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TONUS IN MAMMALIAN UNSTRIATED MUSCLE. I.

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INTRODUCTION.

THEORIES accounting for tonus in unstriated muscle may be divided into two classes: (1) those which depend on some novel mechanism, such as a catch mechanism or gelation, and (2) those which are based on an analogy with similar phenomena in other tissues, such as tetanus in striated muscle. The chief evidence justifying the former kind of explanation was derived from experiments which seemed to show that the tonic contraction of plain muscle was associated with little or no increase of oxygen consumption above that of the relaxed muscle. Recently, Bayliss(1) has calculated, however, that the oxygen consumption corresponding to a tetanus in plain muscle would not necessarily be enough to be detected by the methods employed. This is due to the characteristic slowness of the relaxation, which enables a low frequency of stimulation to produce a fused contraction. The speed of relaxation depends on the so-called "viscosity" of the muscle; and since also it has been shown by Gasser and Hill(2) that the viscosity of skeletal muscle is increased during contraction, it seemed likely that a study of the conditions affecting the viscosity of plain muscle would throw light on the problem of tonus.

Analogy with the reflex tonus of skeletal muscle would suggest that a response to stretch might play a part in the tonus of those unstriated muscles which incorporate a local peripheral nerve plexus, and observations on intestinal and other musculature reinforce this belief. Tonus can be demonstrated, however, in isolated muscles which include no nerve cells, and exhibit no obvious response to stretch. If, then, tonus is to be reduced to its simplest terms, it is evident that it should be analysed first in these simpler muscles. With results so obtained it may be hoped that the superposition of a nervous mechanism will not render insoluble the problem of tonus in the more complex muscles. The retractor penis of the dog was therefore chosen as suitable, since it includes no nerve cells, and it does not appear to be stimulated by stretch. It has the further advantages of having its muscle fibres longitudinally arranged, and usually showing no spontaneous contractions. I am indebted to the courtesy of a number of colleagues who allowed me to remove such muscles from experimental animals which had been used by them for other purposes.

Some mechanical aspects of tonus. The forces with which a contracted muscle resists stretch may be of four kinds: (1) that which is independent of the displacement (comparable with surface tension or weight), (2) that which is a function of the displacement (comparable with elasticity or buoyancy), (3) that which is a function of the velocity of displacement (viscosity), and (4) that which varies with the acceleration. Forces of the last class depend on inertia and will be so small in comparison with the other forces concerned in the slow movements of plain muscle that they can safely be neglected.

The three remaining kinds of force may be related in countless ways, which can be paralleled by the complex networks of resistance, capacity, and inductance studied by the electrical engineer. Although it is now the custom to analyse elaborate mechanical systems by reference to the corresponding electrical models, whose properties are more completely understood, this procedure will not be adopted; it is only mentioned to emphasize that the mechanical models to be described are intended to convey the relations between the tension and length of the whole muscle, and time, in mechanical symbolism, in the same sense as the analysis might have been performed in electrical symbols, or in algebraic symbols. The mechanical model happens to involve the same concepts—force, distance, and time, as are concerned in tonus, but it is only a logical fiction invented in order to simplify the description of the relations between them, and does not aim at representing how the muscle actually produces such relations.

Levin and Wyman(3) examined the effects of stretching skeletal muscles, and found that the changes of tension with time could be represented by two springs arranged in series, the extension of one of which was damped by a vane moving through a viscid liquid as in Fig. 1. The springs obeyed Hooke's Law, and the viscous resistance was proportional to the velocity of the vane at any given moment. Now, although the details are not quite so simple, the qualitative results of stretching unstriated muscle are the same. If the tension in the muscle be recorded, a sudden stretch produces an immediate large increase of tension (equivalent to stretch of the undamped spring only), and if the muscle is kept at the new length this is followed by a gradual falling off of the tension as in curve *A* (gradual extension of the damped spring allowing the undamped spring to shorten without change of length of the whole system). Conversely, sudden shortening of the muscle produces an immediate large fall of tension followed by a gradual recovery till a new equilibrium is established, as in curve *B*. If, on the other hand, the changes in length of the muscle be recorded, the sudden application of a constant tension results in an immediate stretch (extension of the undamped spring) followed by a gradual further stretch (extension of the damped spring, while the undamped spring remains unaffected) as in curve *C*. In the model, the gradual stretch is an exponential function of time; and under ordinary isotonic conditions of recording the curve becomes a straight line only when it is horizontal. It will be shown that the properties of plain muscle deviate from those of the model in this respect. When the load is suddenly removed from a stretched muscle, the corresponding sudden (undamped) and gradual (damped) portions may be distinguished while it shortens as in curve *D*. These general reactions to stretch and release have been observed in many mammalian plain muscle preparations, such as the guinea-pig's uterus, and the rat's duodenum. In those muscles which normally undergo rhythmic contractions, the reactions are most clearly revealed after the spontaneous activity has been abolished by immersion in solutions of chloral or other suitable narcotics. The same type of reaction to stretch and release was found in Holothurian smooth muscle by Hill(4).

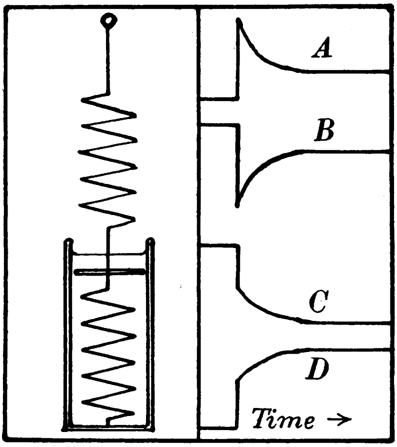

Fig. 1. Viscous-elastic model of Levin and Wyman. The upper curves show the relation between tension and time when the model is suddenly lengthened (*A*), and shortened (*B*). (Increase of tension recorded vertically upwards.) The lower curves show the relation between length and time when an isotonic load is suddenly applied (*C*), and when it is suddenly removed (*D*). (Increase of length recorded vertically downwards.)

It is evident, therefore, that the force maintaining the tonus of plain muscle may be analysed into at least one undamped elastic system, and one viscous-elastic system; and we will consider in turn the variations of the elements of these systems under various conditions.

Experimental methods. The slow time relations which are characteristic of unstriated muscle enable the simplest methods to be employed without undue error. The muscle was immersed in a Ringer's solution of composition described by Burn and Dale(5), which was stirred by a regular stream of air bubbles, and maintained thermostatically within one-tenth of a degree of 36·4° C. The lower end of the muscle was attached to a rigid support, and the upper end to a light aluminium isotonic lever which recorded on a slowly moving drum with a magnification of 2·3. The constant initial isotonic load was about 0·2 g. weight. The experimental weight was attached near the fulcrum of the lever by a thread. It was at first prevented from loading the lever by support from another thread attaching it to a fixed bar placed above and perpendicular to the lever. Sudden application of the load was effected by burning the attachment to the fixed bar. Subsequent sudden release from the load resulted from burning the thread attaching it to the lever. The drum was arranged to move at about 1 cm. per sec. during the first two minutes, in order to secure a sharply defined demarcation between the sudden and gradual phases of the stretch. The later phases of the stretch were recorded with the drum moving more slowly.

The undamped elastic system. The response to sudden stretch of the retractor penis was described in a previous communication ((6), Fig. 5), where it was shown that the immediate tension development due to a series of stretches through equal absolute distances increased with increasing length of a muscle. It may be inferred that the equivalent spring becomes stronger when the muscle is longer. One might expect, and does indeed find, that the application of a series of increasing loads to a muscle would result in extensions which indicate decreasing compliance of the undamped element, as shown in Fig. 2. The sudden shortening which is produced by removing a particular load from the extended muscle is usually less than the sudden lengthening which that load produces in the contracted muscle, as shown in the two pairs of curves (VIII and IX). Two kinds of exceptions to this rule may be mentioned. First, when the muscle is so fully relaxed that the resilience due to the boundary elastic system reinforces that due to the undamped spring, the sudden shortening is abnormally great, as it was when 12½ g. weight was removed in the experiment represented in curve VIII. Secondly, certain muscles consistently show the same or even a greater shortening than the lengthening produced by the same load; and the reactions of one such muscle are represented in curve VII. The conditions producing this anomaly have not been discovered.

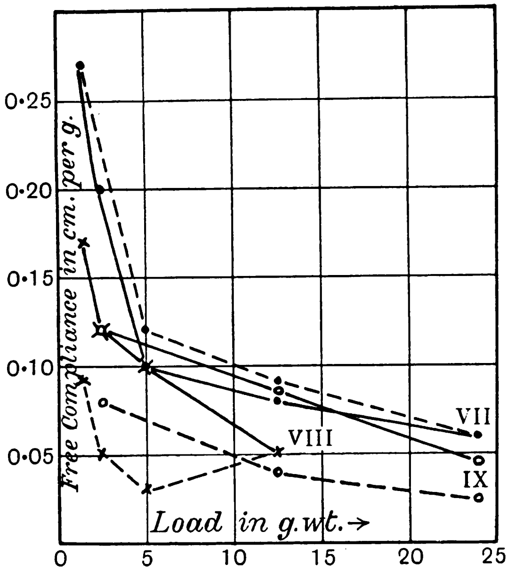

Fig. 2. Variations, with increasing loads, of the compliance of the undamped elastic phase of the stretch (continuous lines) and release (broken lines) of the isolated retractor penis. Each pair of curves corresponds with one of three muscles: Nos. VII, VIII and IX. The curves show increase of the strength of the equivalent spring with increase of load.

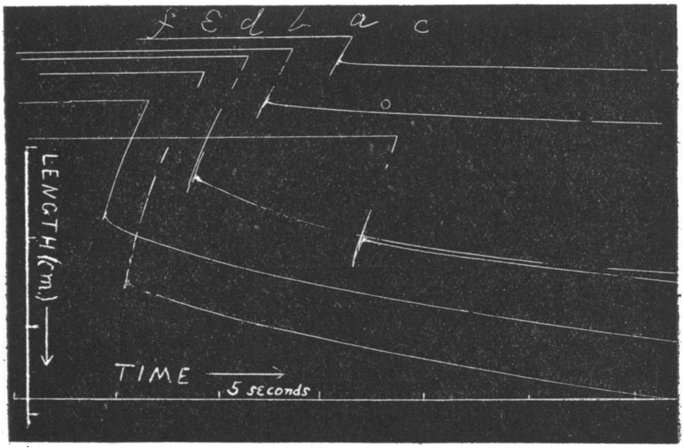

Fig. 3. Record of the stretches of a retractor penis due to sudden isotonic loading. (The early portion only is shown.) Load in curve (*a*) 5 g., (*b*) 12·5 g., (*c*) 24 g., (*d*) 12·5 g., (*e*) 24 g., (*f*) 12·5 g. Curves *d* and *e* represent stretches in the presence of adrenaline (1 : 10^6). The curves indicate the order of accuracy with which the undamped and damped portions of the stretch may be distinguished. Comparison of *b* with *d*, and of *c* with *e*, shows the effect of adrenaline in weakening the equivalent undamped spring.

The strength of the equivalent undamped spring is affected by a variety of other factors; for example, it is strengthened by a fall in temperature, and weakened by the addition of adrenaline (1 : 10^6) to the Ringer's solution (Fig. 3). This rather surprising relation between the free compliance of the muscle and contraction due to a drug cannot be extended to include all kinds of contraction. The development of "Ringer tonus" during the first hour of immersion in Ringer's solution of a muscle under a light load is an instance of contraction associated with the opposite effect on the free compliance, namely, a decrease. The equivalent undamped spring may about double its strength during the development of Ringer tonus (Fig. 6).

"Ringer tonus" is produced under the following conditions. A retractor penis, which may be, for example, 4 cm. long in the living dog, is excised and immediately dropped into cold (17° C. or less) Ringer's solution. After 5 to 10 minutes it has contracted to, say, 2·5 cm. It is then placed in warm (36–37° C.) oxygenated Ringer's solution, with a light isotonic load (*e.g.* 0·20 g.). The muscle relaxes to about 3 cm. in the course of one-quarter of an hour, and then slowly contracts till, at the end of a further hour, its length may be 1·5 cm. This condition of contraction is maintained so long as the muscle survives, and is what I have termed "Ringer tonus." For reference, it may be added that a retractor of the dimensions named would be about 8 cm. long when fully extended, and that the orders of time needed to reach practical equilibrium, when relaxing under an isotonic load of about 10 g., would be one-half an hour if the load were applied when the muscle was first placed in the warm bath, and 5 hours if the load were not applied until Ringer tonus had fully developed. The viscous and elastic properties characteristic of Ringer tonus can be modified by subsequent treatment of the muscle with adrenaline.

The action of adrenaline on the undamped elastic system is shown in Table I, which includes instances where the development of Ringer tonus made it possible to arrange for the initial lengths of the control and drugged muscle not to be widely different.

TABLE I.

		Control		Adrenaline	
Exp.	Load (g. wt.)	Free compliance (cm./g.)	Initial length (cm.)	Free compliance (cm./g.)	Initial length (cm.)
V	10	·040	3·8	·068	4·3
	20	·031	4·1	·063	4·3
VI	12½	·045	2·1	·104	2·2
	24	·048	3·1	·100	2·4

In seven other experiments in which the length of the muscle, under the influence of adrenaline, was shorter than its control length, the immediate compliance in the presence of adrenaline averaged 172, taking the control value as 100. The effect of adrenaline on the sudden release was not so large, the compliance being increased only to 120 (average of nine experiments), as compared with the release control value of 100. This effect of adrenaline is small or absent, when the load applied is 3 g. or less.

The effects of contraction on the viscous-elastic system. These have been observed under isotonic conditions by measuring the progress of the gradual lengthening or shortening of the muscle, which follows the instantaneous changes produced by sudden application or removal of a load.

The addition of adrenaline (1 : 10^6) to the solution in which a retractor is immersed produces a well-marked speeding-up of the relaxation due to a load, as shown in Fig. 4. On the other hand, the muscle does not relax so far in the presence of the drug as it does, if left long enough, in its absence. The rapid initial relaxation is therefore not due to a weakening of the equivalent damped spring, which is actually strengthened; but it must be attributed to a reduction in the viscous

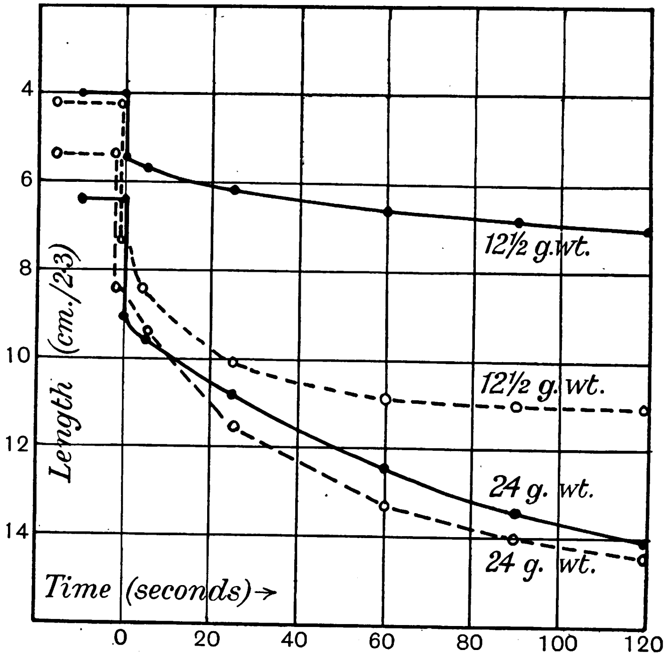

Fig. 4. Isotonic extension-time curves showing the pure elastic and the early part of the viscous-elastic stretch of the retractor penis, in the presence (broken lines) and absence (continuous lines) of adrenaline (1 : 10^6). The curves show the effects of adrenaline in weakening the equivalent undamped spring; and, taken in conjunction with those of Fig. 5, they show its effect in reducing the viscosity of the viscous-elastic component.

resistance. If the relaxation curves be regarded as exponential, as a first approximation, the reduction of "viscosity" due to adrenaline may be calculated to be of the order of twenty-fold. (By "viscosity" is meant the ratio of the viscous resistance in g. wt. to the velocity of the free end of the muscle, in cm. per sec. It is proportional to the product of the time of half-relaxation and the compliance of the equivalent spring.)

The diminution of viscosity due to adrenaline is shown equally well in the release curves (Fig. 5); and the equivalence of the effects of adrenaline on the lengthening and shortening of the muscle gives no support to the hypothesis of a polarized mechanical system, such as the "catch mechanism."

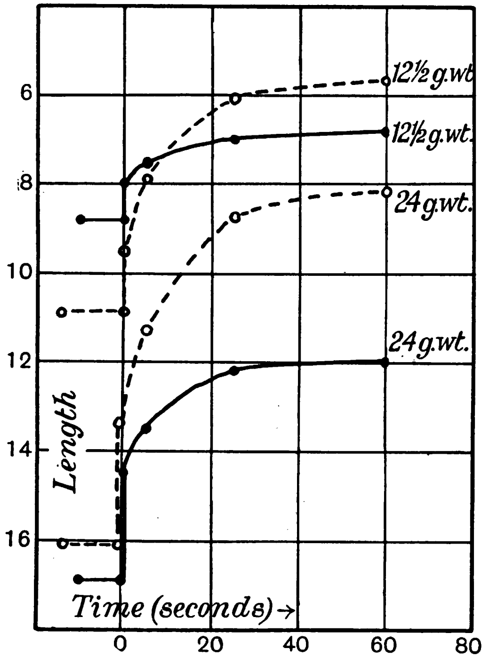

Fig. 5. Isotonic recovery curves showing shortening of the retractor penis after sudden removal of a load, in the presence (broken lines) and absence (continuous lines) of adrenaline (1 : 10^6). The curves show the effects of adrenaline in weakening the equivalent undamped spring; and, taken in conjunction with those of Fig. 4, they show its effect in reducing the viscosity of the viscous-elastic component.

In contrast with the hastening action of adrenaline, the changes associated with the development of Ringer tonus are in the opposite sense, as shown in Fig. 6.

Analysis of the properties of the viscous-elastic system. Inspection of the length-time curves during isotonic stretching of a retractor usually shows at once that there is no simple exponential relation between these

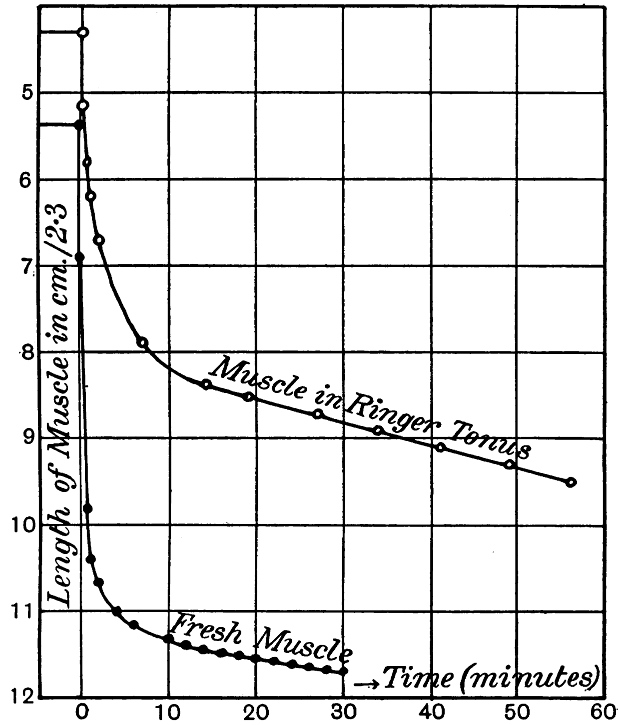

Fig. 6. Isotonic extension-time curves of a retractor penis (1) 20 minutes after removal from a dog, (2) 1 hour later after the development of Ringer tonus. The curves show the influence of the tonic contraction in strengthening the equivalent undamped spring, and in increasing the viscosity of the viscous-elastic component.

two variables. The curves often become practically straight lines, while the slope is still considerable—as illustrated in Fig. 7. The straight portion of the curves represents stretching at a uniform velocity. If the viscosity is constant, the force acting upon the viscous system must therefore also be constant. The damped elastic system has spent its force during the early curved portion of the relaxation, and the muscle then extends like a pure viscous system under constant tension until the boundary region of complete extension is reached. This introduces a new elastic system, which gradually effects an equilibrium length for the given load when the muscle is fully extended, and which persists after death of the muscle.

The disappearance of the elastic component suggests either some nervous inhibitory process due to the prolonged action of the load, and analogous with the lengthening reaction of innervated skeletal muscle, or some irreversible change in the surviving tissue. The first is rendered unlikely by the observation that the same kind of discontinuity in the relaxation curve persists in concentrations of chloral hydrate (1 : 500) more than enough to abolish all spontaneous activity in muscles which have shown it. The second suggestion is contradicted by the subsequent properties of the muscle, as illustrated in Fig. 8. This retractor was first stretched by a light load (2½ g.) and released. It was then fully extended with a large load (24 g.) and released. Finally, it was again stretched by the light load (2½ g.) and released. The curves obtained before and after the complete stretch, which included a period of relaxation at uniform velocity, were practically identical, although insufficient time

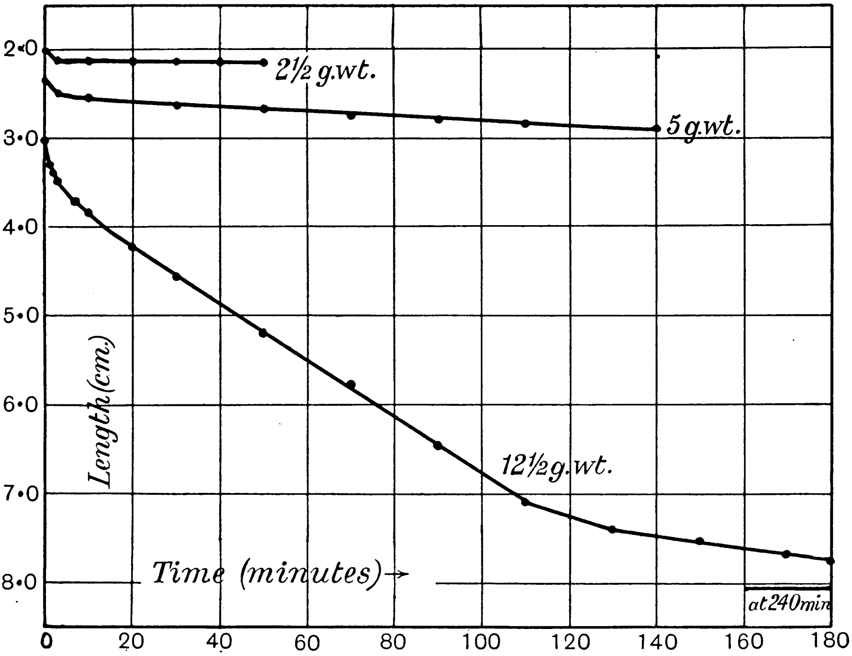

Fig. 7. Isotonic extension-time curves of an isolated retractor penis, stretched successively by loads of 2½ g. wt., 5 g. wt., and 12½ g. wt.—time being allowed for recovery of tone before the application of each. (The undamped stretch is omitted.) The curves show that the viscous-elastic phase is terminated by an inclined straight line, corresponding to a uniform velocity, and attributed to an equivalent pure viscous phase.

was allowed for the muscle to shorten quite to its original length. The curve (Fig. 8) showing lengthening of the same muscle when a heavy

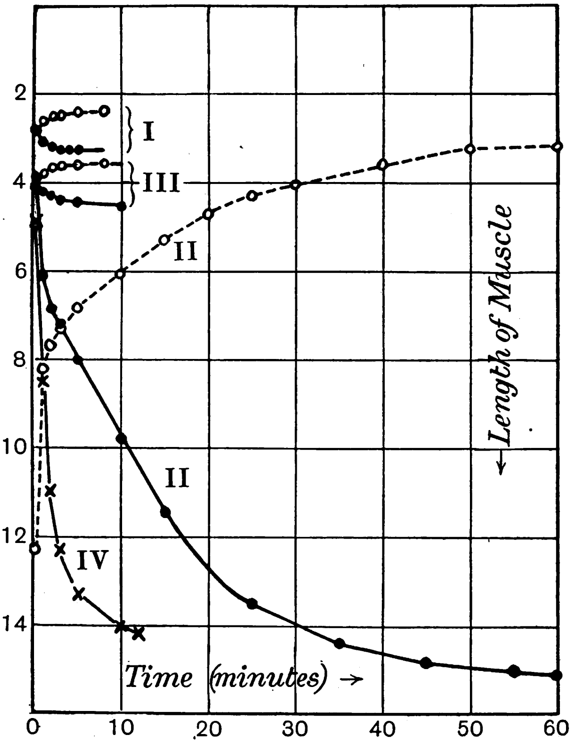

Fig. 8. Isotonic curves showing extension (continuous lines) and recovery (broken lines) of a retractor penis. Curves I = stretch and release with load of 2½ g. Curves II = stretch and release with load 24 g. Curves III correspond with Curves I. Curve IV is the stretch with a load of 24 g. in the presence of adrenaline (1 : 10^6). The curves show that a full extension, including a phase of stretch at uniform velocity, involves only reversible processes. (The undamped phase is omitted.)

load (24 g.) was applied in the presence of adrenaline (1 : 10^6) is included both to amplify the evidence shown in Fig. 4 by describing the changes during a longer period of time, and to indicate some of the conditions under which no straight portion of the relaxation curve is found. The phase of uniform velocity is abolished when the muscle lengthens far enough during the viscous-elastic phase of retardation to reach the second phase of retardation due to complete extension. This tends to occur with large loads, with low viscosities, and particularly when both these conditions are combined, as in the curve shown. Another class of conditions which makes the phase of uniform velocity difficult to detect is the combination of small loads with high viscosities, as illustrated in the top curve of Fig. 7. Here the rate of relaxation is so small, after the early part of the stretch, that errors of measurement prevent a confident distinction between a state of equilibrium and a minute velocity of extension.

We may now enquire what modifications will have to be introduced into the mechanical model in order to make it represent the properties of the muscle more faithfully. The damped spring evidently does not obey Hooke's Law, since the relaxation curve is not exponential. If a more complex relation (*e.g.* a cubic function) between tension and extension be attributed to this elastic element, its damped relaxation curve may be made to approach that of the muscle more nearly. But for our present purposes it is simpler, and sufficiently accurate to regard the curve as compounded of an early exponential portion and a later linear portion. This implies that the spring would have the curious property of resisting a stretch with a force that varied with the extension for a certain distance, and beyond this with a force which was independent of the extension. These two phases are not altogether unlike those found when stretching a wire up to and beyond its yield point. In view, however, of the effects of different loads on the muscle, as shown in the lower two curves of Fig. 7, it is more satisfactory to retain the simple spring in the damped elastic system of the model, and adopt a pure viscous system with a higher viscosity, in series with the viscous-elastic system, to introduce the phase of uniform velocity. Analogous phenomena in wires have been represented by a somewhat similar mechanical model by physicists in order to simplify their analysis (7).

The model constructed in this way is illustrated in Fig. 9, accompanied by a curve showing the three phases—pure elastic, viscous-elastic, and pure viscous—of the length-time curve produced by sudden application of a load under isotonic conditions. In this arrangement the stretch due to the pure viscous system is at a uniform rate throughout, and its amount at any instant can be calculated from the velocity shown by the straight portion of the curve. Thus by subtracting the pure viscous stretch at any instant from the total stretch at that instant, the viscous-elastic stretch can be found. The viscous-elastic stretch, derived in this way and plotted against time, would give a simple exponential curve, represented by the line *B*. From this curve the extensibility of the spring and the viscosity can be calculated. If the relaxation curves obtained from muscle are analysed by this method, the derived "viscous-elastic" curves are approximately exponential in form, and the equivalent spring approximately obeys Hooke's Law.

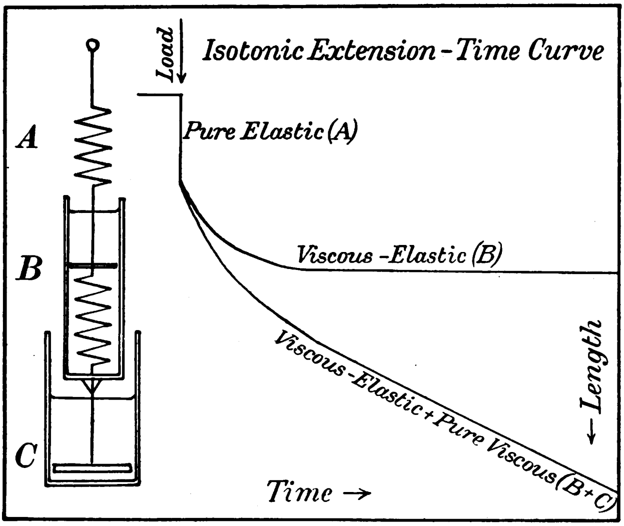

Fig. 9. Triple mechanical model representing the relations between tension, extension, and time, during the stretch or release of a retractor penis. The elastic elements are shown as coil springs, and the viscous elements as vanes moving in viscid liquids. The viscosity of C is much higher than that of B. The diagram of isotonic extension-time curves indicates the contribution of each component of the model: (1) the pure elastic component (A) giving an instantaneous (vertical) response to loading; (2) the viscous-elastic component (B) giving an exponential response, and (3) the pure viscous component (C) giving a linear response. The complete curve ($A+B+C$) represents the response of the whole model.

The development of tonus. When a muscle is released from a load which has stretched it, it shortens to somewhere near its fully contracted length. We have seen that a large part of the stretch could be represented as that of a pure viscous system under the influence of a constant force, presumably equivalent to the isotonic tension. The question arises, what is the restoring force which enables the muscle to shorten through the length corresponding to the non-elastic portion of the stretch? This force is evidently independent of the extension, and resembles surface tension in this respect. The reason why this force does not make the muscle contract up to nothing is suggested by inspection of the fully contracted muscle, which shows parts of the tissue beginning to buckle. Most of the tissue is probably prevented from buckling by the adhesion of adjacent portions, and this introduces a second elastic boundary system corresponding with the completely contracted length of the muscle.

The constant restoring force may be represented in the model (Fig. 9) by adding weight to the damping vane of the pure viscous system. Certain consequences follow from this arrangement, and may be tested. If, for example, the model be stretched with different loads, the velocity of the pure viscous phase will vary not with the absolute value of the load, but with the excess of the load over the restoring force. Fig. 10 shows the velocity of isotonic stretch of a muscle plotted against time for a series of loads. Considering the horizontal portions of the curves, which represent the uniform velocity of the pure viscous phase, it will be seen that a load of 12½ g. produced about ten-fold the rate of stretch which was produced by 5 g. This would be intelligible if the restoring force opposing both these loads were about four grams weight, and the excess of the actual load over the restoring force were the effective force opposing the viscous resistance. Another inference from the model would be that loads exerting a force less than the restoring force would have no effect on the pure viscous system, and should therefore produce an exponential relaxation curve, corresponding with the viscous-elastic

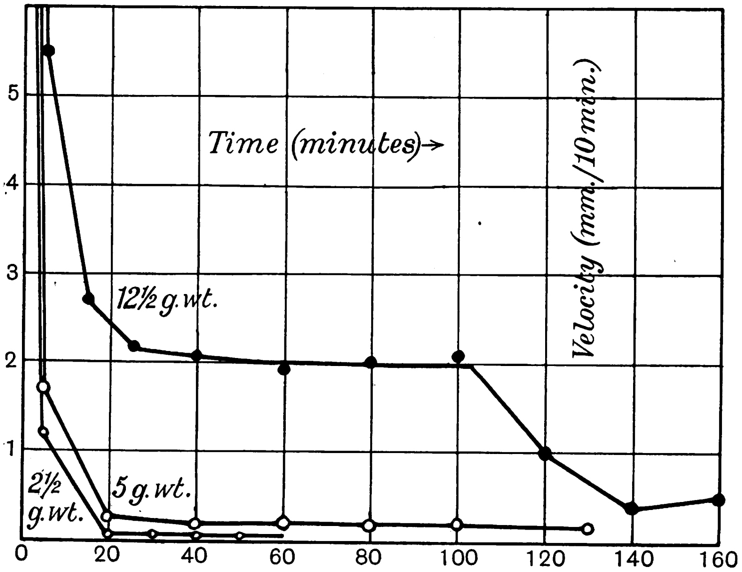

Fig. 10. Velocity-time curves obtained by stretching a retractor penis with a series of constant loads. The curves show (1) the initial exponential phase (viscous-elastic), (2) the phase of uniform velocity (pure viscous), and (3) a terminal viscous-elastic phase when the boundary region of complete extension is approached. A ten-fold increase of the uniform velocity is produced by a two-and-a-half-fold increase of load.

system. The whole model should reach equilibrium at a much shorter length than its fully extended length. It is difficult to be sure whether this is true of muscle, owing to the exceedingly slow stretches induced by light loads, for example, by 2½ g. in Fig. 10, and the consequent difficulty of distinguishing between the almost asymptotic limb of an exponential curve, and a minute superimposed uniform velocity. But the evidence available is clearly not in conflict with the inference. Another deduction from the model would be that a light load (just exceeding the restoring force) might suffice to keep a relaxed muscle extended, though it might take indefinitely long to induce a contracted muscle to lengthen very far; and this is in accordance with the experience of many workers on isolated plain muscle.

Straight portions occur also in the release curves (length-time) of the muscles, but they are not so prominent as those in the stretch curves, and have not yet been so closely scrutinized.

DISCUSSION.

The length of the retractor at a particular time can therefore be represented in terms of the reaction of several mechanical systems to the tension. That the effects of small differences in experimental technique should play so prominent a part in producing apparently inconsistent changes in the length of smooth muscle at different times, and in different places, is hardly surprising when it is regarded as a resultant of so many variables. The action of adrenaline on the retractor penis may be quoted as an example. Adrenaline regularly induces contraction. In only two, out of over a hundred muscles to which adrenaline has been applied, has the reaction to the drug been inhibitory. Both these muscles were tonically contracted. Similar ambiguities in the responses of other plain muscles to drugs and nervous stimulation have been recorded. The ambivalent effects of adrenaline described above on the different components of the equivalent mechanical system would readily account for such anomalies.

Two kinds of contraction in the retractor have been studied in the foregoing experiments, namely, the development of Ringer tonus, and the response to adrenaline. Though shortening of the muscle is common to both, the other properties of the muscle which have been examined vary in opposite directions in the two cases. Ringer tonus involves a small tension, and shortening prevented by a load exceeding 3 to 4 g. This tension appears to correspond with the non-elastic restoring force mentioned above, and is therefore largely independent of the extension of the muscle. Perhaps the most prominent feature of Ringer tonus is the high value of the viscosity which presumably ensures maintenance of a particular length with minimum metabolic expenditure, while opposing a large force to any rapid change of length. It may be convenient to refer to this as the postural contractile mechanism. The response to adrenaline, on the other hand, may involve the development of ten- to twenty-fold the tension, and, as has previously been shown ((6), Fig. 7), the value of this tension varies with the length of the muscle. Associated with this, there is a large reduction in the viscosity which facilitates rapid changes of length. This may be termed the phasic contractile mechanism. Auxiliary evidence favouring the distinction between these mechanisms is derived from observation of spontaneous contractions and the responses to short electrical stimuli occurring during the slow isotonic relaxation under load of a muscle which has developed Ringer tonus. After either of these disturbances, the muscle returns to the length which it would have reached if it had continued in uninterrupted relaxation during the same period of time.

The phasic and postural states may perhaps be regarded as opposite extremes of a continuously variable condition of the muscle—the resting muscle in the living animal probably occupying an intermediate position.

If these mechanisms, found in the isolated retractor penis surviving in Ringer's solution, can also be demonstrated in the musculature of the hollow viscera, the postural system, on the one hand, would be admirably adapted to gripping the contents firmly but not tightly, to showing small changes of tension corresponding with large changes of length so long as these proceeded slowly, and to maintaining its tonus economically. The phasic system, on the other hand, might be regarded as mobilizing the muscle for rapid expulsion of the contents, requiring more force and less viscous resistance for large but transient changes of length—sustained contraction of this kind being uneconomical.

The mechanical analysis of tonus has revealed two boundary elastic systems, corresponding with complete contraction and complete extension; between these limits, the variables concerned are related approximately as in the triple model. Of the relations between the components of the model, only that of the undamped elastic system and the viscosity has been examined under a variety of conditions. The equivalent free spring is strengthened, and the viscosity increased during the development of Ringer tonus or by cooling the muscle. The opposite effects on both systems are produced by adrenaline. The parallelism between these distinct components of the model under a variety of conditions should be a sufficient warning to beware of an attempt to attribute any anatomical significance to the elements of a mechanical model, which is designed only as a trick to simplify the systematic description of the changes in length, tension, and time, of the entire muscle.

The retractor penis is not unique among plain muscles in exhibiting linear portions in the isotonic stretch and release curves, for similar lengthening and shortening at uniform velocity has been observed in the adductor muscle of *Pecten* (8).

SUMMARY.

1. The nature of the force with which a tonically contracted smooth muscle resists stretch has been analysed by sudden application of various loads under isotonic conditions.

2. Two contractile mechanisms may be distinguished in the isolated retractor penis, which is devoid of nerve cells and exhibits no active response to stretch.

(*a*) The postural contractile mechanism, exemplified in the development of Ringer tonus, is associated with (1) a small tension (*e.g.* 3–4 g. wt.) which may be independent of the length of the muscle within a considerable range, (2) a high viscosity, which results in a large tension being opposed to quick increases of length, and may be expected to enable the muscle to remain contracted at the expense of relatively little metabolic activity, and (3) a relatively rigid undamped elastic component.

(*b*) The phasic contractile mechanism, exemplified in the response to adrenaline, is associated with (1) a relatively large tension (*e.g.* 40–50 g. wt. at the optimum length) which is approximately proportional to the length of the muscle within a considerable range, (2) a low viscosity, which results in only a small tension being opposed to rapid changes of length, and may be expected to involve relatively intense metabolic activity during a sustained contraction, and (3) a relatively extensible undamped elastic component.

3. The relations between tension, length, and time, during the lengthening or shortening of a retractor due to application of, or release from, loads can be simply represented by a mechanical model which includes a pure elastic system, a viscous-elastic system, and a pure viscous system controlled by a constant force, arranged in series.

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