612.731.63:612.014.462.7

THE CHANGES IN VISCOSITY OF AN UNSTRIATED MUSCLE (*MYTILUS EDULIS*) DURING AND AFTER STIMULATION WITH ALTERNATING, INTERRUPTED AND UNINTERRUPTED DIRECT CURRENTS

BY F. R. WINTON

(*From the Physiological Laboratory, Cambridge, and the Marine Biological Laboratory, Plymouth*)

(*Received* 18 *September* 1936)

MUSCLE viscosity influences the response to a stimulus in two ways, by opposing rapid shortening or development of tension, and by retarding relaxation. The importance of the former is illustrated by the large reduction in viscosity undergone by the retractor penis of the dog when stimulated with adrenaline [Winton, 1930]: the muscle is changed from a condition in which it is capable of resisting external forces passively and economically, to one in which it can pull relatively powerfully and quickly. The importance of a high viscosity in slowing the relaxation, on the other hand, is due to the consequence that a fused contraction is obtained in plain muscle even with a low frequency of stimulation; the increase of oxygen consumption required to maintain a tetanus might, therefore, be too low to be estimated. Bayliss [1928] showed that this consideration met the objections to the tetanus theory of tonus which had been based on failure to detect an increase of oxygen consumption during tonic contraction. The tetanus theory encounters, however, another difficulty, in that a frequency of stimulus high enough to produce a fused response ordinarily results in the rapid onset of fatigue in plain muscle, whereas normal tonic contraction appears to be unattended by fatigue. A stimulus applied once a minute, for example, produces fatigue with relatively little fusion both in the retractor penis of the dog [Winton, 1926, Fig. 1] and in the anterior retractor of *Mytilus* (Fig. 1B below). Stimulation at a frequency high enough to produce a fused contraction induces fatigue even sooner. If, however, it were found that not all kinds of stimuli reduce the viscosity of plain muscle, but that suitable stimuli may even increase the viscosity, the least frequency of stimulation needed to produce a fused response would be correspondingly lower; consequently the muscle would have time to recover from the ill effects of one stimulus before the next appeared, and fatigue would not develop. It happens that in the anterior retractor of *Mytilus* a direct current stimulus increases the viscosity and an interrupted or alternating current stimulus decreases the viscosity, the changes in viscosity greatly outlasting the duration of the stimulus [Winton, 1934]; this muscle has, therefore, been chosen for studying the changes of viscosity in virtue of which a tetanus theory of tonus may be tenable in plain muscle. In view of the sensitivity of plain muscle to chemical stimulation, it is unlikely that all examples of tonic contraction are due to discontinuous stimulation; the "restoring force" previously described [1930] as present in the isolated retractor penis, and also operative in the isolated retractor of *Mytilus* (Fig. 5 below), is clearly a different affair. The tetanus theory of tonus is particularly applicable to those instances which used to be ascribed to a "catch mechanism", in which nervous activity, possibly of the nature of a stretch reflex, is apparently involved. Since, as far as we know, nervous activity is discontinuous, the problem of how plain muscle yields a tonic response to discontinuous stimulation becomes an important one.

The exact meaning of the term viscosity in connexion with plain muscle was discussed in a previous communication [Winton, 1930]. The viscous-elastic forces with which a retractor penis resists stretch were shown to be capable of representation by a triple component mechanical model, consisting of pure elastic, viscous-elastic, and pure viscous elements, under the influence of a small restoring force which induced slow but ultimately full shortening of the muscle in the absence of an external stretching force large enough to overcome it. Stretch curves indicate that the triple model designed for the dog's retractor penis represents adequately, though not quite so satisfactorily, the mechanical properties of the *Mytilus* retractor, the straight part of the curve being shorter in most of these muscles. The two muscles have in common that they consist of parallel longitudinally arranged unstriated fibres, with relatively little adventitious tissue, and that they are of about the same size and shape, but the individual fibres in the *Mytilus* retractor are very much longer than those in the dog's retractor penis.

Technique. As with other plain muscle preparations, small differences in technique may produce surprisingly large changes in the reactions of the muscle; the experimental results described below were obtained with the isolated anterior retractor of the byssus of *Mytilus edulis*, each end of the muscle being tied with thread and arranged in the stimulation chamber as previously described [Winton, 1926]. The muscles were immersed in sea water, and stimulated by currents passing through it; deep sea water and water from the aquarium tanks of the Plymouth Marine Biological Laboratory did not produce obviously different results, but certain other changes in the solution and aerating with 5 p.c. CO_2 in O_2 instead of with air affected the muscle so considerably that some of the properties described below became masked. Muscles obtained from different batches of animals showed different initial viscosities and variations in the degree of change in tension and viscosity due to various forms of stimulation. This did not appear to be due to the fact that some animals were used as soon as they were brought in from the boat, others after some time in the Plymouth tanks, and others after keeping in a refrigerator in Cambridge for anything up to a fortnight packed in seaweed as sent from Plymouth. If, however, mussels are in bad condition after having been overcrowded in a tank of sea water, their muscles are usually exceptionally viscid and respond poorly to alternating current stimulation.

Good muscles survive under the conditions named for many hours, comparable developments of tension being obtained for 4–6 hours, and good though smaller responses can be obtained 24 hours or more after isolation.

If the responses of any given series are to be comparable with one another, stimulation should be applied not more frequently than once in every 5 min. to avoid fatigue and at intervals not longer than 10–15 min. to avoid the staircase phenomenon which is well marked. Summer temperature is unfavourable for the maintenance of consistent results for long periods, and the experiments here described were mainly conducted, in a bath thermostatically controlled, at temperatures between 8 and 10° C. This temperature is substantially lower than the optimum for tension development.

Polarization was presumably occurring at the silver silver-chloride electrodes during the passage of the relatively large stimulating current, much of which passed through the sea water. The effects described below are, however, unchanged when about ten times the usual stimulating voltage is applied through an appropriate resistance in series with the stimulating chamber. Electrode polarization, therefore, plays no substantial part in producing the characteristic effects on the muscle of direct and alternating currents. Changes of concentration of ions in the sea water due to electrolysis were shown to have a negligible influence by comparing the consequences of stimulation when the sea water in the stimulating chamber was being rapidly replaced by fresh sea water, with those obtained when the liquid in the chamber was stationary. The alternating current employed in these experiments, in which it is not specified that a commutator was used, was derived from the 50 c.p.s. mains supply through a transformer and potential divider.

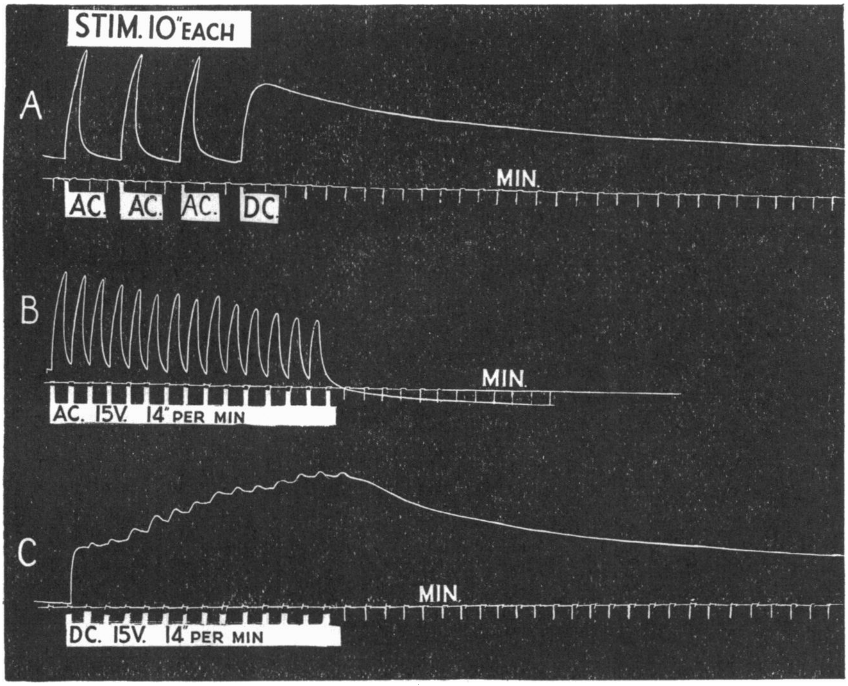


Fig. 1. Isotonic responses of an isolated *Mytilus* muscle stimulated with fluid electrodes. Sea water. 9·2° C. A. Three contractions due to stimulation with A.C. (50 c.p.s.) for 10 sec. involve much quicker relaxation than that due to stimulation with D.C. of the same duration. B. Fatigue curve due to stimulation with A.C. once a minute—a frequency too low to produce considerable fusion of responses. C. The response to stimulation with D.C. once a minute, of the same voltage and duration, showing summation and almost complete fusion.

The contrast in the effects of stimulation with A.C. *and* D.C. Fig. 1 A shows isotonic responses to stimulation for 10 sec. with alternating currents (A.C.) and direct currents (D.C.). In the former the muscle has practically relaxed in a minute; in the latter the same degree of relaxation occupies over an hour. Records of isometric responses to the two forms of stimulation look about the same as records of isotonic responses.

Consider the consequences of repetitive stimulation with the two different kinds of current. If A.C. stimuli of 10–15 sec. duration are applied at varying intervals, there is an optimal range of interval of from 3 to 10 min.; at longer intervals the response is diminished by the "staircase effect", which is very well developed in this muscle at intervals of half an hour or over; at shorter intervals the response is diminished by fatigue, which is well-marked at intervals of one minute or less. One stimulus a minute (Fig. 1 B), though already producing fatigue, still allows almost complete relaxation. More frequent stimulation hastens the development of fatigue; stimulation frequent enough to yield a fused response results in fatigue soon enough and severe enough to reduce the response to about one-quarter in a few minutes. Excitation of the kind produced by A.C. is suitable, therefore, for producing phasic contractions, but is incapable of producing the long-sustained contractions characteristic of tonus.

In contrast with the response to A.C., the responses to D.C. (Fig. 1 C) applied for 15 sec. once a minute involve such slow relaxations that the contraction is almost continuous, and builds up by a process of summation which conceals the effects of fatigue, if there be any. Stimulation with D.C. is, therefore, exceedingly suitable for producing long-sustained contractions, but it is quite unsuitable for producing phasic contractions because the high viscosity opposes the full development of tension and because relaxation is too slow.

If it were supposed that the animal availed itself of this property of its muscles, and sustained tonic contractions on the basis of discontinuous nervous activity, such as a stretch reflex, producing effects like those of repetitive stimulation with D.C., it would be necessary at times to interrupt the tonic contraction by rapid movements of the same muscles. Fig. 2 A shows that the slow relaxation following D.C. stimulation can be rapidly interrupted by an A.C. stimulus with its consequent rapid relaxation. If a series of D.C. stimuli have induced the contraction to build up to a sufficiently high value as in Fig. 1 C, an A.C. stimulus usually produces no further contraction whatever, but only a pure relaxation; this is true whether the A.C. be applied for 10 sec., when the relaxation, as will be shown, is due to a reduction of viscosity, or whether the A.C. stimulation be continued indefinitely, when relaxation is due to the reduction of viscosity together with the rapid onset of fatigue which, as mentioned above, follows an attempt to sustain a contraction with this form of

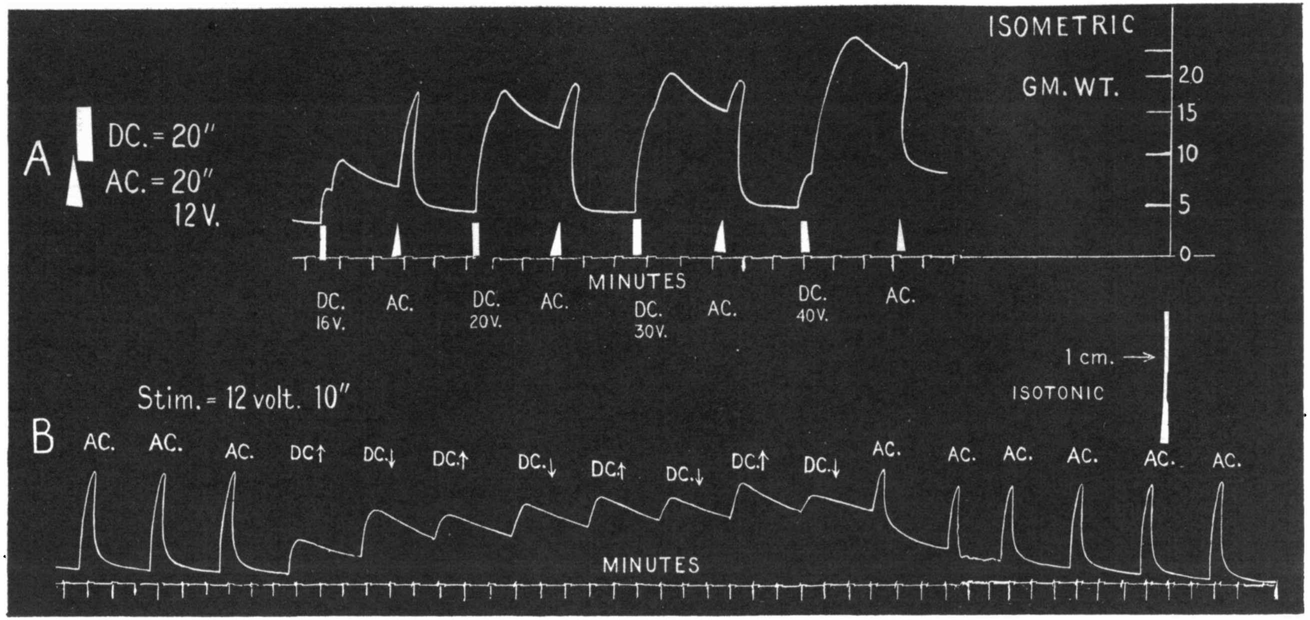


Fig. 2. Mechanical responses of isolated *Mytilus* muscle in sea water at 9·2° C. A. The slow relaxation following a D.C. stimulus (20 sec.) is hastened by intervention of an A.C. stimulus (20 sec., 12 V.). Note that with D.C. stimuli of such long duration the "on" and "off" contractions can be distinguished. B. A series of contractions due to A.C. or D.C., both 12 V., 10 sec. once in 3 min., showing that the responses to A.C. before and after a series of D.C. stimuli are the same, and that the response to D.C. is smaller than that to A.C. but unaffected by the direction of the current along the muscle (arrows indicate the direction).

stimulation. Fig. 2B shows that the D.C. stimuli employed in these experiments were innocuous, the responses of the muscle to A.C. stimuli being the same before and after a series of such stimuli. It also shows that the responses to D.C. stimulation do not depend to any essential degree on the direction in which the current passes along the muscle.

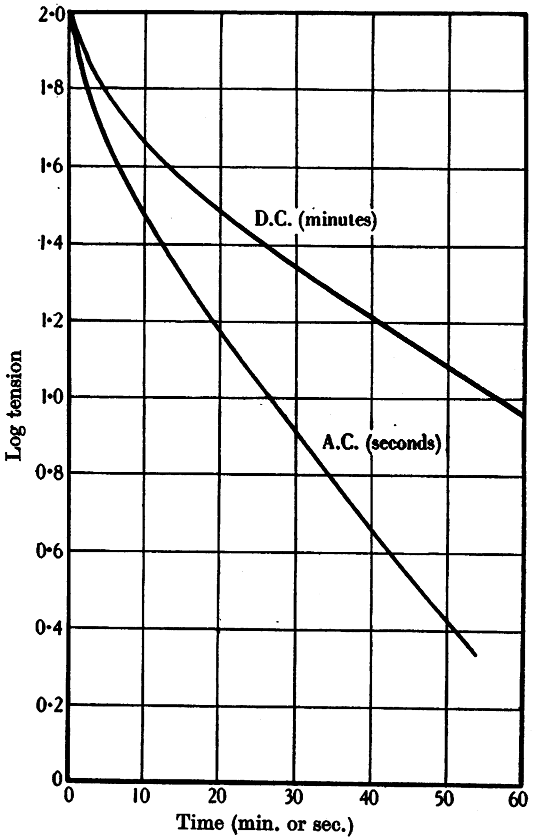


Fig. 3. Isometric relaxation curves after contractions due to stimulation for 10 sec. with D.C. (abscissæ in minutes) and A.C. (abscissæ in seconds). 8·0° C.

The changes of viscosity after cessation of electrical stimuli. The difference between the rate of relaxation of a muscle after an A.C. stimulus and that after a D.C. stimulus is shown quantitatively in Fig. 3. These curves are taken from records of isometric contractions, and correspond with the isotonic records shown qualitatively in Fig. 1A. The isometric relaxation after the A.C. stimulus is 90 p.c. complete in about 30 sec., and that following the D.C. stimulus in 60 min.—a difference of about 120-fold.

The changes in the viscous-elastic properties of the muscle following contraction due to electrical stimulation last for so long a time that they can readily be studied by recording the isometric stretch and release curves obtained after suddenly adding or removing a load [Winton, 1930].

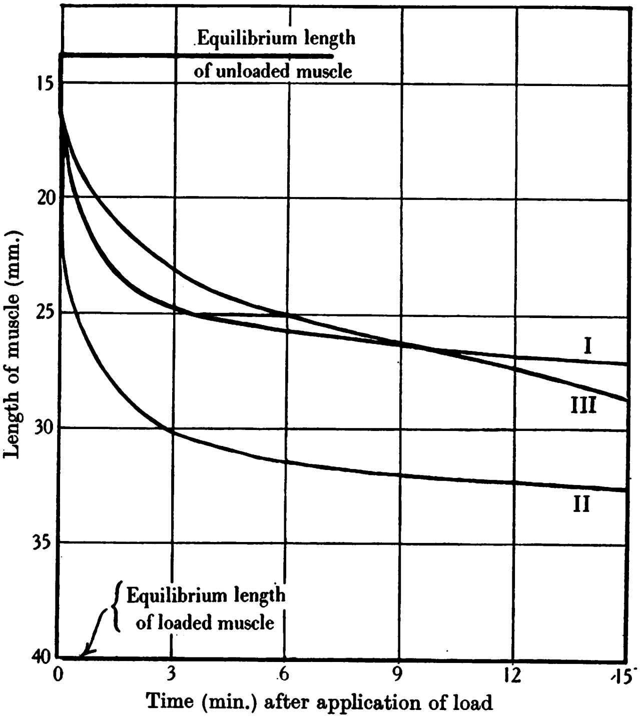


Fig. 4. Isotonic stretch curves following sudden application of a load of 5 g. 8·4° C. Curve I after 4 D.C. stimuli (10 sec.) applied at 3.13 p.m. Curve II after 4 A.C. stimuli (10 sec.) applied at 4.15 p.m. Curve III after 4 D.C. stimuli (10 sec.) applied at 6.0 p.m.

Note. The sudden stretch (undamped compliance) was the same in all three cases; the rate of the subsequent stretch was reversibly hastened by the A.C. stimulation; the final length of the stretched muscle (40 mm.) was the same in all three cases.

Retardation of relaxation after D.C. stimulation might be due either to increase of viscosity, or to the slower disappearance of the tension developed during contraction. The latter alternative is not inherently unlikely, for the tension continues to increase for considerable periods—10 or 15 sec.—after cessation of either an alternating or a direct current, if the duration of the stimulus is relatively short (15 or 10 sec.); a stimulus lasting 30 sec. is usually long enough to produce the maximum tension before it ceases. Which of the two alternatives obtained in the muscle can be discovered by examining the shape of the stretch and release curves following sudden application or removal of weights under isotonic conditions? A decrease in the compliance of the muscle will result in curves of the same shape, but with a new length scale reduced in proportion to the change of compliance which is indicated by the final equilibrium length. An increase of viscosity, on the other hand, will disproportionately extend the time scale, so that both stretch and release curves should be slower. The effects of the previous D.C. stimulation are contrasted with those of previous A.C. stimulation in Figs. 4 and 5. Fig. 4

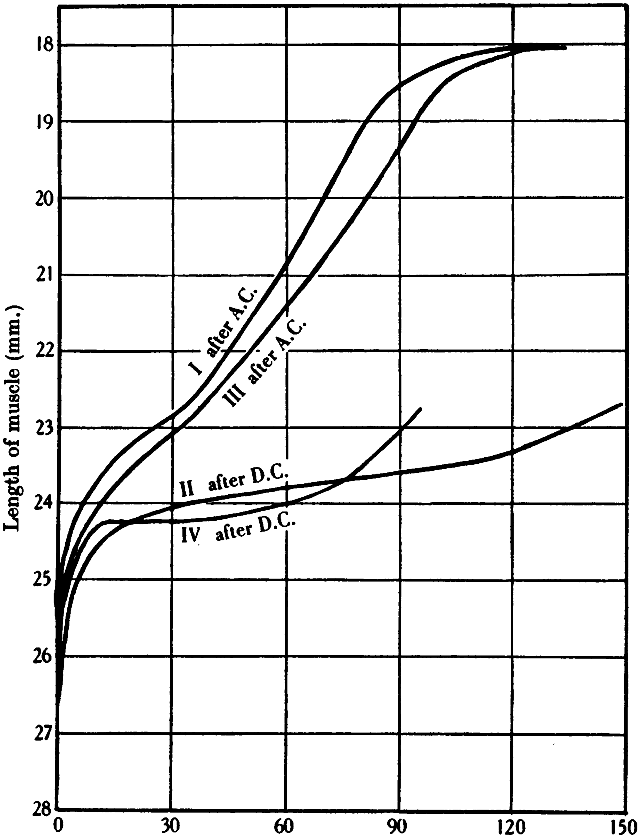


Fig. 5. Isotonic release curves following sudden removal of a load, the remaining load due to the lever being about 0·2 g. The numbers on the curves represent the order in which they were obtained. The stimuli applied were like those in Fig. 4. The rates of shortening due to previous A.C. or D.C. stimulation are different in the same sense as are the rates of stretching (Fig. 4), and the changes are reversible.

shows that the relaxation due to application of a load is slower after D.C. stimulation, and Fig. 5 shows that the shortening consequent upon removal of a load is also slower after D.C. stimulation. The curves show that equilibrium, from which the damped compliance of the muscle can be reduced, takes several hours to achieve, and adventitious changes of compliance may well interfere with the comparisons spread over so long a period. The indications from stretch curves, which ran a quicker course because the applied load was much greater than the "restoring force" in the muscle, are that no considerable change in compliance can be detected as an after-effect of the different forms of stimulation; in any case, such change as there is must be much less than would be needed to account for the changes in time relations of the stretch and release curves. We may infer that the slowing of the stretch and release curves after D.C. stimulation is mainly and possibly entirely due to an increase in viscosity of the muscle. The curves in Figs. 4 and 5 show that the viscosity of the muscle can be changed backwards and forwards between its low and its high value.

The undamped compliance after contraction is sensibly the same whichever form of stimulus is used; the *Mytilus* muscle differs in this respect from the retractor penis of the dog, in which a substantial decrease of undamped compliance was associated with increase in viscosity.

The changes of viscosity during electrical stimulation. Although the study of isotonic stretch and release curves provides a method for detecting changes in viscosity of muscle which is relatively simple, both logically and technically, no observer with experience of plain muscle will be entirely happy in relying on the results of a procedure which involves the sudden jerks due to application or removal of loads. Many plain muscles respond to such jerks by contracting, and although my observations on the retractor penis and the *Mytilus* retractor have never been complicated by the appearance of such a contraction, it is possible that the jerks themselves initiate changes in viscosity. The method is in any case not suitable for studying the changes in the muscle during a contraction, for the rapid onset of fatigue renders the period available too short to yield stretch or release curves long enough for safe interpretation.

To overcome these difficulties, another method of analysing the viscous-elastic properties of muscle was developed. The muscle was fixed at its lower end, while the upper end was attached to a helical steel spring. The end of the spring remote from the muscle was attached to the crank of a Brodie pump, and consequently was submitted to a motion which was approximately sinusoidal. The amplitude of the movement could be varied by the control on the pump, and the frequency could be varied by driving from a synchronous motor through a six speed gear box, with ratios available by turning a knob of 1 : 1, 1 : 2, 1 : 4, 1 : 8, 1 : 16, and 1 : 32. The movement of the junction of the muscle and the spring was recorded; the ratio of this amplitude to that applied to the upper end of the spring depends on the relative compliances of the muscle and the spring. If the muscle has the high compliance of a very weak spring, the two amplitudes will be almost the same. If the muscle is relatively inextensible, its changes of length will be relatively small. Between these limits, the ratio of the two amplitudes depends not only on the relative compliance of spring and muscle, but also on the frequency of the movement; for, as the frequency is increased, the resistance of the viscous components of the muscle to the increasingly rapid change of length becomes greater, and the change of length of the muscle, therefore, becomes less. If the frequency is high enough, the viscous components undergo movements which are negligible compared with the movement of the undamped elastic component. The ratio of the amplitude is then determined entirely by the ratio of the compliances of the undamped elastic component of the muscle and of the steel spring. This range of frequencies can be recognized by the fact that further increase of frequency produces no change in the ratio of the amplitudes. For the *Mytilus* muscle a frequency of 2 per sec. is conveniently within this range. At the other extreme, we can imagine a frequency so low that the amplitude becomes maximal, depending on the ratio of the combined damped and undamped compliances of the muscle to that of the spring. The curves in Fig. 5 would suggest that such frequency would be of the order of 1 in 10 hours, the higher the viscosity of the muscle, the lower the frequency needed to enable the muscle to approach its equilibrium relation between tension and length throughout the cycle.

At an intermediate frequency, the amplitude of the muscle will be intermediate; the ratio of this amplitude, at a frequency of, say, 1 in 2 min., to the minimal amplitude at, say, 2 a second, will depend largely on the viscosity of the muscle; the higher the viscosity, the smaller will be the difference in the amplitude at the two frequencies.

The present series of experiments was concerned with changes in compliance and viscosity of the muscle during contraction, and since, owing to fatigue, the effective maximum duration of a contraction is only a few minutes, only the relatively higher frequencies could be employed. Fig. 6 illustrates the changes of amplitude of a resting unstriated muscle at different frequencies, when the amplitude applied to the spring was constant. It shows that the variations of amplitude over the relevant range of frequencies are measurable but not large. Fig. 7 shows the amplitude at two frequencies, one almost high enough to give the minimal amplitude even in the stimulated muscle, and the second a relatively low frequency. It will be seen that whereas in the unstimulated muscle the amplitude at the low frequency was about 10 p.c. greater than that at the high frequency, in the muscle stimulated with A.C. the amplitude at the low frequency was about 130 p.c. greater than that at the high frequency.

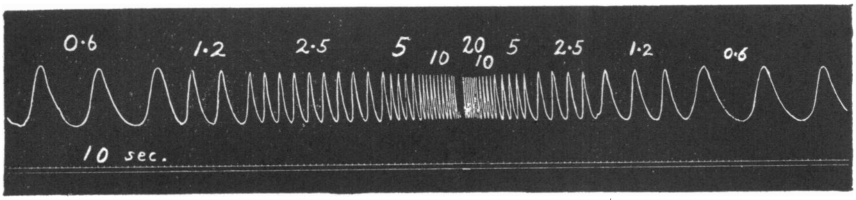


Fig. 6. The effect on the amplitude of movement of a resting *Mytilus* muscle of applying a sinusoidal stretch of constant amplitude through a steel spring at the different frequencies denoted by the numbers at the top of the record (cycles per min.). Time marker 10 sec.

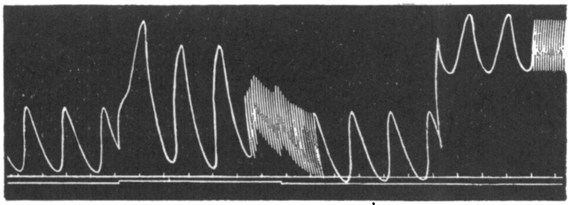
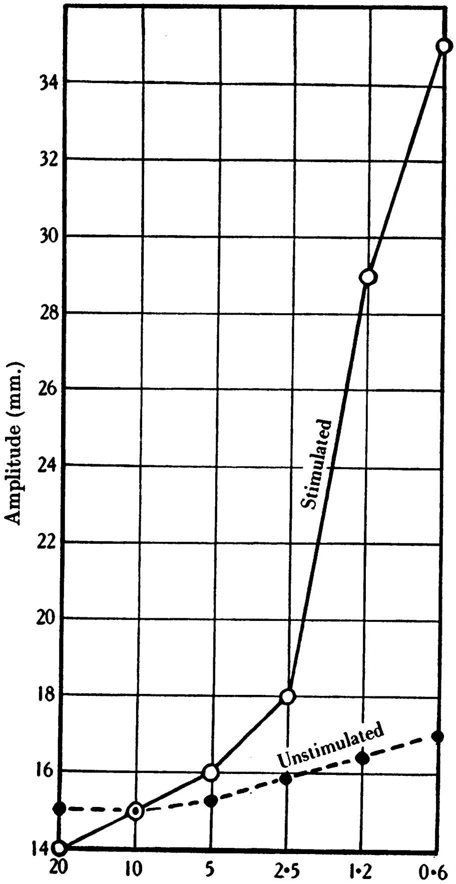


Fig. 7. The effects of alternating current stimulation (3·5 V., 4 per sec., duration given by lower signal) on the amplitude of movement of the muscle when the indirectly applied sinusoidal movement was at a high (20 c.p. min.) and a low (0·6 c.p. min.) frequency. The ratio of the amplitudes at the two frequencies was about 1 : 1·1 in the unstimulated muscle, even if the tension was increased by mechanical stretching, as toward the right end of the record, but it was 1 : 2·3 in the stimulated muscle. Time marker 30 sec.

In Fig. 8 the variation of amplitude with frequency is shown in a muscle during stimulation with alternating current, and in the same muscle unstimulated. The relations are qualitatively of the form which would be expected in a system with undamped and damped compliances in series, as implied by the muscle model mentioned above, and the difference between stimulated and unstimulated muscles shows that a contraction during stimulation with A.C. involves a reduction of viscosity. Contraction during stimulation with D.C., on the other hand, is associated with a viscosity which remains at the intermediate value found after cessation of an A.C. stimulus [Winton, 1935].



Frequency of movement (cycles per min.)

Fig. 8. Curves relating the frequency of the indirectly applied sinusoidal movement of constant amplitude, and the amplitude of movement of the muscle, unstimulated, and stimulated with current alternating at 4 cycles per sec. 3·5 V. 16·2° C.

The significance of frequency of stimulation. Contrasts in the effects on the muscle of direct and alternating currents raise questions such as (1) what frequency of stimulation results in maximum tension development and minimum viscosity, (2) do unidirectional pulses of current raise or lower the viscosity, (3) what are the relations between the effective frequencies of alternating currents and of interrupted unidirectional currents, and (4) using interrupted unidirectional currents, what is the proportion of the cycle which must be occupied by the current flow if its effects are to approach those of continuous current, and does this proportion depend on the frequency?

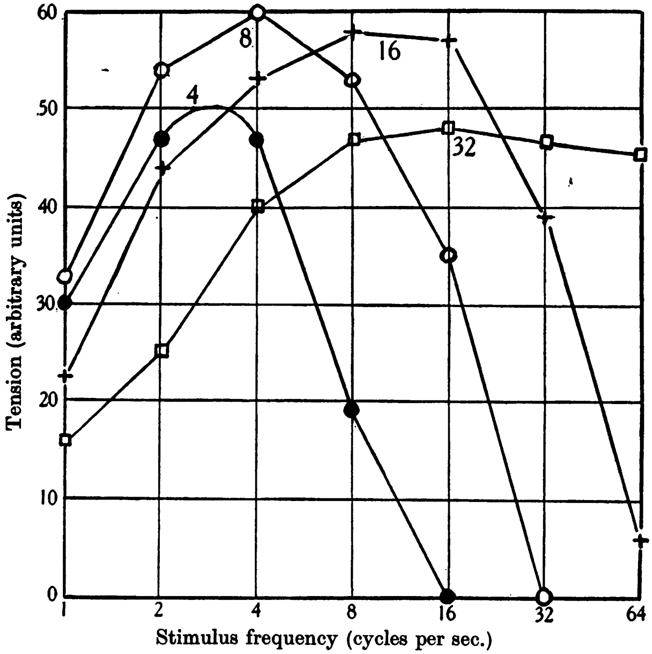


Fig. 9. The relation between the tension developed and the frequency of an alternating current stimulus of 10 sec. duration. The stimulating voltage was constant for any one curve, and proportional to the number on the curve. Note the marked increase of optimum frequency with increase in voltage.

Stimulation with 50 cycle A.C. derived from the mains shows that the optimum voltage is substantially independent of the duration of the stimulus, but that for long continued stimuli (10–20 sec. or more) voltage in excess of the optimum produces actually less tension than the optimum voltage. The rate of relaxation of the muscle, and presumably, therefore, the viscosity, depends on the tension developed in the contraction being quicker the greater the tension. This is true when the contraction is submaximal in virtue of the voltage being too low, and also when it is submaximal in virtue of the voltage being too high.

As sinusoidal currents with a frequency range of 1–100 c.p.s. are not easy to produce, the influence of frequency was studied by stimulating with a commutator which gave rectangular pulses of current; during the first quarter cycle current flowed one way and during the third quarter cycle it flowed the opposite way. No marked differences between the effects of stimulating with the commutator at about mains frequency and those of stimulating with sinusoidal current of the same frequency were noticed.

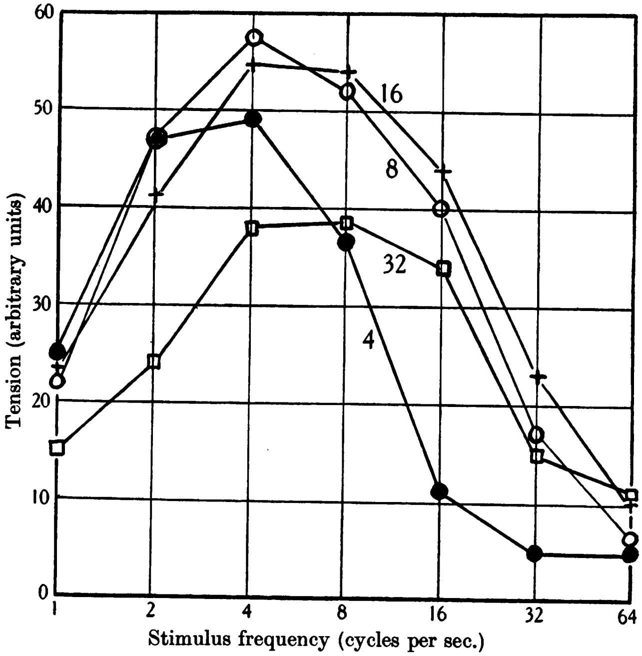


Fig. 10. The relation between the tension developed and the frequency of an intermittent unidirectional current stimulus of 10 sec. duration. The stimulating voltage was constant for any one curve, and proportional to the number on the curve. Note that the increase of optimum frequency with increasing voltage is much less marked than with alternating current stimulation (Fig. 9).

The influence of frequency of such an A.C. stimulus is shown by the typical experiment charted in Fig. 9. In this experiment the duration of each stimulus was 10 sec. The points on any one curve correspond with the same stimulating voltage, and a single curve, therefore, represents the effects of varying frequency when the total stimulating current is kept constant. Errors due to drift in the properties of the muscle were minimized (*a*) by taking a series of observations at each voltage first in ascending and then in descending orders of frequency, and (*b*) by repeating these series, which had been taken in ascending order of voltages, in descending order of voltages. The mean of the four values so obtained is shown as one point on a curve (Fig. 9). The curves show that the optimal frequency increases markedly with increase in voltage.

Intermittent unidirectional current is readily obtained from the same commutator by disconnecting the circuit which gives the reverse pulse of current. In this way the current flows during one-quarter of a cycle only, and the total current passing in a given time is, therefore, one-half of that passing when the connexions are for alternating current as in the experiment shown in Fig. 9. Except for this, the experiments, of which Fig. 10 is a representative, were performed in exactly the same way. They show that the optimum frequency of intermittent unidirectional current stimulation is much less dependent on the voltage than is the optimal frequency of an alternating current stimulus.

The simplest explanation of the existence of an optimum frequency would be to suppose that it resulted from two opposing tendencies: (*a*) an increasing number of pulses increasing the response, and (*b*) a diminishing interval between the pulses reducing their effect when the interval became less than the relative refractory period. This would account for the increase of optimum frequency with increased voltage of alternating current, but it is difficult to see how it can account for the contrast in this respect between alternating and unidirectional pulses as shown in Fig. 11. This phenomenon could, perhaps, be more profitably summarized by a scheme in which each element of excitation was due to the passage of ions through a particular distance, the ions having to retrace their path before the next element of excitation could begin. The velocity of the ions would depend on the potential gradient, or in the absence of an applied potential, on diffusion. The optimum frequency in alternating current stimulation should, therefore, be roughly proportional to the voltage, because up to this frequency the ions would reach their goal more quickly the higher the voltage, and the greater the total number of elements of excitation the greater the response; beyond the optimum frequency, however, ions could not move far enough to excite before the pulse of reverse current drove them back. In an alternating current field the forward and backward movement of the ions would take about the same time. In an intermittent unidirectional current field, however, the backward movement would depend on diffusion; it would be slow compared with the forward movement, except at the lowest effective voltages, and would be independent of the stimulating voltages. The speed of the forward movement would, however, depend on the potential gradient as in A.C. stimulation. Hence the optimum frequency should be much less affected by the voltage of unidirectional pulses than by the voltage of alternating pulses (*vide* Fig. 11). We could predict from such a scheme that if the time for back diffusion of the ions were curtailed by allowing the unidirectional pulses of current to occupy one-half a cycle instead of one-quarter, the optimum frequency should be lower. That this is so is shown in Fig. 12.

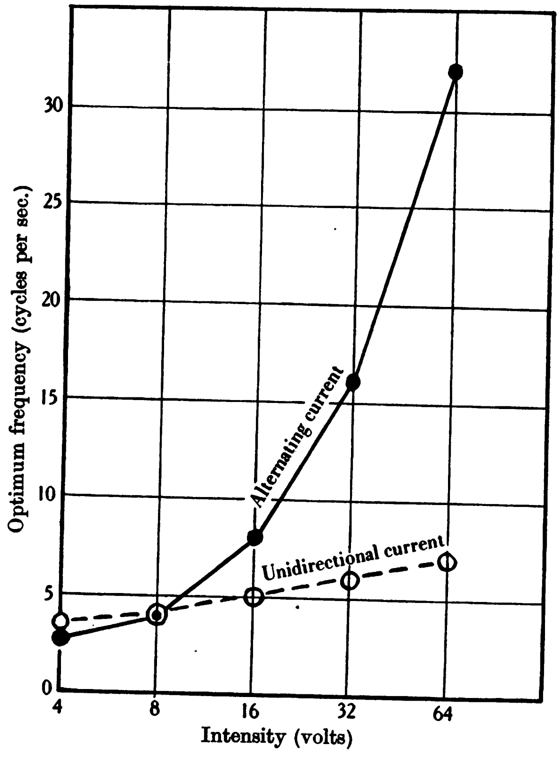


Fig. 11. The relations between optimum frequency and intensity of alternating current and intermittent unidirectional current stimuli of 10 sec. duration in the anterior retractor of *Mytilus*. Sea water 10° C.

The changes in viscosity of muscles due to the different forms of stimuli described in this section have only been investigated provisionally by taking the rate of relaxation as a qualitative guide to the viscosity. The results may be summarized by saying that the rate of relaxation of a muscle is greatest after a maximal contraction, and is lower where for any reason the contraction is smaller. For example, stimulation with unidirectional pulses (one-quarter cycle) results in about the same relaxation rate as stimulation with alternating pulses, when the voltage and frequency of the stimuli are so chosen that the tension development is the same. This point is illustrated in Fig. 12, in which the broken curves show the relaxation rates and tension developments at various frequencies of unidirectional (one-quarter cycle) current stimulation. The relation between relaxation rate and tension development is about the same as that shown in the right-hand column of this figure, where the results of stimulating with sinusoidal currents of 50 c.p.s. are given, the tension development being varied by variation of voltage. This seems to

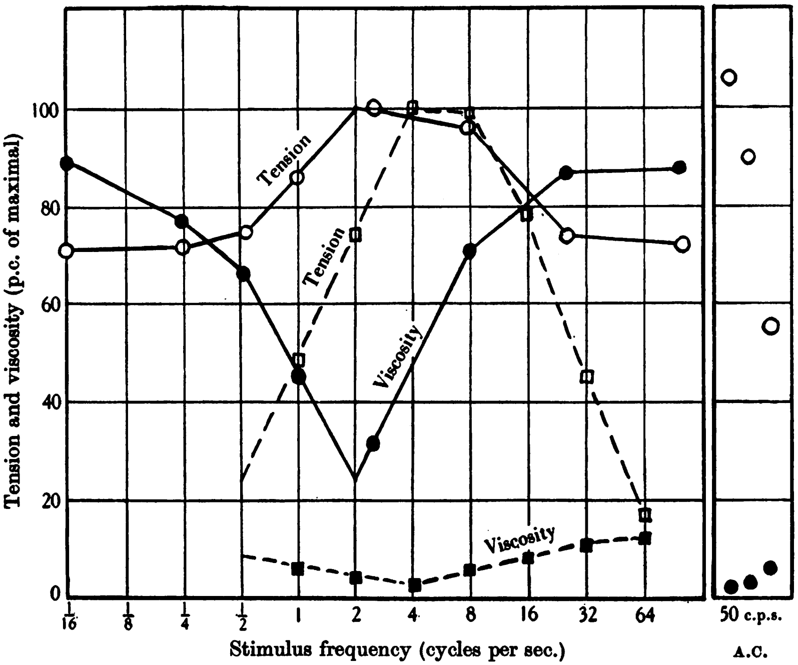


Fig. 12. The effects of frequency of intermittent unidirectional current stimuli (10 sec.) on the tension developed and the relaxation rate (viscosity) of *Mytilus* muscle. The continuous lines correspond with currents occupying one-half of the cycle, the broken lines with currents occupying one-quarter of the cycle. Note that the optimum frequency for the latter stimuli is higher than that for the former; the frequency for maximum tension is the same as the frequency for minimum viscosity.

The column on the right of the figure indicates tensions and viscosities produced by stimulating with mains alternating current (50 c.p.s.) of three different voltages; it is included to show that the relation between tension and viscosity is much the same in alternating current stimulation as in stimulation with unidirectional pulses (one-quarter cycle) of current.

indicate that there is a fundamental connexion between the magnitude of the mechanical response, manifested as tension or shortening, and subsequent viscosity of the muscle, within the range of conditions that can be produced by alternating or unidirectional (one-quarter cycle) currents of various voltages, frequencies, and durations.

The rise of viscosity which follows a response to a direct current stimulus is, however, of an entirely different order from the small rise produced by submaximal stimulation with the other forms of stimulus named. Some light may be thrown on the genesis of this higher viscosity by the unbroken curves in Fig. 12 produced when the stimulus consisted of unidirectional pulses lasting for one-half of the cycle, the total duration of the stimulus being constant and the same as that in the unbroken curve. At the optimum frequency the viscosity falls to a value not greatly exceeding that characteristic of the response to alternating current, but both above and below this frequency the viscosity approaches that characteristic of the response to uninterrupted direct current. Evidently, therefore, the rise of viscosity after a direct current stimulus is no simple consequence of polarization of the stimulating system, or even of polarization in the muscle itself, for it would be difficult to see why polarization should be least for the passage of a given current at some intermediate frequency.

SUMMARY AND CONCLUSIONS

1. The mechanical properties of the anterior retractor of the byssus of *Mytilus edulis*, an unstriated muscle, can be represented by a triple viscous-elastic model as can those of the retractor penis of the dog.

2. Analysis of isotonic stretch and release curves shows that after cessation of an alternating current stimulus the viscosity of the *Mytilus* muscle is much lower (e.g. 100-fold) than it is after a direct current stimulus. The high viscosity due to the latter persists for an hour or two, but can be readily reduced by stimulation with alternating current.

3. These results are confirmed by observations on the changes in tension in muscles submitted to sinusoidal changes of length at different frequencies. This technique has shown further that the viscosity during A.C. stimulation is greatly lower even than it is after A.C. stimulation, but that the viscosity during D.C. stimulation is not very different from that after A.C. stimulation.

4. The tension development due to a single maximal A.C. stimulus is greater than that due to a single maximal D.C. stimulus, presumably owing to the low viscosity. A.C. stimulation produces the powerful type

of contraction followed by quick relaxation suited to rapid movement. D.C. stimulation for a few seconds every minute or two results in a contraction which is fused owing to the high viscosity and powerful owing to summation; such sustained contraction is relatively immune from fatigue and shows how an unstriated muscle may develop one form of tonus with great economy although the exciting agent is discontinuous as it presumably would be if under nervous control.

5. In a preliminary survey of the relations between frequency and voltage of alternating and intermittent unidirectional stimulating currents, the optimum frequency of A.C. stimuli of constant duration, which is the same for maximal tension and for minimal viscosity, is shown to increase markedly with increase in intensity, that of intermittent unidirectional stimuli less so. With the latter, when current passes during only one-quarter of the cycle the effects on the viscosity are much like those of A.C. stimulation, that is, the greater the tension development the lower is the associated viscosity; when the unidirectional impulses of current occupy as much as one-half of the cycle the viscosity is still fairly low at the optimum frequency for tension development, but at frequencies both above and below this, the viscosity is high and approaches the value due to stimulation with continuous current.

REFERENCES

Bayliss, L. E. (1928). *J. Physiol.* **65**, 1*P*.
Winton, F. R. (1926). *Ibid.* **61**, 368.
Winton, F. R. (1930). *Ibid.* **69**, 393.
Winton, F. R. (1934). *Ibid.* **82**, 1*P*.
Winton, F. R. (1935). *Ibid.* **84**, 47*P*.

CAMBRIDGE: PRINTED BY WALTER LEWIS, M.A., AT THE UNIVERSITY PRESS