THE NEURAL CONTROL OF SWIMMERET BEATING IN THE LOBSTER

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INTRODUCTION

One of the most important functions of the nervous system is to produce special patterns of motor nerve activity which can be translated by muscles into co-ordinated movements. If the movements are to have adaptive significance, they must naturally be initiated and modified in accord with sensory information. There is now considerable evidence, however, that the motor patterns underlying many types of animal behaviour are endogenous to the central nervous system, i.e. their major features are determined by the structural and functional connectivity of central nerve cells, and not by sensory inflow or feedback (see Wilson, 1966, for a review).

One of the clearest examples of an endogenous motor output pattern is available in the abdominal swimmeret system of crayfish and lobsters. The elimination of all sensory inflow and feedback to the ganglionic swimmeret 'centres' does not prevent them from producing motor discharge patterns similar to those which cause swimmeret beating. The cyclic patterns occur either spontaneously or in response to continuous electrical stimulation of the appropriate command interneurones (crayfish, Hughes & Wiersma, 1960; Ikeda & Wiersma, 1964; Wiersma & Ikeda, 1964; lobsters, W. J. Davis, unpublished data). Owing to the ease with which the patterns can be elicited from isolated abdominal ganglia, and to the increasing availability of information concerning the structure of the ganglia (Kendig, 1967; Otsuka, Kravitz & Potter, 1967; Stretton & Kravitz, 1968), the swimmeret system offers the possibility of attaining a reasonably complete understanding of the central nervous mechanisms underlying a complex, endogenous motor output pattern. To this end a series of investigations of lobster swimmeret beating has been undertaken. This series has included a study of the swimmeret movements, their behavioural roles and their sensory control by the statocyst receptors (Davis, 1968a, b). A quantitative analysis of high-speed motion pictures of the swimmeret movements has been performed, providing constraints for models of the underlying neural mechanisms (Davis, 1968c). The anatomy and innervation patterns of the swimmeret muscles have been described, and the over-all pattern of neuromuscular activity underlying swimmeret beating has been determined from recordings of the electrical activity of the muscles of intact, unrestrained lobsters (Davis, 1968d).

In the present report the control of the movements of individual swimmerets is described in terms of the activity of single motor nerve cells. Attention is focused in

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particular on the neural regulation of the forces produced during each movement cycle, the relative timing of the activities of the motoneurones supplying a swimmeret, the role of peripheral inhibition in the control of the direction of the powerstroke of each swimmeret, and the temporal patterns of nerve impulses within single swimmeret motoneurones.

MATERIALS AND METHODS

Eastern lobsters (*Homarus americanus*) were used. The electrical activity of the swimmeret muscles of intact, unrestrained lobsters was recorded through electrodes of fine copper wire. The movement of the swimmeret was recorded at the same time, using a movement transducer described by Sandeman (1968). The electromyograms and movement recordings were displayed on a Tektronix dual-beam oscilloscope for streak photography with a Grass camera. Details of the methods are given in another paper (Davis, 1968d).

RESULTS

Interpretation of records

The muscles of arthropods are generally innervated by a relatively small number of motoneurones. As a consequence, the activity of single motoneurones can often be distinguished in electrical recordings made through wire electrodes implanted into the muscles. In some preparations such recordings have been made at the same time as recordings from the motoneurones innervating the muscle (insects, Runion & Usherwood, 1966; crustaceans, Wilson & Davis, 1965). These preparations have provided a direct demonstration of the one-to-one correlation between muscle potentials recorded with implanted leads and action potentials in the corresponding motoneurones.

In the present work the neural activity underlying swimmeret beating has been studied by implanting wire electrodes into the muscles. Potentials recorded from the muscles were considered to correspond to activity in a single motoneurone only if their amplitude was constant within the limits imposed by neuromuscular facilitation, and if they were always separated by at least 4 msec., an interval which approximates the absolute refractory period of single motoneurones. Records meeting these criteria were obtained in about one-quarter of the more than 150 separate experiments.

General features of the motor output pattern

The general spatio-temporal features of the neuromuscular activity underlying the movements of each swimmeret are described in another paper (Davis, 1968d). Each swimmeret is controlled by twelve muscles, which produce six basic movements; the powerstroke, the returnstroke, opening of the rami, closing of the rami, curling of the rami and rotation of the basipodite. Each of the muscles is active cyclically during swimmeret beating, at a characteristic position in the cycle. The temporal sequence in which the muscles become active shows little variation from cycle to cycle.
Variation in the number of muscle potentials per cycle

The number of potentials recorded from a swimmeret muscle during its active period increases as the duration of the corresponding movement cycle decreases, i.e. as the frequency of swimmeret beating increases (Fig. 1). This relationship characterizes the activity of each muscle, regardless of the specific movement it produces. Variation in the number of muscle potentials per cycle could result either

![Graph showing the relationship between the number of muscle potentials and the duration of the movement cycle.](image)

**Fig. 1.** Number of potentials per movement cycle in a powerstroke muscle plotted against the cycle duration (time between the beginning of successive power strokes). $r$ is the correlation coefficient between the two variables. Part of the record analysed in this graph is shown in Fig. 2.

(a) Low-frequency beating, showing the activity of a single motoneurone. (b) High-frequency beating, showing the increase in the number of active motoneurones. In (b), note the frequency division in the 'cross-talk' which was inadvertently recorded from a nearby returnstroke muscle.

from variation of the number of active motoneurones or from variation of the activity of single motoneurones. Both of these methods are in fact employed. As the frequency of swimmeret beating increases, the number of motoneurones which fire during each cycle increases (Fig. 2), and the number of impulses per cycle within single motoneurones increases (Fig. 3).
Exceptions to the above general rule were occasionally seen. In Fig. 4, for example, the number of muscle potentials per cycle in muscle 16, which opens the rami near the beginning of each powerstroke (Davis, 1968d), suddenly began to decrease rapidly despite a maintained and then increased frequency of swimmeret beating. During the latter part of this record the opening movement of the rami was abnormally weak and finally altogether absent, as would be expected, but the remaining swimmeret movements appeared normal. The normal motor discharge to muscle 16, as well as the normal opening movement of the rami, was restored after a short period of rest. These observations suggest that the anomalous motor discharge was caused simply by a localized decrease in the excitability of a small number of motoneurones, rather than by a widespread change in motoneurone responsiveness or by a normal variation in the operation of the central nervous control mechanisms.

Temporal aspects of activity in single swimmeret motoneurones

Duration of bursts in single motoneurones. The duration of the burst of impulses per cycle within each swimmeret motoneurone is independent of the frequency of swimmeret beating (Fig. 5). The burst duration cannot be correctly described as constant, however, because the degree of scatter in its distribution is large relative to the value of the mean. The mean value of the burst duration varies for different motoneurones, ranging between approximately 100 and 250 msec. As shown in the preceding section, the number of impulses per burst increases with the frequency of swimmeret beating. Since the burst duration is independent of the frequency of
Fig. 4. A continuous record from muscle 16, which opens the rami at the beginning of each powerstroke (Davis, 1968d), showing an anomalous decline in the activity of the motoneurones despite an increase in the beating frequency. Normal records were again obtained from this preparation following a short period of rest.

Fig. 5. Duration of the burst of impulses in a single powerstroke motoneurone plotted against the duration of the corresponding movement cycle. The two variables are independent, since the correlation coefficient, $r$, is not significantly different from zero. Part of the record analysed in this graph is shown in Fig. 3.
beating, the average frequency of the impulses in each burst is directly proportional to the frequency of swimmeret beating.

**Duration of the total electrical activity of each muscle.** Each swimmeret muscle is innervated by an estimated one to six excitatory axons (Davis, 1968). The electromyograms recorded from single muscles are therefore often fairly complex, representing the overlapping activities of several motoneurones (e.g. Fig. 2b). In these cases the duration of the total electrical activity of the muscle during each movement cycle is dependent upon the frequency of swimmeret beating. As the frequency of beating increases, the duration of the total activity per cycle decreases (Fig. 6). As described in the preceding section, however, the duration of the burst of impulses within each swimmeret motoneurone is independent of the frequency of swimmeret beating. Variation in the duration of the total electrical activity of a muscle must therefore result from variation in the relative timing of the discharge of the motoneurones which innervate the muscle. This deduction is directly confirmed by results described in the next section.

**Variation in the relative timing of the activities of motoneurones innervating the same muscle.** Although the electromyograms recorded from single swimmeret muscles are often complex, representing the simultaneous activities of several motoneurones, it was nevertheless possible in some records to distinguish clearly the activity of two individual motoneurones innervating the same muscle over the entire range of frequencies of swimmeret beating. In such records it was found that the different motoneurones innervating a given muscle begin to fire at different times during the movement cycle (Fig. 7). The time lag between the beginning of bursts in different motoneurones supplying a single muscle sometimes exceeds 50% of the duration of the total electrical activity of the muscle. The duration of this lag is directly proportional to the duration of the corre-
Neural control of lobster swimmerets

sponding movement cycle (Fig. 8). Moreover, the variation in the time lag is of sufficient magnitude to account for the observed variation in the duration of the total electrical activity of the muscle per movement cycle (compare Figs. 6 and 8).

Changes in the position of bursts within the movement cycle. The relative position in the cycle at which a muscle begins its electrical activity usually varies systematically with the frequency of swimmeret beating. During high-frequency beating the bursts

![Fig. 7. Electromyograms from muscle 13, which helps to produce the powerstroke (Davis, 1968d). (a) High-frequency beating; (b) low-frequency beating. The records illustrate the increase in the time lag between bursts in different motoneurones innervating the muscle as the frequency of beating decreases.](image)

Fig. 7. Electromyograms from muscle 13, which helps to produce the powerstroke (Davis, 1968d). (a) High-frequency beating; (b) low-frequency beating. The records illustrate the increase in the time lag between bursts in different motoneurones innervating the muscle as the frequency of beating decreases.

![Fig. 8. Time lag between the beginning of bursts in two motoneurones innervating the same muscle (Δ on the inset) plotted against the duration of the corresponding movement cycle. r is the correlation coefficient between the two variables. Part of the record analysed in this graph is shown in Fig. 7.](image)

Fig. 8. Time lag between the beginning of bursts in two motoneurones innervating the same muscle (Δ on the inset) plotted against the duration of the corresponding movement cycle. r is the correlation coefficient between the two variables. Part of the record analysed in this graph is shown in Fig. 7.
are initiated relatively earlier in the cycle (Figs. 2, 9). The relationship between the phase position of the beginning of a burst and the frequency of swimmeret beating seldom remained stable for more than twenty consecutive cycles, perhaps reflecting a rotation of the work load among synergistic motoneurones. Variation in the phase position of the bursts is certainly correlated with changes in the relative timing of the activities of different motoneurones, but the main cause is probably mechanical. The inertia of the swimmeret appendage is proportional to its angular velocity,

\[
\frac{d^2 \theta}{dt^2} = \frac{F}{I}
\]

which is in turn proportional to the frequency of swimmeret beating (Davis, 1968c). Thus as the frequency of swimmeret beating increases, the corresponding increase in the inertia of the appendage would be expected to cause the movement response to progressively lag behind the motor command.

An interesting consequence of the change in the phase position of bursts in the movement cycle is that during especially vigorous swimmeret beating, powerstroke muscles become active before the end of the preceding returnstroke (Fig. 9), thereby actively braking the movement of the swimmeret. A similar braking action occurs in the flight system of locusts (Wilson & Weis-Fogh, 1962).

**Peripheral inhibition and the control of the powerstroke direction**

As long as the lobster is upright, the powerstroke of each swimmeret is directed to the rear. If the lobster is forcibly rotated around the long axis of its body, however,
the swimmerets on the side tilted upward beat out toward the side. This change in the direction of the powerstroke is controlled by the statocyst receptors and is caused by a cyclic, outward rotation of the basipodite of each swimmeret immediately before and during the powerstroke (Davis, 1968a).

In the present work the control of the powerstroke direction has been studied in terms of the underlying neuromuscular events. When the powerstroke is directed to the rear, muscles 9 and 10, which cause rotation of the basipodite (Davis, 1968d),

\[ \text{Fig. 10. Electromyograms from muscle 10, which causes outward rotation of the basipodite of the swimmeret (Davis, 1968d). (a) Lobster in the upright position; (b) lobster forcibly rotated about 45° on its long axis so that the swimmeret from which the recordings were made was on the side tilted upward.} \]

\[ \text{Fig. 11. Electromyograms from muscle 13, which participates in the production of the powerstroke (Davis, 1968d). (a) Lobster in the upright position; (b) lobster tilted as in Fig. 10b.} \]

are relatively silent (e.g. Fig. 10a). When the lobster is rotated in order to elicit lateral beating, cyclic activity in the basipodite rotator muscles is greatly increased (e.g. Fig. 10b).

Control over the direction of the powerstroke also involves variation of the activity of two powerstroke muscles which are located in the basipodite, namely muscle 13 and muscle 11-12-14-15 (Davis, 1968d). Muscle 13 is usually active when the powerstroke is directed to the rear, but its level of activity is greatly increased during lateral swimmeret beating (Fig. 11). Muscle 11-12-14-15, on the other hand, discharges vigorously when the powerstroke is directed to the rear, but when the lobster is rotated to elicit lateral swimmeret beating, the activity of this muscle is invariably
suppressed (Fig. 12). This suppression is not an artifact caused by a change in the position of the recording electrode, since the amplitude of potentials from nearby muscles, which were sometimes inadvertently recorded through the same electrode, remained constant during the experiments (Fig. 12). The roll-induced suppression therefore presumably reflects a genuine inhibition of the muscle's electrical activity.

Fig. 12. Electromyograms from bundle 15 of muscle 11-12-14-15, which helps to produce the rearward power stroke (Davis, 1968a). (a)–(c) are one continuous record. In (b) the lobster was rotated as in Fig. 10b. This rotation suppresses the electrical activity of muscle 11-12-14-15, but does not affect the 'cross-talk' recorded from a nearby returnstroke muscle (17-18).

Fig. 13. Muscle potentials associated with activity in a single motoneurone, recorded from bundle 14 of muscle 11-12-14-15. (a)–(c) are one continuous record. In (b) the lobster was rotated as in Fig. 10b. This rotation reduces the amplitude of the muscle potentials, as seen in the first cycle of (b), and then completely suppresses them. When the upright position is restored in (c) the muscle potentials rebound strongly.

The roll-induced inhibition of the activity of muscle 11-12-14-15 could involve either a central inhibition of the motoneurones which supply the muscle, or a peripheral inhibition of the muscle at the neuromuscular junctions. If central inhibition
were the case, the muscle potentials associated with impulses in single motoneurones would be expected to disappear in an all-or-none fashion when the lobster is rolled. In fact, such muscle potentials are gradually and erratically suppressed when the lobster is slowly tilted to one side (e.g. Fig. 13). Moreover, the suppressed muscle potentials are invariably accompanied by small, high-frequency potentials which are usually of the opposite electrical polarity from the excitatory potentials (Fig. 14). Such observations are known to result from activity in peripheral inhibitor axons. These observations leave little doubt that the roll-induced suppression of the activity of muscle 11-12-14-15 is caused by peripheral inhibition.

![Fig. 14. Muscle potentials associated with activity in a single motoneurone, recorded from bundle 15 of muscle 11-12-14-15. (a) Lobster in the upright position; (b) lobster rotated as in Fig. 10b. When the lobster is rotated the excitatory muscle potentials are replaced by a longer burst of small, high-frequency potentials of the opposite electrical polarity, presumably corresponding to the hyperpolarizing activity of an inhibitory axon supplying the muscle.](image)

**Patterning of impulses in single motoneurones**

**Tonic discharge.** In the absence of cyclic movements of the swimmeret, tonic motor discharge has been recorded from some of the swimmeret muscles. This discharge is sometimes associated with the active maintenance of the swimmeret in a constant position while the lobster is stationary. On other occasions tonic discharge is initiated by slowly rotating the lobster around the long axis of its body. In both cases, the muscle potentials associated with the discharge of single motoneurones often occur in a non-random temporal sequence, consisting of pairs, triplets and occasional quadruplets, which are separated from each other by relatively long intervals (Fig. 15). This grouping of motor nerve impulses is strong enough that the histogram of the intervals between impulses displays two modes, corresponding to short and long intervals, separated by a trough which corresponds to intervals of medium duration (Fig. 15). Similar nervous discharge patterns occur in other crustacean motoneurones (Wilson & Davis, 1965; Burrows & Horridge, 1968).

**Cyclic discharge.** Sometimes while a swimmeret motoneurone was discharging tonically in the pattern described above, the swimmeret began to beat weakly. Under these conditions the tonic discharge continued unabated, but its average frequency was modulated in phase with the cyclic movements. Impulse pairs and
Fig. 15. Non-sequential interval histograms for tonic discharge in a single motoneurone, recorded from bundle 11 of muscle 11–12–14–15 (inset). The bimodality of the histogram is caused by the grouping of motor impulses into pairs, triplets, and occasional quadruplets.

Fig. 16. Tonic, patterned discharge of a single powerstroke motoneurone, accompanied by weak, cyclic movement of the swimmeret (arrows). The intervals within impulse pairs and triplets are modulated in phase with the cyclic movements. The three traces represent one continuous record.
triplets continued to occur, but the duration of the intervals within them was also modulated in phase with the movements, reaching a minimum during peaks in the average frequency (Fig. 16).

Pairing of impulses within the rhythmic bursts which occur during swimmeret beating can occasionally be detected, but since the average interval duration within bursts is nearly as small as the intervals which normally separate members of a pair, any possible tendency toward pairing is obscured. The average frequency of the impulses within bursts, however, shows clear trends (Fig. 17). As a generalization, the shortest inter-spike intervals are found in the centres of bursts. This generalization requires modification on the extreme ranges of beating frequencies. When only three impulses are contained within a burst, as often happens during low-frequency beating, the first interval is the shorter of the two. During high-frequency beating, when several impulses are contained within each burst, the last interval is the longest, while the preceding intervals are much shorter and nearly constant in duration. This description applies to the average trends in large numbers of bursts, but the same
trends can also often be seen within individual bursts (e.g. Figs. 2, 3). Moreover, the same trends appear in bursts of impulses recorded from the swimmeret motoneurones of crayfish (e.g. Ikeda & Wiersma, 1964, figs. 3–5).

**DISCUSSION**

The swimmerets of lobsters participate in several and diverse types of behaviour, including locomotion, the maintenance of equilibrium, respiration and reproduction (Davis, 1968a). In all cases, however, their role is the same, namely, the production of cyclic forces by metachronous beating movements. The results described in the present paper provide the basis for discussion of these movements in terms of the activities of single participating motor nerve cells.

**Neural gradation of muscular forces**

As the frequency of swimmeret beating increases, so also does the powerstroke velocity (Davis, 1968c) and therefore the force produced by individual swimmerets (Davis, 1968a). As shown in the present work, increases in the frequency of swimmeret beating are accompanied by increases in the frequency of impulses within single swimmeret motoneurones during each movement cycle, and also by increases in the number of active motoneurones per cycle. Variation of these two parameters is therefore the primary means of regulating the force produced by each swimmeret. Since the activity in all of the swimmeret muscles is cyclic and correlated in the same way with the frequency of beating, all of the movements of each swimmeret, including those which regulate the direction of the powerstroke (see below), presumably result from the common influence of a single, central nervous oscillator on the entire population of motoneurones supplying the swimmeret. The analysis here of the activity of the swimmeret motoneurones points to the same conclusion drawn independently from analysis of the swimmeret movements (Davis, 1968c), namely that the period of the central nervous oscillation is inversely proportional to its amplitude.

**Neural regulation of the temporal distribution of muscular forces**

Although the duration of the burst of impulses within each motoneurone is independent of the frequency of swimmeret beating, the total duration of the overlapping activities of all of the neurones which innervate a given muscle is nevertheless strongly related to the frequency of beating, owing to systematic changes in the relative timing of the discharges of the motoneurones. As the frequency of beating increases, the time lag between the initiation of the bursts in synergistic motoneurones decreases. The effect is presumably to distribute the force produced by the muscle evenly throughout movement cycles of variable duration.

Two neurones with different thresholds for spike generation will of course begin to fire at different times in response to identical and increasing excitatory inputs, but the time lag between the beginning of bursts in the neurones innervating a given swimmeret muscle is probably too large, and varies over too great a range, to be explained by such a mechanism. Instead, it must be postulated that during each cycle of beating the different neurones which innervate the same muscle receive their inputs at different times. Since the time lag between the beginning of bursts in neurones which supply
Neural control of lobster swimmerets

A given muscle varies by the same ratio and in the same way as the time lag between bursts in antagonistic motoneurones, variation of both time lags can be explained in terms of the action of the same neural mechanism.

Biological 'noise' in the output of the swimmeret motoneurones

The movements of each swimmeret, as well as the sum of the forces which they produce (Davis, 1968a), show little variation from cycle to cycle during constant-frequency swimmeret beating. In contrast, numerous measures of the activity of single swimmeret motoneurones and muscles display a large degree of non-systematic variation, superimposed on the systematic variation associated with changes in the beating frequency (e.g. Figs. 1, 5, 6). The movements are apparently insensitive to this 'noise' in the output of single motoneurones, probably because of the damping effects of the excitation-contraction coupling processes between the nerves and the muscles, and because of inertial damping by the mass of the swimmeret appendage in the conversion of the muscular tension to an average mechanical response. Owing to the insensitivity of the swimmeret movements to neural noise, fewer restrictions need be placed upon the operation of the central nervous control mechanisms. The oscillator need only provide for a general inverse relationship between the amplitude and the period of the oscillation, and for the activation of the swimmeret motoneurones in the same sequence during each movement cycle (Davis, 1968d).

Neural control of the direction of the powerstroke

The change in the direction of the powerstroke which occurs when the lobster is tilted to one side is accomplished by an increase in the cyclic activity of muscles which rotate the basipodite, and by a reciprocal change in the cyclic activity of two powerstroke muscles. One of these muscles displays an increased level of excitatory activity when the lobster is tilted. The other probably also receives an increased excitatory discharge, but the resulting electrical activity of the muscle is suppressed by simultaneous high-frequency discharge of a peripheral inhibitor axon. Since the excitatory muscle potentials are abolished by the inhibitory discharge, the tension response of the muscle is presumably also eliminated.

Concurrent activity also occurs naturally in the excitor and inhibitor axons which innervate the opener muscle of the crayfish claw (Wilson & Davis, 1965). In that case the inhibitor axon appears to provide an additional mechanism for grading the tension response of the muscle over a large range of excitatory discharge frequencies. In other arthropod muscles, however, the role of peripheral inhibitor axons is not clear (insects, Hoyle, 1966; crustaceans, Evoy, Kennedy & Wilson, 1967). In the swimmeret system the muscle which is inhibited by tilt presumably directs the powerstroke only to the rear, while the muscle which is excited by tilt directs the powerstroke either to the rear or, when the basipodite rotator muscles are active, to the side. These two powerstroke muscles may therefore be considered antagonistic with respect to the lateral powerstroke, in which case the role of the peripheral inhibitor axon is to neutralize the tension produced by an antagonistic muscle.

The use of peripheral inhibition greatly simplifies in principle the central nervous machinery needed to achieve fine control over the direction of the powerstroke. Since the necessary functional reciprocity between muscle 13 and muscle 11-12-14-15

Exp. Biol. 50, 1

113
need not be determined centrally, the entire population of motoneurones innervating muscles which alter the powerstroke direction is free to respond as a unit to the excitatory influence of the central nervous oscillator. Arrangements need only be made to influence the responsiveness of this cell population in direct proportion to the degree to which the lobster is tilted, and such an influence is potentially available in the form of input from the statocyst receptors.

**Patterning of impulses in single motoneurones**

**Tonic discharge.** The pattern of pairs and triplets of motor impulses recorded during tonic discharge of the swimmeret motoneurones also occurs in the excitor axon which innervates the opener muscle of the crayfish claw (Wilson & Davis, 1965) and in the optomotor neurones of crabs (Burrows & Horridge, 1968). In the case of the crayfish, the tension produced by the muscle is especially enhanced by the pattern. The swimmeret muscles may show a similar sensitivity to the pattern of impulses which occurs naturally during tonic discharge, since the muscles are presumably specialized to respond to the 'bursty' discharge associated with swimmeret beating. Paired impulses in the opener muscle of the crayfish claw may be produced by a process of refractory oscillation in the motoneurone membrane during a single fundamental input cycle (Wilson & Davis, 1965). A similar process could underlie the temporal grouping of impulses during tonic discharge in single swimmeret motoneurones.

**Cyclic discharge.** The rhythmic modulation of the tonic pattern discussed above during weak swimmeret beating suggests that both the cyclic burst pattern of the motoneurones during swimmeret beating and the micro-structured tonic discharge pattern originate, or at least interact, at a common integrative site. The most satisfactory hypothesis is that both types of pattern are generated at the level of the motoneurone itself, in response to independent presynaptic inputs.

The frequency trend of the impulses contained within the bursts of single swimmeret motoneurones (Fig. 17) provides clues about the nature of the excitatory input to individual motoneurones during swimmeret beating. At medium frequencies of beating the impulse frequency is greatest in the middle of the burst and less at the beginning and end. This temporal structure suggests that the excitatory input to the cell oscillates in a sinusoidal fashion, increasing during the first half of each burst, and decreasing during the last half. The temporal structure of the bursts during low-frequency beating is consistent with this hypothesis. At high frequencies of beating, however, the impulse frequency is high and constant until the end of the burst, when it declines markedly. This pattern of output could result in principle from a sinusoidal excitatory input if the inter-spike intervals were small compared to the duration of the relative refractory period of the motoneurone. Alternatively, the pattern could represent the response of the cell to a sinusoidal input, modified by accumulating motoneurone refractoriness during the course of the burst. These possibilities are explored in the following paper (Davis & Murphey, 1969).

**Nature of the central nervous oscillator underlying swimmeret beating**

In a previous paper, constraints for models of the neural mechanisms underlying swimmeret beating were provided from analysis of the limb movements (Davis,
Neural control of lobster swimmerets

1968c). As discussed there, these constraints are consistent with a model in which the source of the central nervous oscillation underlying the movements of each swimmeret is a wave of neural activity, consisting of a synchronized barrage of action potentials, which is propagated through the neuropilar network of each ganglion, recruiting the swimmeret motoneurones in the proper sequence. According to the model, the neuropilar wave is generated repetitively at the same frequency as that of swimmeret beating by a process of refractory oscillation.

Although the above model was developed exclusively from analysis of the swimmeret movements, it is entirely consistent with the results of the present study of the activity of the swimmeret motoneurones. For example, the required inverse relationship between the amplitude and period of the neuropilar wave, which can be explained in terms of conventional synaptic interactions (Davis, 1968c), provides a satisfactory explanation for the lack of dependence of the burst duration of single swimmeret motoneurones on the frequency of swimmeret beating (see also Davis & Murphey, 1969). Moreover, according to the model, the average excitatory influence on each motoneurone should wax and then wane as the neuropilar wave sweeps past its dendrites. The results described here and in the following paper (Davis & Murphey, 1969) indeed suggest that the excitatory input to single swimmeret motoneurones oscillates sinusoidally with time. Finally, the required frequency-correlated variation in the conduction velocity of the hypothetical neuropilar wave provides an adequate explanation for the observed variation in the relative timing of bursts in synergistic and in antagonistic swimmeret motoneurones, as illustrated in Fig. 18.

The proposed model requires extensive testing before it can be considered useful as an expression of ‘reality’. In particular, data must be obtained which permit alternative models to be rejected. The proposed model accounts well for the available data, however, and it certainly provides a reasonable hypothetical basis for further work on the swimmeret system.
SUMMARY

1. The neural basis of swimmeret beating in the lobster *Homarus americanus* was studied by recording the cyclic motor output to the swimmeret muscles of intact, unrestrained specimens.

2. The force produced by each swimmeret is regulated by changes in the number of impulses within single motoneurones during each movement cycle, and by changes in the number of motoneurones which discharge during each cycle. Both of these parameters increase with the frequency of swimmeret beating.

3. The burst duration of single swimmeret motoneurones is independent of the frequency of swimmeret beating. The duration of the total electrical activity of each muscle nevertheless increases with the cycle duration, owing to changes in the relative timing of the activities of the motoneurones which innervate the muscle. By this method the forces produced by each muscle are presumably distributed evenly throughout cycles of variable duration.

4. As the frequency of swimmeret beating increases, the movement response progressively lags behind the motor nerve activity. At high frequencies of beating powerstroke motoneurones fire during the returnstroke of the preceding movement cycle because of this phase change, thereby actively braking the swimmeret.

5. Tilting the lobster to one side changes the direction of the powerstroke of each swimmeret on the side tilted upward. This change is achieved by an increase in the activity of muscles which rotate the appendage outward on its long axis, by an increase in the activity of a muscle which directs the powerstroke out toward the side, and by a decrease in the activity of a muscle which directs the powerstroke to the rear. The latter decrease is accomplished through the use of a peripheral inhibitor axon.

6. Under some conditions individual swimmeret motoneurones discharge in continuous trains rather than in bursts. This tonic activity is characterized by the occurrence of a disproportionate number of impulse pairs and triplets, a pattern to which the swimmeret muscles may be especially sensitive.

7. During swimmeret beating, all of the swimmeret motoneurones discharge in cyclic bursts. The temporal structure of the bursts suggests that the underlying excitatory input oscillates sinusoidally with time at the same frequency as that of swimmeret beating.

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Neural control of lobster swimmerets


