the stretch receptors increases over many cycles. It is even true that at the beginning of flight the number of discharges of each stretch-receptor neuron decreases during the first few cycles (records may be seen in Wilson, 1961), so that the argument for a gradually increasing effect is exaggerated.



Fig. 8. Frequency declines after onset of flight following destruction of the four stretch receptors. The three traces form a continuous record from the mesothoracic first basalar muscle. Activity of an elevator muscle is seen in the deflexions of lower amplitude.

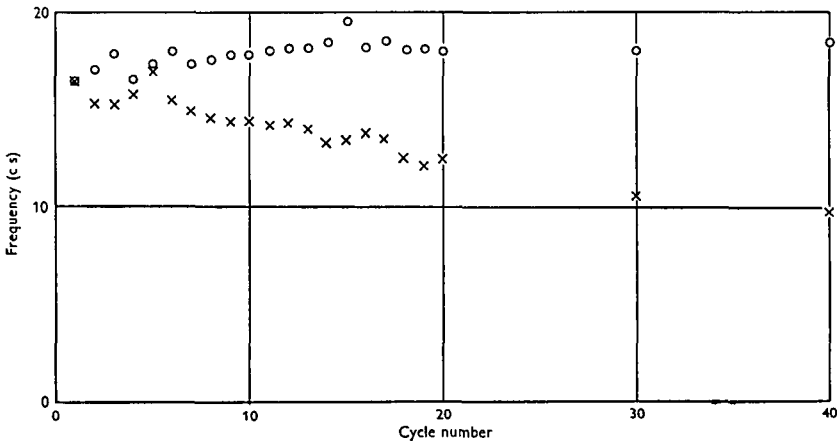


Fig. 9. Wingstroke frequency at the beginning of flight before (O) and after (x) destruction of the four stretch receptors. Exact data from one particular experiment.

Interference with normal timing

We next desired to leave the stretch receptors intact but to alter the time at which they fired and measure the effect upon the motor output pattern. One easy means was available. Since the receptors in the two segments each discharge normally within 2 or 3 msec. of the top of their respective wingstroke and since the two wings are out of phase by about 8 msec. (Weis-Fogh, 1956a) there must also be asynchrony between the anterior and posterior receptors in normal flight. It was possible to fix the forewings and hindwings together so that they moved as a unit, thus decreasing the mechanical asynchrony to zero and presumably altering the time of firing of the stretch receptor similarly. From a separate study (Gettrup, 1963) we know that in

hemisected thoracic preparations when the receptor is stimulated sinusoidally it always responds at the same phase instant at any one frequency regardless of amplitude, and while the argument is indirect we are rather confident that the wing fixing would have the effect of changing the relative time of firing of the pairs of receptors by not less than 5 msec. When the trailing edges of the forewings were waxed to the leading edges of the hindwings animals were not stable in free flight, nor could they lift their own weight in the flight balance. The aerodynamic conditions were thoroughly



Fig. 10. The first basalar muscles (*a*) and subalar muscles (*b*) of the metathorax (upper trace) and mesothorax (lower trace) fire in their usual pattern even though the forewings and hindwings are waxed together so that they move as a unit. The ordinary segmental delay is still manifested in the motor output pattern.

disturbed. But they could maintain a flapping response which had a normal frequency and they would continue this abortive sort of flight as long as the wind stimulus lasted. The forewings continued to pronate on downstroke but the hindwings were fixed so that they could not. The stroke amplitude was usually large. It is probable that the hindwings pushed the forewings since the former have the more powerful driving mechanism and they are the leading pair in normal flight.

Not only did this manipulation not upset the frequency control but it also left unaffected the basic features of the motor output pattern including the segmental time difference. Recordings were made of the activity of the main wing control muscles, the first basalars and the subalars, of the two segments before and after fixing the wings together (Fig. 10). These pairs of homologous muscles continued to exhibit action potentials in the same temporal pattern as in free flight even though the wings were mechanically limited so that the command could not be followed and the stretch-receptor feedback must have had an altered timing. This was the first important evidence that the time of firing of the stretch receptor is not very important. It certainly demonstrates that the stretch receptors do not control the segmental phase difference as suggested by Pabst & Schwartzkopf (1962).

In another attempt to alter the relative timing of the stretch receptor three-quarters of each forewing was cut off and records were made of the time of firing of the first basalar muscle of the forewing relative to the wing movement. With the decreased inertial and air-resistance loads the wing muscles were capable of accelerating the wing much more than usually and the duration of the upstroke was shortened considerably. This should have the effect of causing the stretch receptor to fire somewhat

early. The wing began the downstroke early also, due to the activity of the dorsal longitudinal muscles and to elasticity of the thorax. However, the basalar muscle (a downstroke muscle) did not fire until the normal interval had elapsed so that its mechanical effect did not begin until the wing had nearly returned to the down position where it paused until the cycle resumed. The timing of the wing-twist controlling depressor muscles does not seem to be affected by the wing reflexes.

Effect of non-phasic stimulation

From the foregoing results it could be predicted that electrical stimulation of the nerve *IBb* (containing the stretch-receptor axon) of de-afferented preparations should produce an increase in the frequency of the centrally inherent flight pattern. The experiment was arranged as follows. The animal was bisected except for the head along a plane cutting the median dorsal line and a paramedial ventral line just lateral to the nerve cord and ganglia. The gut, air sacs, and fat body were removed. The preparation was pinned firmly to a mount which could be placed in a wind stream so the wind-on-head flight stimulus could be utilized. It had already been shown that such a preparation 'flies' at about half normal frequency. Paired stimulating electrodes were placed under the two remaining stretch-receptors nerve. Monopolar recording electrodes were placed on selected muscles and a ground wire was placed in the abdomen. The exposed tissues were covered with petroleum jelly to prevent drying and to increase insulation between the various electrodes. In quiescent preparations stimulation of the nerves *IBb* had no effect. At high voltages the dorsal longitudinal muscles twitched due either to direct stimulation or to stimulation of the nearby large motor axons. These muscles were chosen for recording so that a non-reflex effect could be easily checked, as is desirable, since possible effects on flight of antidromic activity in these axons are totally unknown.

Since only half the stretch-receptor inputs were available it was necessary, in order to produce a conspicuous effect, to stimulate at a higher frequency than the flight frequency. In order to avoid a situation in which a particular response might seem to be related to a particular stimulus the stimuli were grouped and the repetition of groups was at a low frequency which was different from the response frequency (see Fig. 11). In this way the stimuli fell in all possible phase relationships with the response over a series of several response cycles. In the best preparation it was thus possible to increase the frequency by about 30% above the natural frequency in response to the non-phasic stimulus of wind-on-the-head. The response is steady, that is, it does not vary from cycle to cycle depending upon the input timing. The response builds up slowly over many cycles after the stimulus has begun and it likewise wanes slowly after cessation.

It is clearly to be seen in Fig. 11 that stimulation of these sensory nerves, besides affecting frequency, also increases the number of active motor units of the flight system and increases the activity of individual units causing multiple firing within a single cycle. Both elevator and depressor muscles show these effects and as in the case of frequency control the response waxes and wanes slowly. The stretch receptors seem to add to the general excitation of the flight control system but do not seem to be used to provide any specific information about wing position.

It should be pointed out again that the nerve *IBb* contains in addition to the stretch-

receptor axon some other sensory axons. It is possible that these were stimulated also but as the stretch-receptor axon is the largest it is highly improbable that it was not stimulated. The more specific ablation experiments show that the scolopoforous organ has little effect on frequency while the stretch receptor is highly important.



Fig. 11. Effect of non-phasic electrical stimulation of the nerves *1Bb* on the motor output during flight. Upper trace, the dorsal longitudinal (depressor) muscle (upward spikes) and the tergosternal (elevator) muscle (downward spikes) of the metathorax. Lower trace, 50 c/s and stimulus marker. (a) Stimulated only by wind on the head. (b) Steady response during a long period of electrical stimulation. Frequency is increased about 25 %. Note small effect if any, of the phasing of the stimulus. (c) The stimulation causes multiple firing of the downstroke muscle even when there is not much frequency change.

Notes on other reflexes

Although the timing of the stretch receptors seems unimportant, and the main flight output-pattern can operate either when they fire at the wrong time or not at all, *some* reflexes are more disruptive when abnormally stimulated. If the wing sense-organs are left intact but the wings held still, then when the head receives wind the animal may still attempt flight. When the wings are held down only elevator muscles fire and when they are held up the depressors fire at higher than normal frequency but erratically in small bursts which are themselves at a frequency lower than that of normal flight. Some reflexes acting on specific muscle groups seem to be in operation. These reflexes probably have their sensory source in the structures innervated by nerve *IA*.

Records from nerve *IA* taken during flight have been published already (Wilson, 1961). These show many nerve impulses occurring mainly during the downstroke of the wing. We have made somewhat more detailed study of isolated preparations and find that the main inputs through nerve *IA* are from sensory hairs on the tegula and from the campaniform sensilla on the main wing veins. The latter receive detailed attention elsewhere (Gettrup & Wilson, 1963). They appear to have no effect on frequency or gross shape of the wingbeat. Their function is probably related to the control of lift.

The 15–20 small sensory hairs of the tegula are stimulated whenever the wing moves downward below the horizontal position. The tegula folds under the base of the costa-subcosta and radius-media veins and the hairs are bent by contact with the wing vein in much the same way as the hairs of the coxal hair plates of cockroaches (Pringle, 1938). This has been observed under stroboscopic illumination during flight. The discharge is a phasic one involving the largest axons in nerve *IA*. In mature animals in good flight condition destruction of all four tegulae by surgery or cautery has very little effect on flight. There may be a slight decrease in frequency but the animal is still capable of a good performance. In less mature animals the frequency decrease is greater and in some cases it is of the same order as when the stretch receptors are removed. In these immature animals the effects of the tegula receptors and the stretch receptors are additive. Experiments on *Melanoplus differentialis* have all given this result but it is possible that the animals were never in optimal flight condition. In mature *Schistocerca* the tegular hairs are not necessary, the stretch receptors being sufficient to maintain normal frequency without them.

In addition to these wing reflexes other factors may influence frequency. The velocity of wind on the sensory hairs of the head in wingless preparations has the effect that within limits the frequency of the motor output-pattern is higher with higher wind speed. Flashing lights or sudden sounds often cause transient increases in frequency.

Animals which are mounted with tarsi out of contact with solid objects often respond to vibration by a quick elevation of the wings. This is most conspicuous if the forewings are already unfolded. The wing nerves, head, and tympanum are unnecessary for this reaction. It may be due to the scoloparia of the thorax (Slifer, 1936; Campbell, 1961). The reaction may be part of the normal start of flight and may be particularly sensitive without tarsal inhibition. It is interesting that the same response

results when the wing nerves are intact. If the wings are given a quick pull upwards they actively twitch upwards as well. There is no ordinary stretch reflex.

DISCUSSION

The evidence all leads to the conclusion that the effect of the stretch-receptor input outlasts a single period of the wing oscillation and that the effect summates for several cycles. We do not wish to imply that the effect might not be facilitated when the input occurs at some particular part of the cycle but such a specific timing is not necessary for a reaction of normal magnitude.

Another argument for the same case can be made from facts from two other papers. It has been found (Wilson & Weis-Fogh, 1962) that with increasing wingbeat frequency the wing muscles are excited earlier with respect to wing position. For example, at low frequency the majority of downstroke muscles fire 0–2 msec. before the wings reach the top position; at high frequency they fire several msec. before the top and thus help to brake the upward movement. Gettrup (1963) has found that during sinusoidal mechanical stimulation of the stretch receptor the first impulse always occurs at the same phase of the stretching movement regardless of amplitude, but that the phase at which it fires becomes later as frequency is increased. If this holds true in the flying animal then as wingbeat frequency increases the muscles fire earlier and earlier while the stretch receptor fires later and later. This seems inconsistent with the idea that the stretch receptor supplies specific timing information to keep the muscles firing properly with respect to the wing movements. The argument depends upon a lack of efferent control of sensitivity of the stretch receptor and this is the best assumption at present. There is no sensitivity-controlling muscle and evidence is lacking on a direct nervous control of sensitivity.

It has often been suggested that proprioceptive reflex loops are responsible for the timing of various muscle groups undergoing cyclic activity and such a model has been proposed for the present case (Weis-Fogh, 1956*b*). Although we have not dealt with all of the sensory apparatus of the locust flight system we have now surveyed the likely possibilities and find no evidence in favour of that kind of model.

An alternative model along the following line may now be suggested. A central oscillator has its frequency set by input from several sources, most important among these being the stretch receptors. At the optimal frequency muscles begin their activity at the appropriate time for maximal efficiency, that is, the downstroke muscles begin to shorten just as the wings reach the top position, etc. At a higher frequency of the nervous oscillator the half cycle of the wing movement which is initiated by the elevators is not over when the downstroke command arrives and so the downstroke muscles help to stop the upward movement of the wings before their energy has been absorbed in other ways. With this muscular brake acting at both the top and bottom wing positions the wings can be driven at the higher frequency. A reflex which caused muscle groups always to fire at a certain phase of the wing movement would preclude this means of adjusting frequency to the behavioural needs. The system may be thought of as being composed of two oscillators, a peripheral mechanical oscillator whose frequency is influenced by a central nervous oscillator. The peripheral oscillator has a natural frequency, i.e. a frequency of maximum efficiency for converting muscular

work into aerodynamic work. But it is not always an advantage to an organism to be maximally efficient in any particular process and in the case of grasshopper flight the mechanical oscillator may be driven to higher frequency and therefore greater power output but at decreased efficiency.

The role of the stretch receptor in this system seems to be to excite in a non-specific way the flight control system so that it operates faster. The central nervous oscillator has its frequency adjusted in part by the stretch receptors but the effect of this input is phase-independent. Since there may be one to several impulses from the stretch receptors during each upstroke it does not follow that increased wing frequency will result in increased total number of input impulses, in fact the contrary is probably true. It can be pointed out that the wingstroke amplitude is less at higher frequencies because higher frequencies are associated with greater braking activity by the muscles and with greater overlap in the time of activity of antagonistic muscle groups. This can lead to fewer stretch-receptor impulses per wingstroke (Gettrup, 1963; see also Lowenstein & Finlayson, 1960). The effect is illustrated in Fig. 1. The system has then the characteristic of a negative feedback loop; a frequency-increasing input decreases as frequency increases.

The argument favouring a predominantly central nervous origin of output pattern is further strengthened by the finding that the central oscillator is independent of input phase.

SUMMARY

1. The stretch receptors of the wing hinge of the locust *Schistocerca* fire once or twice at the top of the wingstroke during normal flight.
2. Removal of the four stretch receptors results in a decrease of the wingstroke frequency to about one-half normal.
3. Interference with the normal timing of the stretch-receptor input (mechanically or by electrical stimulation) does not affect the normal wingstroke frequency. With respect to this sensory source the centrally generated motor output pattern is independent of input phase.
4. The results are discussed briefly in relation to the question of central *v.* peripheral control of locomotion.

The work was supported by grants from the Carlsberg Foundation, Copenhagen and the Rockefeller Foundation, New York, to Prof. T. Weis-Fogh and a grant from the U.S. Public Health Service to Dr D. M. Wilson (N.I.H. grant no. B3927). E. Gettrup received support from the Carlsberg Foundation. The locusts (*Schistocerca*) were supplied by the Anti-Locust Research Centre, London.

We are indebted to Prof. Weis-Fogh for his interest and hospitality during the work.

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