
Tetanic potentiation in motor units of rat medial gastrocnemius

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Abstract. Tetanic potentiation is a phenomenon, which expresses the ability of a motor unit (MU) to increase its force output in tetanic contractions above that predicted with an assumption of algebraic summation of single twitch responses. To quantify tetanic potentiation, a coefficient *TPC* (tetanic potentiation coefficient) was defined as a ratio of the areas below tetanic force recording corresponding to the single stimulus contribution and that of the single twitch. Single MUs (27 Slow, 71 Fast, Fatigue Resistant, and 47 Fast, Fatigable) were isolated from the rat medial gastrocnemius muscle (MG) by ventral root splitting. *TPC* value was rate-dependent, with the maximum TPC_{max} at a certain optimal rate. The largest values of the TPC_{max} were obtained in the weakest and most fatigue resistant (S and weak FR) MUs. The different manifestation of staircase effect, post-tetanic and tetanic potentiation in individual MU types indicates that these phenomena may be independent of each other. We suggest that these phenomena as well as the fatigue resistance should be reexamined with protocols adjusted to the MU optimal frequency.

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INTRODUCTION

In mammalian skeletal muscle, three essential types of MUs can be distinguished, which differ according to their metabolism and function: Slow (S), Fast, Fatigable (FF), and Fast, Fatigue Resistant (FR) (Burke et al. 1973). With increasing muscle force, MUs are recruited in an orderly fashion according to the “size principle” (Henneman 1957, Henneman and Mendell 1981, Milner-Brown et al. 1973). This means that S MUs are recruited on the lowest and FF MUs on the highest levels of muscle contraction. Thus, in daily activity the most fatigable MUs are utilized only occasionally, whereas the majority of contractions (e.g., posture maintenance) involve MUs which are weak, but fatigue resistant (Hennig and Lomo 1985, Lomo 1985).

The maximal force of single MU twitches is graded in the order $S < FR < FF$. However, when MUs are stimulated repetitively, several nonlinear phenomena concerning summation of twitches can be observed, which are different in different MU groups. There are experimental data indicating that the condition of muscle fibers depends on the history of previous excitations (Burke et al. 1976, Celichowski 2001, 2005, Celichowski et al. 2004, Van Cutsem and Duchateau 2005). The “all or none” principle is applicable to the single twitch only when interstimulus intervals are long enough to allow for the termination of all biochemical processes before the next stimulus delivery. Even when interstimulus intervals are close to the single twitch duration, a long stimulus train results in a gradual change of twitch force and shape, which is known as the staircase phenomenon (Desmedt and Hainaut 1968, Krarup 1981). Another phenomenon, post-tetanic potentiation, is observed after tetanic stimulation: single twitch of a MU recorded immediately after the tetanic stimulation is stronger than that recorded before the stimulation. Post-tetanic potentiation was observed mostly in fast MUs (Bagust et al. 1973). Its strength was inversely correlated with contraction time; most of the slow MUs demonstrated post-tetanic depression (Krarup 1981).

Nonlinear summation of the twitch components corresponding to single stimuli can also be expected in tetanic contractions (Raikova et al. 2006). However, whereas a change in single twitch parameters in staircase or post-tetanic potentiation may be measured directly, a change due to tetanic potentiation is difficult to assess without a special analysis. Probably this is the

reason why this phenomenon was not widely investigated. To our knowledge, only one study (Parmiggiani et al. 1982) was published, which used the term “tetanic potentiation”. This study, however, was conducted on the whole muscle and did not allow for comparison between different MU types. We introduced a simple method of analysis of tetanic mechanogram applicable to single MU studies, where measured mean force value is compared with that which would be predicted by linear summation of twitches. This method allowed us to find more-than-linear summation of single twitches in a small sample of MUs from various rat muscles (Piotrkiewicz et al. 1986). The strongest tetanic potentiation was observed in S MUs. However, the number of MUs was too small (30 MUs, among them 5 slow) to draw definite conclusions.

In this paper we report the results of tetanic potentiation investigation on the much larger sample of MUs from the rat MG.

METHODS

Experiments

The present results are based on the experimental data underlying another study (Celichowski et al. 2000), where experimental conditions are described in detail. Here, only a brief description will be given.

Experiments were performed on 11 adult Wistar female rats (5–10 months old, average body mass \pm SD 284.1 ± 30.0 g), under pentobarbital anesthesia, in accordance with Polish Law on Animal Care. After the experiments the animals were given a lethal dose of pentobarbital.

The distal portion of the MG muscle was isolated from the surrounding tissues and the Achilles tendon was attached to an inductive force transducer. Single MUs were isolated by standard splitting of the ventral roots. The isolated spinal cord, ventral and dorsal roots as well as the muscle studied were immersed in non-conducting media (paraffin oil) and automatically kept at constant temperature ($37 \pm 1^\circ\text{C}$). Ventral root filaments were stimulated by rectangular electrical pulses (duration 0.1 ms, amplitude up to 0.5 V). The muscle was stretched with a constant force of 100 mN (Celichowski et al. 2000). Experimental data from the force transducer was fed into a PC for off-line analysis via an A/D 12-bit converter (RTI-800 Utilities) with a sampling frequency of 20 kHz.

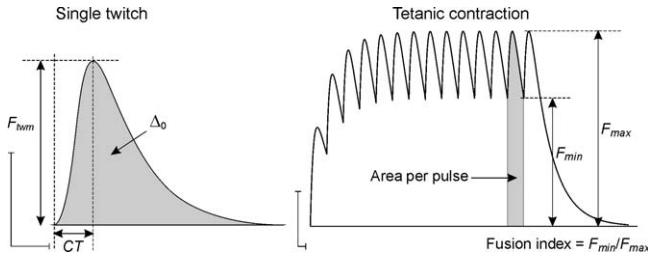


Fig. 1. Essential parameters of twitch (left panel) and tetanic (right panel) contractions. Shaded are force-time areas under single twitch (Δ_0) and single stimulus contribution (area per pulse); F_{twm} , maximal twitch force; CT , contraction time; fusion index calculated as ratio of minimal (F_{min}) and maximal (F_{max}) force values at end of 500 ms contraction. Calibration bars: vertical 5 mN, horizontal 10 ms.

For each MU its contraction time, CT , and maximal force, F_{twm} , were measured. Then the MU was stimulated with 500 ms trains of pulses at rates: 10, 20, 30, 40, 50, 60, 75, 100, and 150 Hz. Successive trains were delivered at 10 s intervals. The tetanic force F_{tet} was measured as the maximum tension of the fused tetanus at 150 Hz. For each stimulation rate, the fusion index and the force-time area per pulse, Δ_m , were calculated (definitions in Fig. 1). The experiment was concluded with the fatigue test (Burke et al. 1973).

MUs, which demonstrated a “sag” in partially fused tetanus at 40 Hz stimulation, were classified as fast, and non-sagging ones as slow MUs (Burke 1981, Grottel and Celichowski 1990). The further classification of fast units was based on their fatigability: MUs with the fatigue index higher than 0.5 were classified as FR type, and those with smaller index, as FF type (Grottel and Celichowski 1990, Kanda and Hashizume 1992).

Tetanic potentiation analysis

If we assume that during tetanic contraction single twitches sum algebraically, an integral mean force value may be estimated as:

$$F_e = \frac{1}{T} \int_{t_0}^{t_1} \sum_{i=1}^n f(t) dt, \quad (1)$$

where n is the number of stimuli, $f(t)$ is single twitch time course (mechanogram) and $T = t_1 - t_0$. The values t_1 and t_0 should be chosen so as to correspond to this fragment of tetanic contraction, where the mean force value stabilizes (as in Fig. 1). For most experimental

recordings, this condition was fulfilled at the end of 500 ms stimulation period.

Further,

$$F_e = \frac{n}{T} \int_{t_0}^{t_1} f(t) dt. \quad (2)$$

Since $\frac{n}{T} = r$ (stimulation rate, expressed in s^{-1}), and the integral is an area under the single twitch mechanogram, Δ_0 (expressed in Ns), the formula becomes

$$F_e = r \Delta_0. \quad (3)$$

The force value actually measured can be analogously expressed as

$$F_m = r \Delta_m, \quad (4)$$

where Δ_m is an area under the tetanic contraction mechanogram, corresponding to the single stimulus contribution, thus an area per pulse, as defined above (cf. Fig.1).

As a measure of tetanic potentiation, Tetanic Potentiation Coefficient is introduced as

$$TPC = \frac{F_m}{F_e} = \frac{\Delta_m}{\Delta_0}. \quad (5)$$

TPC was correlated with other mechanical parameters of a MU, namely: twitch contraction time, CT , maximal twitch force, F_{twm} , and tetanus-to-twitch ratio, which is defined as

$$TTR = \frac{F_{tet}}{F_{twm}}, \quad (6)$$

where F_{tet} is the maximal force of fused tetanus. Tetanus-to-twitch ratio was chosen here instead of the more commonly used twitch-to-tetanus ratio, since the former value reflects the ability of a MU to increase its contraction force due to tetanic stimulation.

The correlation analysis was performed using the Spearman Rank Order Correlation test (STATISTICA).

RESULTS

The analysis was performed for 27 S, 71 FR, and 47 FF MUs. An example of the typical dependency of mean force value, calculated from (4), and TPC on

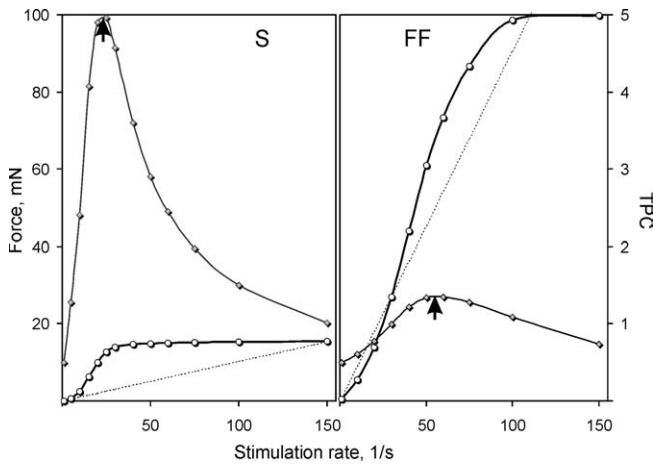


Fig. 2. Two examples of force and TPC dependency on stimulation rate for single S (left panel) and FF (right panel) MUs: circles, left scale, MU force; diamonds, right scale, TPC ; dotted line, force calculated from (3). Note that force record of S MU is always above the dotted line ($TPC > 1$), whereas for FF MU the force record is below the dotted line until 30/s ($TPC < 1$)

stimulation rate is presented in Fig. 2 for a slow (a) and a fast FF (b) MU. The bell-shaped TPC dependency has a maximum, TPC_{max} (marked by an arrow) at the stimulation rate, which will be further denoted as the optimal rate. The optimal rate and corresponding value of TPC_{max} were determined from individual plots for each MU and are correlated below with other characteristic MU parameters. MU force at the optimal rate was close to 75% of the force of the fused tetanus, which corresponded to the fairly fused contraction (the fusion index slightly exceeded 0.9, cf. Celichowski et al. 2000 and Fig.1).

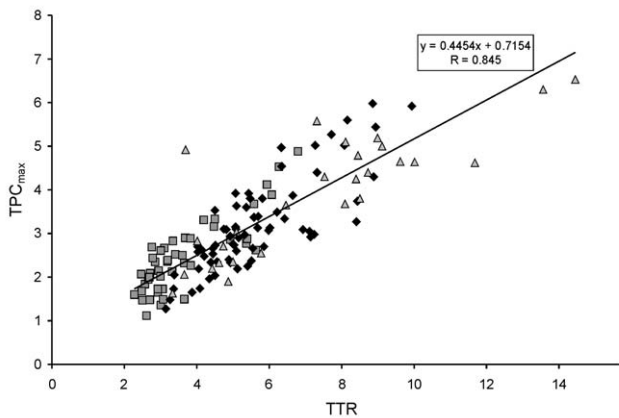


Fig. 4. TPC_{max} for single MUs plotted against their tetanus to twitch ratio, TTR: triangles, S; diamonds, FR; squares, FF MUs; solid line fitted to pooled data by least squares method

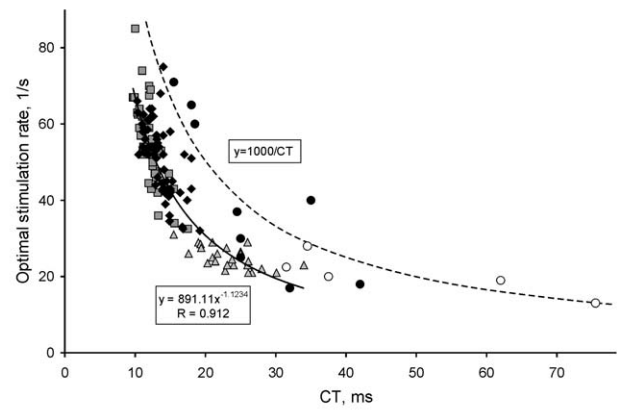


Fig. 3. Dependency of optimal stimulation rate for single MUs on their contraction time, CT : triangles, S; diamonds, FR; squares, FF MUs; broken line, inverse of contraction time; solid line, result of fitting a power function to the main cluster of data; circles, data from the preliminary study (Piotrkiewicz et al. 1986): open circles, S; filled circles, F MUs.

The optimal rate for each MU was inversely correlated with CT (Fig. 3). However, in contrast to the previous results (Piotrkiewicz et al. 1986), shown also in Fig. 3 (circles), the majority of points were grouped below the line representing an inversion of CT . The main cluster of data (after the rejection of outliers) was fitted with a power function.

TPC_{max} was linearly correlated with TTR for all MU types (Fig. 4). An inverse correlation was found between TPC_{max} and twitch maximal force (Fig. 5).

TPC_{max} for FF and FR MUs was correlated with contraction time, CT (Fig. 6) and optimal stimulation rate

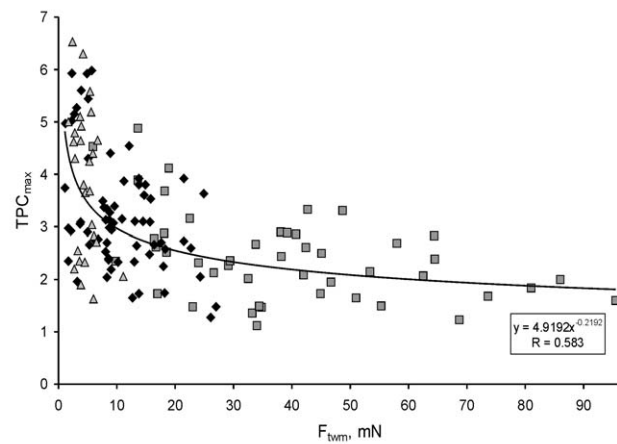


Fig. 5. Relation between TPC_{max} for single MUs and their twitch maximal force, F_{twm} : triangles, S; diamonds, FR; squares, FF MUs; solid line, power function fit for the main cluster of data

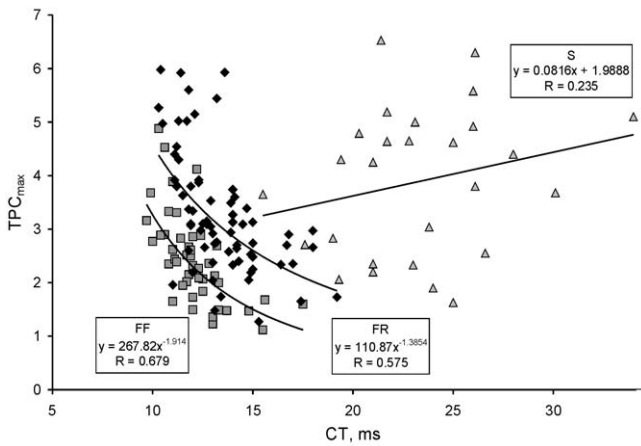


Fig. 6. TPC_{max} for single MUs plotted against their contraction time, CT : triangles, S; diamonds, FR; squares, FF MUs; solid lines fitted to data for each MU type by least squares method

(not illustrated). All regressions were statistically significant ($P < 0.0003$), except those for S MUs, between TPC_{max} and contraction time and between TPC_{max} and optimal stimulation rate ($P > 0.1$). The correlation coefficients are collected in Table I.

Table II illustrates the comparison of mechanical properties analyzed in this work between different MU types. FR MUs were subdivided into two groups on the basis of their twitch forces: weak FR MUs, with twitch forces in the range of those for S MUs ($F_{t_{wm}} < 11$ mN), and strong FR MUs ($F_{t_{wm}} > 11$ mN). Note that with respect to the parameters collected in the table, weak FR were much closer to S MUs than to the other types. Note also that both maximal and mean values of TPC_{max} for slow MUs were larger than those for fast MUs (Fig. 5, Table II).

Table I

Correlation coefficients for different types of MUs					
Variables		Fig. number	Correlation coefficient R		
X	Y		S	FR	FF
Opt. rate	CT	3	-0.8292^{*1}		
TPC_{max}	TTR	4	0.8453^{*1}		
TPC_{max}	$F_{t_{wm}}$	5	-0.5658^{*1}		
TPC_{max}	CT	6	-0.2717^{NS}	0.4575^{*}	0.5100^{*}
TPC_{max}	Opt. rate	—	0.2503^{NS}	-0.6007^{*}	-0.7005^{*}

(1) Correlation coefficient for all MUs taken together (cf. appropriate figure); (*) statistically significant correlations ($P < 0.0003$); (NS) non-significant correlations ($P > 0.1$)

Table II

Mean values \pm SD of essential mechanical parameters of MUs				
MU type	S	FR weak ¹	FR strong ²	FF
MU number	27	44	27	48
$F_{t_{wm}}$	4.61 ± 1.92	6.15 ± 2.96	17.21 ± 4.59	38.12 ± 21.1
TPC_{max}	3.82 ± 1.45	3.51 ± 1.21	2.83 ± 0.87	2.52 ± 1.0
Tet/tw ratio	7.34 ± 3.01	6.81 ± 2.86	4.64 ± 0.90	4.84 ± 1.39
Mean $F_{t_{wm}}$ related to that of S MUs	1	1.35	4.23	8.27
Mean fused tetanus force related to that of S Mus	1	1.20	2.75	3.90

(1) FR MUs with $F_{t_{wm}} < 11$ mN; (2) FR MUs with $F_{t_{wm}} > 11$ mN

DISCUSSION

The results confirmed our preliminary finding (Piotrkiewicz et al. 1986) that slow MUs demonstrate the largest ability to increase their force during tetanic contractions. Not only the mean values of TPC for slow MUs were greater than those for FR and FF type, but also the two largest TPC_{max} values recorded in the study belonged to the S MU. A slightly lower value of the mean TPC_{max} was obtained for FR MUs with maximal twitch forces comparable to those of S MUs. Thus, F_{twm} seems to be the crucial factor for tetanic potentiation.

S and weak FR MUs participate in the majority of the daily movements of an animal or human being (Hennig and Lomo 1985, Lomo 1985). These small and weak muscle elements are provided with marked resistance to fatigue. Moreover, their action is supported by several mechanisms enhancing their performance during unfused tetani, thus the regime under which they usually operate (Kernell et al. 1999). Tetanic potentiation is one of these mechanisms, which is remarkably expressed in these MU types. The TPC_{max} value is correlated with another mechanical parameter, TTR, which also reflects the ability of a MU to increase its force output in tetanic contractions. The maximal and mean values of this parameter are the highest in S and weak FR MUs as well. This confirms an earlier finding (Celichowski and Grottel 1993) that the weakest units have the lowest values of twitch-to-tetanus ratio. As the result, in our MU sample mean twitch force of FF MUs was more than 8 times larger than that of S MUs, whereas when forces of fused tetani were compared, this proportion decreased more than twice (cf. Table II). It should be noted, however, that TTR and TPC_{max} are not equivalent. TPC_{max} characterizes the MU ability to increase its force output above that predicted by algebraic summation (it could thus in principle be less than 1), whereas TTR would be always larger than 1, even if a MU did not demonstrate tetanic potentiation. The present experimental data do not contain MUs of this type; in the previous work we observed a few of them, all fast and extremely fatigable. Such MUs could not be included in the present sample, since their endurance was so low that the experiment had to be terminated after the first few series of stimuli.

The positive staircase effect, post-tetanic, and tetanic potentiation seem to be interrelated phenomena.

However, the different manifestation of these effects in individual MU types indicates that they may be independent of each other, as was suggested for other phenomena related to repetitive stimulation (Powers and Binder 1991). The mechanism of force generation is far from being fully understood. The linear summation of twitches was applied here to reveal tetanic potentiation; it is not, however, a proper method for description of the muscle contraction, even as a first approximation. A model based on current knowledge of the molecular structure of muscle fiber filaments could provide a key to the explanation of the above-mentioned discrepancies and other intriguing phenomena. It has already been shown that mechanical parameters of rat muscles are correlated with the pattern of myosin heavy chain isoform expression (Gallo et al. 2004). In this respect, the new model of myosin filament (Skubiszak 1996, Skubiszak and Kowalczyk 2002) certainly deserves attention. The model introduces helical structure of the filament and its verification has shown that in contrast to other existing models it is able to explain virtually all published experimental data.

The dependency of optimal stimulation rate on the twitch CT for MUs of rat MG was different from that found in our preliminary study (Piotrkiewicz et al. 1986). The reason for this discrepancy may be the difference in muscles studied. Mrówczyński and coauthors (2006) found that force-stimulation rate relationships in slow motor units in cat and rat muscles were identical despite evident differences in CT. This result indicates that the dependency of optimal stimulation rate on the twitch CT would be different for cat and rat MUs. The differences in this respect may also be expected between various muscles of the same animal.

The existence of an optimal frequency range specific to a given MU (Celichowski et al. 2000, Kernell et al. 1983) has also another aspect. MU fatigability is usually tested in stereotyped conditions, with the same stimulation rate of 40 Hz applied to all MU types (Burke et al. 1973). This stimulation rate is close to the optimal rates for the majority of our FR MUs. When the fatigability was tested in fast MUs with stimulation rate of 60 Hz (which is close to the optimal rates of the majority of our FF MUs), the fatigue indices for FF MUs increased (Nowak 1996), i.e., these MUs were found to be less fatigable. The influence of stimulation rate on fatigability of S MUs was not so straightforward. Slow MUs were usually able to maintain constant force for

a much longer time when tested with 20 Hz (which is close to their optimal rates) than in routine 40-Hz fatigability test, although the 20-Hz force value was lower (Celichowski and Grottel 1995). Moreover, the daily activity of slow MUs consists of rather long periods of constant force contractions. When slow MUs are stimulated with constant rate producing unfused tetanus, they usually increase their force for a long time (e.g., Baldissera and Parmiggiani 1975, Cope et al. 1991, Piotrkiewicz and Miller-Larsson 1986). It seems therefore reasonable to reexamine the fatigue resistance with protocols adjusted to the individual MU properties. Also the reexamination of other phenomena, such as, e.g., the staircase effect, posttetanic potentiation or tetanic depression, with stimulation protocols adjusted to the MU optimal frequency, could certainly yield interesting, unpredictable results.

CONCLUSION

It has been shown that tetanic potentiation influences MU force in frequency-dependent manner. The maximal TPC was greatest in weakest MUs, i.e., S and FR with lowest values of maximal twitch forces. It is suggested that the fatigue resistance as well as the staircase effect, posttetanic potentiation or tetanic depression should be reexamined with stimulation protocols adjusted to the MU optimal frequencies.

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