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RELATIONSHIP BETWEN THE TENSION-TIME AREA AND THE FREQUENCY OF STIMULATION IN MOTOR UNITS OF THE RAT MEDIAL GASTROCNEMIUS MUSCLE

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The tension-time area is an estimation of the work performed by contracting motor units. The relationship between tension and frequency of stimulation and between tension-time area and frequency have been studied on 148 single motor units of the rat medial gastrocnemius muscle, under isometric conditions. Motor units were classified as fast fatigable (FF), fast resistant to fatigue (FR) or slow (S). Trains of stimuli of increasing frequency and constant duration were used. For all motor units a half of the maximum tetanic tension corresponded to lower frequencies compared to frequencies at a half of the maximum tension-time area. Moreover, the slopes of tension-frequency and area-frequency curves (change of tension or area per 1 Hz rise in frequency) were higher for slow than for fast motor units. The tension-time area per one pulse was calculated for different frequencies of stimulation. For slow units the maximum area per pulse corresponded to significantly lower frequencies than for fast ones, especially of FF type. However, for all three types of motor units this optimal frequency corresponded to sub-fused tetani with a tension of about 75% of the maximum tension, and with the fusion index slightly over 0.90. The absolute values of the maximum tension-time area per pulse revealed that in one contraction within the tetanus, slow units are generating greater work than FR units. The work performed by FF units is nearly two times larger than for S units, although the tension of slow units is over eight times lower. The presented results reveal that the contraction of slow motor units is much more effective than was suggested based on their low tension.

K e y w o r d s: *motor unit, contraction, tension-time area*

INTRODUCTION

Motor units, during their activity, contract with a tension changing in relation to the discharge frequency of motoneurons. Therefore, the relationship between the motor unit tension and the frequency of stimulation was investigated in numerous studies (11, 21, 26, 30, 31, 32). It was found that the course of the tension-frequency curve correlated to the contraction time. For slow units a steep part of this curve, corresponding to the unfused tetani of these units, was observed at significantly lower frequencies than for fast units.

The tension-time area was used as a measure of the output of motor unit and muscle contractions (3, 4, 7, 8, 35, 24). This tension-time area is a good estimator of the work performed by contracting motor units (12) and the area is related to energy utilized by the activated skeletal muscles during contraction (24). The work performed during a twitch of slow units appeared to be higher than it was estimated based on tension measurements alone (12). Moreover, it was found that the course of a twitch (including tension, contraction and half-relaxation times) strongly influenced the tension-time area of a single motor unit twitch (12). During the natural activity of muscles their motor units contract in unfused tetani (18, 29). Results of experiments performed by Tansey *et al.* (34) suggested that during this activity the tetani of contracting motor units are relatively well fused. The tetanus results from the summation of contractions evoked by repeated firings of a motoneuron. However, each contraction of muscle fibre require certain amount of energy and therefore with an increasing frequency of contractions the total energy cost of the tetanus rises. The tension of this tetanus is also increasing but it can change only within a limited range of frequencies corresponding to unfused tetani of muscle fibres (2, 23, 26). An excessive rise in the frequency of stimulation is not effective in relation to the tension, whereas the increasing number of muscle fibre contractions evokes a parallel rise in metabolic costs. On the other hand, it can be expected that at a very low frequency of stimulation both the tension of a tetanus and the work performed by this tetanus will be rather low and not optimal for the metabolism of muscle fibres. Zajac and Young (35) performed experiments on cat medial gastocnemius motor units and described the optimal pattern of stimuli i.e., giving the maximal tension-time area per pulse. However, they have not studied tetani evoked at different frequencies of stimulation. Therefore, in the present paper we aimed to study the relationship between the frequency of stimulation and the work performed by evoked contractions. Based on these results it is also possible to find the frequency of stimulation which is optimal for the work performed by one contraction during the tetanus.

In the present series of experiments we have stimulated motor units of the three main types with trains of stimuli at different frequencies and recorded their variable-tension tetani. In these tetani the tension, the tension-time area and the fusion have been measured. Moreover, the area corresponding to a single contraction in this tetanus was measured. This analysis enabled us to find the frequency of stimulation optimal for the work performed by motor units during the tetanus. Moreover, this analysis makes it possible to compare the work performed by various types of motor units, which has never been done before. Finally, our previous paper revealed that the fusion of a tetanus is a factor determining the sensitivity of the motor unit tension to temporary changes in the stimulation frequency (20). Therefore, it is also important to find and compare the fusion of tetani which is optimal for the work performed during the activity of single motor units of different types.

METHODS

Materials and anaesthetization

Experiments were performed on 11 adult Wistar female rats (average body mass$\pm$S.D. 284.1$\pm$30.0 g), under pentobarbital anaesthesia (Vetbutal, Biovet, 60 mg/kg I.P., supplemented during the experiment as required, according to the observation of the pinna reflexes and the shape of the pupils, approximately after 3 h at the rate of 5 mg/kg/h). Experiments were performed in accordance with Polish Law on Animal Care. After the experiments animals were killed with an overdose of pentobarbital.

Surgical preparation

During surgery, the medial gastrocnemius muscle was partly isolated from the surrounding tissues, the blood vessels and the sciatic nerve branch were left intact. The Achilles tendon was prepared in order to connect the muscle to a force transducer. All muscles of the hindlimb except the studied medial gastrocnemius were denervated. The laminectomy was performed over L2-S1 segments. Dorsal as well as ventral roots were cut as proximal to the spinal cord as possible. The isolated spinal cord, ventral and dorsal roots were covered with warm paraffin oil (37 $\pm$ 1°C) in a small pool made by skin around the laminectomy. The muscle studied was also immersed in a special metal pool filled with this mineral oil kept automatically at the same temperature. Animals were immobilized with two steel clamps on tibia and on the processus of the sacral bone.

Isolation of single motor units

Electrical stimulation of very thin filaments split from ventral roots (usually L5) evoked contractions of muscle fibres in medial gastrocnemius. When the contraction and action potentials of muscle fibers were both of the "all-or-none" type this kind of muscle activity was accepted as the contraction of the single motor unit. Filaments of ventral roots were stimulated with a bipolar silver electrode. Rectangular electrical pulses (amplitude up to 0.5 V) were used for the stimulation. Action potentials in the muscle studied were recorded with a pair of thin-wire silver electrodes inserted into the muscle and amplified. The tension of contraction was recorded under quasi isometric conditions with an inductive force transducer (compliance of 1 μm/1 mN). During recording, the studied muscle was stretched with a constant force of 100 mN, because under this condition a majority of its motor units generate the highest twitch tension (9).

Experimental procedure

When activity of a single motor unit was obtained, this unit was stimulated in the following manner: 1/ a series of 10 stimuli at 1 Hz (10 twitches were recorded and an average twitch was obtained); 2/ a series of 20 stimuli at 40 Hz (the unfused tetanus was recorded); 3/ a series of 30 stimuli at 150 Hz (the fused tetanus was recorded); 4/ 9 series of 500 ms trains of stimuli at frequencies of 10, 20, 30, 40, 50, 60, 75, 100 and 150 Hz (a series of tetani fused at variable degrees were recorded); 5/ fatigue test (tetani, evoked by trains of stimuli at 40 Hz frequency and at a duration of 330 ms repeated every second for 4 minutes).

Classification of motor units

The studied motor units were divided into three types: slow (S), fast resistant to fatigue (FR) and fast fatigable (FF) (5). Slow/fast division was based on the "sag" phenomenon visible in unfused tetanus of fast units at 40 Hz stimulation (5,19). The division of fast units onto FF and FR types resulted from the different ability of these units to keep tension during the fatigue test. This ability was expressed by the fatigue index, which was the ratio of the tension generated two minutes after the maximum tension was recorded at the beginning of the fatigue test to this maximum tension (5, 27). When the fatigue index was lower than 0.5 a motor unit was classified as FF type, whereas when this index exceeded 0.5 — as FR type (19, 25).

Analysed motor unit properties

On the single twitch record the contraction time (time interval from the beginning of a twitch up to the peak in tension), the half-relaxation time (time interval from this peak up to the moment when tension decreased to a half of the peak) and the twitch tension (measured from the baseline up to the peak) were measured. On the fused tetanus recording (at 150 Hz stimulation) the maximum tetanic tension was measured. For tetani recorded at various frequencies of stimulation the tension of these tetani was measured as the amplitude from the baseline to the highest point in the recording (*Fig. 1A*). Moreover, for single twitches and tetani the tension-time area (area between the baseline and the record of tension) was also measured (*Fig. 1A*). This area was expressed in [ms · mN]. The tension-time area per one pulse was calculated as a part of the tension-time area between two vertical lines in two neighbouring points of the lowest tension (*Fig. 1B*). Finally, the fusion index was calculated for the tetani studied (1,10). This index was expressed as an a/b ratio (*Fig. 1B*), where a was the distance from the baseline to the lowest tension before the last contraction within the tetanus and b was the amplitude of the last contraction.

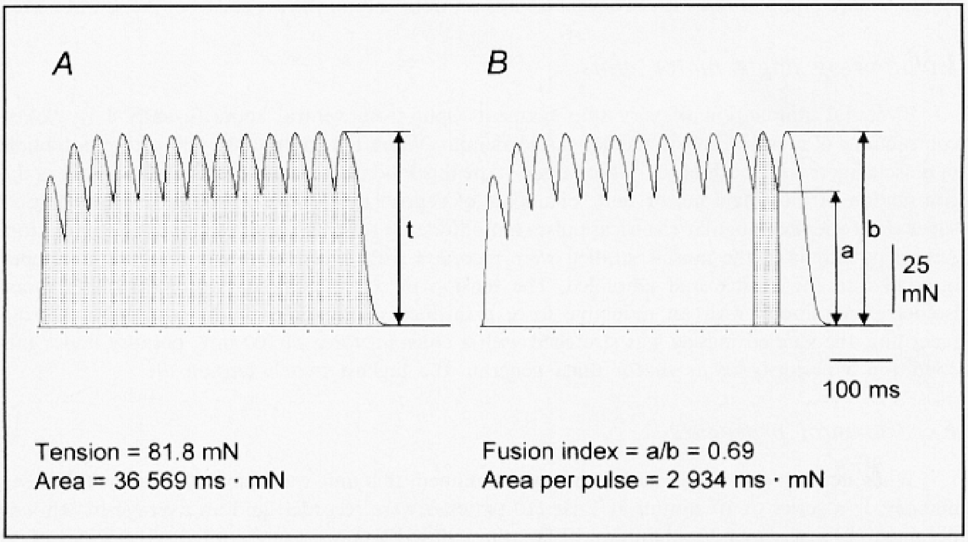

Fig. 1. An example of the FF motor unit tetanus, evoked at 50 Hz frequency of stimulation. A. t, the tension (measured at the peak of recording); dotted area, the tension-time area (expressed in [ms · mN]). B. The calculation of the fusion index and area per pulse in train of stimuli. Stimulation pattern is visible under the recording of tension, each point denotes one pulse.

Statistics

For statistical analysis of the presented results the ANOVA Kruskal-Wallis rank test, Mann-Whitney test, and the Wilcoxon matched pairs tests were used.

RESULTS

The study was performed on 148 motor units of the rat medial gastrocnemius muscle (49 FF, 72 FR and 28 S type units). The main contractile properties of units investigated are summarized in *Table 1*.

Table 1. Mean values ± S.D. of contractile properties of motor units studied. CT, the contraction time; HRT, the half-relaxation time; TwT, the twitch tension; TetT, the maximum tetanus tension; FI, the fatigue index; Tw area, the tension-time area for the twitch. Under the Table, results of the ANOVA Kruskal-Wallis rank test and the Mann Whitney test are presented, *** $P<0.001$, N.S. — difference non-significant, $P>0.05$.

Type of motor unit	CT (ms)	HRT (ms)	TwT (mN)	TetT (mN)	FI	Tw area (ms·mN)
FF	12.2 ±1.9	11.9 ±3.3	38.4 ±20.8	132.2 53.2	0.25 ±0.13	814.4 ±551.7
FR	13.6 ±2.6	15.6 ±4.5	11.4 ±10.6	59.0 ±41.8	0.86 ±0.09	292.1 ±271.8
S	23.3 ±3.9	36.2 ±9.2	4.6 ±1.9	32.7 ±9.9	0.93 ±0.05	230.4 ±96.6
ANOVA Kruskal-Wallis rank test						
	H = 71.7 **	H = 80.8 ***	H = 85.2 ***	H = 78.8 ***	H = 99.1 ***	H = 53.1 ***
Mann-Whithney test						
FF-FR	***	***	***	***	***	***
FF-S	***	***	***	***	***	***
FR-S	***	***	***	***	***	***

Fig. 2 presents examples of the FR motor unit tetani evoked at several frequencies of stimulation. Values of the tetanic tension, the tension-time area and the area per pulse are given under the recordings. In these examples the greatest area per pulse was observed in the tetanus at the stimulation frequency of 40 Hz. This tetanus had the fusion index of 0.92, and its tension amounted up to 76.6% of the maximum tetanic tension.

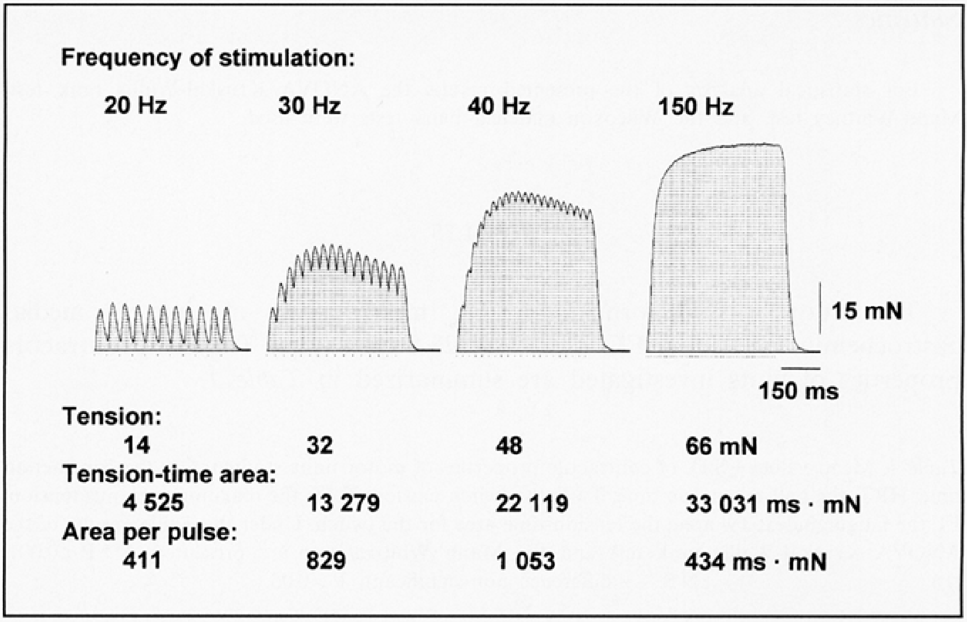

Fig. 2. Examples of tetani of the FR motor unit, evoked at different frequencies of stimulation. The values of tension, tension-time area, and the area per pulse, calculated for these tetani are given under the recordings. The greatest area per pulse was observed at 40 Hz stimulation. The stimulation pattern is also visible under the recordings of tension.

Changes in the tetanic tension and the tension-time area were observed as a function of the stimulation frequency. *Fig. 3* shows the averaged values of the tetanic tension (upper part), the tension-time area (middle part), and the area per pulse (lower part) presented as a percentage of the maximum, as a function of the frequency of stimulation for the three types of motor units.

When the three types of motor units were compared it was found that in the tension-frequency and area-frequency curves 50% of the maximum values were obtained at the lowest frequencies in the slow units, whereas in the FF units at the highest frequencies of stimulation (*Fig. 3, Table 2*). For all three types of motor units 50% of the maximum tetanic tension corresponded to lower frequencies compared to frequencies at 50% of the maximum tension-time area (*Table 2*; differences significant for all three types of motor units, $P<0.01$, Wilcoxon test). Moreover, the slopes of the tension-frequency and area-frequency curves were estimated at a level of 50% of the maximum values. The slope was expressed in percentage of this maximum value per 1 Hz change in stimulation frequency. In the fast units, the tension-frequency curves were steeper than area-frequency curves (*Table 2*). The reverse relationship was found in the slow motor units (*Table 2*). These differences within each of the three motor unit types were significant ($P<0.001$, Wilcoxon test).

Table 2. Mean values ± S.D. for properties of tension-frequency (T-f) and area-frequency (A-f) curves. Slope, the slope of the curve; 50% frequency, the frequency of stimulation corresponding to 50% of the maximum value. For the optimal frequency of stimulation, when the area per pulse was maximal: frequency, the frequency of stimulation evoking optimal tetanus; tension, the tension of this tetanus, expressed in % of the maximum tension; area, the tension-time area for the optimal tetanus, expressed in % of the maximum area; FuI, the fusion index of the optimal tetanus; area per pulse, the absolute value of the area per pulse in optimal tetanus. Under the Table, results of the ANOVA Kruskal-Wallis rank test and the Mann Whitney test are presented, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, N.S. — difference non-significant, $P > 0.05$.

Type of motor unit	T-f slope	A-f slope	T-f 50% frequency	A-f 50% frequency	Maximal area per pulse				
					Frequency	Tension	Area	FuI	Area per one pulse
	(%/1Hz)	(%/1Hz)	(%)	(%)	(Hz)	(%)	(%)		(ms·nN)
FF	1.9 ±0.4	2.6 ±0.6	39.6 ±8.1	43.2 ±7.5	55.8 ±11.3	75.8 ±6.0	73.9 ±7.1	0.91 ±0.03	1653.1 ±938.1
FR	2.6 ±0.5	2.8 ±0.6	37.8 ±7.2	40.7 ±8.3	50.0 ±9.8	74.1 ±6.6	69.8 ±6.8	0.92 ±0.03	756.8 ±527.5
S	4.9 ±1.3	4.3 ±1.2	17.2 ±3.8	20.5 ±3.4	25.2 ±5.8	79.5 ±7.8	66.5 ±8.4	0.93 ±0.03	955.1 ±504.4
ANOVA Kruskal-Wallis rank test									
	H = 80.0 ***	H = 34.9 ***	H = 64.9 ***	H = 64.2 ***	H = 69.6 *****	H = 8.3 *	H = 14.2 ***	H = 9.9 *	H = 41.93 ***
Mann-Whithney test									
FF-FR	***	N.S.	N.S.	N.S.	*	N.S.	**	N.S.	***
FF-S	***	***	***	***	***	N.S.	***	**	***
FR-S	***	***	***	***	***	*	N.S.	*	N.S.

For each motor unit the tension-time area per one pulse was analysed (*Fig. 3*). The optimal frequencies of stimulation (i.e., giving the maximum area per pulse) for the three types of motor units differed significantly. This frequency was the highest for FF units and the lowest for S type units (*Table 2*). However, for all types of motor units the optimal frequency of stimulation corresponded to sub-fused tetani with a tension of approximately 75% of the maximum tetanic tension (*Table 2*). Moreover, the fusion index for these tetani slightly exceeded 0.90. These differences between the three types of motor units were significant at low levels of confidence only (*Table 2*).

Finally, the absolute values of the tension-time area per pulse for all types of motor units were compared. It was found that FF motor units were characterized by the highest values of this area, whilst FR units had the lowest values (*Table 2*). Slow units, producing the lowest tension (*Table 1*) generated greater tension-time area per pulse than stronger FR units. Differences between the tension of motor unit types were highly significant (*Table 1*) while those for the analysed areas appeared to be significant only when FF units were compared to FR or S type units. The maximum area per pulse for tetani of FR and S units was not different statistically (*Table 2*).

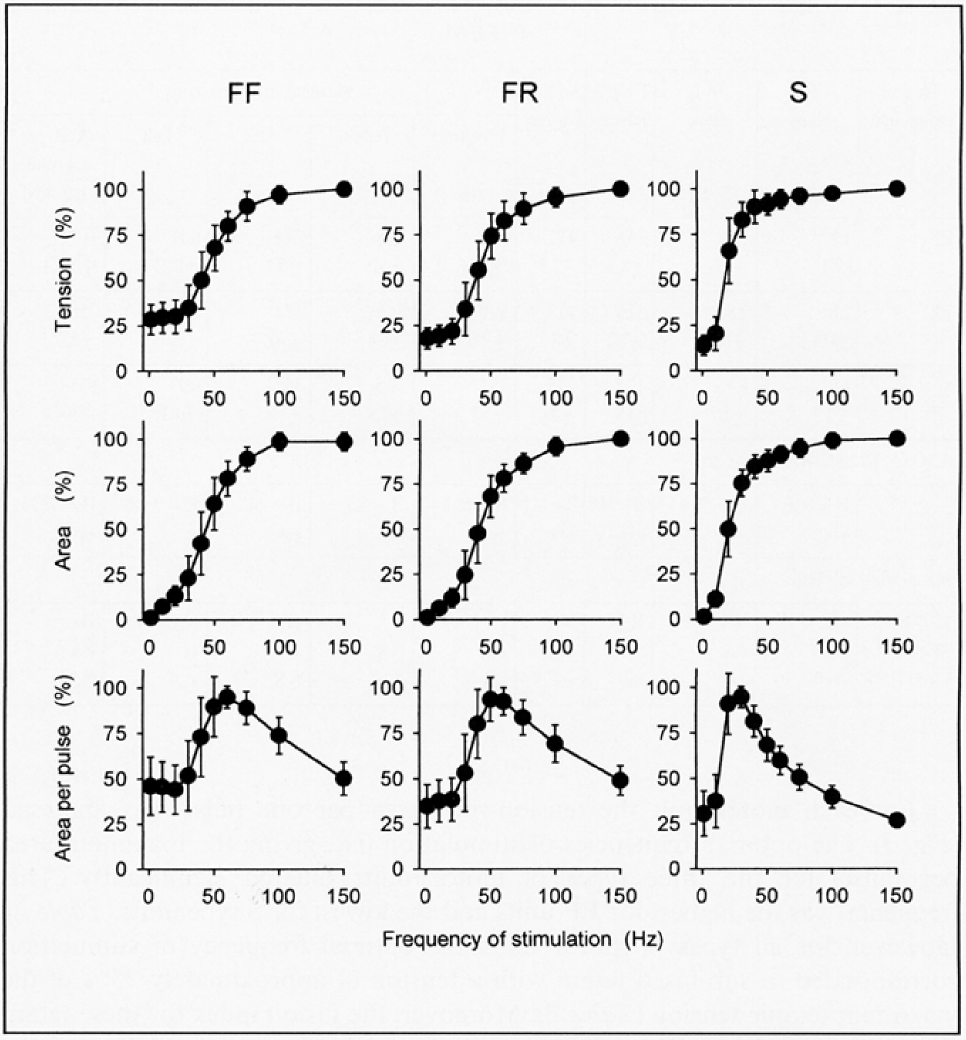

Fig. 3. The tension (upper row), the tension-time area (middle row), and the area per pulse in stimulation (lower row) as a function of stimulation frequency for the three types of motor units. Each point represents the mean value whereas vertical bars are the standard deviations. All analysed parameters of tetanic contractions are expressed in relative values, 100% corresponds to the maximum values.

DISCUSSION

The tension-time area which can be used as an estimation of the work performed by a contracting motor unit, depends on the frequency of stimulation. The shape of the area-frequency relationship has been generally similar to the tension-frequency curve (21, 26, 30, 31). However, the steep part of area-frequency curve corresponded to higher frequencies of stimulation than that of tension-frequency curve and the tension-time area for a tetanus changed in a wider range of relative values than the tension. Moreover, the tension-frequency curve for fast units has been less steep than the area-frequency curve, whereas for slow units the reverse result was obtained.

The measure of the tension-time area per pulse permits us to evaluate the work performed during one contraction within the tetanus. It has been found that in each motor unit type this area attained the maximum value in sub-fused tetanus but at various frequencies of stimulation. However, these optimal tetani had a similar relative tension and were fused to a similar degree in the three types of motor units. The optimal frequency corresponded to tetani with a high fusion index (above 0.90) and a tension of 75% of the maximum, approximately. Experiments of Tansey *et al.* (34) revealed that during natural activity motor units contracted in relatively well fused tetani, with the tension kept at the level >70% of the maximum output, which was probably optimal for the work performed by individual contractions within these tetani. Zajac and Young (35) found that the tension of tetani evoked at the stimulation pattern producing maximum tension-time area ranged between 50 and 80% of the maximum tetanic tension. In their next paper they revealed that the discharge patterns of cat hindlimb motoneurons, recorded during locomotion induced by mesencephalic stimulation, were similar to the optimal trains of stimulation (36).

In our previous paper (20) the effects of irregularity in the pattern of stimulation on the tension produced by motor units were studied. We found that motor units of all three types were less sensitive to a decrease in the interpulse interval the more fused the profile of tetanus was produced, whereas they were the most sensitive to an increase in the interpulse interval when the fusion index of tetanus was about 0.75. Therefore, the optimal tetanus for the tension-time area per pulse with a fusion index over 0.90 is rather insensitive to temporary interruptions in the pattern of motoneuronal discharges. It means that small irregularities in these discharges, visible during the natural activity of motoneurons (13, 14, 16, 17, 33) do not influence significantly the course of motor unit contractions. The regulation of tension of the optimal tetanus of the motor unit can be performed with a strong change in the pattern of discharges of motoneurons.

Evaluation of the work performed in response to one pulse during the tetanus enables the comparison of metabolic costs relevant to the contractions of different types of motor units. Each contraction within the tetanus is performed with a release of certain amount of energy. It has been found that slow units, which were over eight-times weaker than FF units, were able, in one contraction within the tetanus, to perform the work which was less than two-times lower than in FF units and even higher than for FR units. Kanda and Hashizume (25) studied the innervation ratios for the three types of motor units in the rat medial gastrocnemius muscle and found that slow units were composed of 41—80 muscle fibres, FR units — 116—198 fibres and FF units — 221—356 fibres. This means that slow units have 3—5 times fewer fibres than FF units and 2—3 times fewer fibres than FR units. Therefore, the present results point out that fibres of slow units are able to perform significantly more work than fast ones, at lower metabolic costs. The total daily time of activity of slow units can be about 5—8 hours (22, 28), whereas FF type units are active daily a few minutes and FR units are active roughly an hour. Therefore, slow units are responsible for the main part of normal daily muscular activity. The ability of slow units to contract with low metabolic costs is their very important property. With high resistance to fatigue (5, 6, 15, 19), and low sensitivity of tension to changes in interpulse intervals during tetanic activity (20) slow motor units are well prepared to participate in long-lasting contractions, at a nearly constant level of tension, and at low metabolic costs.

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