

BIFUNCTIONAL MUSCLES IN THE THORAX OF GRASSHOPPERS

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INTRODUCTION

Studies of grasshopper flight cannot provide a complete picture of the activities of certain of the flight muscles. Throughout the flight studies (Wilson & Weis-Fogh, 1962) we have recognized that some of the muscles must exert forces on the legs as well as the wings. It was dissection of a flightless species showing the differences in proportions between the pure wing muscles and wing-to-leg muscles that emphasized the need for further analysis. The purpose here is to report on activities of these muscles which are not related to flight and to indicate what meaning the results have for understanding the flight control system.

MATERIALS AND METHODS

The two species of grasshoppers used were *Melanoplus differentialis* (Thomas) and *Romalea microptera* (Beauv.), the melanistic variety, *marci* Serv.

Melanoplus were from a culture maintained in the laboratory for many generations. Adults of this species are capable of vigorous flight and are similar in general form and in details of thoracic anatomy to well-known animals such as *Locusta*, *Schistocerca*, and *Dissosteira*. Their length (from frons to tip of abdomen) is between 3 and 4 cm., females being slightly larger than males. The wings are long, extending a few millimetres past the tip of the abdomen.

Romalea were obtained from the Waubun Laboratories near Schreiver, Louisiana, U.S.A. They were purchased as second and third instars and raised to breeding adults. Adults are 6-8 cm. long and heavy-bodied. The wings are short and used only for audible and visible display. The animals are incapable of flight. The internal thoracic anatomy is correspondingly different. The wing muscles are thin and the large thoracic cavity is filled mostly by gut and air sacs.

Anatomical study was on living or formalin-fixed specimens. Muscle stimulation was by means of a Grass S4 stimulator and platinum-wire electrodes of 0.1 mm. diameter. Muscle potentials were led through similar wires insulated except at the tip. The potentials were amplified with Tektronix type 122 preamplifiers, displayed on a Tektronix type 502 oscilloscope, and recorded by means of a Grass C4 oscilloscope camera.

Flying animals (*Melanoplus*) were tethered by waxing the sternum or pronotal shield to a stationary support. Often the legs were cut off in order to eliminate the flight-inhibiting tarsal contact. The stimuli for flight were wind puffs or continuous but

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turbulent wind from a compressor. All flights were of short duration. Flight movements were observed under flashing light from a General Radio Corporation Strobotac.

Walking animals were usually restrained as little as possible and provided with horizontal and vertical surfaces, smooth and also irregular.

Recording electrodes were placed through small holes in the cuticle and waxed in place at two spots so that the point of entry into the animal was never strained. The ground electrode was a long bare wire similarly waxed into the abdomen. For nearly freely moving animals long flexible leads were trimmed so as not to interfere with leg movements. These were insulated copper wires sufficiently light that the animal could drag them without apparent extra effort.

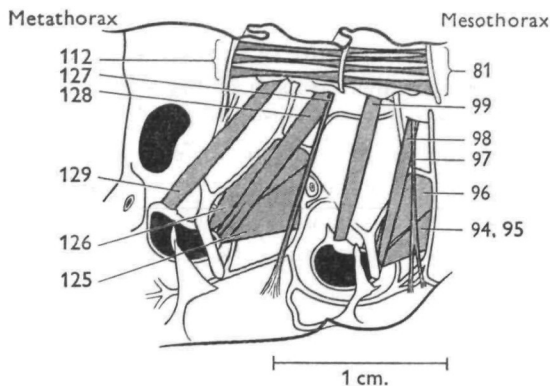


Fig. 1

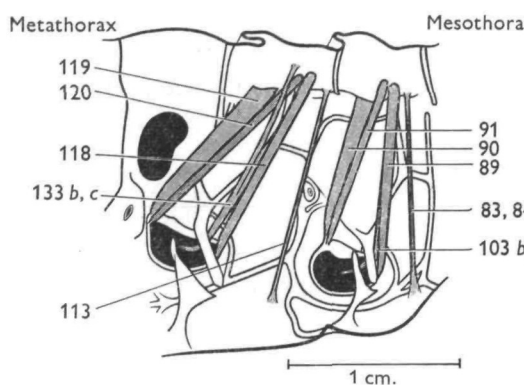


Fig. 2

Fig. 1. The wing depressor and pleurocoxal muscles of *Romalea*. See Table 1 for explanation of numbers. The nota and sternum have been pulled somewhat apart to give a fuller view of the muscles.

Fig. 2. The wing elevator muscles of *Romalea*. See Table 1 for explanation of numbers. The skeleton is distorted as in Fig. 1.

Anatomy

The wing muscles of *Melanoplus* and *Romalea* appear to be entirely homologous. Those of *Melanoplus* are similar not only in arrangement but also in proportional size to those of the flying grasshoppers such as *Schistocerca*. The sagittally split thorax gives the appearance of being packed with muscles (see Wilson & Weis-Fogh, 1962). *Romalea*, on the other hand, has a reduced wing musculature with the individual muscles thin and with small groups separated from one another (see Figs. 1 and 2). In *Romalea* those muscles which are attached so that they can move only the wings are mere threads which presumably can exert little force. Those attached to the legs as well are relatively robust. This observation led to the main suggestion of this paper that some of the wing muscles of grasshoppers may be used also as leg muscles. As this is true, the origins and insertions of these muscles are functionally interchangeable and depend upon the behaviour of the whole animal.

In Table 1 the various muscles studied are listed according to the numbers of Snodgrass (1929). Names based upon attachments, and synonyms based on presumed function, are given. The functions during flight are taken from Wilson & Weis-Fogh (1962) while the actions on the legs are new observations which only partly confirm

the functions assigned on anatomical basis alone (Snodgrass, 1929). The action on the legs was determined on thoracic preparations with the central nervous system and most tissue other than muscle and skeleton removed. Windows were cut in the thin parts of the cuticle when necessary, but the main structural elements of the thoracic box were not damaged. Single muscles were stimulated electrically or pulled in the direction of their long axis with forceps and the direction of movement of the limb was observed visually. The bifunctional muscles of special interest here are indicated in the table by asterisks.

Table 1. *Numbers, names, and functions of the muscles illustrated in Figures 1 and 2*

Number (Snodgrass, 1929)		Name	Synonym (Snodgrass, 1929)	Functions
Meso- thorax	Meta- thorax			
81	112	Dorsal longitudinal muscle	—	Depressor of wing
83	113	First tergosternal muscle	—	Elevator of wing
84		Second tergosternal muscle	—	Elevator of wing
*89	*118	Anterior tergocoxal muscle	Tergal promotor of coxa	Elevator of wing. Promotor of coxa
*90	*119	First posterior tergocoxal muscle	First tergal remotor of coxa	Elevator of wing. Remotor of coxa
*91	*120	Second posterior tergocoxal muscle	Second tergal remotor of coxa	Elevator of wing. Remotor of coxa
94	125	First pleurocoxal muscle	First abductor of coxa	Promotor of coxa
95		Second pleurocoxal muscle	Second abductor of coxa	Promotor of coxa
96	126	Third pleurocoxal muscle	Third abductor of coxa	Abductor of coxa
97	127	First basalar muscle	First pronator extensor of wing	Pronator depressor of wing.
*98	*128	Second basalar muscle	Second pronator extensor of wing	Pronator depressor of wing. Promotor of coxa
*99	*129	Subalar muscle	Depressor extensor of wing	Supinator depressor of wing Remotor of coxa
*103 b, c	*133 b, c	Tergotrochanteral muscle	Depressor of trochanter	Elevator of wing. Depressor of trochanter

RESULTS

Romalea microptera

All of the muscles studied were capable of response to electrical stimulation and gave visible twitches to single shocks. The very small dorsal longitudinal muscles, tergosternal muscles, and first basalar muscles of *Romalea* appear normal in this respect, but, due to their small size, records of their activity in the intact animal have not been obtained. They may contribute to wing movements in spite of their small size. Records have been obtained from the other muscles during wing movements and walking. These records usually contain several recognizable motor units and presumably represent small groups of muscles. Precise identification of the source of a particular electrical event was seldom possible because the muscles are relatively smaller and placed farther from the cuticle than in the flying forms. Post-mortem examination usually showed the electrode to lie next to a muscle or between two muscles but not to be set within the body of one.

Notwithstanding these deficiencies, the records from *Romalea* show clearly the following things. First, the thoracic muscles which are used during flight in many

grasshoppers also move the wings of *Romalea*. Two reactions are common: a long-maintained elevation of both pairs of wings which exposes the brightly coloured hind wings, and a flapping response in which elevator and depressor muscles alternate in a clear rhythm and the wings produce a characteristic sound. This flapping is at a frequency of about 12 times a second, a value in proportion to the size of the animal (Greenewalt, 1960) but much too low in proportion to the length of wings as compared to flying grasshoppers. Secondly, many of these 'wing muscles' are activated during certain kinds of terrestrial locomotion, especially climbing, groping for a hold when suspended from irregular objects, and straining against an abnormal resistance to movement over a level surface. These muscles seem to be quiet during ordinary low-speed walking on a flat surface; at least large action-potentials are absent. Their use is especially conspicuous when an animal is suspended so that the legs are out of contact. The stronger movements made possible by the use of these extra muscles may make reaching a hold more likely.

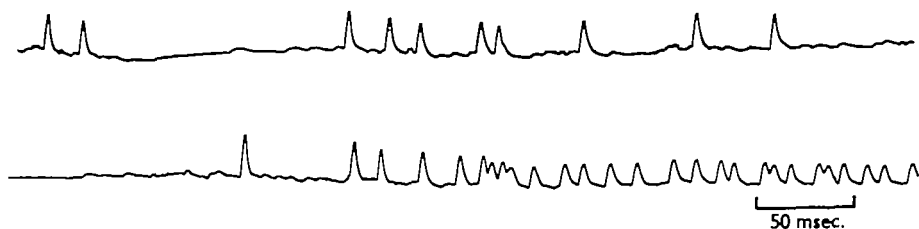


Fig. 3. Action-potentials from the metathoracic first pleurocoxal muscle (125) of a fifth-instar *Romalea* while the leg is swung forward under restraint. This is a near-maximal performance.

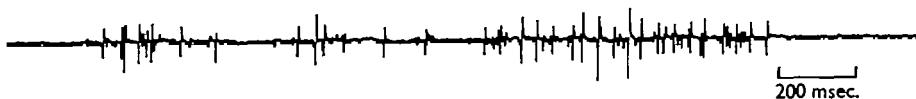


Fig. 4. Activity in the 'flight muscles' of *Romalea* during leg movements with the wings still. The electrode is in the metathoracic subalar region. The largest spikes are over 4 mV. deflexions from the baseline and do not represent distant activity.

Action-potentials from a purely leg-moving muscle (125, the metathoracic pleurocoxal muscle, a promotor) are presented in Fig. 3. This muscle was active only when the leg was drawn forward under restraint. In a series of muscle action-potentials the first is always largest and at highest frequency the potentials begin to fuse but never facilitate. This effect is similar to that of the repetitively firing flight muscles of *Schistocerca*.

In Fig. 4 is seen a typical picture of activity in the dorso-ventral thoracic muscles of *Romalea*. The electrode was in the metathoracic epimeral region and the electrical record was taken during a period of groping movements by the leg. There were no simultaneous wing movements. All of the muscles of this region are used in flight in fully winged grasshoppers. The several sizes of spikes probably represent different units in the subalar and posterior tergocoxal muscles which together form a small bundle. The largest unit did not fire during wing elevations whereas at least some of the others did. It is probably one of the subalar muscle units. As crude as these interpretations are they nevertheless establish the leg-moving function of these

muscles. Experience has shown that electrodes of the kind used will not pick up comparably large potentials (several millivolts) from distant muscles in the thorax of these animals.

Fig. 5*a* shows activity in the posterior tergocoxal muscles of the mesothorax during the beginning and ending of a long-maintained wing elevation. Fig. 5*b* shows activity at the same electrode a little later when the wings were still and the mesothoracic leg was pulling against a large resistance. The two records show that the same small group of muscles may be involved in either wing or leg movements.

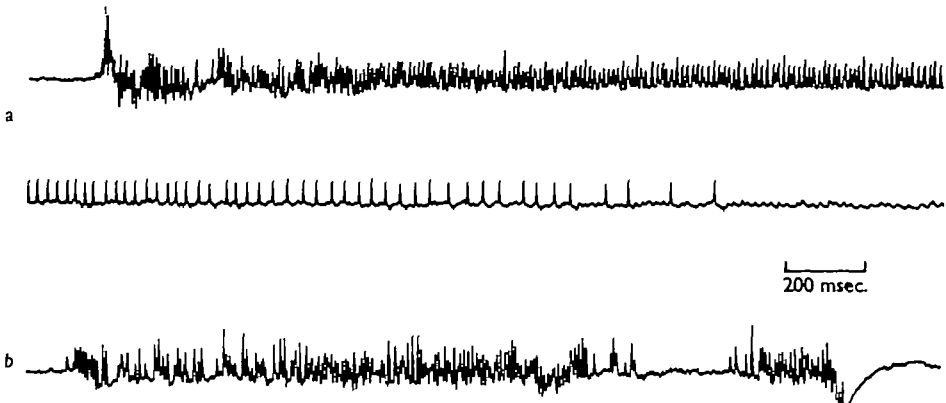


Fig. 5. Records from deep in the mesothoracic subalar region of *Romalea*. (a) Activity during a long-maintained elevation of the wings. About $\frac{1}{3}$ of the middle of the record is deleted. (b) Activity during leg movements while the wings are still.

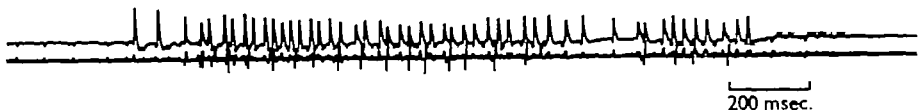


Fig. 6. The subalar muscle (above) and adjacent elevator muscle (below) of the metathorax of *Romalea* are active simultaneously during some leg movements. The electrodes were positioned under visual control directly on the exposed muscles.

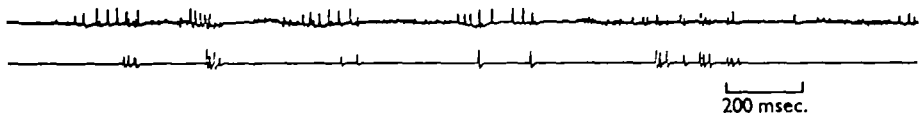


Fig. 7. The mesothoracic second basalar muscle (above) and a nearby elevator, the anterior tergocoxal muscle (below), are active at the same time during repetitive leg movements (*Romalea*).

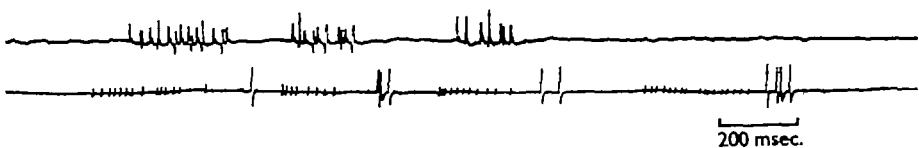


Fig. 8. The mesothoracic second basalar muscle (above) and subalar muscle (large unit, below), which are synergists during flight, reciprocate during repetitive leg movements. The small potentials in the lower trace are uninterpreted (*Romalea*).

Somewhat more precise localization of the source of the potentials was possible when the animal was mounted, windows cut in the thoracic wall, and the gut removed. In this situation the muscles were mostly insulated from each other by air spaces and pairs of electrodes could be placed carefully on adjacent groups and their activities distinguished. Push-pull amplification was used in order further to reduce pick-up from distant muscles. Simultaneous visual observations of contractions were also possible. The metathoracic subalar muscle (a wing depressor) and underlying elevator muscle are compared in Fig. 6. These two muscles which are antagonists for flight here operate at the same time as synergists for swinging the coxa posteriorly. Fig. 7 shows activity of the mesothoracic second basalar muscle and its adjacent elevator muscle during several repeated limb movements. Both fire as the leg swings forward. Fig. 8 compares the second basalar muscle (upper trace) and subalar muscle (large unit, lower trace) of the mesothorax during repeated leg movements. These muscles which are synergic for flight are antagonists regarding coxal movements. The records establish the double function of the whole muscles in *Romalea*, but interpretation at the single motor unit level is not yet possible.



Fig. 9. Use of the mesothoracic subalar muscle of *Melanoplus* during climbing (a) and groping for a hold (b). The two units used during flight are both detectable here as well.

Melanoplus differentialis

Having found that the muscles of the wings of *Romalea* may be used as leg muscles I wished to find whether this was true also of flying grasshoppers, since such a fact must influence hypotheses on the mechanism of nervous control of flight. Not surprisingly, it turned out that the flying and flightless forms are similar with respect to the use of these muscles for leg movements. In the case of *Melanoplus* it is possible to be quite certain of the source of the action-potentials since the muscles are relatively large and placement of the electrodes within single muscles is easy.

The mesothoracic subalar muscle is used during climbing (Fig. 9a) and groping for a hold (Fig. 9b). The first portion of Fig. 9a shows a single unit firing many times at a fluctuating frequency. The amplitude of any one muscle action-potential depends upon the time since the last, and closely spaced firings result in decreasing amplitude. The latter part of the records in Fig. 9a, b show a second unit. Records during flight also show two units in the subalar muscles (see Wilson & Weis-Fogh, 1962). Recordings taken under a variety of conditions as well as electrical stimulation of the muscle consistently show two fast units. Efforts to demonstrate more than two fast units have failed. It is therefore probable that not just the same muscle, but actually the same

motor neurons are used for the different activities. There could be in addition some slow innervation but it has not been detected.

Wing elevator and depressor (the subalar) muscles of the mesothorax may be active together, sometimes firing synchronously (Fig. 10). The second basalar and subalar muscles may operate together or separately (Fig. 11) and show a tendency toward antagonism except during flight when they are always nearly synchronous. Activating both at once should have the effect of stiffening the joint. Simultaneous action of slow units of antagonistic leg muscles during rapid walking has been noted by Hoyle (1957,



Fig. 10. The first posterior tergocoxal muscle, an elevator of the wings (above), and the subalar muscle (below) of the mesothorax of *Melanoplus* are active during leg movements while the wings are still. The two are often synchronous and show similar trends toward high and low frequency.

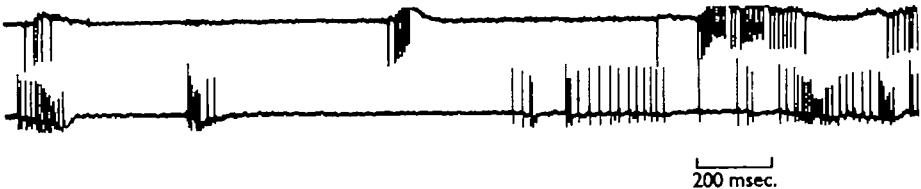


Fig. 11. From the same experiment as Fig. 10, the second basalar muscle (above) and the subalar muscle (below) of the mesothorax show all degrees of simultaneous and independent action during movements of the leg.

and personal communication) and he suggests one muscle may remain active continuously and provide an elastic force against which the second may operate with the advantage that quick recovery is possible. Figs. 10 and 11 are from a preparation which was fixed by the sternum and which had windows cut in the pleuron. The subalar and second basalar muscles could be seen to fibrillate during the leg movements. Records from these adjacent muscles show that electrodes on or in one muscle do not pick up large voltages from nearby ones. The first basalar muscle, which does not attach to the leg, remained still and electrically inactive while the second basalar muscle moved the leg, again demonstrating the independence of muscles which are closely coupled in activity during flight.

DISCUSSION

The results bear out the expectation based on observation of the anatomy that some of the thoracic muscles are used both as wing and leg movers. Since the two kinds of movement are not usually simultaneous some further explanation of how the double function is accomplished is necessary. In order for these muscles to move the wings the wings must be open or free to open. Ordinarily the wings are folded with the hindwings under the forewings, and the latter are clicked in place. A description of how the muscles do open the wings has not yet been worked out, but it is probable

especially vigorous activity. Hoyle (1957, and personal communication) finds that the fast units within the legs themselves are also brought into action only during strong movements. How some of the motor neurons of the intrathoracic musculature can be involved in two locomotory systems will be a subject for future analysis. It is possible that the two systems are rather different in mechanism: that there may be a centrally inherent flight system and a reflex-dependent walking system.

In describing the attachments of these muscles the uselessness of the terms *origin* and *insertion* is apparent. The same is true of many other muscles, for example, the axial muscles of the vertebrate spine, the shell adductors of clams, and the muscle sheets of animals with hydrostatic skeletons. In fact, neatly defined origins and insertions are a special case. For the bifunctional muscles it is also inappropriate to speak of an action in terms of direction of movement of a particular limb. The action of a muscle is to shorten or resist lengthening; what moves depends upon the configuration of the skeleton and other forces applied to it.

SUMMARY

1. Recording electrical activity of certain dorso-ventral muscles in the thorax of grasshoppers has shown that the same muscles and (in at least one muscle) the same motor units may be used to move either the wings or the legs.

2. The anatomical connexions are such that muscles which are antagonists with respect to the wings are synergists with respect to the legs, and vice versa.

3. These muscles, which operate in a nearly perfectly repeating, fixed pattern during flight, show complete independence during manœuvres involving the legs and it is concluded that the flight pattern is not due to a fixed set of connexions between the motor neurons.

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