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Review article

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MECHANISMS UNDERLYING THE REGULATION OF MOTOR UNIT CONTRACTION IN THE SKELETAL MUSCLE

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The control of movements is made posible thanks to the activity of motor units in skeletal muscles. In the present paper the influence of frequency and pattern of motoneuronal firing on the tension of contraction and the tension-time area is presented and discussed. The most resistant to fatigue slow-twitch motor units are low susceptible to changes in a pattern of impulses and therefore they are well prepared to participate in long-lasting movements at low but rather stable levels of tension. Moreover, their contraction is very effective and it is performed at a low metabolic charge. Fast-twitch units have lower resistance to fatigue and they have higher tension but they have high susceptibility to a pattern of pulses and their tension can be effectively regulated by an increase or a decrease in the interpulse interval. Therefore, fast motor units are specialized to participate in the regulation of the movement force. The existence of different functional groups of motor units in skeletal muscles enables the performance of different motor tasks very effectively and at possibly low metabolic costs.

Key words: *motor unit, contraction, regulation of tension.*

INTRODUCTION

Mammalian skeletal muscles are composed of small functional units, called "motor units". A motor unit is a complex of one motoneuron and a bundle of muscle fibres innervated exclusively by this neuron and dispersed in a limited territory within one muscle (1). All of the muscle fibres of one motor unit are synchronously contracting in response to each action potential generated by motoneuron and all of the fibers belonging to one motor unit are of the same type. Therefore contractile properties of different motor units vary significantly. Slow units (S) are composed of type I muscle fibres, fast resistant to fatigue (FR) are composed of type IIA muscle fibres and fast fatigable (FF) are composed of type IIB muscle fibers (2). Each muscle activity engages a number of motor units. Moreover, during activity motor units are contracting in unfused tetani (3, 4). Therefore, the tension of muscular contraction depends on two main factors: the number of motor units recruited into contraction and the tension of active motor units depends on the frequency and pattern of firing of motoneurons. The present review will deal with the mechanisms regulating the tension of active motor units. The studies were performed on motor units in the rat medial gastrocnemius muscle.

The influence of stimulation frequency on the tension of motor unit contraction

The tension of motor units can vary in range between the tension of a single contraction (the lowest tension) of the fused tetanus (the maximum tension) (*Fig. 1*). The tension of unfused tetani depends on the firing rate of motoneurons. *Figure 2* presents the averaged plots of relationship between the

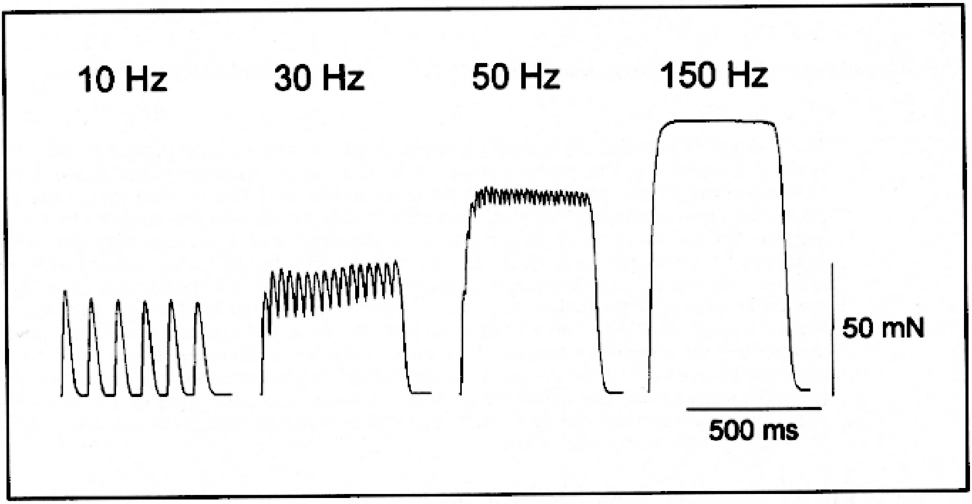

Fig. 1. Tetani of an FF motor unit evoked at four different frequencies of stimulation indicated above the records.

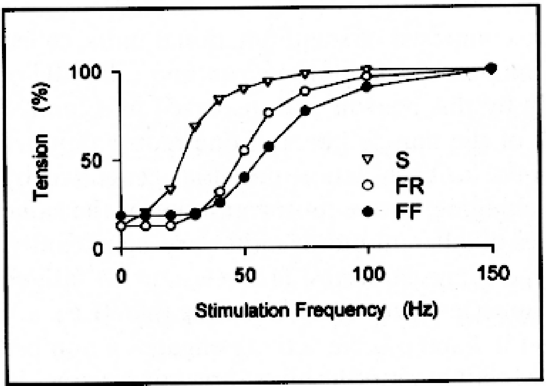

Fig. 2. The tension-frequency of stimulation relationships for the three types of motor units. Each point represents the average value for a given frequency of stimulation. 100% corresponds to the tension of the maximal fused tetanus. From Grottel *et al.* (5).

motor unit tension and the stimulation frequency for the three types of motor units (5). The steep part of the tension-frequency curve corresponds to unfused tetani. Slow units are able to generate unfused tetani at lower frequencies of stimulation than fast units, especially of FF type (5, 6). During voluntary contractions motor units contract in unfused tetani and the rate of motoneuronal firing corresponds to the steep part of the tension-frequency curve (7—10).

The tension-frequency relation is a dynamic property and this is changing during activity of fast motor units, especially fast fatigable. Experiments in which changes in tension-frequency curves were observed during long-lasting activity of motor units showed first the influence of potentiation and then of fatigue on this relationship (11). For the fast units, especially of FR type, it was observed that the potentiation resulted in a shift of the steep part of the tension-frequency curve towards lower frequencies (*Fig. 3*, the second curve for FR unit). For FF units when fatigue developed the tension-frequency curve shifted towards higher frequencies (*Fig. 3*, the tenth curve for FF unit). These changes were parallel to the changes of the contraction time visible on single

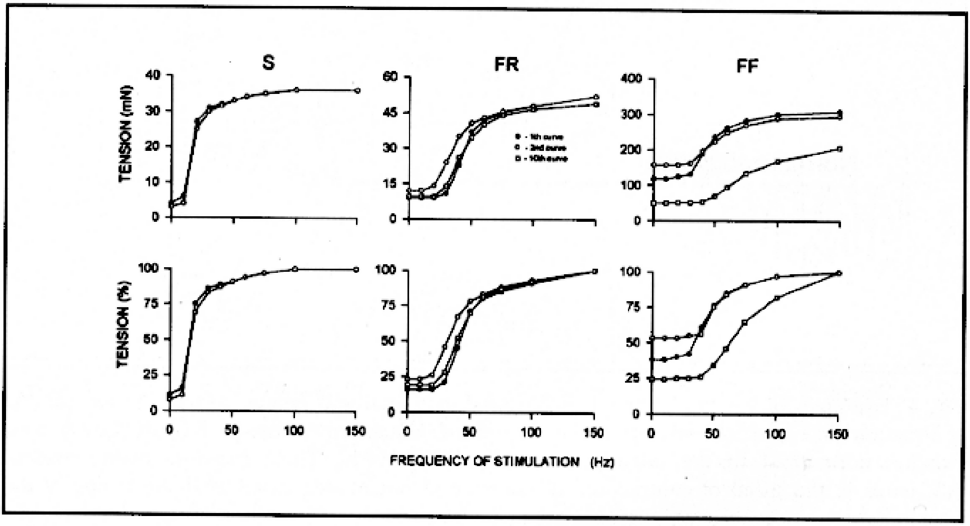

Fig. 3. Motor unit tension — frequency of stimulation curves for S, FR and FF motor unit. Each motor unit was stimulated with a series of trains of stimuli at the frequency increasing from 1 to 150 Hz. These series were repeated ten times. Each frequency corresponds to one point on a plot. The tension is expressed in absolute values (higher plots) and in relative values (lower plots, expressed in % of the maximal tetanic tension). Filled circles, the first curve; open circles, the second curve; squares, the tenth curve. For fast units (FR and FF) the second curve shows potentiation of twitch and unfused tetani, whereas the tenth curve of FF unit shows a fatigue. To make the Figure easy to understand for fast units the third — ninth curves are nor presented: the steep part of these curves shifts progressively towards higher frequencies in the field between the second and the tenth curve. For slow units the second and the following curves overlap and therefore only the two first curves are presented. From Celichowski and Grottel (11).

twitches (*Fig. 4*). It is known that the potentiation is accompanied by the slowing of contraction (12—18), whereas the fatigue is parallel to the shortening of contraction time (19, 20). These results show that the relationship between the motoneurone firing rate and the tension is changing during contractions and must be taken into consideration in the motor control studies. Especially, significant changes in the steep part of tension-frequency curve occurring during potentiation and fatigue are very important because during muscular activity motor units are contracting in unfused tetani.

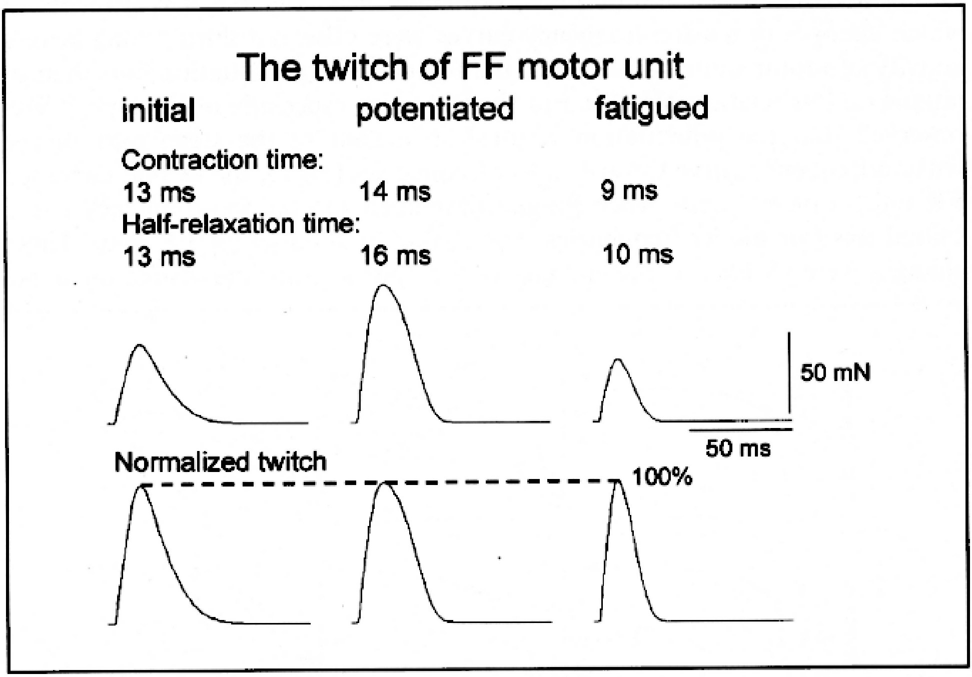

Fig. 4. Examples of FF motor unit twitch: initial, potential and fatigued. Over the records the contraction time and half-relaxation time are given. Higher row, original records. Lower row, twitches normalized to the same peak amplitude of 100%. This procedure makes evident differences in the speed of contraction: the slowing of potentiated twitch and shortening of the twitch in fatigue.

The increase in stimulation frequency results not only in the increase in tension of an unfused tetanus but in parallel also evokes a rise in the tetanic fusion. The fusion of contraction can be measured by the fusion index (*Fig. 5*). This index can be calculated as a ratio of the distance from the baseline to the relaxation before the successive contraction to the amplitude of this contraction (21, 22). Values of the fusion indices vary from 0.0 (for repeated but not-summated twitches) to 1.0 (for fused tetanus) whereas unfused tetani can be described by intermediate values of the fusion index. *Figure 6* presents the

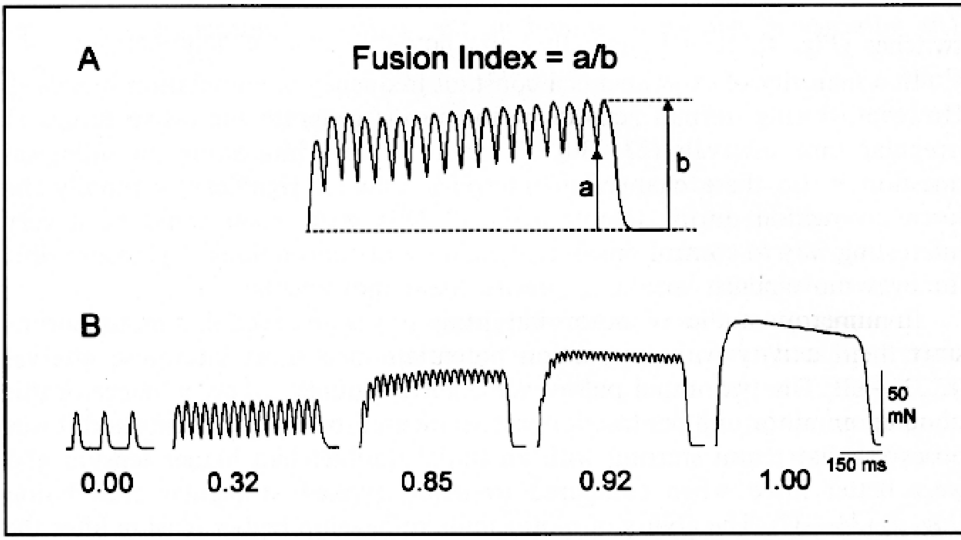

Fig. 5. The fusion index. A, the method of calculation of the fusion index as the ratio of the amplitude from the baseline to relaxation before the following contraction to the peak amplitude of the following contraction. B, examples of FF motor unit tetani and the values of the fusion index calculated for these tetani (under the records).

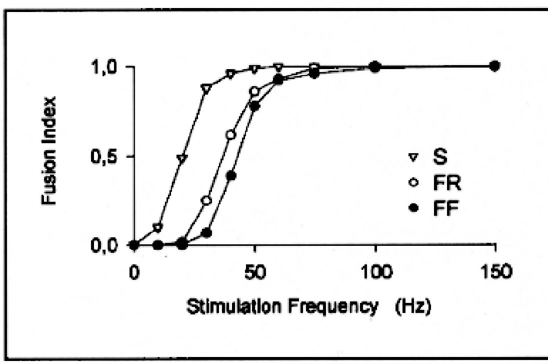

Fig. 6. The fusion index as a function of the stimulation frequency. Each point represents an average value for a given frequency of stimulation. From Celichowski and Grottel (21).

relationship between the frequency of stimulation and the fusion index for the three types of motor units. The course of the fusion index — frequency curve is similar to the tension — frequency curve (*Fig. 2*). However, the tetanic fusion develops faster than the tension rise and the steep part of the fusion index — frequency curve corresponds to lower frequencies of stimulation than for the tension — frequency curve. As an effect, for all motor units the tetanus with a fusion index of 0.5 corresponds to lower frequency of stimulation than the frequency used to evoke the tetanus with a tension at 50% of the maximum.

The influence of pattern of stimuli on the course of contraction

In a majority of experiments a constant frequency of stimulation was used. However, during normal activity motoneurons generate successive firings at irregular time intervals (23—30). Therefore, a very interesting physiological question is: do these changes in interpulse interval significantly modify the force production during tetanic activity? This mechanism could be a very interesting way to control precisely the course of contractions (e. g. responsible for eyes movements, speaking, precise hand movements).

In numerous studies of motor unit firings it was observed that motoneurons start their activity with two action potentials in a short interpulse interval (8, 31—33). The two initial pulses were called "doublet". The influence of this doublet on motor unit contraction was studied in some experiments and it was observed that tetani starting with an initial doublet had higher tension and were better fused when compared to tetani evoked at regular stimulation (*Fig. 7*) (34—37). The ability of motor units to develop higher tension after the doublet was called the "catch effect" (34). This effect is important for the metabolic costs of contraction because it enables the develop of tension similar to that during the stimulation with higher frequency of pulses in regular interpulse intervals but with a lower number of contractions.

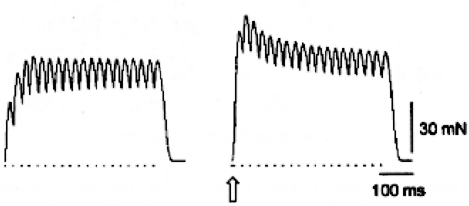

Fig. 7. The influence of a doublet on the tension of FF motor unit tetanus. Points under the record denote the pattern of stimuli used to evoke the tetanus. The initial doublet (two pulses in a short interpulse interval) is indicated by an arrow under the right record.

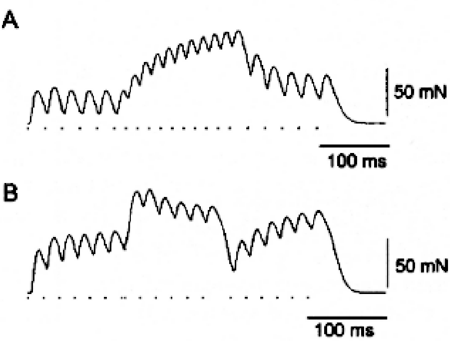

Fig. 8. The influence of stimulation pattern on the course of FF motor unit tetanus. The pattern of stimuli used to evoke the contraction is shown under the record of tension. In the higher record (A) the tension was influenced by an increase (from 40 to 60 Hz) and later by a decrease (from 60 to 40 Hz) in stimulation frequency. In the lower record (B) the changes in tension resulted first from the 75% decrease and then from the 75% increase in only one interpulse interval.

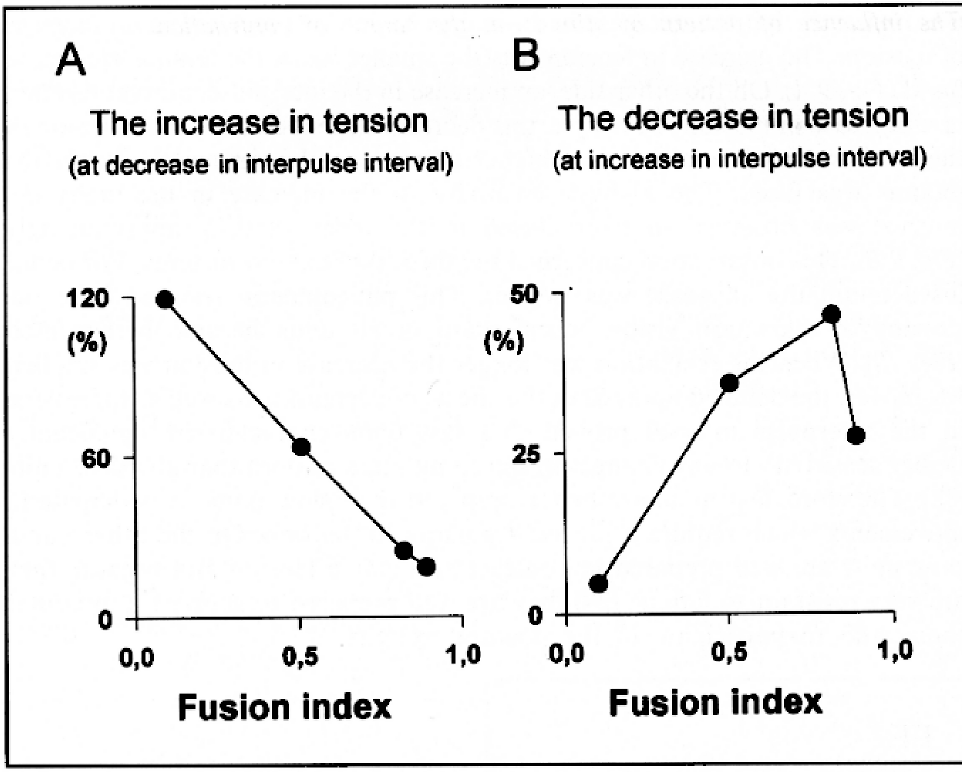

Fig. 9. The increase (A) in tension of tetanus resulting from the decrease in interpulse interval and the decrease (B) in tension of tetanus resulting from the increase in interpulse interval as a function of the fusion index. An example of FF motor unit. Four points on both plots correspond to four applied frequencies of stimulation (30, 40, 50 and 60 Hz) whereas the changes in tension were an effect of 75% decrease in one interpulse interval (left) or 75% increase in one interpulse interval, as shown in Fig. 8 B. The change in tension is expressed in relative values, 100% is the tension of tetanus before the interruption in the stimulation pattern was introduced. From Grottel and Celichowski (38).

The doublet was the phenomenon which occurred *at the beginning* of tetanus. However, the change in the stimulation frequency *during* the tetanus also results in the regulation of tension. *Fig. 8 A* presents the influence of an increase and a decrease in the stimulation frequency on the tension produced by the contracting motor unit. Moreover, it was found that not only a rise of a fall in the stimulation frequency modified the tension of motor units but even temporary changes in stimulation frequency (i. e. decrease and increase of only one interpulse interval) influenced the following part of contraction (*Fig. 8 B*) (38). This interruption in the stimulation pattern modified the tension of at least a few successive contractions. These effects were studied in tetani evoked at different frequencies of stimulation, in tetani fused to a variable degree. It was observed that the decrease in an interpulse interval resulted in an increase of tension. The increase in tension was the smaller when the tetanus was more fused (*Fig. 9 A*). On the other side, an increase in the interpulse interval resulted in a decrease of tension. Of course, this decrease depended also on the fusion of the tetanus. First, we observed a higher decrease in the tension the better the tetanus was fused. The highest sensitivity to the increase in the interpulse interval was observed in tetani fused to the index of 0.75, approximately (*Fig. 9 B*). This observation concerned the three types of motor units. For better fused tetani this decrease was smaller. This phenomenon resulted from the slowing of relaxation visible when tetani of all units became better fused (*Fig. 10*). When the relaxation was longer the decrease in tension was smaller. Moreover, the detailed analysis of the effects of decreasing as well as increasing in the interpulse interval proved that fast units characterized significantly higher sensitivity to any changes in the stimulation pattern than the slow units (38). Therefore, fast units are better prepared than slow units to paticipate in movements which require a precise regulation of tension. On the other hand, slow units are well prepared to contract at a stable tension and because they are very resistant to fatigue (39) they are well prepared to support a muscular tonus and to participate in the postural activity.

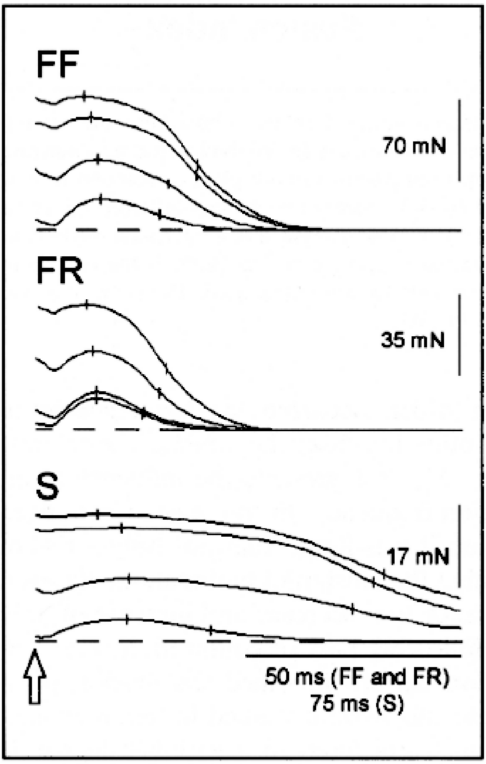

Fig. 10. Examples of the course of the last contractions of FF, FR and S motor units within tetani fused to various degrees. Small vertical bars point to the peak force and the time when the tension falls to a half of the peak value. A prolongation of the relaxation parallel to a rise in the fusion index is visible. From Grottel and Celichowski (38).

The comparison of the effects of increasing the interpulse interval to the effects of decreasing the interpulse interval permits us to estimate the fusion index of a tetanus in which this increase or decrease in the interpulse interval evokes similar amplitudes of tension decrease or increase, respectively. Plots of the decrease and the increase in tension as a function of the fusion index were superimposed (*Fig. 11 A*). The point where both plots overlap each other enables this estimation. Similar method enabled to estimate the level of tension of this tetanus (*Fig. 11 B*). It was found that for all three types of motor units this tetanus had a fusion index of about 0.70 and its tension corresponded approximately to 40% (slow units) or 45—50% (fast units) of the fused tetanus tension (*Table 1*). These observations concerned both tetani beginning with a regular stimulation and tetani beginning with a doublet (*Table 1*). It seems to be important that this pattern-susceptible contraction is also the tetanus nearly maximally sensitive to a decrease in the interpulse interval (38). Moreover, this tetanus could be optimal for precise movements because each change in the interpulse interval is highly effective in the regulation of tension. The contraction at the level of 40—50% of the maximum tension is rather weak contraction. Therefore, this observation could explained why the high precision of the movement must be performed with a low force.

Table 1. Properties of the best tetanus for precise movements (means ± S.D.). This tetanus is similarly sensitive to an increase and a decrease in the interpulse interval. The relative tension of this tetanus is expressed as a percentage of the maximal tetanic tension. The differences between the values of the fusion index for the three types of motor units were non-significant (ANOVA Kruskal Wallis test, $P > 0.05$) whereas the level of tension for the three types differed (ANOVA Kruskal Wallis rank test, $P < 0.05$) and differences between (FF and S) units appeared to be significant (Wilcoxon test, $P < 0.01$). These analysis were performed in tetani beginning with regular stimulation and with a dublet. Non-doublet tetanus — the tetanus beginning with a regular stimulation; doublet tetanus — the tetanus beginning with two initial pulses at a short interpulse interval.

Motor unit type:	FF	FR	S
The fusion index			
non-doublet tetanus	0.72 ± 0.07	0.69 ± 0.06	0.75 ± 0.11
doublet tetanus	0.71 ± 0.07	0.66 ± 0.06	0.69 ± 0.14
The relative tension (% of the maximal tetanic tension):			
non-doublet tetanus	48.3 ± 6.2	43.3 ± 6.7	41.0 ± 4.8
doublet tetanus	50.4 ± 8.0	44.5 ± 7.0	39.1 ± 7.4

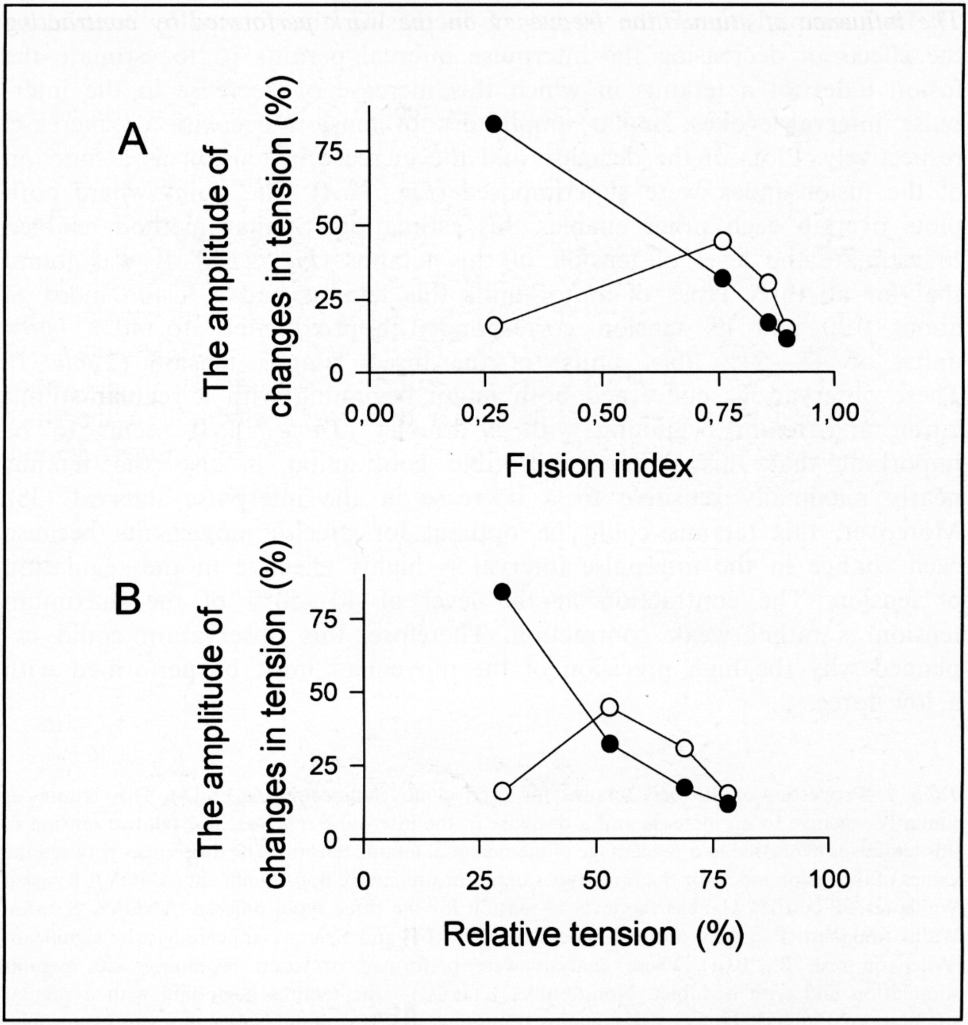

Fig. 11. The method of estimation of the fusion index and of the relative tension at which a tetanus is similarly sensitive to an increase and a decrease in the interpulse interval. An example of FR motor unit. A, superimposed plots of the tension increase and decrease evoked by 75% changes in the interpulse interval (ordinate) as a function of the fusion index (abscissa). A crossing of both plots indicates the value of the fusion index of the tetanus (0.68 for this unit) at which both changes in the interpulse interval evoke similar amplitudes of an increase and a decrease in tension. B, superimposed plots of the tension increase and decrease evoked by 75% changes in the interpulse interval (ordinate) as a function of relative tension (abscissa). A crossing of both plots indicates the level of the tetanic tension (50% of the maximal tetanic tension in the case) at which both changes in the interpulse interval evoke similar amplitudes of an increase and a decrease in tension. Four points in each plot correspond to four applied frequencies of stimulation: 30, 40, 50 and 60 Hz. Filled points, the increase in tension at the decrease in the interpulse interval; non-filled points, the decrease in tension at the increase in the interpulse interval.

The influence of stimulation frequency on the work performed by contracting motor units

The area between the baseline and the record of tension (the tension-time area) was used in many experiments as a measurement of the output for motor units and muscle contractions (34, 35, 40—43) and the work performed during contraction can be estimated by a measure of this area (44). A very simple example of records of single twitches of three motor units: S, FR and FF (*Fig. 12*) shows that the tension of these units vary. A slow unit has the smallest tension whereas an FF unit is the stongest. However, the tension-time area for slow units is the biggest whereas for the FF unit — the smallest. This observation turns our attention to the time course of contraction: for slow units the contraction time is significantly longer than for fast units and the work performed during the twitch is higher than it could be estimated exclusively on the base of the twitch tension.

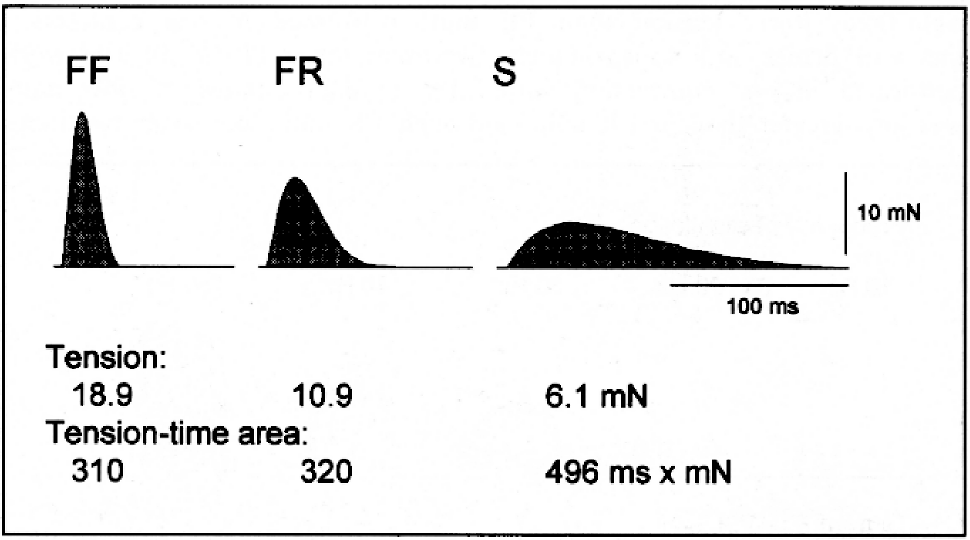

Fig. 12. Examples of FF, FR and S motor unit twitches. Values of the twitch tension and of the tension-time area (the grey area on the records) are given under the records.

During usual movements motor units contract in unfused tetani. Therefore, the tension-time area performed during this kind of motor unit contraction was studied. The tension-time area for tetani fused in various degrees was measured. The tetanus results from the summation of successively repeated contractions. Therefore, the tension-time area corresponding to one contraction was additionally analysed for tetani evoked at different frequencies of stimulation

(*Fig. 13*). Each successive contraction causes a new unit of metabolic costs and therefore this analysis of the effects of one contraction enables the estimation in which the work is performed at the lowest metabolic charge. This tension-time area of tetanus and the tension-time area per one pulse within this tetanus were presented as a function of the stimulation frequency (*Fig. 14*). The tension-time area – frequency curve is also similar to the tension – frequency curve, although the steep part of this curve corresponds to slightly higher frequencies. However, we observed that for the three types of motor units the optimal contraction i.e. when the tension-time area per pulse was maximal, was evoked at different frequencies of stimulation (the lowest for slow motor units and the highest for FF units) but for all types of motor units the tetanus had the fusion index of about 0.90 and its tension corresponded to 75% approximately of the maximal tetanic contraction (*Table 2*). Moreover, the analysis of absolute values of tension-time areas corresponding to one contraction within the optimal tetanus revealed that slow units which had over eight-times lower tension than FF units performed in one contraction the work which was approximately two-times lower (*Table 2*). The work performed in one contraction within the optimal tetanus of slow units was also greater than in FR units, although FR units were over two-times

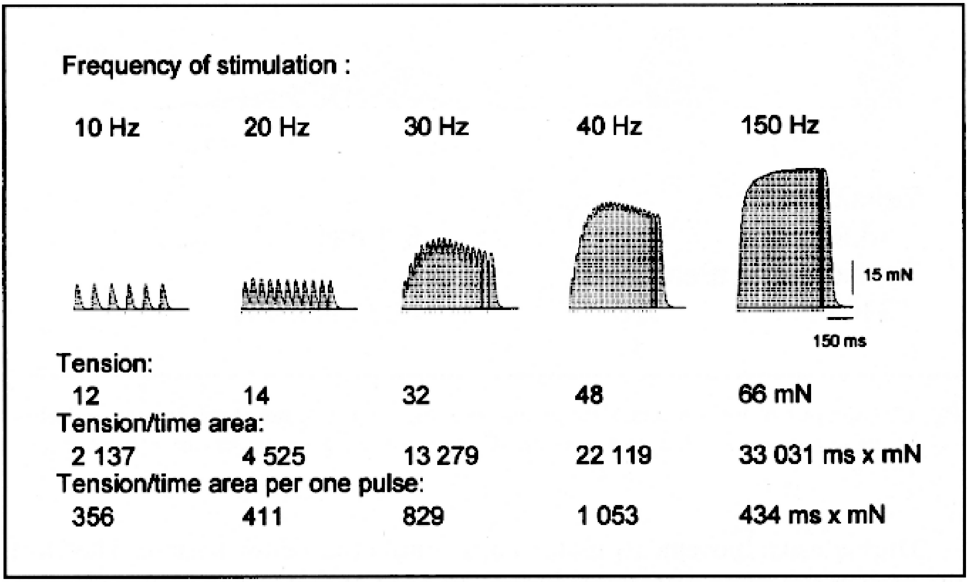

Fig. 13. Examples of FR motor unit tetani evoked at stimulation frequencies given above the records. For each tetanus values of the peak tension, the tension-time area and the tension-time area per pulse are given under the record. The tension-time area for tetanus is the grey area on the record. The tension-time area per pulse corresponds to the area between two vertical lines.

stronger than slow units. The tension is nearly directly dependent on the number of muscle fibers constituting the motor unit. Slow units have the lowest number of muscle fibers whereas FF units are composed of the highest number of these fibres (45). Therefore, the results presented in *Table 2* revealed that the contraction of slow units is significantly more effective and performed at significantly lower metabolic charges than the contraction of fast units.

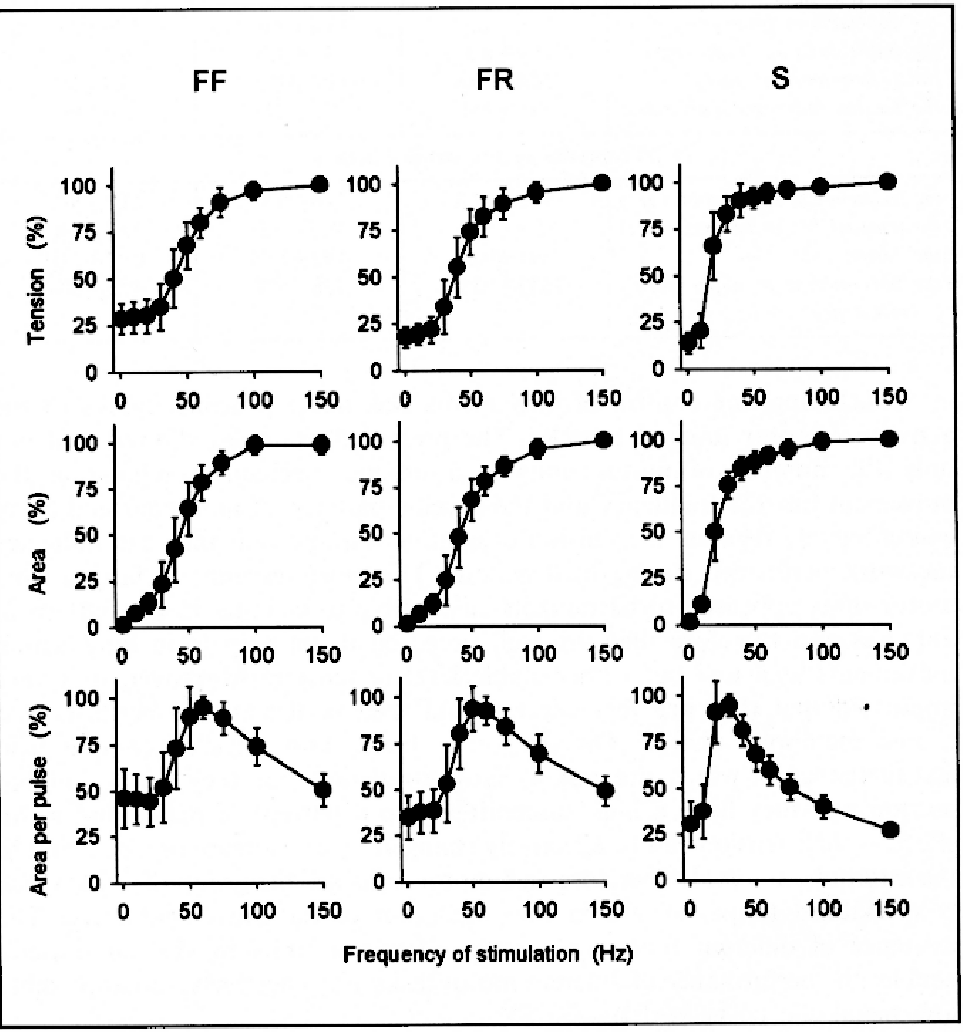

Fig. 14. The tension-frequency curves, the area-frequency curves and the area per pulse-frequency curves for FF, FR and S motor units. Each point on the records indicates the mean value and the standard deviation. The tetanus with the highest value of the tension-time area per pulse is accepted as an optimal tetanus.

Table 2. The mean values (±S.D.) of the main properties of the twitch and of the optimal tetanus (with the maximal tension-time area per pulse), for the three types of motor units. The contraction time was measured from the beginning of the twitch to a peak in tension record, the half-relaxation time was measured from the peak tension to a moment when tension falled down to a half of the peak value. The tension of the optimal tetanus is given in relation to the tension of the maximal fused tetanus.

Motor unit type	FF	FR	S
Properties of the twitch:			
the contractiom time (ms)	12.2±1.9	13.6±2.6	23.3±3.9
the half-relaxation time (ms)	11.9±3.3	15.6±4.5	36.2±9.2
the twitch tension (mN)	38.4±20.8	11.4±10.6	4.6±1.9
the tension-time area (nN × ms)	814±551	292±271	230±96
Properties of the optimal tetanus:			
the frequency of stimulation (Hz)	55.8±11.3	50.0±9.8	25.2±5.8
the tension (% of the maximum)	75.8±6.0	74.1±6.6	79.5±7.8
the fusion index	0.91±0.03	0.92±0.03	0.93±0.03
the tension-time area per pulse (mN × ms)	1653±938	756±527	955±504

Concluding, the control of movements was made possible thanks to the activity of motor units in muscles. The presented examples showed that not only the number of motor units is a unique mechanism regulating the movement but the frequency and the specific patterns of motoneuronal firing can effectively regulate the tension of contraction and that they can influence the work performed during contractions. The most resistant to fatigue slow motor units appeared to be unlikely susceptible to changes in the pattern of impulses and therefore they are well prepared to participate in long-lasting movements at a low but rather stable level of tension. Moreover, it is very important that they are very effective and their contraction is performed at a low metabolic charge. On the other hand, and muscles contain also fast-twitch units which are not as fatigue-resistant but they have a higher tension and they have a high susceptibility to a pattern of pulses and as an effect — their tension can be effectively changed by an increase or a decrease in the interpulse interval. Therefore, fast motor units are the group of units which is specialized to participate in the regulation of the movement force. The existence of different functional groups of motor units in skeletal muscles enables the performance of different motor tasks very effectively and at possibly low metabolic costs.

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