

Muscle Twitch Tension—Influence of Electrical Stimulating Conditions at Different Temperatures

IV. Time Rate of Rise of Tension

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§ 1. INTRODUCTION

THE first paper in this series (Kelly, Fry and Fry 1964, referred to as I), was concerned primarily with the problem of the variation of the amplitude of isometric twitch tension of frog sartorius muscle with temperature, and indicated the importance of the choice of values of the electrical stimulating parameters in relation to the amplitude of twitch tension elicited. However, in any investigation of the effect of temperature on the peak amplitude of isometric twitch or tetanus tension, in which whole muscle is employed, the nature of the mechanical attachment of the muscle to the recording device is critical. Since the time rate of rise of tension during muscle contraction increases with increasing temperature, the effect of a compliant attachment on the amplitudes of recorded tension will change with temperature. One of the first considerations in the investigations outlined in I was whether the discrepancies between the results of various authors on the effect of temperature change on the amplitude of twitch tension could be correlated with the different mechanical attachments employed to fasten the muscle to the recording apparatus.

Exact comparison of the tension data of various investigators is often impossible because of the difficulty of evaluating the physical parameters of the attachments used to fasten the muscle to the transducer. In many cases, this information is not published and it does not appear unreasonable to us to conclude that the structure of the attachments significantly influenced the results reported in most of these cases. In general, the mechanical response (strain) of various types of attachments (such as strings or threads) to a sudden force is non-linear, i.e., the response of a string to a muscle contraction depends in a complex manner on a number of parameters including length, elastic modulus as a function of tension and temperature and on construction features (stranded, monofilament, etc.). Therefore, prior to investigating the influence of the stimulus parameters on the amplitude of twitch tension as reported in I, an attempt was made to determine an experimental arrangement whereby (1) the muscle could be attached to the transducer with a minimum of connecting material and (2) the type of mechanical attachment could be

easily and exactly duplicated by other investigators. As the result of a large number of experiments on the effects of various types of attachments, it was found that an optimum arrangement, for the purposes of the stated investigations, was the use of the muscle with its natural tendons and a section of the attached bone at each end. A hole was drilled through each piece of bone and small steel loops attached the bones directly to the experimental apparatus. This arrangement satisfies the two criteria just indicated and was used in all studies reported in this series of papers. As indicated in the first paper, the large amplitudes of twitch tension obtained with this arrangement can be attributed to the combined effect of more adequate electrical stimulation and improvement in the mechanical attachment of the muscle to the transducer, but the large amplitudes of *tetanus* tension obtained must be attributed primarily to the improvement of the mechanical attachment alone since no unique stimulation techniques, basically different from those employed by previous investigators, were used. The present paper presents data on the time rate of rise of tension obtained with the type of preparation described and correlates these data with those presented in I and in II (Kelly and Fry 1964).

§ 2. INSTRUMENTATION AND GENERAL PROCEDURE

The frog sartorius muscles (*Rana pipiens*), mounted as indicated above, were stimulated by means of a mass electrode. The stimulus pulse durations applied to elicit isometric twitch responses ranged from 0.2 to 10.0 msec. The isometric tetanus response was elicited by stimuli (1.0 msec pulses) with a frequency of 20/sec at 2°C and 100/sec for temperatures of 18°C and above.

The instrumentation for recording the tension of the muscle consisted of a photoelectric strain gauge transducer capable of measuring tensions from 0 to 225 g, an oscilloscope, and a camera. The transducer employed contains a spring with a light gate mounted on one end, the linear displacement of the spring amounting to 0.006 mm per gramme of applied tension. The value of the voltage output of the transducer, for the magnitude of the force applied by the muscle, was in the millivolt range. This relatively high output response was a distinct advantage because it permitted the transducer to be directly connected to an oscilloscope without any intervening preamplifier which often limits the overall frequency response capability of a system. The oscilloscope had a vertical deflection sensitivity of 1.0 mV/cm, a minimum sweep speed of 1.0 cm/sec, and a frequency response "flat" from 0 to 300 kc/sec. In addition to determining the resonant frequency (250 c/sec) by simply observing the response to shock excitation, a determination of the frequency response characteristic of the transducer and its associated oscilloscope was made. This was accomplished by driving the transducer at frequencies in the range 0 to 200 c/sec with a variable frequency, variable displacement (amplitudes ranging from 0 to ± 1.0 mm from the equilibrium position),

linear motion device designed for this purpose. As a result of this determination, it was concluded that for the temperature range 0 to 25°C, the transducer-oscilloscope system recorded the full tension developed by the muscle without reduction caused by frequency response limitations. Reference should be made to I for further details of the instrumentation and experimental methods.

§ 3. EXPERIMENTS AND RESULTS

The results obtained by employing the muscle attachment described above exhibited time rates of rise of tension at high temperatures considerably greater than those reported by previous investigators. However, one can question whether the compliant elements represented by the tendons in our experiments, in particular the longer tibial tendon, influenced unfavourably the amplitudes of recorded tension. Investigation of this indicated that although the tendon attachments caused a decrease in the recorded maximum time rate of development of tension, the final amplitudes of isometric tensions recorded (in the temperature range of 0 to 25°C) were essentially the same for preparations with the natural tendon attachments as for those in which almost all the tendon lengths were eliminated. The latter preparations were supported by two clamps which were attached to each end of the muscle as close as possible to the tendon-muscle junction without injury to the muscle fibres. These clamps in turn were attached directly to the recording apparatus. It may be of interest to mention that in addition to the clamps, a variety of mechanical attachments were tested including the commonly employed wire and thread. The least successful of these, with regard to time rate of rise of tension, was thread, even though the amount used was just sufficient to make a tie between the tendon stub and the steel loop. Of course, it is understood that none of these arrangements eliminate the compliant elements distributed along the muscle, nor do they eliminate completely the tendon attachments at the two ends of the muscle. The purpose of the experiments with the clamped-off tendons was not the determination of the mechanical impedance of muscle; these experiments were designed to investigate the validity of using whole sartorius muscle with attached tendons (a preparation readily reproducible from one investigator to another), as described in the Introduction, in order to compare the conflicting conclusions of a number of investigators who used the sartorius muscle with a different mechanical attachment.

3.1. *Time Rate of Rise of Tension—Low Temperatures*

The form of the isometric tetanus myogram has been of considerable interest since Hill's (1938) publication on the dynamic constants of muscle. More recently, Jewell and Wilkie (1958) have attempted to verify Hill's theory that the form of the myogram is determined by the force-velocity curve of the contractile component and the stress-strain curve of the elastic component. Their experimental approach differs

from that of previous studies in that data on the three parameters (force-velocity, stress-strain, and isometric rise of tension) were all obtained on the same muscle. The experiments were carried out at 2° c and considerable attention was centred on eliminating compliant elements in the attachment of the muscle to the transducer. The experimentally determined force-velocity and stress-strain data were used to predict the form of the isometric tetanus myogram and this computed curve was compared with the experimentally determined isometric relation. It was found that the time rate of rise of tension exhibited by the experimentally determined relation was considerably less than that calculated.

Since Jewell and Wilkie's experiments are particularly pertinent to the investigations reported in I, a number of tension experiments were performed by us at the same temperature (2° c) in order to make a direct comparison of data. These experiments yielded maximum time rates of rise of tension faster than Jewell and Wilkie's experimentally determined relation, but not as fast as their theoretical curve. This is of considerable interest with regard to the interpretation of Jewell and Wilkie's results, particularly when it is realized that in our investigations the long tibial tendon was included in the connection of the muscle, while in the former case the tendon was tied off close to its insertion in the muscle. If Jewell and Wilkie had been successful in achieving a minimum of compliant connecting material and in stimulating all the muscle fibres to full response, their tension rise times should have been faster than ours. In view of our results in regard to the use of thread as a coupling agent between muscle and transducer, it is possible that Jewell and Wilkie's longer duration rise times may be the result of their use of a plaited silk loop to tie the tibial tendon to the steel wire.

In discussing various underlying causes for the discrepancy between their experimentally observed relation and the computed curve, Jewell and Wilkie state that their experiments were made with "very inextensible apparatus" because their isometric myograms exhibit tension rises 2-3 times faster than comparable ones in the literature. The literature quoted is that of Katz (1939), Hill (1953) and Macpherson and Wilkie (1954). It is of interest to examine this statement in detail because it is not immediately apparent, from the statement itself, that its content depends on a very specific method of treating tension data. Jewell and Wilkie's comparison of tension rise times is based on normalization of the tension relations, that is, comparisons are based on the time required to reach a chosen fraction of peak value. It appears to us that the *maximum* time rate of development of tension might constitute a more appropriate indicator of the capability of the muscle than the time to attain a fixed fraction of the maximum measured tension. At the present state of knowledge of muscle mechanisms, it seems reasonable that the maximum time rate of development of tension may be more readily related to basic mechanisms than the time required to realize some fixed fraction of peak value, since the latter involves not only the process of

tension development but also processes that are important in the levelling off of the tension to a maximum. It is not possible, in our opinion, to predict with certainty whether the maximum amplitude or the initial development of tension might be more readily handled by basic theory (normalization involves both), but at least one might expect that a state of the muscle determined by two or more mechanisms of comparable importance is a poor choice to consider first. Consideration should also be given to the fact that the usual argument for normalization of data, such as that applied in electrical measurements of nerve action potential, where the measurements represent relative values rather than absolute magnitudes, does not apply in this case. In the case of muscle, the tension measurements represent the absolute level of developed tension under the conditions of the experiment.

The comparison of speed of response, when the maximum tension output of one muscle is much smaller than that of another, on the basis of the time required to reach a chosen fraction of the maximum value, seems particularly misleading. This is especially evident from comparing Katz' and Jewell & Wilkie's myograms reproduced in fig. 1. It is quite true

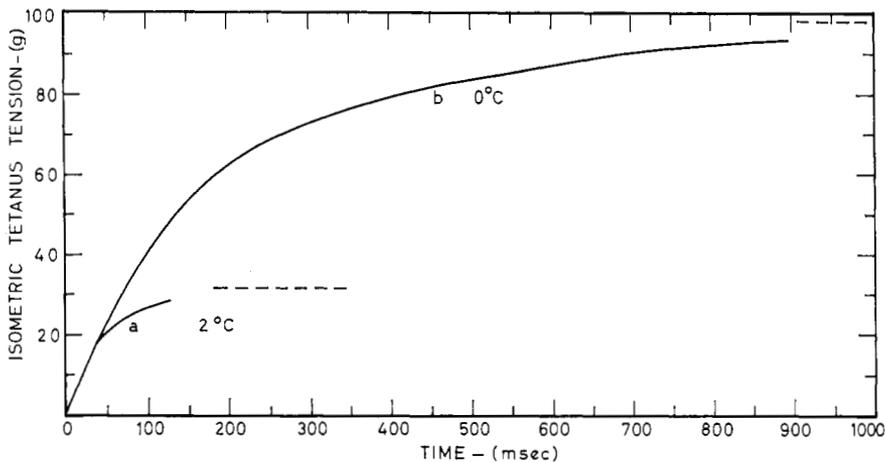


Fig. 1. Isometric tetanus responses of excised frog sartorius muscle at low temperature: (a) reproduced from fig. 7, Jewell and Wilkie (1958); (b) reproduced from fig. 3a, Katz (1939).

that the time required to attain half the peak value in the Jewell and Wilkie case is about $\frac{1}{3}$ of that of Katz, but the maximum tension reached is less than $\frac{1}{3}$ of that reached in the experiment reported by Katz. When compared on the basis of the maximum time rate of development of tension, the Katz and the Jewell and Wilkie results are about the same. Comparison on this basis should, of course, be done on the basis of the tension output per unit cross-sectional area but these data are not available in either case. Table 1 lists values for the maximum time rate of tension development obtained from the data of different authors. Since

Table 1. (Excised frog sartorii) †

Author	Temp. °C	Max. Time Rate of Development of Tension (Tetanus) g/msec	Peak Tetanus Tension g
Katz (1939, fig. 3a)	0	0.52	98
Jewell and Wilkie (1958, fig. 7)	2	0.53	32.3
Macpherson and Wilkie (1954, fig. 1)	0	0.20	25 (est.)
Present paper typical case	2	0.70	67

† Katz (1939) obtained his data on either *R. temporaria* or *R. esculenta*; Macpherson and Wilkie (1954) data obtained on *R. temporaria*; our data obtained with *R. pipiens*; Jewell and Wilkie (1958) do not indicate frog species.

no tension values are indicated by Hill (1953 fig. 6D) his data do not appear in table 1. The Macpherson and Wilkie data are included only because of Jewell and Wilkie's specific reference to them. It is questionable, however, whether such data should be used for a comparison of rise times since in the description of their experimental technique Macpherson and Wilkie indicate "there was no need for conditions to be very strictly isometric so the muscle was connected to the transducer by a length of silk braid which had been oiled to make it hang limply". Under such conditions one would expect the time rate of rise of tension to be extremely low. It is of some interest that a rather early publication (Hartree and Hill 1921) included a myogram of a twitch which indicated a maximum time rate of rise of tension of 1.0 g/msec and a tension amplitude of approximately 118 g (0°C). This represents the best response in the paper. The myograms exhibit a considerable range of values of both rate of rise of tension and amplitude of developed tension.

3.2. Time Rate of Rise of Tension—High Temperatures

Table 2 lists values for the maximum time rate of rise of tension for the high temperature twitch responses discussed in the present series of papers. The fastest time rate of rise of tension is 5.2 g/msec for a temperature of 23.6°C (fig. 2). It would be of considerable interest to compare maximum time rates of tension development for the Jewell and Wilkie (1958) work at high temperatures with ours, but unfortunately no such data are given by them. However, Sandow's (1958) paper on the form of the isometric

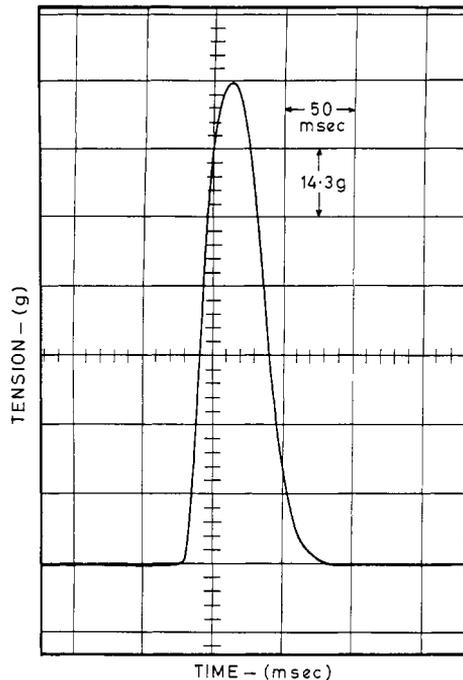


Fig. 2. Illustration of fast maximum time rate of rise of tension (5.2 g/msec) at 23.6° c, of an excised, uncurarized frog sartorius muscle mounted with intact tendons, in response to a single stimulus (10 msec) delivered by a mass electrode.

tetanus myogram and its relation to active state theory does show an oscilloscope trace of a tetanus myogram of a sartorius muscle at 20° c. Table 3 gives a comparison of data obtained from fig. 1 of Sandow's paper and fig. 3 of I.

§ 4. DISCUSSION

As discussed in III (Kelly and Fry 1965) we feel that it is essential, prior to formulating theories on mechanisms of muscle contraction based on observed differences in amplitude of developed tension (of whole muscle) caused by changes in controlling parameters, that the full tension of the muscle be elicited by an adequate stimulus and that the recorded tension be minimally affected by the influence of the mechanical attachments between muscle and transducer. With regard to the latter, the advantages of using muscle with fully intact tendons instead of muscles inadequately coupled by strings, threads or wires, seems apparent from the data on rates of rise of tension presented here.

In II we have indicated that the large increases in *amplitude* of twitch tension for muscle in nitrate Ringer's solution, recorded by a number of previous investigators, over those amplitudes measured for muscle in

Table 2 (Unneurized excised frog sartorii—twitch responses)

Author	Figure Number (original journal of reference)	Stimulus Pulse Duration msec	Ringer's	Temp. °C	Peak Tension g	TL ₀ /M (kg/cm ²)/(g/cm ³)	Max. Time Rate of Development of Tension g/msec.
Kelly, Fry and Fry (1964)	1 ^a	0.2	Chloride	24.5	31.8	0.94	2.8
		10.0		24.5	83.5	2.47	4.2
A. V. Hill (1951)	2D (lower row)	Not given	Chloride	21.5	14.7	0.39 ^b	0.84
Kelly, Fry and Fry (1964)	2	6.0	Chloride	21.5	74.0	2.43	3.5
Hill and Macpherson (1954)	7 ^c	0.3 ^a	Chloride	18.0	27.0	0.72	0.85
		0.3 ^a		18.0	53.0	1.40	1.3
Kelly and Fry (1964)	2 ^a	0.3	Chloride	18.0	63.1	2.60	2.7
		2.0		18.0	79.5	3.30	3.1
		6.0		18.0	90.1	3.71	3.5
		10.0		18.0	95.0	3.91	3.5
		0.3	Nitrate	18.0	103.5	4.26	3.8
Present Paper	2	10.0	Chloride	23.6	100.1	2.87	5.2

^aData refer to a single muscle.^bCalculated from Hill's data.^cData are for a single muscle.^dAssumed on basis of pulse duration indicated for fig. 5 of publication.

chloride Ringer's, are the result of stimulating the muscle, when in chloride Ringer's, with pulses of comparatively short duration. When the muscle is adequately stimulated in chloride Ringer's by a single pulse of appropriate duration, the large increases in tension are not observed when nitrate Ringer's is substituted for chloride Ringer's. In view of these findings it is of interest to consider the data of table 2. The results listed show that the increased *time rate of rise* of tension, as indicated by the data of Hill and Macpherson (1954) (normally characteristic of the data of other investigators when solutions containing nitrate, bromide, or iodide are substituted for that containing chloride), is similar to the increase in time rate of rise of tension elicited by prolonging the duration

Table 3

Author	Temperature °C	Peak Tetanus Tension g	TL ₀ /M (kg/cm ² /g/cm ³)	Maximum Time Rate of Development of Tension g/msec
Sandow (1958)	20	48.3	2.16	1.65
Kelly, Fry and Fry (1964)	18	117.0	4.82	3.73

of the stimulus. For example, a progressive increase in the time rate of rise of tension from 2.7 to 3.5 g/msec occurred as the pulse duration was increased from 0.3 to 10.0 msec for a muscle at 18°C. Substitution of nitrate Ringer's for chloride Ringer's resulted in only a small additional increase in rate of rise of tension. Thus the time rate of rise of tension for the twitch response exhibits no appreciable increase when the ionic environment of the muscle is changed from chloride to nitrate Ringer's, and therefore is similar to the behaviour of the tension amplitude, provided the full response of the muscle has been elicited in the chloride Ringer's by the application of single stimuli of appropriate duration.

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SUMMARY

Various arrangements for coupling whole frog sartorius muscles to transducers were investigated, with special attention to a configuration readily reproducible from one investigator to another and consistent with a minimum influence of the characteristics of the attachments on the recorded values of tension. An arrangement satisfying these two criteria was achieved, and the time rates of rise of tension observed at various temperatures were greater than those normally reported for other methods of attachment. The values of the time rates of rise of tension measured in chloride and nitrate Ringer's are considered in relation to basic muscle mechanisms.

RÉSUMÉ

Tension de secousse musculaire—l'influence de conditions stimulantes électriques à différentes températures. IV. Taux de variation de l'augmentation de la tension en fonction du temps.

On a étudié différents dispositifs servant pour accoupler le muscle couturier entier de la grenouille aux transducteurs, en s'attachant surtout à une configuration qui serait aisément reproductible lorsqu'on passe d'un investigateur à l'autre et compatible avec le minimum d'influence des caractéristiques des accouplements sur les valeurs enregistrées de la tension. On a exécuté un dispositif qui satisfait à ces deux critères, et les taux de variation de l'augmentation de la tension en fonction du temps, observés à de différentes températures, étaient plus grands que ceux signalés d'ordinaire pour d'autres méthodes d'accouplement. On étudie les valeurs de taux de l'augmentation de la tension en fonction du temps, mesurés en solutions de Ringer au chlorure et au nitrate, par rapport aux mécanismes fondamentaux musculaires.

ZUSAMMENFASSUNG

Muskelzuckungsspannung—der Einfluss elektrischer Reizbedingungen bei verschiedenen Temperaturen. IV. Zeiträte des Spannungsanstiegs.

Verschiedene Vorrichtungen zur Kopplung des ganzen Frosch-Sartoriusmuskels mit Wandlern wurden untersucht. Insbesondere wurde eine experimentelle Anordnung gesucht, die am besten reproduzierbar ist und den geringsten Einfluss der Charakteristik der Befestigungsanordnung auf die Messung der Spannungswerte zeigt. Eine Anordnung wurde entwickelt, die den angeführten Kriterien genügt, wobei gefunden wurde, dass die bei verschiedenen Temperaturen beobachteten Zeiträten des Spannungsanstiegs grösser waren, als sie für andere Kopplungsverfahren gemeinhin angegeben werden. Die in Chlorid- und Nitrat-Ringerlösung gemessenen Werte der Spannungsanstiegs-Zeiträte werden in Zusammenhang mit einigen fundamentalen Muskel-Mechanismen diskutiert.

Резюме

Напряжение мышечной судороги — влияние электрических стимулирующих условий при разных температурах. IV. Скорость подъема напряжения во времени.

Исследовались различные установки для соединения целых портняжных мышц лягушки с трансдукторами, причем особое внимание уделялось конфигурации, легко воспроизводимой от одного исследователя к другому и совместимой с минимальным влиянием характеристик закреплений на зарегистрированные значения напряжения. Выполнена была установка, удовлетворяющая эти два критерия; оказалось, что наблюдаемые при разных температурах скорости подъема напряжения во времени были больше скоростей, обычно получаемых для других методов закрепления. Измеренные в хлоридном и нитратном растворе Рингера значения скоростей подъема напряжения во времени обсуждаются по отношению к основным мышечным механизмам.

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