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The area under the record of contractile tension: estimation of work performed by a contracting motor unit

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Short communication

Abstract. The area under twitch tension records was measured for motor units in rat medial gastrocnemius. These measures were compared to measures of tension. The tension varied in significantly larger range than the area. The area of slow motor units was similar to the area of fast resistant units, whereas their tensions differed significantly. The area depended mainly on the amplitude of contraction and to a smaller degree on its time course. The measure of area under the tension record gives a more exact evaluation of the work performed by contracting motor units than the measure of tension alone. The obtained results show that motor units in mammalian muscle are less variable in their ability to perform contractile work and moreover, that slow motor units play a more significant role during contractions than was supposed based on tension measures.

Key words: motor unit, tension, contraction, area, work

Motor units in mammalian skeletal muscles can be divided into three main types: fast-twitch fatigable (FF), fast-twitch resistant to fatigue (FR) and slow-twitch (S), basing on their contractile properties (Burke et al. 1973, Burke 1981). In numerous studies on the contractile properties of motor units, tension was the main motor unit property measured (e.g., Filippi and Troiani 1994, Bakels and Kernell 1995, Kadhiresan et al. 1996, Rafuse and Gordon 1996, de Ruiter et al. 1996, Tansey et al. 1996). This tension can vary significantly for different types of motor units. The tension of the weakest units can be 100 times lower than that of the strongest ones (Burke 1981). This observation suggests that slow units - the weakest ones - have a very small influence on the work done by muscles. However, the contraction of slow units is significantly longer and therefore one might expect that the work performed by these units would not be as low as suggested based on their tension alone. The measure of the area under the tension record can be a useful tool to study the work done during contraction of muscle fibers. The aim of the present paper was to measure the area under the twitch tension records for motor units and to estimate in this way the work done during contraction of different types motor units.

The study was performed on 15 adult Wistar rats (mean weight 287 ± 3 2 g), under pentobarbital anesthesia (Vetbutal, 35 mg/kg I.P. supplemented as required during experiments). The procedure of surgery and isolation of single motor units in medial gastrocnemius muscle was described in our previous paper (Celichowski 1992). Briefly, the L5 ventral root was split into very fine filaments, containing only a single axon going to the investigated muscle. Because all muscles except the investigated one were denervated, electrical stimulation on ventral root filaments evoked an "all - or - none" contraction of single motor units in medial gastrocnemius. The muscle and spinal cord were covered with warm (37 ± 1°C) paraffin oil. The muscle was stretched to a tension of 100 mN. Under these conditions the maximal tension of motor unit twitches can be recorded (Celichowski and Grottel 1992). Isometric tension was recorded using an inductive tension transducer, sampled with an A/D converter at a 10 kHz rate and stored on a computer disc.

For each motor unit the averaged twitch (at 10 repetitions) was first recorded. Then, unfused tetanus (stimulation frequency of 40 Hz during 500 ms), fused tetanus (stimulation frequency of 150 Hz during 200 ms) and fatigue test (tetani repeated each second during 4 min and evoked by 14 pulses trains at 40 Hz) were recorded.

In the averaged twitch record the tension (from the baseline to the peak), contraction time (from the onset of tension record to the peak), half-relaxation time (from the peak to fall of tension to half of peak value) and the area under tension record (Fig. 1) were measured using a special computer program. The area was measured for the first part of the twitch (from the onset to the peak), for its second part (from the peak to the end of twitch) and for the whole twitch record as well.

Motor units were classified into three types: slow (S), fast resistant (FR) and fast fatigable (FF). Slow/fast classification was based on "sag" property in unfused tetani of fast motor units (Burke et al. 1973, Grottel and Celichowski 1990). Fast units were classified as FR when their fatigue index was higher than 0.5 whereas for FF units this index was lower than 0.5 (Kernell et al. 1983, Grottel and Celichowski 1990). 106 units were investigated in the present study: 34 of the FF, 43 of the FR and 29 of the S type.

Table I summarizes the results of measures made on twitch records for each of the three types of motor units. The twitch area appeared to be significantly less variable than its tension. For example, the mean twitch tension of FF motor units was more than 11 times higher than for S units, whereas the twitch area was only 4 times greater. Moreover, it is very interesting that the tension of FR units was significantly higher than for slow units, but that there was no significant difference between their twitch areas.

The twitch area correlated with the twitch tension (R = 0.963, Spearman rank correlation, $P<0.001$). This correlation was present for FF, FR and S units separately (R = 0.982, R = 0.890 and R = 0.792, respectively, $P<0.001$

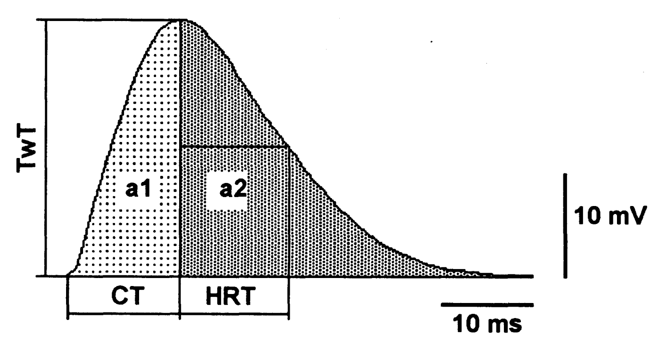

Fig. 1. Parameters measured for single motor unit twitch. An example of FR type motor unit. CT, contraction time; HRT, half-relaxation time; TwT, twitch tension; a1, the area under the first part of twitch; a2, area under the second part of twitch. The twitch area was calculated as a sum of a1 + a2.

TABLE I

Mean ± SD, ranges of variability and variability coefficients of investigated twitch properties for three motor unit (MU) types. CT, contraction time; HRT, half-relaxation time; TwT, twitch tension; Area, area under the twitch tension record; Area1:2, ratio of areas of the first to the second part of the twitch; Area/TwT, ratio of the twitch area to its tension; Area/CT+HRT, ratio of the twitch area to the sum of contraction and half-relaxation times. In the lower part of the Table the results of ANOVA Kruskal-Wallis rank test (of differences between three types of motor units) and results of Mann-Whitney test (significance of differences between pairs of individual types of motor units) are shown (***, *P*<0.001; **, *P*<0.01; *, *P*<0.05; NS, difference non significant, for both tests)

MU type	CT (ms)	HRT (ms)	TwT (mN)	Area (ms*mN)	Area1:2	Area/TwT (ms*mN/mN)	Area/CT+HRT (ms*mN/ms)
FF	11.8 ± 1.5	12.4 ± 2.7	47.5 ± 35.1	1058 ± 1028	0.56 ± 0.08	20.4 ± 3.8	40.3 ± 30.8
	8.0-16.0	8.0-21.0	2.5-175.2	58-5235	0.42-0.78	14.5-33.2	2.0-153.9
	12.75	22.36	73.93	97.14	14.56	18.96	76.63
FR	13.2 ± 1.8	15.4 ± 3.1	12.3 ± 14.8	306 ± 387	0.51 ± 0.06	25.5 ± 4.5	10.8 ± 13.1
	10.0-18.0	12.0-25.0	2.9-89.4	64-2368	0.37-0.64	19.2-37.2	2.6-78.9
	13.88	20.24	121.05	126.49	12.04	17.66	121.13
S	25.0 ± 4.8	39.5 ± 8.0	4.2 ± 1.4	245 ± 89	0.44 ± 0.09	58.0 ± 12.6	3.8 ± 1.4
	17.0-35.0	23.0-61.0	1.7-8.5	95-561	0.30-0.74	32.3-90.4	1.4-7.6
	19.35	20.42	33.59	36.52	21.57	21.71	36.26
ANOVA Kruskal-Wallis rank test:							
	H = 69.9***	H = 73.4***	H = 61.6***	H = 30.3***	H = 30.7***	H = 75.4***	H = 61.1***
Mann-Whitney test:							
FF-FR	***	***	***	***	**	***	***
FR-S	***	***	***	NS	***	***	***
FF-S	***	***	***	***	***	***	***

in all cases). Contractile time parameters (contraction time, half-relaxation time or their sum) did not correlate significantly with the twitch area (*P*>0.05) either across all types of motor units or within individual types.

Multiple regression analysis was used to investigate the relationship between the area under twitch record and the other twitch parameters studied. The relationship can be described according to the following equation:

$$y = -266.214 + 25.990x_1 + 6.490x_2$$

where y is the twitch area, x_1 is the twitch tension and x_2 is the sum of the contraction and half-relaxation times. The determination coefficient is 95.13%. This analysis shows that twitch tension has the strongest influence on the area under the tension curve, whereas relaxation and contraction times exert a smaller influence. It should be stressed that in the present study twitch tension showed a significantly larger range of variability than did duration of relaxation or contraction (Table I).

The ratio of areas of the first to the second part of a twitch and both the ratio of area to tension of the twitch and the ratio of area to the sum of contraction and half-relaxation times appeared to be significantly different for the three types of motor units (values of these ratios are given in Table I). These differences correspond to the variability in the time courses of the twitches. For slow units contraction and relaxation are significantly longer than for fast units, whereas within fast units they are longer for FR than for FF units (Table I). These differences influence the ratio of twitch area to tension. Therefore, this ratio may show the influence of twitch time on the analysed area. On the other hand, the ratio of the twitch area to the sum of contraction and half-relaxation times seems to be a good measure of the influence of twitch tension on twitch area. Moreover, the ratio of the first to the second part of the twitch area is influenced by different ratios of contraction to relaxation times in particular types of motor units. The ratios of contraction to half-relaxation times for FF, FR and S units amounted to 0.97 ± 0.14, 0.87 ± 0.11 and 0.64 ± 0.12, respectively (differences significant, $P<0.01$).

Measures of the area under the tension record appear to be an interesting tool for the analyses of muscle contractile activity. This parameter gives a better evaluation of the actual work performed by a contracting muscle than the amplitude of the tension record alone. Moreover, this method of analysis shows that the ability of different types of motor units to perform work during contractions is not as variable as was believed based on tension measures only. The present measures of twitch area also show that slow motor units characterized by the lowest tension can work with efficacy similar to FR units. These results concern single twitches of motor units only. Previous studies of twitch/tetanus ratios showed that slow units have a lower ratio than fast ones (Stephens and Stuart 1975, Dum and Kennedy 1980, Gardiner and Olha 1987, Celichowski and Grottel 1993). This means that within a tetanus they are able to summate their tension better than fast units. All these observations suggest that slow motor units play a more significant role during contractions than was previously supposed. It should be stressed that slow motor units are responsible for a significant part of muscle work because they are active during various forms of muscular activity, e.g., postural activity and locomotion.

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