VISCOUS-ELASTIC CHANGES IN MUSCULAR CONTRACTION

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INTRODUCTION.

IN demonstrating the viscous and elastic changes which accompany muscular contraction a dynamical method is essential in order to discriminate between possible effects of fatigue and those essentially characteristic of the contracted state. Such a method is indicated in an important memoir on "The Dynamics of Muscular Contraction" by Gasser and Hill (1924). As an approximate estimate these authors state that during short contractions the viscosity of the frog's sartorius increases to about ten times its value in the resting condition, while Young's modulus increases to about sixteen times its normal value. It seemed possible therefore, that a study of the viscous-elastic properties of muscle might be undertaken in connection with studies commenced (Hogben, 1925) to throw further light on the relation of electrolytes to the contractile and excitatory processes in muscle. Experiment, however, has not encouraged this expectation, since the changes we have observed are not of the order of magnitude recorded by Gasser and Hill. Though the latter state very explicitly that the figures quoted above are intended only as a rough approximation, it would seem justifiable to place on record the results of experiments designed to confirm the conclusions of Gasser and Hill on account of the theoretical interest which attaches to the issue as it bears on our views of the physical mechanism of contraction and the efficiency of the process.

Gasser and Hill employed in their experiments a flat steel spring of dimensions 25 × 2 × 0·1 cm. clamped at one end and carrying at the other a light extension to write on a smoked surface. A pair of sartorius muscles fixed at one end were connected by a silk thread with the spring at such a distance from its attachment that there was no slack in the shortest position and the tension in the longest position of the resting muscle was comparatively small when the spring was made to vibrate by release of tension. Records of the vibration of the free spring and the coupled system were taken; and in the latter case the muscle was stimulated to contract in the course of the experiment. Measurements were made of the amplitude of successive swings and the period of the vibration in each case. From these data the elastic and damping coefficient were calculated as indicated in what follows. The tension to which the resting muscle was subjected is not recorded.

PRINCIPLE OF THE METHOD.

The damped vibrations of a steel spring are given by an equation of the familiar form

$$m\frac{d^2x}{dt^2} + \mu\frac{dx}{dt} + Kx = 0 \qquad \ldots\ldots(1),$$

when the system is not subject to disturbing forces which are a function of the time. If the ratios of μ and K for successive operations are alone involved, m may be neglected; and the solution of (1) is then

$$x = ae^{-\frac{\mu t}{2}}\cos\left[\left(\sqrt{K - \tfrac{1}{4}\mu^2}\right)t + \epsilon\right] \qquad \ldots\ldots(2)$$

where K and μ are elastic and viscous coefficients respectively. It follows from (2) that if λ is the natural logarithm of the ratio of two successive amplitudes, and T the periodic time

$$\frac{2\lambda}{T} = \mu \qquad \ldots\ldots(3),$$

and

$$T = \frac{2\pi}{\sqrt{K - \tfrac{1}{4}\mu^2}} \qquad \ldots\ldots(4)$$

from which K and μ may be calculated.

For the coupled system in which the spring vibrates against the resistance of a pair of sartorius muscles, Gasser and Hill calculate K and μ for (*a*) the spring alone, (*b*) the system composed of spring and resting muscle, (*c*) the system composed of spring and contracted muscle. The validity of Gasser and Hill's method depends upon the assumption that the configuration of the vibrating system remains the same in successive operations. Preliminary experiments led the writers to doubt whether this condition was realised in the experiments described by Gasser and Hill, from whose descriptions it would appear that the spring was flexible beyond the point where the muscle was attached. To avoid this a modification was introduced. To a piece of flat steel spring 2 cm. broad, 1·4 cm. long and 0·9 mm. thick a ribbed and rigid aluminium extension 30 cm. long was fixed. The point of attachment of the muscle was on the rigid portion 2·5 cm. from the junction of the latter with the spring. With the object of testing at the same time the reliability of the modification and the formal considerations stated in the foregoing paragraph, an experiment was carried out to compare the elastic constants of three helical springs determined previously by a statical method. The values in the two right-hand columns in the table below refer to the reciprocal of the extension per unit length for a fixed tension; and the results do not give any justification for the suspicion that the different values obtained by the dynamical method with this arrangement are due to differences in the configuration of the vibrating system.

Spring	Dynamical method T 200 gm.	Statical method	
		(*a*) T 1000 gm.	(*b*) extrapolated to T 200 gm.
1	1·00	1·00	1·00
2	0·15	0·18	0·15
3	0·69	0·72	0·84

In these experiments, as in others herein described, optical records were made to avoid errors due to variable surface friction inevitable in kymographical procedure. The time was recorded in hundredths of a second by means of a standard tuning-fork.

In their treatment of the problem, Gasser and Hill subtract the constants for the spring from those of the complete system to obtain the corresponding constants of the muscle. This is not rigidly valid; but a consideration of the equations of motion at the point of attachment of the muscle shows that for a small angular deflection it is a reasonable approximation. This point has to be borne in mind in the method of conducting the experiment.

Needless to say, it is absolutely essential to base comparison of the period and amplitude of the swings of the coupled system spring plus contracted muscle, with those of the coupled system spring plus resting muscle, only after the new equilibrium point in the former case has been reached. A safe criterion in this case is that when equilibrium is reached, the logarithmic decrement for two successive pairs of swings should not be significantly different. To avoid vitiating the interpretation of the data through the effects of fatigue, the logarithmic decrement of the first five swings after shortening is completed was taken in all cases. If the logarithmic decrement has not reached an approximately constant value, it is clear that equilibrium has not been attained.

EXPERIMENTAL DATA.

The data here recorded refer only to experiments carried out with the modification indicated above. Previous experiments with a form of apparatus identical with that described in the publication referred to had yielded results which were very variable though in no case indicative of an increase in the viscous and elastic constants of the muscle during contraction of the order suggested by Gasser and Hill's experiments. In these preliminary experiments both gastrocnemius and sartorius muscles of *Rana Catesbiana* and *R. pipiens* were used. In those recorded below, only the gastrocnemius of *R. pipiens* was employed. The temperature throughout was 20–22° C. It was desired especially to obtain more definite information with regard to change in the elastic properties of the muscle during contraction, an issue which, aside from its relevance to the physico-chemical mechanism of contraction, bears upon an important problem in the comparative physiology of contractile tissues, namely, the "catch" muscle. For this reason, in view of the possibility that considerable deviations from Hooke's Law may be anticipated in the case of muscle, it seemed desirable to know in every case the average tension to which the resting and contracted muscle in each experiment were subjected. In the case of resting muscle, this is achieved by observing the deflection of the spring for a given tension applied to the point of attachment of the muscle, the cord being subsequently tightened until a corresponding deflection is registered.

In the experiments summarised in Tables I–III, series A, the muscle was attached as stated in the Introduction at a distance of 2·5 cm. beyond the junction of the inflexible extension with the spring itself. This gives a high value for the logarithmic decrement of the coupled system and makes the error of measurement for the former rather high. On the other hand, the measurement of the difference between the period of the spring and coupled system is thereby made more accurate than is the case in Hill's experiment, since the logarithmic decrement does not very materially affect the value of K. The comparison of the elastic condition of the muscle in the resting and contracted state in this arrangement is not susceptible to the very considerable source of arithmetical error involved in the manner in which Gasser and Hill's experiments were conducted. It is of course impossible to arrange the experiment so that there is a difference in the periodic time of the spring alone and of the coupled system of an order of magnitude which permits any measure of confidence in calculating the K ratio of resting and contracted muscle, while at the same time, to keep the damping of the vibration within such limits as to make the calculation of the viscous effect consistent.

In series A, of which Tables I–III are representative of a very large number of experiments repeated many times, the method of recording was optical to minimise the sources of mechanical error in calculating the damping effect. Table I gives the results of a series of experiments, each one of which was performed upon the muscle of a different animal. The muscles varied greatly in size, and the values of the spring constants are therefore calculated separately for each muscle to take into account the appreciable effect of differences in the weight of the muscle when exerting no damping effect on the spring. All spring constants are calculated with the muscle hanging freely from the spring.

Table I. *Series A.*

No. of exp.	Initial tension (gm.)		λ	T	μ ratio	K ratio
1	25	Spring alone	0·02632	0·098		
		With resting muscle	0·16814	0·090		
		With contracted muscle	0·27268	0·076	2·0	3·7
2	50	Spring alone	0·01903	0·099		
		With resting muscle	0·16973	0·089		
		With contracted muscle	0·15998	0·090	0·89	0·88
3	100	Spring alone	0·02120	0·099		
		With resting muscle	0·24324	0·082		
		With contracted muscle	0·22712	0·080	0·95	1·2
4	150	Spring alone	0·01961	0·099		
		With resting muscle	0·20743	0·083		
		With contracted muscle	0·23405	0·077	1·2	1·5

It will be seen from Table I that when the resting muscle was exerting a tension of 50 or more grams on the spring, the ratios of μ and K (contracted to resting) approximated to unity. It is necessary, however, to explain why higher values were obtained at lower tension. In the case of the K ratio, this might be because the muscle departs widely from Hooke's Law, but that would not explain the apparent increase of the viscous coefficient in contraction. The meaning of this discrepancy can be further explored by performing the same series of operations upon a single muscle. In the experiment summarised in Table II, this has been done, and the order in which the operations were carried out is indicated in the left-hand column. This was such as to insure that the interpretation of these data was not vitiated by the effects of fatigue, or by irreversible changes produced by over-stretching the muscle itself.

Table II. *Series A.*

No. of exp.	Initial tension (gm.)		λ	*T*	μ ratio	*K* ratio
—	—	Spring alone	0·0182	0·099	—	—
4	25	With resting muscle	0·139	0·090		
		With contracted muscle	0·337	0·076	3·1	3·3
1	50	With resting muscle	0·205	0·092		
		With contracted muscle	0·282	0·076	1·7	4·4
3	100	With resting muscle	0·268	0·078		
		With contracted muscle	0·288	0·070	1·2	1·6
2	150	With resting muscle	0·215	0·076		
		With contracted muscle	0·225	0·068	1·1	1·6

From the data presented in Table II, there emerges very clearly the fact that the relatively high ratio found at the low tension in the previous series of experiments is not fortuitous; this at once gives rise to the suspicion that when the resting muscle exerts on the spring only a relatively small tension, it does not have its full damping effect on the latter when the spring is caused to vibrate. In other words, during part of the period, there may be a slackening of the cord which attaches the muscle to the spring. To test this possibility, the experiment may be carried out in the following way. Having calibrated the deflection of the spring when tensions of different magnitudes are applied to the point of attachment of the muscle, the muscle is connected with the spring with sufficient play of the cord to permit it to exert, when contracted, a tension of 25 gm. Thus it is possible to compare the behaviour of the contracted muscle when exerting a mean tension of 25 gm. with that of the resting muscle subjected to the same mean tension in the manner adopted in the previous series of experiments. The result of such an experiment as set forth in Table III confirms the suspicion adumbrated above.

Table III. *Series A.*

	λ	*T*	μ ratio	*K* ratio
Spring alone	0·022	0·099	—	—
Resting muscle (initial tension 25 gm.)	0·10218	0·096	—	—
Contracted muscle (maximum tension 25 gm.)	0·07568	0·096	—	—
			0·67	1·0

In the experiments summarised in Table IV, the muscle was attached to the point of junction of the spring with the inflexible extension. The results are inserted because the figures for the logarithmic decrement were more satisfactory when the experiment was carried out in this way. With this arrangement, when springs of known elastic ratio were substituted for the muscle in the coupled system, the effects were not of an order of magnitude to give calculated values by the dynamical method, conclusively indicating that the coupled system vibrated with the same configuration as the free spring. Hence they are put forward somewhat tentatively. The data in Table IV refer to the same muscle. The difference in the spring constants is due to the fact that a different extension was used, the experiments being graphically recorded.

Table IV. *Series B.*

No. of exp.	Initial tension (gm.)		λ	T	μ ratio	K ratio
—	—	Spring alone	0·02186	0·103	—	—
1	25	With resting muscle	0·05649	0·100		
		With contracted muscle	0·13865	0·85	4·0	3·45
2	50	With resting muscle	0·08618	0·095		
		With contracted muscle	0·13014	0·082	2·11	2·89
3	100	With resting muscle	0·10197	0·091		
		With contracted muscle	0·13755	0·080	1·66	2·34
4	150	With resting muscle	0·10674	0·088		
		With contracted muscle	0·16625	0·081	1·84	1·68
5	200	With resting muscle	0·13081	0·087		
		With contracted muscle	0·13866	0·082	1·14	1·44
6	250	With resting muscle	0·10824	0·084		
		With contracted muscle	0·11326	0·086	1·02	0·86
7	300	With resting muscle	0·10070	0·084		
		With contracted muscle	0·13186	0·080	1·45	1·31

CONCLUSIONS.

As the differences dealt with are very small, the appropriate corrections for the natural length and cross-sectional area of the contracted and resting muscle have been left out of account. Taking into account all the data cited in the above tables, it does not seem certain that there is a significant increase in the viscosity or decrease in the extensibility of the gastrocnemius muscle of *R. pipiens* when subjected to a tetanus of short duration, at least if the dynamical method is valid.

The differences between these observations and those of Gasser and Hill may possibly be due to (1) the fact that a larger muscle was deliberately used because of the greater ease with which it is possible to obtain independent confirmation of the experimental validity of this method for calculating elastic as opposed to viscous coefficients; (2) the difficulty of insuring, unless special precautions are taken, that the resting muscle, when exerting a small tension on the spring, is not given a certain amount of free play; (3) the danger that, when the point of attachment of the muscle is made on the flexible surface of the vibrating spring, the latter does not oscillate through the whole series of observations with the same configuration.

In any case, even when the experiment was carried out precisely in the manner indicated by Gasser and Hill, the present authors were unable to obtain values pointing to a change in the elastic and viscous coefficients of muscle in the resting and contracted state comparable to those recorded in their communication. Further, it may be mentioned that a few experiments in which the muscle was attached to a lever vibrating against the resistance of a helical spring yielded results consonant with those obtained with the modification of Gasser and Hill's apparatus employed. Were the changes in the elastic properties of muscle of the order indicated by Gasser and Hill, it would, moreover, be necessary to make a very careful investigation of the deviation of normal resting muscle from Hooke's Law at different tensions before the precise meaning of the calculated ratio could be appreciated in its right perspective. It is interesting to note that Scarth, in a recent investigation of the relation of the hydrogen-ion concentration to the elastic qualities of gelatine, finds that there is a slight decrease in the value of Young's modulus as this protein is brought nearer to its isoelectric point from the alkaline side.

When correction is made for the different natural dimensions of contracted and resting muscle, the average K ratio of the previous series of observations is for high tensions slightly less than unity, so that a small decrease in the elastic coefficient of contracted muscle is compatible with these observations. However, the sources of error inherent in this method are such that one would not wish to lay any emphasis on this conclusion.

REFERENCES.

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