

## ON THE EXCITATION OF CRUSTACEAN MUSCLE

## III. QUICK AND SLOW RESPONSES

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(With Four Text-figures)

## INTRODUCTION

It was shown in a previous paper (Pantin, 1936) that the rate of contraction of the flexor and extensor muscles of the dactylopodite of the walking legs of *Carcinus maenas* varied with the frequency of stimulation of the nerve in a perfectly continuous manner. There was no abrupt transition in rate between the imperceptibly slow development of tension caused by low-frequency stimuli and the response to a frequency sufficiently great to call forth the maximum rate of contraction the muscle can give. Evidence was brought to show that the rate of contraction was controlled through neuromuscular facilitation, each shock in a succession bringing more and more muscle fibres into action as the contraction proceeds. No evidence was obtained for the existence of more than a single excitable system in the nerve supplying the flexor muscle. With one exception, to be considered presently, this is true of all the other leg and claw muscles studied.

Despite this underlying continuity of mechanism, certain properties of the neuromuscular system render possible apparently abrupt changes in rate of contraction which have sometimes been referred to the existence of more than one excitable system. One of the causes of this is the very great rapidity with which the contraction rate increases as the frequency is increased over a certain somewhat limited range. A small change in frequency can change the rate of contraction five or tenfold. Unless great care is taken to map out this critical region, an impression is easily taken that there exists an abrupt transition from slow to relatively rapid contraction with increase in frequency.

A more obvious transition from a slow to a quick type of response occurs when the intensity of stimuli of low frequency is very greatly raised. Evidence from many sources was brought to show that this transition does not involve a second excitable system but was due to repetitive excitation of a nerve. These things may account for some of the phenomena observed by earlier workers. Thus Blaschko, Cattell and Kahn (1931) found that in *Maia* an increase in either frequency or

intensity led beyond a certain point to a sudden increase in contraction rate. The results, however, were obtained with the claw and not with the walking leg. When, however, all allowance is made for the factors we have just discussed, abrupt changes still appear in the rate of contraction in crustacean muscle under certain conditions, and these we will now discuss.

In the following experiments the limbs of *Carcinus maenas* were used. The method of stimulation usually employed was the neon-lamp stimulator and has been described in a previous paper (Pantin, 1936). All stimuli were applied by needle-shaped silver-silver-chloride electrodes pushed through the meropodite of the limb on either side of the nerve.

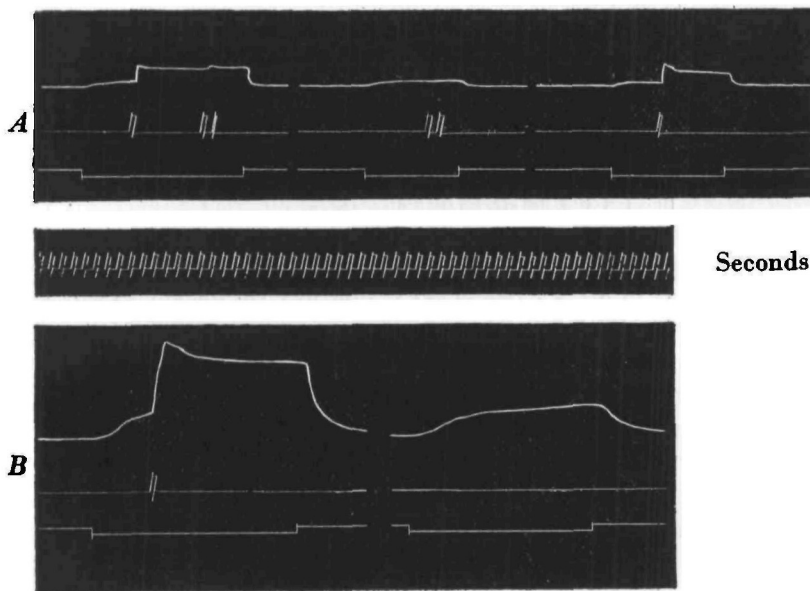


Fig. 1. Flexor of dactylopodite of leg. Blaschko, Cattell and Kahn's effect. *A*, lower signal stimulation rate 13 per sec. Upper signal, single shocks. *B*, lower signal stimulation rate 31 per sec. Upper signal, 10 shocks at 200 per sec.

#### BLASCHKO, CATTELL AND KAHN'S EFFECT

Blaschko, Cattell and Kahn, while working on the claws of *Maia*, discovered a phenomenon of very great importance. They demonstrated that if while a slow contraction is in progress in response to a battery of low-frequency shocks a single extra stimulus is interjected in the series, the muscle responds to this with a rapid twitch. The tension so developed is often maintained for a considerable time and may only be terminated by the cessation of the low-frequency stimulus. This effect can even be produced when the frequency of the background stimulus is so low that there is scarcely any visible response.

There is no difficulty in reproducing these effects in the flexor muscle of the dactylopodite in the walking legs of *Carcinus* despite its small size. Fig. 1*A* shows

responses of this kind. Induction shocks of frequency 13 per sec. and of strength 10 per cent. above the threshold were sent in (lower signal). The response to such a stimulus is barely perceptible. During the course of these barely perceptible responses, single induction shocks are thrown in (upper signal). Some of these produce abrupt increases in tension, and when they do so this extra tension continues to be maintained by the very low-frequency stimuli. By itself, such a single shock is quite ineffective. By repeated successful interjection of such stimuli, tetani of considerable magnitude can be built up.

In the figure it will be seen that the tension produced by the interjected shocks falls slightly after its initial appearance. This fall becomes exaggerated by fatigue.

If instead of the interjection of a single stimulus a short battery of shocks at a relatively high frequency is thrown into the nerve, this effect can assume remarkable proportions. Fig. 1*B* shows the result of interjecting about 10 shocks at a frequency of 200 per sec. during a slow tetanic response to a frequency of 31 per sec. The tension abruptly rises from 17 to nearly 70 per cent. of the maximum tension the muscle can develop. The greater part of this additional tension is maintained during the remainder of the low-frequency stimulus.

Blaschko, Cattell and Kahn pointed out that this effect of interjected stimuli was of considerable functional importance because it resulted in an economy of activity necessary in crustacean nerve. The effect is not only significant from this point of view but also for the whole question of neuromuscular activation among invertebrates. It is evident from these experiments that if there is present in the motor nerve a background of nervous impulses of low frequency, the muscles can be thrown into prolonged action merely by the sending out of a very short series of high-frequency impulses. The normal slight degree of tone in the muscles of a crustacean suggests in the light of the experiments described in the previous paper that there is such a low-frequency background normally present. For the animal to throw its muscles into a state of tension, therefore, it does not appear necessary for it to send out a continuous stream of high-frequency impulses. A brief series suffices to put the muscle into tension, and it will automatically remain in this condition until something prevents the tension being maintained further by the low-frequency background. We shall see in the next paper that this abolition of tension can be effected through inhibition. This is very different from the arrangement which apparently obtains in vertebrate skeletal muscle where the tension is continuously maintained by a volley of comparatively high-frequency impulses just so long as the volley lasts.

We may now consider the question of how this effect is brought about. There is no reason to suppose that it is due to the existence of a new excitable system, or of one which acts in a different way from that analysed in a previous paper. That is, the effect is wholly explicable in terms of neuromuscular facilitation. The rate of contraction which takes place in response to interjected stimuli never exceeds the maximal rate which can be caused by stimuli of high frequency applied in the ordinary way. There is therefore no evidence here for a different type of contractile mechanism. On the other hand, the sudden increase in tension caused by an inter-

jected stimulus might be expected to produce the observed effect simply from what is already known of the rapid increase of neuromuscular facilitation with the frequency of the applied stimuli. For an interjected stimulus is in fact equivalent to momentarily increasing the frequency of stimulation to at least double its value. An increase in frequency of this order was shown in the previous paper to produce a great increase in the rate of contraction. Just how great the increase would be might be expected to depend upon where the interjected stimulus fell in relation to the preceding and subsequent stimuli of the low-frequency background. This is borne out by experiments such as Fig. 1A, which shows that a single interjected stimulus is not always effective.

While these data serve to explain the phenomena in a general way it is evident that the rate of contraction and the increase in tension caused by the interjection of a single stimulus or a very few stimuli is disproportionately large. Further, the important fact that the tension continues to be maintained must be considered. Both these features have in fact a strong analogy to central phenomena associated with facilitation. A low-frequency stimulus succeeds in causing a response in only a few muscle fibres. But after the stimulus has progressed for some time there must be a large number of muscle fibres in a condition of partial facilitation, which we may liken to the subliminal fringe of excitation in the vertebrate central nervous system (Creed, *et al.* 1932). The fact that once the muscle fibres are excited they continue to maintain their tension with stimuli of very low frequency is also parallel to the central phenomenon of sustained facilitation. Once through conduction has been established between nerve and muscle, it is not easily broken down, even though its original cause has ceased.

A parallel effect to this can be produced in a very different muscle, the sphincter of the anemone *Calliactis parasitica*. It seems therefore that Blaschko, Cattell and Kahn's effect is not restricted to the claw muscles of *Maia*, but is to be found in other muscles and in other organisms.

Blaschko, Cattell and Kahn also made the interesting observation that when a stimulus of low frequency is applied to the nerve a sustained tension of considerable magnitude could be produced not only by the interjection of stimuli in the manner described above, but also by mechanically raising the dactylopodite so as to increase the tension. Mechanical closure of the claw could thus be maintained against a very considerable tension. This phenomenon suggests that stretching a muscle may increase its excitability so that a low-frequency stimulus which previously only affected a few muscle fibres might now affect a majority. It is of interest to note that Katz (1934) finds that stretching frogs' skeletal muscles causes an increase in activity, and Katz suggests that this may provide a basis for the well-known rule of von Uexküll that excitation tends to flow into a stretched effector. The production of Blaschko, Cattell and Kahn's effect by mechanical means might appear to be a direct expression of this widespread rule. This effect is one of considerable importance, but there is no reason to suppose that it involves more than one excitable system in the leg muscles.

## RESPONSES OF THE CLAW MUSCLES

The experiments recorded here and in the previous papers have dealt chiefly with the flexor muscle of the dactylopodite of the walking legs of *Carcinus*. No evidence has been obtained in this muscle of a double contractile system. The extensor muscle agrees entirely with the behaviour of the flexor. Experiments conducted upon *Maia verrucosa* showed that the leg muscles behaved in an essentially similar manner in this species also.

The most definite evidence for the existence of a double contractile mechanism was obtained by Lucas (1907 and 1917) in the claws of the crayfish and lobster. In some of his evidence, particularly that involving the use of a series of stimuli, the duration of the shocks he applied was very long (10σ). Shocks of this duration are liable to cause multiple excitation in the nerve as we have shown in the previous paper. The same difficulty is to be found in the experiments of Lapique (1903). He obtained two types of contraction from the claws of *Carcinus*. The contractions were large. A rapid one from a direct current stimulus of several hundredths of a second duration, and a much slower one from induction shocks. Both these must involve multiple excitation. A single impulse produces a scarcely perceptible response in the claw muscles, just as in the leg muscles. The constant current stimuli are of a duration which is bound to cause multiple excitation, while the induction shocks were so strong (coil at 4 cm., 2 volts in primary) that the shock may well have been 100 times the true threshold; such stimuli cause prolonged after-discharge in the nerve. Lucas, however, found other evidence which it is almost impossible to interpret except by the existence of a double mechanism in the claw, particularly a doubling of the refractory period curve which could be related to the occurrence of two different kinds of response. Lucas noted that not all the claws showed evidence of such doubling.

The fact that Lucas and others employed the claw and not the walking leg is of considerable importance. In the first place, compared with the walking leg, the claws are morphologically specialised. Not only is this true but also the claws of the decapod Crustacea are usually differentiated to a greater or less extent from each other. This differentiation may consist of little more than a slight difference in size of the two chelae as frequently is found in *Astacus*. But in extreme cases this difference of size may be accompanied by more obvious morphological features such as change of tooth pattern. This extreme differentiation occurs among all groups of the Decapoda. It is well shown in the "cutter" and "crusher" claws of the lobster, *Homarus vulgaris*, and an exactly parallel modification is found in the claws of *Carcinus maenas* amongst the crabs. In these cases it is easy to see that the claws are differently employed by the animal during life. In the face of such morphological differentiation one has no right to assume in any member of the decapod Crustacea that the claw muscles and leg muscles are physiologically identical or even that the muscles are similar in the two claws.

Experiments on the claws of *Carcinus maenas*, however, show that in the cutter claw, despite its huge size, the muscles behave in a similar manner to the flexor

of the walking legs. As in the flexor, there is a well-defined threshold above which contractions are obtained whose rate and amplitude are normally independent of intensity of stimulus over a certain range, while they increase rapidly with the frequency of excitation. If the intensity of the stimulus is sufficiently increased, the threshold for inhibition is reached, and the response is lessened. The frequency range for the muscles of the cutter claw is about the same as that for the leg flexor.

While the adductor muscle of the cutter claw behaves invariably as a single contractile unit, *there is the strongest evidence of a double contractile mechanism in the crusher adductor and in this alone of all the muscles of the limbs investigated.* The adductor muscle of the crusher claw shows the unique phenomenon illustrated in Fig. 2. At a constant frequency, increase in intensity above the threshold pro-

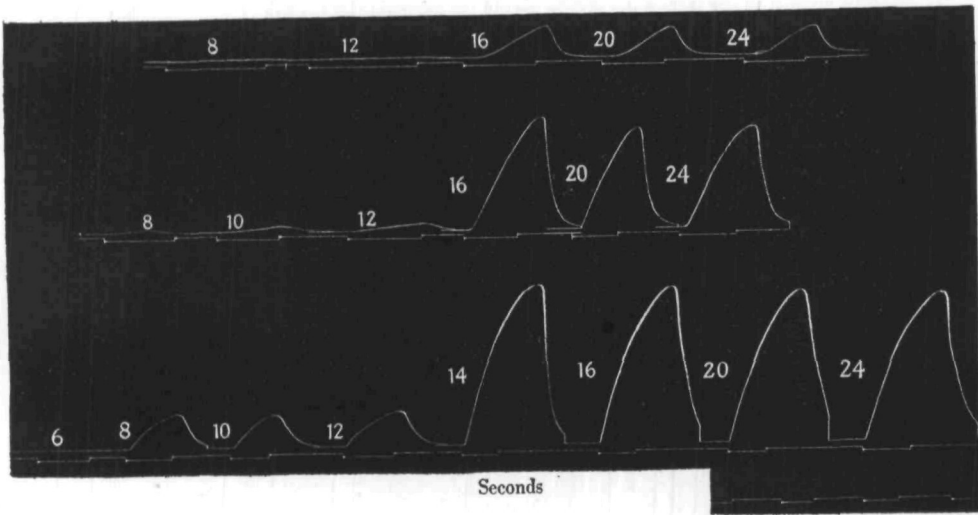


Fig. 2. Adductor of crusher claw. Effect of increasing intensity of repetitive stimulation at stimulation intervals of  $25\sigma$ ,  $12.5\sigma$  and  $6.2\sigma$ .

duces no change in the nature of the contraction up to a certain point. But when the intensity reaches this point the contractions abruptly become much more rapid and very much greater. It is as though there existed two distinct muscles, a smaller one served by a nerve with a lower threshold and a greater one with a higher threshold, and that these muscles were brought into action successively as the intensity of stimulus passes the threshold of first one and then the other.

Apart from this special feature, the general behaviour of the crusher adductor muscle is essentially the same as the other muscles. Fig. 2 shows that within the range of intensities at which each of the two types of contraction is evoked, the rate of contraction is independent of the intensity. If the intensity is still further increased, inhibition of contraction may ensue as in the other muscles. At low frequencies of excitation of the muscle inhibition by inhibitory stimuli can be complete, so that both contractile systems would appear to be inhibited simul-

taneously. As in the other muscles, inhibition becomes less effective as the frequency is increased.

There is little doubt that this double mechanism of *Carcinus* crusher claw is identical with that found by Keith Lucas in the claws of the lobster and crayfish. Lucas noted that evidence for the double mechanism is not obtained with all claws. He does not state with which type of claw, cutter or crusher, his experiments were made. Mr P. A. Gorer very kindly allowed me to see the results of some unpublished investigations in which he repeated many of the experiments of Lucas on the lobster. This work shows that whenever evidence for the existence of a double mechanism is obtained, it is the *crusher* claw which has been employed. These facts suggest that this physiological specialisation of the crusher claw may

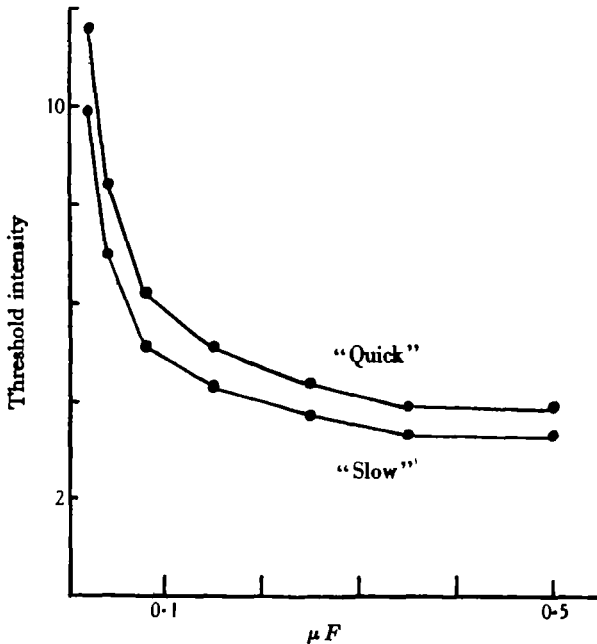


Fig. 3.

be widespread in the Decapoda. The existence of such specialisation must warn one of the danger of generalising as to the nature of neuromuscular action in Crustacea on the basis of experiments conducted on the claw.

Employing the neon-lamp method described in a previous paper, excitation-times of the quick and slow systems were traced. The thresholds remain distinct throughout a wide range of stimulus durations (Fig. 3). Lucas found a similar doubling of the intensity-duration curve for the crayfish and lobster claws. In that case, however, the curves usually cut one another at a certain point, so that when the duration of stimulus exceeded a certain value, the slow type of contraction was first obtained at a lower intensity than the quick type; whereas, for stimuli of brief duration, the quick type of contraction was obtained at the lower intensities of

stimulus. The curves obtained by the neon-lamp method in the crusher of *Carcinus* did not usually cut one another.

The crusher adductor behaves as though it consisted of two distinct muscles served by separate nerves. Apart from the distinct intensity-duration curves, the responses of the two contractile systems are quite distinct. However high the frequency, a stimulus of intensity sufficient only to evoke the slow contraction never brings the quick system into action. This behaviour distinguishes the quick and slow mechanisms of this muscle from the twitch-like contractions which can be produced in various ways described earlier in the flexor of the dactylopodite of the walking leg. It has already been shown in these cases that such twitches never exceed in rate of contraction or in tension developed the maximal rate of contraction which can be evoked in the flexor muscle by high-frequency stimulation near threshold value.

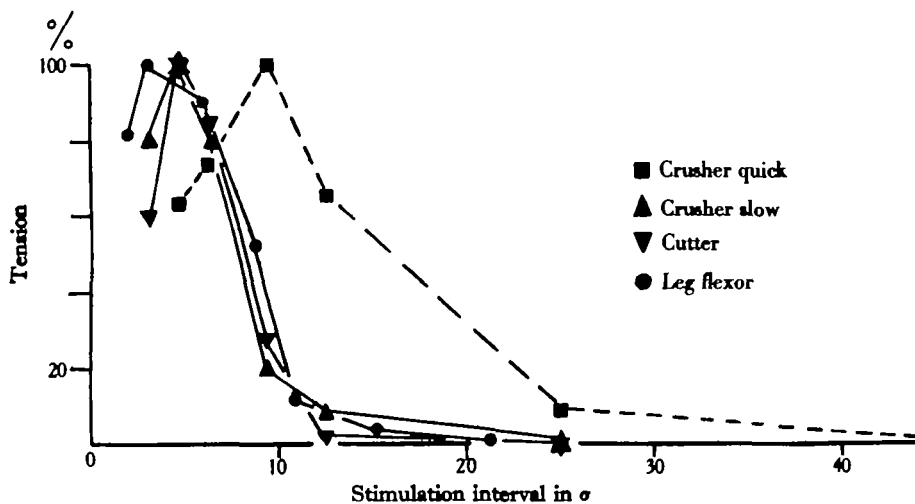


Fig. 4. Tension expressed as per cent. of tension developed in 0.2 sec. at maximum rate of contraction.

The independence of the quick and slow systems in the crusher adductor can be shown in many other ways. Prolonged stimulation of the slow system tends to fatigue it without producing any obvious modification of the quick response.

Apart from these differences, there is one of very great significance between the quick and slow mechanisms. Within their range both of them are more or less independent of intensity and even behave like single motor units, just as does the entire flexor muscle of the dactylopodite of the walking leg. Both systems increase rapidly in rate of contraction with increasing frequency (Fig. 2). But the quick system does so far more rapidly than the slow. Indeed, the quick system begins to respond at far lower frequencies than any other muscle investigated in *Carcinus*. By choosing a suitable low frequency it is possible to bring about an almost maximum tension of the quick response while the slow system is scarcely contracting at all. Since one can invoke the slow system alone by a high frequency but of lower



intensity, one can in this way distinguish sharply between the two kinds of contractions.

The difference in the frequencies at which the two systems begin to respond is exceedingly important. Fig. 4 shows the rate of contraction plotted against the stimulation intervals corresponding to various frequencies of the applied stimuli. The rate is measured by determining the height of contraction reached after a given interval from the beginning of the battery of stimuli. The height of contraction is expressed as percentage of the maximum rate, so that all curves may be comparable. Curves *A*, *B* and *C* are obtained respectively for the flexor of the dactylopodite of the walking leg, for the adductor of the cutter claw, and the "slow" mechanism of the crusher claw. The relation between rate of contraction and frequency is almost identical in all of these. A high frequency of the order of about 300 per sec. is required for the maximum facilitation rate to be achieved. On the other hand, curve *D* shows the rate of contraction of the quick mechanism of the crusher claw. This is most correctly expressed by subtracting from the "quick" tension developed in a given time the small component due to the "slow" contraction. The ordinates in Fig. 4, curve *D*, thus represent the tension developed in response to stimuli of sufficient intensity to evoke the quick contraction, less the slight tension developed by the slow system at the same frequency. This correction does not very greatly affect the form of the curve. It will be seen that in the case of the quick mechanism, the maximum contraction rate is actually achieved at a frequency of 100 per sec., and contraction begins to be evident at extremely low frequencies. At frequencies of 100 per sec. and less, the rate of contraction of the slow system is very small.

The relation of the two systems in the crusher claw to the other muscles shown in Fig. 4 would lead us to suppose that the "slow" mechanism in the crusher claw is physiologically equivalent to the unmodified flexor muscle of the dactylopodite in all the other limbs. On the other hand, three-quarters of the crusher adductor have been specialised to form a "quick" mechanism with extremely rapid facilitation. This differentiation has a clear functional significance. The living crab uses the crusher claw in two ways. On the one hand it is used in conjunction with the cutter simply as a prehensile organ for conveying small particles of food to the mouth, and it is used in a manner which is quite in accordance with the use of the other limbs; no great physical strength is demanded of the contractions. On the other hand, the crusher claw is also used specifically for producing prolonged contractions of immense force in breaking up the shells of the animals on which the crab feeds. The big isometric tensions registered in Fig. 2 correspond to a tension of some 500 gm. at the tip of the dactylopodite of the chela; and tensions considerably greater than this can be registered. For such purposes the specialised so-called "quick" machinery is ideal, for owing to its ease of facilitation a few impulses even of low frequency are sufficient to bring the whole of this powerful part of the muscle into action.

While there is a considerable degree of correspondence between the results obtained with the crusher claw of *Carcinus* and the experiments of Lucas on the

claws of the crayfish and lobster, there are some points of difference. Lucas' evidence appears to show that the optimum for the quick response takes place at a shorter stimulation interval than that for the slow: whereas for the *Carcinus* crusher the quick is more easily facilitated and has an optimum at a longer stimulation interval than the slow. It must be remembered that the quick and slow responses observed by Lucas were based on the relatively small contractions in response to one or to two stimuli; whereas the responses of the *Carcinus* muscles described here involve the whole muscle and took very many stimuli to produce. The "quickness" and "slowness" of the responses depend on rather different factors in the two cases.

#### CONCLUSION AND SUMMARY

1. The cases where there appears to exist a "quick" and "slow" contractile system in the same crustacean muscle are reviewed.

2. Blaschko, Cattell and Kahn (1931) showed that in the claws of *Maia* a stimulus of very low frequency produced a scarcely perceptible response. But the interjection of a single stimulus during such low-frequency excitation brought about a sudden rapid contraction which was subsequently maintained by the low-frequency stimulus. This effect is to be found in other muscles, including the flexor of the dactylopodite of the walking leg of *Carcinus*.

3. The effect is not due to the presence of a second excitable element in the neuromuscular system. The flexor in *Carcinus* leg can be shown to behave as though there were only one excitable element present. The effect is due to neuromuscular facilitation. The low-frequency excitation is unable to reach the majority of the muscle fibres; but it leaves their neuromuscular junctions in a condition in which the transmission of an interjected impulse by momentarily increasing the frequency, is so greatly facilitated that it reaches almost all the muscle fibres. Once the conduction path has been established between nerve and muscle in this way, the low-frequency excitation is sufficient to maintain it.

4. The most certain evidence for the existence of a double excitable mechanism in any crustacean limb muscle is that of Keith Lucas on the claws of lobster and of *Astacus*. These are highly specialised, and further are differentiated into cutter and crusher claws in *Carcinus* and many decapods. The muscles of the cutter claw show the same behaviour as the muscles of the walking leg. The muscle behaves as a single excitable unit when the nerve is excited near the base of the limb.

5. *The adductor of the crusher claw and this muscle alone exhibits a double excitable system.* Two distinct types of response are obtained at different thresholds. Two intensity-duration curves can be traced. The systems show very different rates of contraction. The whole system behaves as though there were two distinct muscles. The "slow" system has a lower threshold than the "quick" system.

6. The "quick" system differs sharply from the "slow" in the frequency of stimulation required to bring it into action. The frequency range of stimulation required to activate the "slow" system of the crusher claw is identical with the range for the whole adductor of the cutter claw and the flexor and extensor muscles

of the dactylopodite of the walking leg. The "quick" system, on the other hand, is brought into action at a much lower frequency range. Apart from this, the behaviour of both systems is the same as that of all the other muscles investigated. Over their own characteristic ranges, the higher the frequency the more rapid the contraction.

7. The crusher adductor is equivalent to two units physiologically differentiated. The unit corresponding to the slow system is used in the normal movements of the crab, while the unit corresponding to the quick system is used when great tensions are suddenly required for the crushing of hard objects. The differentiation thus has a decided functional significance.

Part of this work was done while holding the Cambridge University Table and the Bidder Fund at the Stazione Zoologica, Naples. I wish to express my sincere thanks to Dr R. Dohrn and his staff for their hospitality and for the great facilities they gave me. I also wish to thank my wife for valuable help during this work. The cost of some of the apparatus was defrayed by a grant from the Government Grant Committee of the Royal Society.

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