During natural contractions of a muscle, motor units (MUs) are activated by irregular discharge patterns of motoneurones. The aim of this study was to analyze changes in contractile forces of MUs following patterns of stimulation at variable frequency. Experiments were performed on 33 functionally isolated MUs of the fast-type in the medial gastrocnemius (MG) muscle of adult Wistar rats, under pentobarbital anaesthesia. The MUs forces evoked at five different regular stimulation patterns of constant frequencies were compared to forces generated during five random patterns of irregular stimulation with the same mean values of interpulse intervals, between 10 and 75 ms, and variability of these intervals of ±50% in each case. These values cover the natural range of the preferred firing rates of the MG motoneurones from unfused to nearly fused tetanic contractions. Analysis of changes in tetanic forces indicated a linear relationship between the interpulse interval as well as the initial level of the force and the amplitude of the force increase of the next contraction. It was demonstrated that variability of the instantaneous tetanic force during the irregular discharge pattern depends on the level of tetanic fusion. Moreover, it was demonstrated that for low and moderately-fused tetani, effectiveness of a MU contraction (expressed as the force-time area) is considerably higher for contractions evoked by irregular stimulation patterns. On the basis of the results of this study it was supposed that during voluntary contractions, the influence of changes in the motoneuronal firing rate on the motor unit force depends on the initial level of force.

Keywords: irregular stimulation pattern, interpulse interval, unfused tetanus, motor unit, rat
INTRODUCTION

The rate of motoneuronal firing is a major factor regulating the force of motor units (MUs), what has been demonstrated in numerous studies on functionally isolated MUs in animal species (1 - 4). During voluntary activity of a muscle, its MUs generate unfused tetanic contractions, which are characterized by variable force and variable degree of fusion (5 - 8). However, in the majority of experimental studies only the constant stimulation frequencies have been applied to investigate properties of tetanic contractions.

Irregular patterns of MU activation have been introduced in several studies, but authors have implied only small changes in regular stimulation rates, by adding or deleting impulses or by applying a linearly varying frequency of stimuli to evoke MU tetanic contractions (9 - 13). These authors have proved that even minimal and temporary changes in the pattern of impulses generated by motoneurons significantly modify the force generated by muscle fibers. Other studies have shown that in some motoneurons two firings in a short interval (doublet) appear at the beginning of MU activity or during a train of pulses in slightly fused tetani, what leads to immediate and considerable increase of the generated force (14 - 17). Moreover, fast MUs are sensitive to even very small changes in the pattern of interpulse intervals of a motoneuronal firing (12, 14, 15, 18,) and therefore, force of unfused tetani of fast MUs is highly susceptible to modifications of the firing rate. Slow MUs, being less sensitive to changes in the stimulation pattern, are suitable for tonic activity with the force kept at a stable level.

The above observations do not bring full explanation of mechanisms of force generation in MUs during natural voluntary contractions. Numerous electromyographic studies, performed either on animal species or human subjects, have revealed considerable variability of interspike intervals measured for individual MUs recruited during voluntary activity of a muscle. Tansey and Botterman (19) have measured firing rates of the medial gastrocnemius motoneurones during contractions evoked by stimulation of the mesencephalic locomotor region in the cat. They have revealed differences in the instantaneous frequencies of the recorded action potentials that ranged between 4 and 100 Hz. Differences between discharge frequencies of individual MUs between 5 and 18 Hz have been reported in the EMG study performed on the human rectus femoris muscle (5). Similar results have been obtained in the tibialis anterior muscle in man by Erim et al. (20), who have detected myoelectric signals from one MU ranged between several Hz and more than 30 Hz.

The purpose of this study was to analyze unfused tetanic contractions of MUs evoked by irregular patterns of stimulation in functionally isolated fast MUs of the rat medial gastrocnemius (MG) muscle. For comparison we applied five stimulation patterns at constant frequencies and five patterns of random stimuli at the same mean frequencies, corresponding to regular rates. We aimed
at analysing changes in the force and differences in the relative force increase during subsequent components of unfused tetanic contractions. We addressed three main questions related to this research (1). Whether the interpulse interval and/or the initial level of the force in the individual tetanic contraction can be used for prediction of the force developed by successive contractions within this tetanus? (2) To what extent the level of fusion of tetanus influences variability of the force during irregular stimulation? (3) How the level of fusion influences effectiveness of a MU work expressed as the area under the tetanic contraction record?

MATERIALS AND METHODS

Experimental procedure

Experiments were performed on 4 adult Wistar rats weighing 445 - 500 g. During experiments the animals were anaesthetized with pentobarbital (initial dose of 60 mg/kg, i.p., supplemented as required). The depth of anaesthesia was verified by controlling the withdrawal reflex. The principles of laboratory animal care, as approved by European Union and the Polish Law on Animal Protection were followed. After the experiments, the animals were killed with an overdose of pentobarbital (180 mg/kg).

MUs of the MG muscle were investigated. The studied muscle and the respective branch of the sciatic nerve were partly isolated from surrounding tissues; other muscles were denervated. Laminectomy over L2-S1 segments was performed, and dorsal as well as ventral roots of spinal nerves were cut proximally to the spinal cord. The animal was immobilized with steel clamps on the tibia, the sacral bone and the L1 vertebra. The operated hind limb and the spinal cord were covered with the paraffin oil; its temperature was kept at 37 ± 1°C by automatic heating system. The muscle was connected to an inductive force transducer to measure the contractile force under isometric conditions and stretched up to the passive force of 100 mN (21). The MU action potentials were recorded with a bipolar silver electrode inserted into the muscle. All the recorded data were stored on a computer disc using a 12-bit analog-to-digital converter (sampling rate 1 kHz and 10 kHz for force and action potentials, respectively). The functional isolation of single MUs was achieved by splitting the L5 or L4 ventral roots into thin filaments, which were electrically stimulated with suprathreshold rectangular pulses (amplitude up to 0.5 V, duration 0.1 ms). The “all-or-none” appearance of the twitch contractions and MU action potentials in response to stimuli of increasing amplitude indicated the activity of a single MU.

The pattern of stimulation

All MUs tested during experiments were stimulated according to the following protocol: 1) 5 stimuli at 1 Hz (5 single twitches were recorded and then the averaged twitch was estimated); 2) two trains of stimuli with 41 pulses: first at 40 Hz (the unfused tetanus was recorded), and second at 150 Hz (a fused tetanus was recorded) with 5 s interval between the trains; 3) five stimuli at 1 Hz; 4) two trains of stimuli with 41 pulses: the first at 20 Hz with the constant 50 ms interpulse interval (IPI) (an unfused tetanus at the regular stimulation pattern was recorded), and the second at the mean frequency of 20 Hz, but with variable random IPI (an unfused tetanus at the irregular stimulation frequency was recorded). The trains were separated by 10 s intervals. The procedure 4 was repeated four times, for the mean frequencies 25, 33, 40 and 50 Hz, i.e., with the mean
interpulse intervals 40, 30, 25, and 20 ms, respectively. The mean frequencies of irregular stimulation patterns corresponded to the respective regular patterns, but the intervals between individual pulses were randomly set at values in the range of the mean IPI ± 50%. Therefore, the IPIs in five types of unfused tetanic contractions evoked by irregular stimulation varied between 25-75 ms, 20-60 ms, 15-45 ms, 12-37 ms, and 10-30 ms, (Figs 1 and 3); 5) the fatigue test - 14 impulses at 40 Hz repeated every second throughout 3 min.

Data analysis

During the experiments all MUs were classified as fast or slow ones on the basis of the sag effect, visible exclusively in unfused tetani of fast MUs at 40 Hz stimulation (1, 22). The additional criterion of the division into fast and slow was the contraction time, which was shorter than 20 ms in fast MUs and longer than 20 ms in slow MUs (22). Only fast MUs were taken for further stimulation (i.e., the experiments continued with points 3 - 5 of the protocol). Fast MUs were

![Fig. 1. Parameters analysed in the unfused tetanic contractions evoked at regular and irregular stimulation patterns. A – unfused tetanus of an FF MU, recorded during regular 25 Hz stimulation. Ful, the fusion index, calculated as the ratio of the distance from the baseline to the maximal relaxation before the last contraction of the tetanus (a) to the amplitude of this last contraction (b). B – the same FF unit during irregular stimulation with a pattern of the mean frequency 25 Hz (IPI 40 ± 20 ms). In A and B, only parts of the tetani in the indicated windows (from the 11th component) were used for force analysis to avoid uneven effects of initial summation of tetanic components. C - an FF MU, recorded during regular 30 Hz stimulation. D - the same FF unit during irregular stimulation with a pattern of the mean frequency 30 Hz (IPI 30 ± 15 ms). Dotted parts of the records in C and D were used to calculate the ratio of force-time areas (FTAr / FTAi).](image-url)
divided into fast fatigable (FF) and fast resistant to fatigue (FR) on the basis of the fatigue index, which is below 0.5 for FF and over 0.5 for FR MUs (2).

The analysis concerned the unfused tetani evoked during regular (Fig. 1A and C) and irregular stimulation (Fig. 1B and D). For each unfused tetanus at the regular stimulation pattern, the fusion index (FuI, the ratio of the initial force of the last contraction within a tetanus to the maximal force of this contraction) was calculated (23, 3) (Fig. 1A). For each successive component (i.e., the contraction evoked by one pulse) of the unfused tetanus at the irregular stimulation pattern (Fig. 2), the preceding interpulse interval (IPI), the contraction time (CT, the time from the onset of the force increase to the force peak), the minimum force (F_{min}, from the baseline to the onset of the force development) and the maximum force (F_{max}, from the baseline to the peak) were measured, and the increase of force (F_{inc}, the difference between F_{max} and F_{min}) was calculated. In order to avoid incomparable differences caused by various rates of initial force development during regular and irregular stimulation patterns, the above parameters were analyzed for distant parts of tetanic contractions (from 11th component, as indicated by windows in Fig. 1A and B). For all studied tetani (at regular and irregular stimulation) the areas between the baseline and the line of the force record (FTA, force-time area) were measured, and the regular to irregular ratio of FTA was calculated (Fig. 1C and D).

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Fig. 2. Parameters measured for individual components within unfused tetani evoked at irregular stimulation pattern. A - unfused tetanus of an FF MU, recorded during irregular stimulation with the mean frequency 40 Hz (IPI 25 ± 13 ms). B - enlarged part of A, as indicated by the window. IPI, the interpulse interval; F_{min}, the minimum force of the component at the beginning of the force development; F_{max}, the maximum force of the component (peak); F_{inc}, the increase of force in the component; CT, the contraction time.
RESULTS

33 MU, 14 of the FF type and 19 of the FR type were analyzed in the study. In all cases the complete protocol of stimulation was applied, and all the contractile parameters were measured and compared between components of tetanic contractions evoked by the regular and irregular patterns of stimulation with comparable mean stimulation frequencies (i.e., mean interpulse intervals).

*Fig. 3* presents examples of unfused tetanic contractions of one FF motor unit stimulated with five different regular stimulation patterns (*Fig. 3A*) and with the respective irregular patterns of the same mean frequencies, but with a considerable variability (± 50%) between successive interpulse intervals (*Fig. 3B*). Irregular stimulation patterns evoked unfused tetani with highly variable peak force of successive contractions.

For each fast MU studied, at contractions evoked by irregular stimulation patterns, relationships between CT as well as the amplitude of the force increase during each successive contraction ($F_{inc}$) and the IPIs preceding each component of a tetanus were analysed (*Fig. 4*). Similar and comparable results were observed for all fast MUs studied. In less fused tetani, evoked by patterns with the mean IPIs of 30, 40 and 50 ms, respectively, longer contraction times and higher force

![Diagram](image_url)

*Fig. 3.* Unfused tetani of one FF MU recorded during application of regular (A) and irregular stimulation patterns (B). IPI, the interpulse interval; FuI, the fusion index. The bars indicating time and force scales are the same for A and B.
Fig. 4. Relationship between selected parameters measured for successive components of tetanic contractions evoked in one FF MU by five various irregular stimulation patterns with mean interpulse intervals from 50 to 20 ms (A-E). Left column - relationship between the contraction time (CT) and the interpulse interval (IPI), middle column – relationship between the force increase ($F_{\text{inc}}$) and the IPI, right column - relationship between $F_{\text{inc}}$ and the minimum force preceding each component ($F_{\text{min}}$) The regression equations are given for each chart.
increase were observed when longer interpulse intervals were applied. However, these relationships tended to be weaker in more fused tetanic contractions and could not be noticed in tetani evoked with the mean IPIs of 20 and 25 ms (Fig. 5).

Fig. 5. A - the relationship between variability of the force developed during unfused tetani evoked by irregular stimulation patterns and the fusion indices of respective tetani evoked by regular patterns of stimulation. This variability is expressed as the standard deviation (SD) of the mean tetanic force in percents. Data for the whole sample of fast MUs studied are presented on the chart. B - the relationship between mean values of variability of the force developed during five types of irregular unfused tetani and the mean interpulse intervals of these contractions. Mean values ± standard deviations are indicated.
$4D$ and $E$). Stronger relationship was observed between the force increase after each stimulus (for explanation of $F_{\text{inc}}$ see Fig. 2) and the initial force preceding each component of a tetanus ($F_{\text{min}}$). The higher was the initial force, the lower was its increase during the subsequent component of the tetanus. In all cases, as in the MU presented in Fig. 4, this relationship was clearly visible in all tetanic contractions evoked by irregular stimulation patterns, except the nearly fused tetani (the fusion index at regular stimulation exceeding 0.8) evoked with the 50 Hz mean stimulation frequency (the mean IPI of 20 ms). The above observations point to the fusion degree of a tetanus as a factor that might be used to predict the subsequent force increase.

For each tetanic contraction caused by the irregular stimulation pattern, the range of force changes (either increase or decrease) developed during subsequent components was calculated as the standard deviation of the mean force in percents. Fig. 5A presents the relationship between this variability and the values of $F_{\text{UI}}$ calculated for respective contractions evoked by regular stimulation patterns. The mean $F_{\text{UI}}$ of tetani evoked by trains of stimuli with the IPIs of 20, 25, 30, 40, and 50 ms amounted to $0.92 \pm 0.07$, $0.85 \pm 0.13$, $0.68 \pm 0.20$, $0.35 \pm 0.29$, and $0.23 \pm 0.28$, respectively. Relation between the force variability during irregular stimulation and various mean IPIs is shown in Fig. 5B. It was indicated that the highest variability of the tetanic forces (more than 20%) could be obtained at frequencies that produce contractions of moderate fusion degrees. For the majority of MUs, changes of the force were only minimal when the fusion indices of respective regular tetanic contractions were close to 0.0 or above 0.8 (Fig. 5A).

The mechanical output at the regular or irregular stimulation pattern was estimated as the force-time area (FTA). Values of the FTA obtained for tetani evoked by regular stimulation patterns were higher or lower than respective areas under force records of tetanic contractions evoked by the irregular stimulation patterns. The chart in Fig. 6A shows the ratios of the FTA for regular tetanic contraction to the FTA of irregular tetanus of the same mean IPI as a function of the fusion index for the regular tetani for the whole sample of motor units studied. One can notice that relatively high fusion degrees of regular tetani produced differences between FTA in favour of tetani evoked by regular stimulation rates (ratios > 1.0). However, the FTAs in tetani of low and moderate levels of fusion were higher for irregular than for regular contractions (ratios < 1.0). The mean values of the FTA ratios for regular and irregular tetani generated with the same mean IPIs amounted to $1.00 \pm 0.11$, $1.03 \pm 0.09$, $1.01 \pm 0.08$, $0.95 \pm 0.11$, and $0.91 \pm 0.11$, for IPIs of 20, 25, 30, 40, and 50 ms, respectively. The relationship between these values is shown in Fig. 6B. Stimulation with shorter mean IPIs (20-30 ms, corresponding to mean $F_{\text{UI}}$ of regular tetani 0.68 – 0.92, see above) resulted in similar values of the FTA for both types of tetani or slightly higher for contractions evoked by regular stimulation rates. However, areas under force-time curves of tetani evoked by
stimulation with longer mean IPIs in (40 and 50 ms, corresponding to mean FuI 0.23 - 0.35) were considerably higher for contractions evoked by irregular stimulation patterns.

Fig. 6. A - the ratio of the areas under records of tetanic contractions evoked at regular and irregular stimulation of the same mean frequencies (regular/irregular ratio) in the range of interpulse intervals (IPIs) between 20 and 50 ms, as a function of the fusion index, for all studied motor units. B - the relationship between this ratio of the areas and the mean IPIs. Squares on the curve reflect mean values and vertical bars standard deviations for each type of irregular stimulation patterns. Horizontal dotted lines in A and B denote the ratio of areas under regular to irregular tetani amounting to 1.0, what indicates identical force output in contractions evoked by respective regular or irregular patterns.
DISCUSSION

Patterns of motoneuronal firing

Irregular patterns of motoneuronal firing are typical for muscle activity during natural voluntary contractions. The recruitment order and range of discharge frequencies depend to a certain degree on intrinsic properties of motoneurones, as excitability, membrane electrical properties, duration of afterhyperpolarization (24 - 26). However, irregularity of the discharge pattern reflects mainly effects of supraspinal commands transmitted by descending pathways to motoneurones (27) and of afferent signals from muscle, joint and cutaneous receptors serving as a feedback control during performed movements (28 - 31).

In our study performed on the rat MG muscle we have used random patterns of stimulation of MUs to simulate, as closely as possible, conditions of voluntary contractions. The experimental recordings of a preferred firing range of motoneurones during voluntary contractions across vertebrate species, from turtle to human, have indicated that the lower mean motoneuronal discharge frequencies coincide with higher contraction times of MUs (32). Hennig and Lømo (6) have investigated discharge patterns in MUs of extensor digitorum longus and soleus muscles in the rat and have recorded firing rates ranging from 48 to 91 Hz, and from 18 to 21 Hz, respectively. Tansey and Botterman (19) in the cat MG muscle have measured 48.4 ± 6.2 Hz and 27.8 ± 9.0 Hz, for fast and slow MUs, respectively. In human muscles discharge rates of individual MUs varied between 5 and about 30 Hz (5, 20). However, in all these studies considerable differences in the instantaneous frequencies of the recorded action potentials have been reported, sometimes exceeding 100% of the mean value (19). The mean firing rates and the ranges of frequencies measured in individual MUs depend on the type and strength of a contraction.

Therefore, application of five different random patterns of stimulation with interpulse intervals between 10 and 75 ms and variability ± 50% in each case, enabled us to obtain the range of instantaneous frequencies of tetanic contractions between 13 and 100 Hz. One may expect that such patterns cover the natural range of the preferred firing rates of MG motoneurones from unfused to nearly fused tetanic contractions. Such wide range of stimulation frequencies would reflect activity of MUs recruited either during weak or strong contractions of the muscle. Our previous experiments on MUs of the rat MG muscle have shown that unfused tetanic contractions of various fusion degrees can be evoked in fast MUs at frequencies between 15 - 20 and 75 Hz (4, 33), what corresponds to the range of IPIs analyzed in this paper for contractions evoked by irregular stimulation patterns.

Variability of force

It has been reported in numerous previous studies that the discharge rate of motoneurones positively correlates to the absolute force of tetanus during
centrally evoked or voluntary contractions of MUs (5, 20, 34). The results of the present study have revealed that the instantaneous force developed by a MU during tetanus evoked by the irregular pattern of stimulation depends both on the interpulse interval and on the initial force level. Two main findings should be emphasized. First, that longer IPIs and lower initial levels of force ($F_{\text{min}}$) result in higher force increase during next components of tetanic contractions. Second, that these relations are stronger for tetani evoked with relatively low mean stimulation frequencies (longer IPIs) generating lower forces, than for high-frequency tetani (shorter IPIs) generating higher levels of force. The latter observation seems to be due to considerably higher level of fusion of high-frequency tetani resulting in relatively small changes of force (compare examples of force records in Fig. 3 and charts in Fig. 4) (12). One should also notice that higher initial forces measured for individual components of a tetanic contraction usually reflect its higher fusion. From this point of view, it can be concluded that values of IPIs influence the force increase during tetanus by regulating the rate of the force decline, thus allowing achieving lower force level during a longer interval, what in turn induces higher force increase following the next impulse of the firing pattern. Our previous study, devoted to analysis of the relaxation phase in regular tetani of variable fusion degree, has revealed that in tetani with the FuI above 0.8, the biphasic relaxation (first slow, and then fast) is observed (35). The slow initial relaxation in tetani of relatively high fusion (and high force level as well) prevents the significant force decrease even at relatively long IPI. This may help explain why irregularities in the stimulation pattern do not produce considerable force changes during tetani when mean IPIs are relatively short, coinciding with high force levels.

For regular tetanic contractions, the relationship between the force level (as well as the corresponding FuI) and the stimulation frequency has been widely described by analysis of force-frequency curves in various mammals and in man (20, 2, 33, 36). These investigations have indicated high ability of MUs to increase the tetanic force in response to small changes in stimulation frequency in the relatively wide range of frequencies that evoke unfused tetanic contractions. However, during the regular pattern of stimulation, the force of individual components of the tetanic contraction is relatively stable, while variability of forces observed during irregular stimulation in many cases has exceeded 30% of the mean force of the tetanus. The range of this variability of force (instantaneous changes in force of successive components of tetanus in relation to the mean tetanic force) appears to highly depend on the fusion of tetanus. Since calculation of the FuI for tetani evoked by irregular stimulation brings different results for each component, instantaneous changes of force could only be analyzed with respect to FuI of regular contractions evoked with the same mean frequencies, in which stable levels of force are obtained. As presented in Fig. 5, this variability is most pronounced for moderately fused irregular contractions, evoked with the mean IPIs of 30 and 40 ms. On the other hand, instantaneous changes of force are
much smaller for low-fused contractions evoked with mean IPIs of 50 ms (FuI < 0.2) as well as high-fused tetani with mean IPIs of 20 and 25 ms (FuI > 0.8). It has been previously described that small changes in the stimulation pattern (increase or decrease of the IPI, a doublet at the beginning of the tetanic contraction) can significantly change the force of the contraction and these changes depend on the fusion index (17, 37). Results of this study point on the high influence of the level of fusion on the variability of the instantaneous tetanic force during the irregular discharge pattern, what leads to the conclusion that during voluntary contractions, the significance of changes in the motoneuronal firing rate on the MU force depends on the initial level of force.

The force-time area

The area under the record of a contraction in view of classical mechanics is named an impulse and reflects potential to develop changes of the momentum of an object, on which the force acts during a given time (38). In numerous earlier studies it has been assumed that the area under the force-time curve of tetanus reflects the effectiveness of this contraction, and depends on a frequency of the MU stimulation (14, 15, 39, 40). It has been suggested by Zajac and Young (16) that the FTA represents the total amount of activated and bound Ca2+ during an isometric contraction. Modifications of the contractile force and/or the time of its increase by changes in interpulse intervals influence the FTA during various stimulation patterns which allows determining parameters of the optimal tetanus, i.e., the maximal generated FTA per pulse.

Moreover, the analysis of the FTA is important in view of the economy of a MU contraction. The economy of the isometric tetanus can be calculated by dividing the FTA by the total energy consumption (41), which comes principally from the ATPase activity of the actomyosin system and that of the sarcoplasmic reticulum Ca2+ pump, and to a lesser extent from other energy-producing processes (42). The energy cost of a single twitch is independent from the contraction frequency (43, 44), but the total amount of energy utilized during a tetanus is a function of the number of applied stimuli and intervals between successive tetani – less energy is consumed when contractions are repeated with brief intervals (41, 45). Despite the fact that this study does not provide direct data concerning the energetic cost of a MUs contraction, several assumptions on the economy of contraction may be drawn from our results since experimental protocols applied for each pair of compared tetani have created comparable conditions: the constant number of pulses within each tetanus (n = 41), the same duration, and identical (10s) intervals between tetani. Therefore, it is supposed that the levels of energy consumption during respective contractions evoked by regular and irregular stimulation patterns do not differ between each other. One can assume that analysis of the FTA may also be related to the economy of these tetani.
We have demonstrated that FTA under tetanic contractions obtained at irregular stimulation patterns may be lower or higher than FTA for tetani developed at regular stimulation frequencies of the respective mean IPI and this depends on the fusion of the tetanus and the mean IPI. The application of the regular stimulation pattern appears to be similarly or slightly more effective than irregular stimulation of the same mean frequency only for tetanic contractions of IPIs between 20 and 30 ms, in majority of cases corresponding to relatively high levels of fusion. The reversed results, in favour of the irregular stimulation pattern, concern low-fused tetani evoked with the mean IPIs of 40 and 50 ms. As discussed above, during tetanic contractions with Ful exceeding 0.8, high levels of force can be achieved, but variability of force is considerably lower in comparison to less fused contractions. These observations suggest that the irregular stimulation pattern produces higher output of MUs (and higher economy of contraction) than the regular frequency during relatively weak tetanic contractions. Moreover, the variability of the MU output may be more precisely regulated by changing intervals between pulses during motor tasks requiring low or moderate level of force.

To sum up, we have compared selected time and force parameters of tetanic contractions evoked in individual MUs by respective regular and irregular stimulation patterns. On this basis we have demonstrated that application of regular stimulation patterns during experimental analysis of contractile properties of functionally isolated MUs can lead to several conclusions that do not correspond to activity of MUs during natural voluntary movements. This concerns contractile parameters of successive components of tetanic contractions, the contraction time, the instantaneous force and its variability as well as the effectiveness and economy of the MU’s contraction.

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