

## STUDIES OF THE INNERVATION AND ELECTRICAL ACTIVITY OF FLIGHT MUSCLES IN THE LOCUST, *SCHISTOCERCA GREGARIA*

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### INTRODUCTION

The main flight muscles of the locust are large and are considered to be of the 'fast', non-facilitating type (Wilson & Weis-Fogh, 1962). However, some of the accessory group of indirect flight muscles in the locust, e.g. the tergopleural and sternopleural muscles, are thought to be 'slow' muscles (Wilson & Weis-Fogh, 1962). These 'slow' muscles probably help to determine the elasticity of the thoracic box and could be innervated by inhibitory neurones as well as by excitatory neurones. Furthermore, several of the muscles involved in flight are also involved in walking and maintenance of posture, and these bi-functional muscles (Wilson, 1962) may also require the very fine central nervous control normally associated with an innervation containing tonic components.

Ewer (1954, 1957) found that certain prothoracic muscles of the cricket *Acanthacris* did not respond with twitch contractions when directly stimulated with low-frequency shocks. Further experiments on the thoracic muscles of acridids, this time on muscles of *Locusta*, led him to conclude that there are functional differences between the various thoracic muscles. Muscles which gave a large mechanical response to a single direct stimulus were termed 'twitch' muscles, whereas those which only gave an appreciable contraction to high-frequency stimulation were termed 'tonic' muscles. Other muscles with properties intermediate between those of the 'twitch' and 'tonic' types were classified as 'twitch/tonic'. Usherwood (1962) studied the innervation and electrical activity of some of these muscles and found that most of the 'twitch' muscles were exclusively innervated by 'fast' motoneurones, whereas a few 'twitch' muscles and the 'tonic' and 'twitch/tonic' muscles received endings from 'slow' excitatory neurones as well as 'fast' excitatory neurones. Indeed, in some fibres of the 'tonic' muscles two types of 'slow' potential were recorded in response to neural stimulation. At the time these two potentials were identified as  $S_{1a}$  and  $S_{1b}$  potentials (Hoyle, 1955).

The majority of the investigations of the flight motor system of the locust have been made using extracellular electrodes for monitoring the electrical activities of the flight muscles (e.g. Wilson, 1962, 1964; Wilson & Weis-Fogh, 1962). Although information on 'fast' excitatory muscle potentials can be readily obtained with these electrodes they are much less suitable for studying smaller responses such as 'slow' excitatory and inhibitory potentials (Runion & Usherwood, 1966). These smaller potentials can,

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however, be readily recorded using intracellular micro-electrodes, and it is somewhat surprising that the intracellular recording technique has rarely been used for studying the innervation and electrical activity of locust flight muscles. With this in mind it seemed pertinent to investigate the neurally evoked electrical responses of some of the flight muscles of *Schistocerca*, using intracellular micro-electrodes. In doing so we have selected on the one hand two large power muscles and on the other hand two accessory flight muscles. The results of this study together with a summary of the results obtained by Usherwood (1962) are made the subject of this publication.

#### METHODS

Adult male locusts (*Schistocerca gregaria*) were used. They were obtained from colonies fed on grass and Bemax and maintained at 32° C. The abdomen, legs and wings were removed and a half-side preparation of the right thorax was made. The gut was cut in the neck and pulled out leaving the head, connectives and thoracic ganglia unimpaired. The preparation was then pinned down on a wax block with the tergum and coxal segments fixed so as to reduce to a minimum movement of the thoracic muscles during contraction.

One metathoracic muscle (M 120) (Snodgrass, 1929) and three mesothoracic muscles (M 90, M 91 and M 99) were studied in this investigation. These muscles were excited indirectly, either by electrical stimulation of their innervation or by reflex stimulation using an air stream to excite sense organs on the head (Weis-Fogh, 1956). The electrical activity of these muscles was recorded intracellularly (3 M-KCl glass micro-electrodes) and extracellularly (copper electrodes, 70  $\mu$  diam.). The extracellular electrodes were inserted right into the centre of the muscles. The nerves to the surrounding muscles were cut. Electrical recordings from the nerves which innervate M 90, M 91, M 99 and M 120 were made using bipolar electrodes (Ag/AgCl). The muscles were perfused continuously with locust saline (Usherwood, 1968), care being taken to ensure that the spiracles were not blocked as a result of this since the muscle preparations quickly deteriorated when their air supply was cut off. The experiments were carried out at room temperature (approx. 22° C.).

M 90, M 91, M 99 and M 120 and their nerves were also studied histologically. They were fixed in Bouin's solution, embedded in paraffin wax and cut transversely (6  $\mu$  sections). The sections were stained by the Haematoxylin-Eosin method.

#### RESULTS

The three mesothoracic muscles, M 90, M 91 and M 99 are innervated by about eight large axons (up to 20  $\mu$  diam.), three medium axons (up to 5  $\mu$  diam.) and at least three small axons (< 2  $\mu$  diam.) which run in mesothoracic nerve 4 D (Fig. 1 and Table 1). M 120 is homologous with M 91 and is innervated by axons contained in metathoracic nerve 4 D.

#### *M 99 (The mesothoracic subalar muscle)*

Two groups of muscle fibres, a rostral group and a caudal group, can be clearly discerned in transverse sections of M 99 (Fig. 2). A branch of mesothoracic nerve 4 D containing two large axons enters the gap between the two groups of fibres about

halfway along the muscle. The two axons initially run and branch together but they finally separate, with one axon innervating the caudal fibres and the other the rostral fibres.

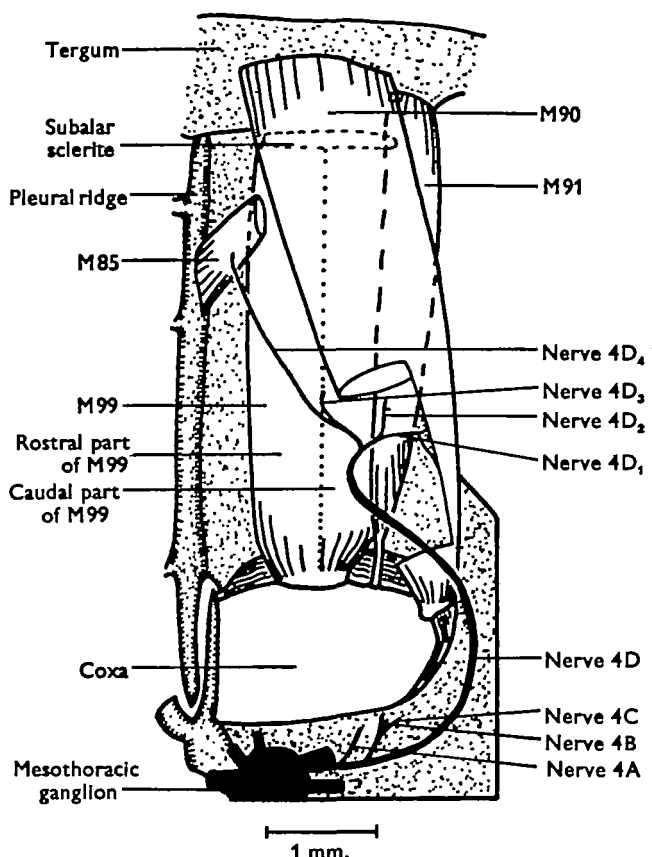


Fig. 1. Right half of mesothorax of *Schistocerca gregaria*. Musculature and innervation of the epimeral part. Muscles numbered according to Snodgrass (1929). Nerves numbered according to Campbell (1961).

Most intracellular recordings from M 99 were obtained from superficial fibres which gave resting potentials ranging from  $-40$  to  $-60$  mV. Similar resting potentials were recorded from fibres of M 90, M 91 and M 120. When mesothoracic nerve 4 D was stimulated maximally more or less identical electrical responses were seen in all fibres of M 99. They consisted of a large excitatory postsynaptic potential plus a large graded electrically excited response which sometimes overshoot zero potential. By grading the intensity of stimulation it was possible to demonstrate two steps in the height of the extracellular potential recorded from M 99 (Fig. 3). The first step in the extracellular record represents firing of one motor unit, either the rostral or the caudal unit, while the second step results from the additional activity of the other unit. This confirms the findings of Wilson & Weis-Fogh (1962) and our anatomical findings described above. Small differences in latency between the responses of the rostral and caudal units and differences in the thresholds of the two 'fast' axons were sometimes seen but these probably resulted from asymmetries in the stimulation system

Table 1. *Summary of electrophysiological and histological studies of some thoracic muscles of Schistocerca and Locusta*

Muscle no.	Neurally evoked responses	Innervation			Results for <i>Locusta</i> (Ewer, 1957)
		Large axons (5-20 $\mu$ ) diam.	Medium axons (2-5 $\mu$ ) diam.	Small axons (< 2 $\mu$ ) diam.	
90	3 'fast' excitatory	3	0	?	Twitch muscle
91	1 'fast' excitatory 1 'slow' excitatory 1 inhibitory	3	3	0	Tonic/twitch muscle
99	2 'fast' excitatory	2	0	0	Twitch muscle
120	1 'fast' excitatory 1 'slow' excitatory 1 inhibitory	3	2	3	Twitch muscle
60*	1 'fast' excitatory 1 'slow' excitatory	—	—	—	Tonic muscle
81*	1 'fast' excitatory	—	—	—	Twitch muscle
87*	1 'fast' excitatory 1 'slow' excitatory 1 inhibitory?	1	1	1	Twitch muscle
88*		—	—	—	Tonic muscle
92*		1	1	1	Twitch muscle
94*		—	—	—	Tonic muscle
95*		—	—	—	Tonic muscle
96*	—	—	—	Twitch muscle	

\* Results of studies made by Usherwood (1962) on *Locusta* and *Schistocerca*.

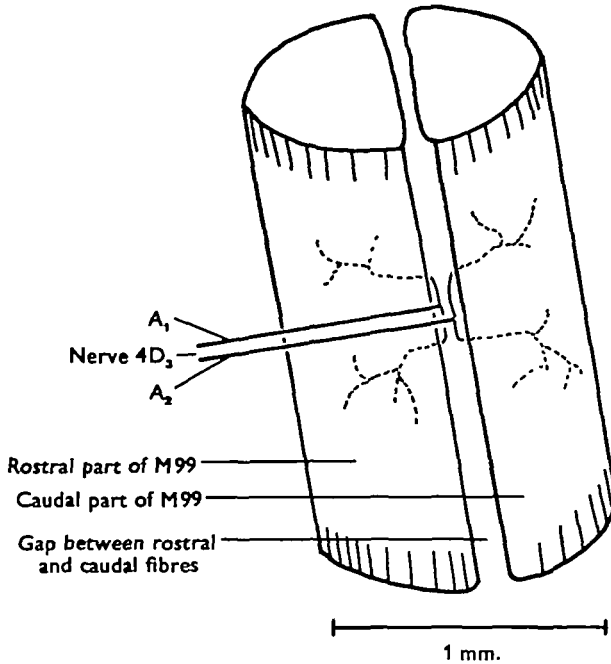


Fig. 2. Schematic drawing of the right mesothoracic subalar muscle (M99) and its innervation. Each part of this muscle is innervated by a separate large motor axon (A<sub>1</sub>, A<sub>2</sub>).

rather than from differences in the properties of the two axons which innervate M 99. It is concluded, therefore, that each fibre of M 99 receives endings from one 'fast' axon and that this muscle consists of two 'fast' motor units only.

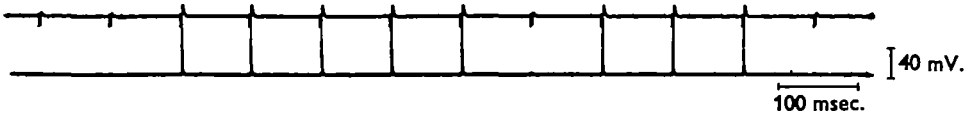


Fig. 3. Extracellular (upper trace) and intracellular recording (lower trace) from M 99. The muscle was excited indirectly through mesothoracic nerve 4 D. The extracellular record shows the responses of two units occurring at different stimulus intensities. The intracellular record was obtained from a fibre in the caudal part of M 99 and shows that this fibre is innervated by only one of the motoneurons which supplies M 99.

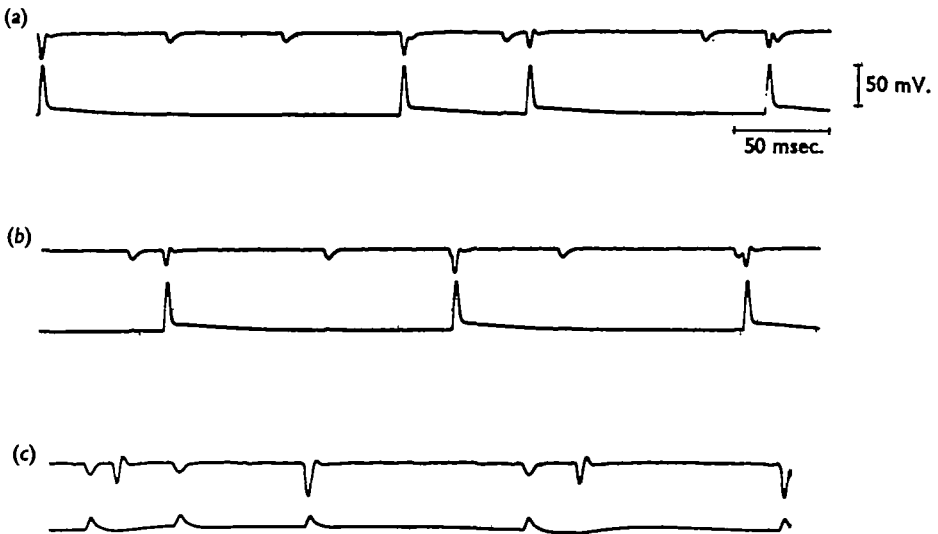


Fig. 4. Extracellular (upper trace) and intracellular recordings (lower trace) from M 99 during 'flight' activity. The intracellular electrode was first located in a fibre of the caudal unit of M 99 (a-b) and then in a slightly damaged fibre of the rostral unit (c). Although the two motor units sometimes fired independently there was a tendency for simultaneous activity of both units (see Fig. 5).

During normal flight M 99 fires at a constant frequency of about 17 Hz, i.e. the wing-beat frequency. The firing frequency is influenced to some extent by the input from a stretch receptor associated with the wing articulation (Wilson & Gettrup, 1963). In our preparations regular activity of M 99 was obtained by blowing on the head of the locust (Fig. 4). 'Fast' potentials occurred at a frequency of 10-20/sec. and the pattern of activity was not unlike that which occurs during normal flight (Wilson & Weis-Fogh, 1962). However, since the thoracic box was firmly fixed in position during exposure of M 99 and mesothoracic nerve 1, which contains the afferent fibres from the wing stretch receptor, was cut, it would be unwise to assume that it was normal flight activity. Nevertheless, the firing frequency during this reflex response was normally very constant and close to the flight frequency, and it was possible to obtain information on the relative activities of the two units comprising M 99 during this

'flight' response. To some extent the units functioned independently during this reflexly-evoked activity, although there was always a tendency towards simultaneous firing of both units (Wilson & Wyman, 1965), with the rostral unit the more active member of the pair (Figs. 4 and 5).

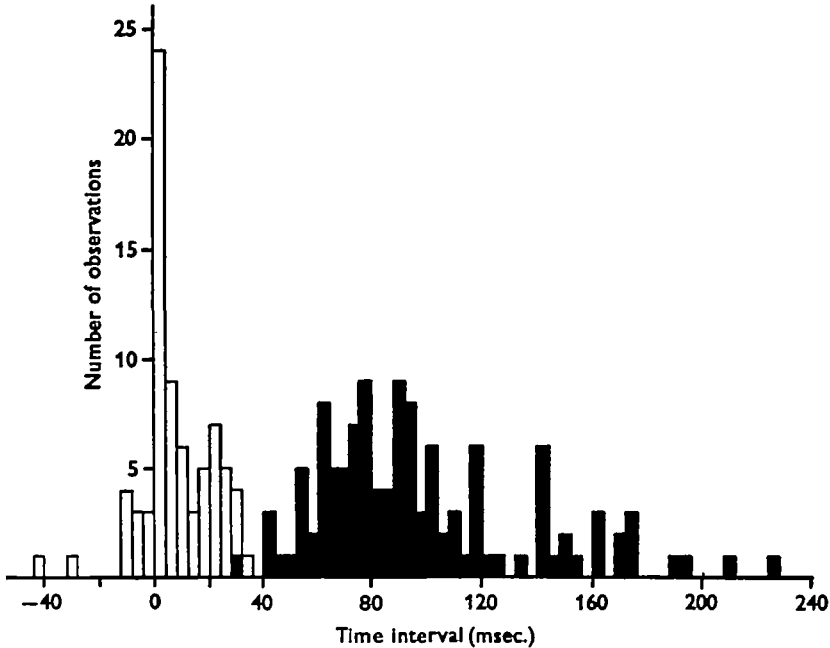


Fig. 5. Analysis of data from M 99 obtained during 'flight' activity. ■ Distribution of time intervals ( $\Delta t_1$ ) between spikes of the rostral unit of M 99. □ Distribution of time intervals ( $\Delta t_2$ ) between spikes of rostral unit and caudal unit. When the caudal unit fired before the rostral unit the time interval was given a negative value. Ordinate: number of occurrences. Abscissa: time interval ( $\Delta t_1$  or  $\Delta t_2$ ) in msec. Since the time between firing of the rostral and caudal units is usually less than half the peak time interval between the spikes of the rostral unit it follows that the two units do not fire independently but are loosely coupled, i.e. there is a tendency towards synchronous firing. In fact there was a significant ( $P < 0.05$ ) bivariate distribution of the intervals between spikes of the rostral unit and caudal unit (Kolmogoroff-Smirnoff test).

During normal flight some of the flight muscles of *Schistocerca* are activated twice or even three times per wing-beat cycle (Wilson & Weis-Fogh, 1962). It seemed of interest, therefore, to investigate the effect of closely spaced nerve impulses on the intracellular responses of M 99. Both axons innervating M 99 were refractory for about 5 msec. after generating an action potential (Fig. 6). The absolute refractory period of the electrically excitable membrane of M 99 could not be measured accurately using neural stimulation because of the refractoriness of the motor axons. However, neural stimulation of M 99 could be used to investigate the relative refractoriness of this muscle. Apparently this lasts for about 30 msec. During 'flight' activity, M 99 was often activated three times in quick succession, the last two responses occurring within the relative refractory period of the first response. To determine how the third response was influenced by the refractoriness induced in the electrically excitable muscle membrane by the first two

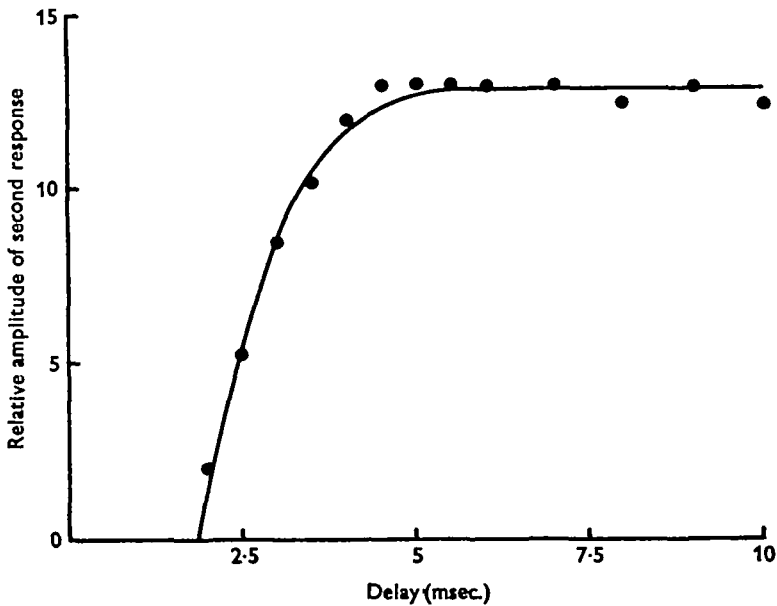


Fig. 6. Graph demonstrating refractoriness of nerve 4D<sub>2</sub>. The nerve was excited with pairs of stimuli, the delay between the first and second stimulus being progressively reduced. The recording and stimulating electrodes were placed very close together on nerve 4D<sub>2</sub> and it was possible, therefore, to measure relative and absolute refractory periods.

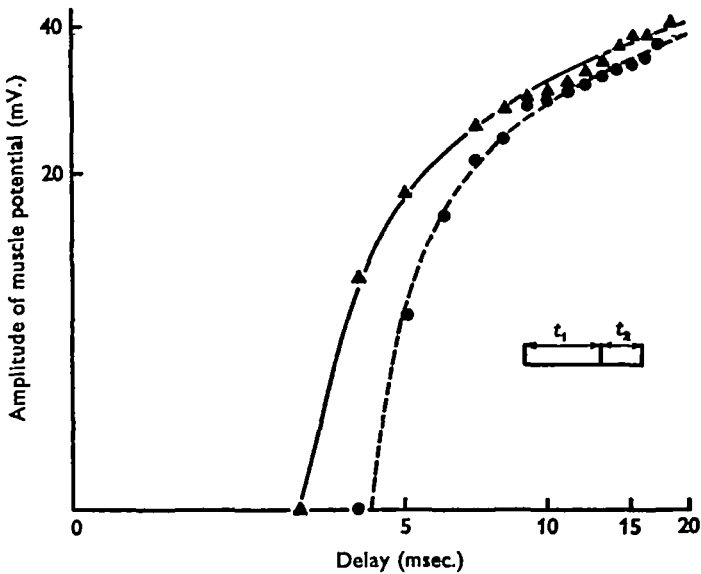


Fig. 7. Refractoriness of a fibre of M 99. Abscissa: delay between the first stimulus and the second stimulus ( $t_1$ ) and the second stimulus and third stimulus ( $t_2$ ). Ordinate: amplitude of the second response (circles) and third response (triangles). The muscle was stimulated through mesothoracic nerve 4D. The three stimuli were given within a period of 20 msec. (see inset) and repeated at 1 sec. intervals. The muscle potentials were recorded intracellularly and the amplitude of the first response was 45 mV. See text for further explanation.

responses, M 99 was stimulated indirectly three times within 20 msec., the set of three stimuli being repeated at 1 sec. intervals. The time interval between the first two stimuli ( $t_1$ ) and the second two stimuli ( $t_2$ ) was varied between 1 and 19 msec. The results of this analysis are illustrated in Fig. 7 and clearly demonstrate how the magnitude of the neurally evoked potential can be graded by varying the interval between responses. The upper limit to the firing frequency of M 99 is determined by the duration of the refractory period of the motoneurons which innervate this muscle. Even if M 99 is activated when its electrically excitable membrane is in a state of absolute refractoriness, an excitatory synaptic potential will still be generated. This is because the synaptic membrane does not exhibit refractoriness (Cerf, Grundfest, Hoyle & McCann, 1959). However, the magnitude of the synaptic response is profoundly affected by synaptic fatigue. Indeed, when M 99 is excited continuously at a frequency of 20 Hz the amplitude of the muscle response declines owing to a decrease in the height of the synaptic component. At a frequency of 40 Hz the muscle units no longer responded to every stimulus and sometimes fired alternately. At even higher frequencies the relationship between stimulus and response of M 99 became very unclear.

#### *M 90 (The first mesothoracic remotor coxae muscle)*

The fibres of M 90 are not clearly divided anatomically into distinct groups. The neurones which innervate this muscle branch profusely within the muscle. It was not clear from the histological studies whether individual fibres are innervated by more than one neurone.

Potentials of three different sizes were recorded extracellularly from M 90 during graded electrical stimulation of mesothoracic nerve 4 D. The stepwise increase in height of the extracellular response which occurred as the stimulus intensity was raised, was due to the recruitment of first one, then two and then finally three populations of fibres. Each population of fibres was found to be innervated by a single 'fast' motoneurone and therefore, during maximal stimulation of nerve 4 D every fibre of M 90, gave a typical 'fast' electrical response. This was the only type of electrical response recorded from M 90 so presumably this muscle contains three physiologically distinct 'fast' motor units as described previously by Kutsch (1969).

#### *M 91 (The second mesothoracic remotor coxae muscle)*

Some fibres of M 91 are clearly innervated by only a single 'fast' neurone. However, other fibres of this muscle are polyneuronally innervated and from these fibres three different-sized potentials were often recorded intracellularly during both reflex stimulation and electrical stimulation of nerve 4 D (Fig. 8). The largest responses recorded from the triply innervated fibres were 'fast' excitatory potentials, about 40 mV. in amplitude. Medium-sized depolarizing potentials 15–30 mV. in amplitude and about 15 msec. in duration and small depolarizing potentials 3–10 mV. in amplitude and about 30 msec. in duration were also recorded. The small responses were evidently depolarizing inhibitory post-synaptic potentials (IPSPs) (see later), because the medium-sized potentials were attenuated when they occurred during a small potential, the attenuation being most pronounced when the medium-sized potential



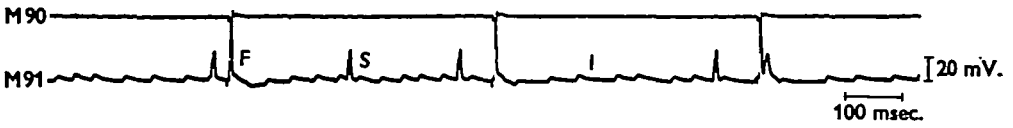


Fig. 8. Upper trace: extracellular recording from M 90. Lower trace: intracellular recording from a triply-innervated fibre of M 91. Note synchronous 'fast' activity (F) of M 91 and M 90. Also note the occurrence of medium-sized potentials ('slow' excitatory) (S) and small potentials (IPSPs) (I) in record from M 91. The large 'fast' potentials were evoked by stimulating nerve 4 D and are followed in the intracellular record by a mechanical artifact.

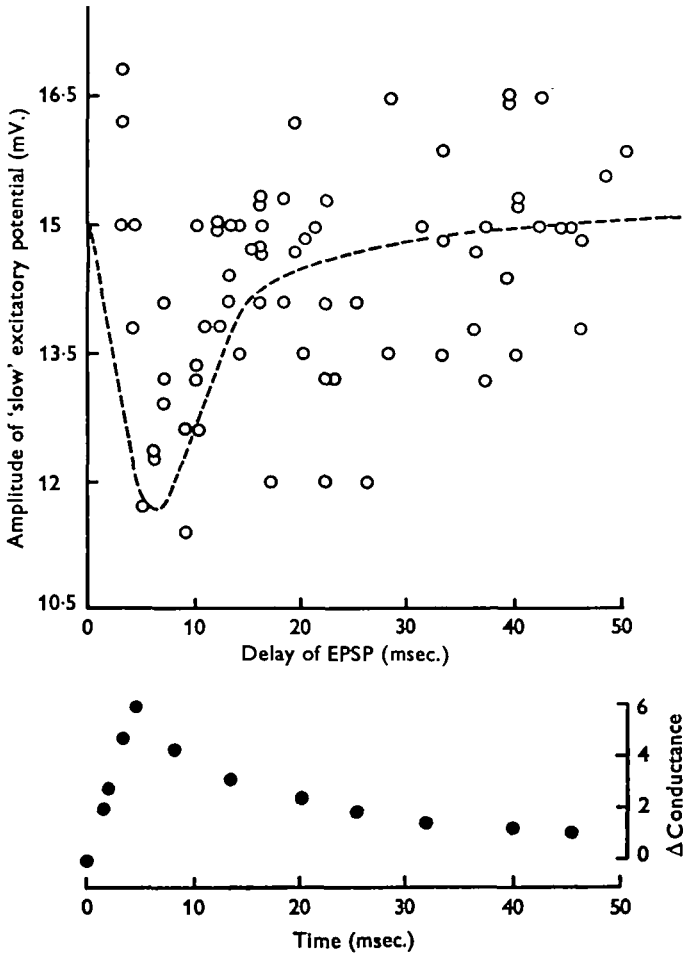


Fig. 9. Change in amplitude of a medium-sized ('slow' excitatory) potential recorded intracellularly from a fibre of M 91, when it occurred during a small depolarizing potential (IPSP). Abscissa: delay between beginning of IPSP and beginning of 'slow' response. Ordinate: amplitude of the 'slow' response measured from the resting membrane potential to the peak of the response (i.e. includes IPSP). Note that the amplitude of the 'slow' potential shows considerable variation. (Curve fitted by eye.)

Below: time course of the increase in membrane conductance during an IPSP (adapted from Usherwood & Grundfest (1965)). Note that time of maximum attenuation of EPSP by a small depolarizing potential corresponds with time of maximum conductance increase at inhibitory synapses.

occurred 5–10 msec. after the beginning of the small potential (Figs. 9 and 10*a*). Only 'fast' potentials were recorded from fibres in the rostral part of M 91 whereas all three types were seen in fibres in the middle part of this muscle. In the caudal part the small potentials were absent.

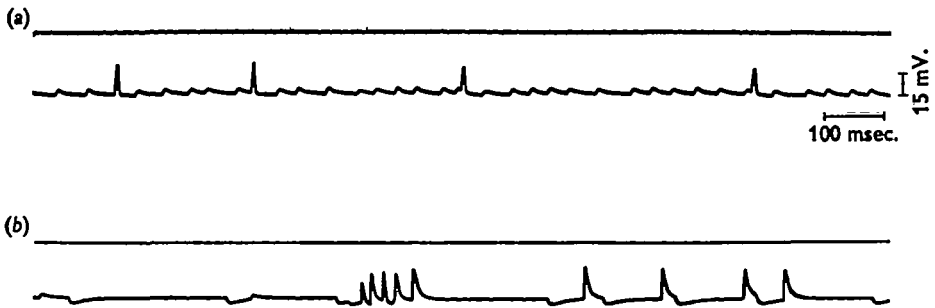


Fig. 10. Intracellular recordings from (a) M 91 and M 120 showing attenuation of 'slow' excitatory potentials by IPSPs. In (a) the IPSPs were depolarizing responses whereas in (b) they were hyperpolarizing responses. The top trace in each record represents zero potential.

#### *M 120 (The second metathoracic remotor coxae muscle)*

A nerve branch containing two large axons enters the rostral part of M 120. The caudal part of this muscle is innervated by one large axon and several smaller axons (Table 1). During neural stimulation large 'fast' excitatory responses were recorded intracellularly from all the fibres of M 120. These were the only type of potential recorded from the rostral fibres whereas medium-sized and small depolarizing responses were also recorded from the caudal fibres (Fig. 11). In two preparations of M 120 the small depolarizing potentials were absent and in their place hyperpolarizing postsynaptic potentials (IPSPs) were observed (Fig. 10*b*). In all probability, therefore, the small depolarizing responses represent depolarizing IPSPs arising from the activity of an inhibitory neurone whereas the medium-sized potentials represent 'slow' excitatory responses. Although the IPSPs recorded from insect muscle fibres are normally hyperpolarizing responses, Usherwood (1968) has demonstrated that under certain conditions (e.g. where difficulty of dissection results in exposure of the muscle preparation to high levels of potassium) the IPSPs are reversed to depolarizing responses.

#### *Summary of earlier observations*

The results of studies by Usherwood (1962) on some of the mesothoracic muscles of *Schistocerca* and *Locusta* are summarized in Table 1. These muscles include some of Ewer's 'tonic' muscles (Ewer, 1957) and all are innervated by at least one 'fast' excitatory neurone. What distinguishes Ewer's 'tonic' muscles from his 'phasic' muscles is that whereas the latter receive endings from only 'fast' excitatory neurones, the former are also innervated by neurones of the 'slow' excitatory type and by inhibitory neurones. At the time these earlier observations were made the inhibitory responses were classified as  $S_{1a}$  responses (Hoyle, 1955). However, it has since been demonstrated that in M 92 these  $S_{1a}$  potentials are in fact IPSPs i.e. Hoyle's  $S_2$  potentials (Usherwood, 1968). M 92 has since been studied very thoroughly by Hoyle

(1966*a, b*) and by Usherwood (1968) and has been shown to be innervated by one 'fast' and one 'slow' excitatory neurone and a single inhibitory (inhibitory conditioning) neurone. In this muscle only a fraction (about 40%) of the fibres respond to the 'slow' excitatory neurone and to the inhibitory neurone, and there is a clear-cut anatomical and physiological differentiation of the muscle into 'phasic' and 'tonic' regions. All the fibres of M 87 on the other hand are innervated by the three types of motor neurone.

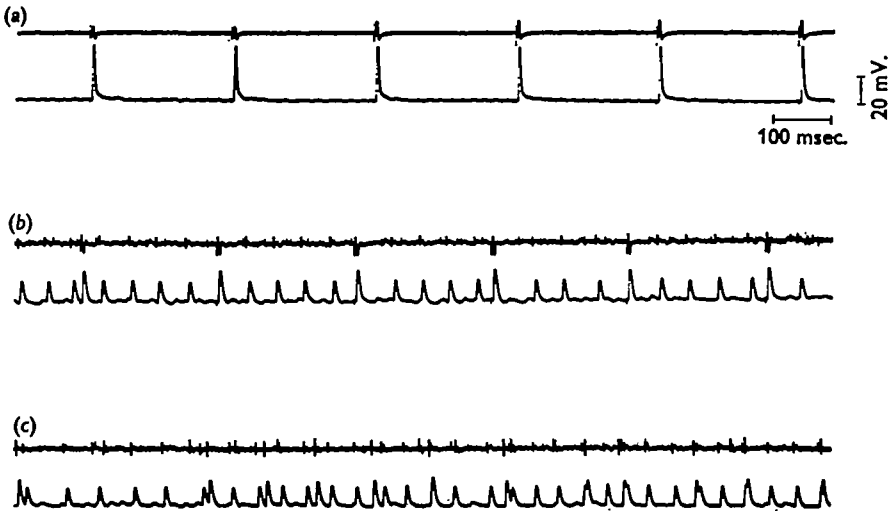


Fig. 11. Intracellular recordings (lower traces) from a fibre of the rostral part (*a*) and caudal part (*b-c*) of M 120. The rostral fibre was innervated by a single 'fast' neurone only and responded only during stimulation of metathoracic nerve 4 D. The upper trace in (*a*) is an extracellular recording from M 120. The caudal fibres (*b-c*) were triply-innervated. 'Fast' and 'slow' excitatory responses and depolarizing IPSPs were recorded from these fibres (see text). The excitatory and inhibitory neurones were spontaneously active while 'fast' responses were evoked by stimulating metathoracic nerve 4 D (*b*) or by mechanical stimulation of the metathoracic ganglion (*c*). The 'fast' and 'slow' muscle potentials can be clearly correlated with the potentials recorded extracellularly from the nerve innervating M 120, which are illustrated in the upper traces of (*b*) and (*c*).

#### DISCUSSION

Wilson & Weis-Fogh (1962) suggested that muscles containing a few all-or-nothing elements or 'fast' motor units were sufficient for satisfactory performance of flight activity in the locust. Indeed it has been clearly confirmed in the present studies that two of the flight muscles of this insect, a depressor (M 99) and an elevator (M 90) are of this type. However, other flight muscles, e.g. the two elevators M 91 and M 120 contain a distinct population of fibres innervated by three different types of neurone and two of these neurones, i.e. the 'slow' excitatory neurone and the inhibitory neurone, probably serve a tonic rather than a phasic function. Undoubtedly the phasic activity of M 91 and M 120 during flight is controlled through their 'fast' motor innervation. Since every fibre in these muscles is innervated by a 'fast' motoneurone it follows that every part of the muscle can be used to move the wings, provided of course that the muscle fibres themselves are phasically responsive (Usherwood, 1967;

Cochrane, Elder & Usherwood, 1969). The role(s) of the 'slow' excitatory and inhibitory neurones which innervate M<sub>91</sub> and M<sub>120</sub> is uncertain since they appear to discharge tonically even during 'flight' activity. Perhaps these neurones are involved in determining the elasticity of the thoracic box as proposed by Wilson & Weis-Fogh (1962). There certainly appears to be no reason why the two modes of activity, i.e. tonic and phasic, should not proceed together during flight and involve the same muscle fibres.

It should be recalled that most of the big thoracic muscles in *Schistocerca* are attached not only to the wings but also to the coxae. Although the wings are held in position during walking by a skeletal disk mechanism there are no known skeletal mechanisms for holding the legs in position during flight. It has been proposed that the absence of leg movements during straight flight depends upon the fact that the bifunctional muscles are antagonistic during walking but synergistic during flight. Therefore the coxae are held in position during flight by simultaneous activation of the bifunctional muscles (Wilson, 1962). It is equally probable, however, that during flight tonic activity of the bifunctional muscles ensures that the coxae are held firmly in position. Very fine control of the tension developed by these muscles could be achieved through their inhibitory innervation, and changes in the magnitude of the tonic contractions could be used to adjust the position of the legs. It is known that steering during flight can be accomplished by controlling the position of the legs (Dugard, 1967).

This is, of course, not the first account of flight muscles in insects with surprisingly complex innervations. The intracellular micro-electrode technique was used by Ikeda & Boettiger (1965*a, b*) to investigate the innervation and electrical activity of the longitudinal and dorsoventral flight muscles of the bumble bee, *Bombus*, and the basalar flight muscle of the beetle, *Oryctes rhinoceros*. They found that the dorsoventral muscle of the bee was innervated by 'fast' and 'slow' excitatory neurones and probably also by an inhibitory neurone. The basalar muscle of the beetle was also found to have a very complex innervation which included an inhibitory neurone. Darwin & Pringle (1959) proposed that this muscle provides power for the downstroke as well as adjusting the angle of attack of the wing. Presumably the power response could be controlled by its 'fast' motoneurones whilst the regulatory properties could be mediated via its 'slow' excitatory and inhibitory innervation. The reason for the complex innervation of the dorsoventral muscle of the bee remains somewhat doubtful since there is no evidence that this indirect flight muscle has the regulatory action during flight that would require the fine control that could be achieved through its 'slow' excitatory and inhibitory innervation (Ikeda & Boettiger, 1965*a*).

Usherwood & Grundfest (1965) pointed out that in the metathoracic extensor tibiae muscle of *Schistocerca* only fibres innervated by a 'slow' excitatory neurone receive endings from an inhibitory neurone. Apparently this is also the rule in the thoracic muscles of this insect. In some muscles with inhibitory as well as excitatory input the muscle fibres are arranged in groups according to their innervation properties, fibres with inhibitory and excitatory endings being spatially separate from those with excitatory endings only. Since all the fibres in these muscles have a common insertion the reason for this spatial arrangement is not readily apparent. Perhaps the mechanical properties of the fibres varies according to their innervation, those with 'fast' endings

only being phasically responsive; those with 'slow' excitatory and inhibitory innervation being tonically responsive.

The discovery of inhibitory neurones innervating locust flight muscles is not particularly surprising. It was thought at one time that this type of innervation in insects was a rarity but recent work has demonstrated that this is far from the truth and that peripheral inhibitory neurones in insects may be very 'common' indeed (Pearson & Bergman, 1969).

## SUMMARY

1. Four flight muscles, one depressor (M 99) and three elevators (M 90, M 91 and M 120) of the wings of the locust *Schistocerca gregaria* have been investigated using extracellular and intracellular recording techniques. The innervation and anatomy of these muscles have also been studied histologically.

2. Every fibre in each of these muscles is innervated by 'fast' motoneurones. M 99 contains two anatomically distinct 'fast' motor units. M 90 contains three 'fast' motor units.

3. M 91 and M 120 are innervated by at least one 'slow' excitatory and one inhibitory neurone as well as by a 'fast' excitatory neurone. Sometimes the inhibitory responses recorded from fibres of these muscles appeared as depolarizing IPSPs.

4. The roles of these muscles in the behaviour of the locust, especially during flight performance, are discussed.

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