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The Relationship between the Rate of Rise of Isometric Tension and Motor Unit Recruitment in a Human Forearm Muscle*

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Summary. The recruitment properties of single motor units from the human extensor indicis muscle were investigated during voluntary isometric contractions of different rate of rise but equal amplitude. Both the electrical and the contractile events associated with recruitment were analyzed. The threshold force of recruitment (measured as the total muscle force at firing onset) decreased with increasing rate of rise of isometric tension. This was consistently found for all units. Differences between low and high threshold units indicating a preferential tonic or phasic mode of activation were not observed.

The contractile events associated with recruitment were analyzed analoguously to the electrical events. For this purpose, muscle force was measured at the time of the first twitch as it was measured at the time of the first spike. This separate measurement of the electrical and mechanical recruitment of a unit is necessary, because during a change of muscle force, force is different at firing onset and during the subsequent twitch contraction. Muscle tension at the time of the peak of the first twitch contraction was calculated from measurements of the twitch contraction time of the single motor units.

In contrast to firing onset, the peak of the first twitch of a motor unit occurs at approximately the same muscle tension no matter how fast the contraction is performed.

This is the consequence of the result that the average decrease of the threshold force of recruitment at successively faster contraction has the same value as the corresponding increase of total muscle force during the mean contraction time of the motor units. On the basis of this precise matching between these two changes, the mechanical recruitment of motor units occurs at approximately the same force level irrespective of the rate of rise of tension.

Key words: Human motor units – Recruitment threshold – Rate of rise of isometric tension.

INTRODUCTION

The recruitment properties of human motor units during voluntary isometric contractions are closely correlated to their size. This correlation has been established, if either the conduction velocity of the corresponding nerve fibre [3,4], or the contractile properties of the motor unit [7] were used as an estimator of unit size. In these studies it had already been noticed that the threshold force of recruitment varies strongly with the rate of rise of tension (RRT).

The present experiments were performed in order to examine these changes of motor unit recruitment systematically. Particular attention was drawn to two questions.

The first refers to the question whether the changes of recruitment during variation of RRT are similar for all units or whether small and large motor units are preferentially activated by slow and fast contractions.

The second concerns the mechanical aspects of recruitment. It seems reasonable to assume that the changes of firing onset are arranged to match the mechanical properties of the muscle and to achieve a precise timing of the tension development in the individual motor units. The analysis of the tension development of the single units and their relation to the mechanical output of other units indicated by the

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The experiments reported in this paper are adherent with the principles embodied in the declarations of Helsinki. Informed consense was obtained from each subject and they were aware that they could withdraw from the experiment at any time. Pain was minimal equivalent to that experienced during routine clinical electromyography.

whole muscle tension leads us therefore to expect a better understanding of the neuronal mechanisms underlying the regulation of RRT.

METHODS

Single motor units were recorded from the extensor indicis muscle of the right forearm of twelve healthy male subjects. The electrical activity of the motor units was recorded using a multi-electrode (produced by Gösta Lovén, Uppsala) which contains an array of 14 platinum leading-off surfaces with a diameter of 25 μ on the side of a stainless steel cannula. The diameter of the needle was 0.6 mm. The distance between the leading-off surface was 200 μ. For further details see [2]. The shaft of the needle served as reference electrode and a surface pad electrode as earth connection. For the examination of rapid contractions the multi-electrode has two advantages as compared with tungsten microelectrodes: 1. the pickup area is broader, so that the risk of loosing a unit during fast and strong contractions is smaller; 2. two, or sometimes 3, different units can be recorded simultaneously through different channels. If the lead-off area is close enough to the muscle fibre, single fibre potentials can be recorded up to high force levels. Electrical activity was amplified by a Tönnies differential amplifier and displayed on an oscilloscope. Visual and auditory feedback of the signals was provided. Further details about the measurement of the recruitment of single motor units have been described elsewhere [3]. The forearm and the hand were rigidly fixed to a flat support which left a 3 cm wide slit for the index finger. A rigid band was attached to the proximal phalanx of the index and this band was fixed to a strain gauge mounted rigidly 11 cm below the hand.

For tension recording resistance strain gauge transducers supplied by a d.-c. power supply were used. The output was connected to an oscilloscope placed in front of the subject and to an a.-c. coupled amplifier (time constant 0.3 s) which supplied the force record to an averager (Nicolet Model 1072, Instrument Computer). For the measurement of the contractile properties of single motor units according to the method described by Milner-Brown et al. [6], 256 force records were sampled. Each force record was triggered by the single unit action potential, which was connected to the address advance and for control, to a second signal input. Electrical stimulation was performed using 0.1 ms shocks either applied through the recording electrode or by a surface electrode.

In order to obtain standardized rates of rise of isometric tension the subjects were asked to track triangular wave forms of equal amplitude but different cycle time. The triangles were generated by a function generator and displayed on an oscilloscope in front of the subject. The traces of the pulse generator and the force display were superimposed so that the base of the triangles corresponded to zero force and their maximum to the amplitude of the required force level. The force range investigated was below 60% of maximal voluntary contraction. Usually, the data from five contractions of similar amplitude (see Fig. 1) were averaged.

RESULTS

The Influence of the Rate of Rise of Isometric Tension on Firing Onset. In a preceding paper [3] a close correlation between the threshold force of recruitment (TFR) of motor units and the conduction velocities of the corresponding nerve fibres has been described. The rate of rise of isometric tension (RRT) used in those experiments was 50 g/s representing a slow contraction. During this condition, the small, slowly conducting units were earlier recruited than larger, faster conducting units. This earlier recruitment of smaller units could, however, be due to that particular experimental condition.

According to the hypothesis of a grouping of alpha motoneurones into two types, small units are more adequately recruited by tonic contractions whereas larger units become preferentially activated by brisk contractions. In recent investigations of the changes in the recruitment of human motor units associated with different rates of rise of voluntary isometric contractions, Tanji and Kato [9] found no evidence for such a preferential mode of activation. The fastest RRT examined did not, however, exceed 250 g/s, which is still a relatively slow contraction. The investigation of a larger range of RRT including fast contractions (Büdingen et al. [1]) came to the same result. In the experiments reported here, the RRT was systematically varied, covering a range from very slow (50 g/s) to brisk (2000 g/s) voluntary, isometric contractions.

The threshold force of recruitment (TFR) was determined as the total force at which a particular unit started firing. A typical experiment on a motor unit from the extensor indicis is illustrated in Figure 1. During increasingly faster isometric contractions of approximately constant strength, the motor unit starts firing at successively lower force levels. The examination of 7 different units recorded from the same muscle of 3 subjects shows that this decrease of TFR with increasing RRT has similar slopes for all 7 units (Fig. 2). This monotonic decrease of the TFR during increasing RRT was constantly found for all units tested.

The slopes of low and high threshold units did not show consistent differences. There were, however, small random variations in TFR at repetitive measurements [3]. Therefore, sometimes the curves of units with small differences in TFR may cross each other. Except for these changes by small fluctuations of the TFR, which were also observed by Tanji and Kato [9], the orderly recruitment of motor units remains unchanged for the whole range of RRT tested.

The TFR does not change at RRT below 50 g/s. This is in agreement with observations on motor units from the abductor digiti minimi [9]. The TFR at RRT less than or equal to 50 g/s has therefore the same value as the tonic threshold of the motor units. The tonic threshold is the lowest steady force level where a particular unit remains continuously active no matter what RRT was used to activate it [3]. This implies that a unit which is recruited during contractions slower than 50 g/s remains tonically active, if the force is fixed to a constant level immediately after firing onset. This is illustrated in Figure 3A for a higher threshold unit recorded from the extensor indicis. In

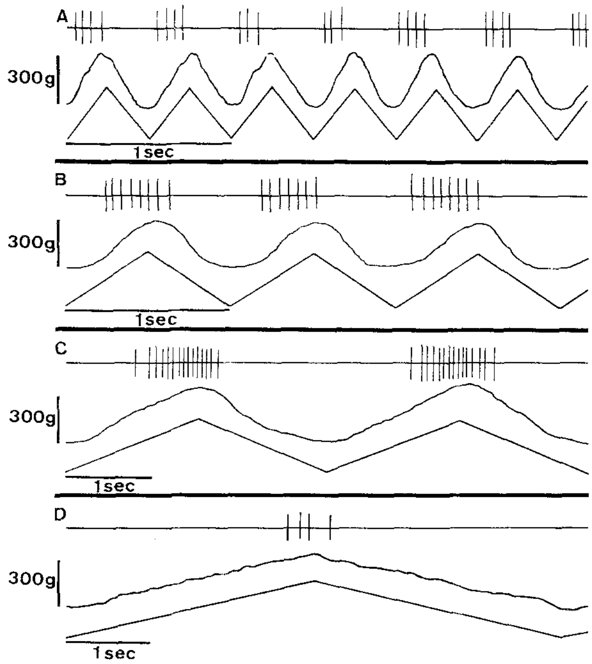


Fig. 1 A–D. Firing pattern of a high threshold unit recorded from the extensor indicis during isometric contractions of different rate of rise of tension (A–D). Each registration shows from top to bottom the spike record, the isometric force and the tracking signal which was visually displayed to the subject. Time scale in the lower 2 records is half that of the upper 2 records. During increasingly faster contractions the unit starts firing at successively lower force levels

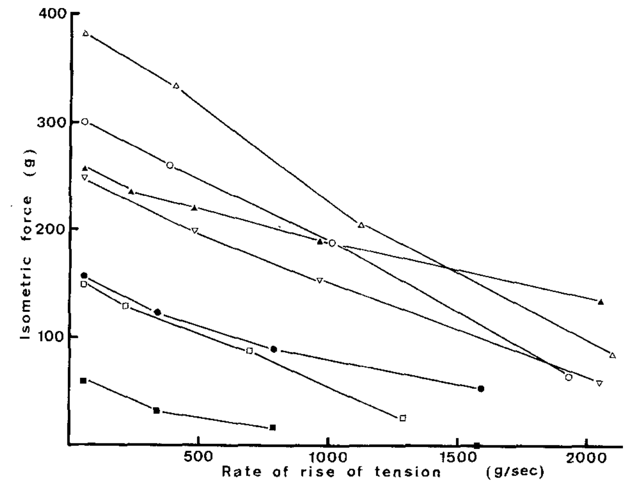


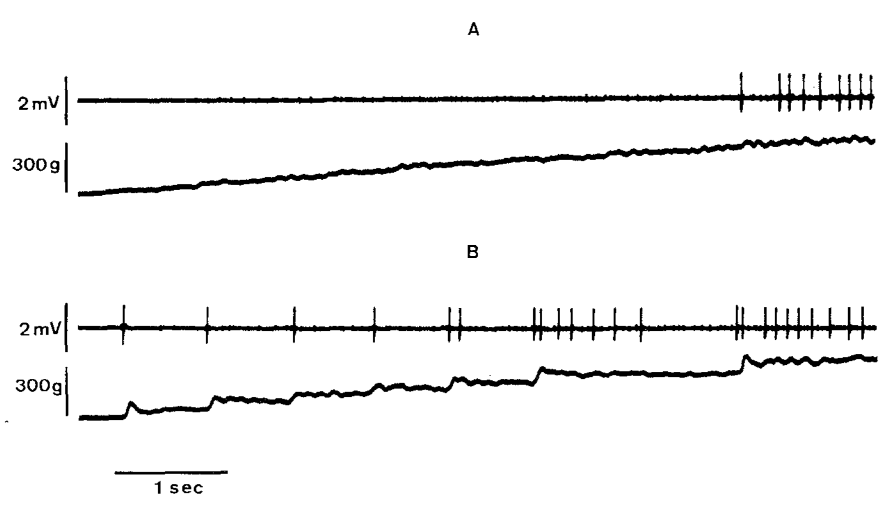
Fig. 2. Change of the threshold force of recruitment (TFR) (ordinate) associated with the variation of the rate of rise of isometric tension (RRT). Recordings from seven motor units of the extensor indicis of three subjects. ■, ▲, ● = units from H.J.B., △, □ = units from K.H.,▽ , ○ = units from R.S.

this experiment, the subject was asked to increase the force slowly until the unit started firing, but then to keep that force level constant as soon as possible after firing onset. The unit discharges continuously as long as the force level is maintained.

If the contractions rise faster than 50 g/s, the units become activated at lower force levels. If then the force is again kept constant as soon as possible, the unit stops firing during the subsequent plateau. This is shown in Figure 3B for the same unit. During stepwise increasing contractions, the unit discharges only during the steps and stops firing during the subsequent plateaus until the force is further increased above tonic threshold. In this way, all units (except those with the lowest threshold) could be transiently and continuously activated.

As a consequence of the decrease of TFR with increasing RRT the time between the recruitment of the low and high threshold units diminishes considerably. This can be seen in Figure 4 where the time between the beginning of the muscle contraction and firing onset is plotted for 3 units on a double logarithmic scale. At high RRT, the time between the activation of units with different threshold becomes very

Fig. 3 A and B
Activity of a high threshold unit of the extensor indicis during continuously (A) and stepwise (B) increasing isometric contractions



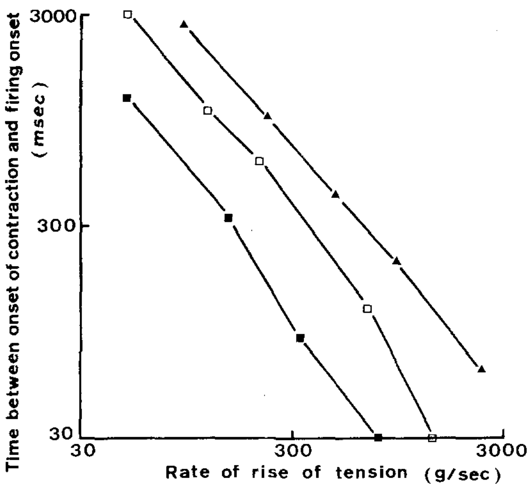


Fig. 4. Dependence of the time between the begin of muscle contraction and firing onset of 3 motor units on the rate of rise of tension. Double logarithmic scale. The faster the contraction, the earlier the recruitment. The units are shown with the same symbols as in Figure 2

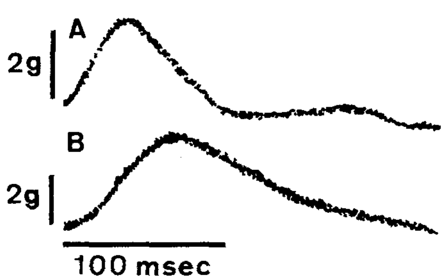


Fig. 5 A and B. Comparison of the contraction curves of a single motor unit from the extensor indicis measured during steady isometric contraction (A, see methods) and after intramuscular stimulation (B) through the recording electrode

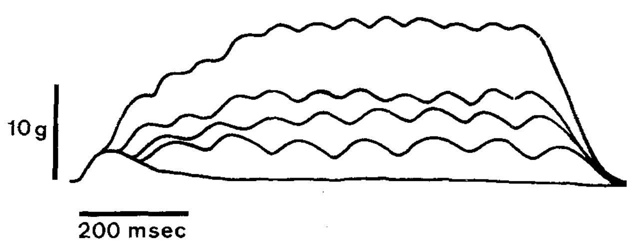


Fig. 6. Contraction curves of a single motor unit from the extensor indicis (same unit as shown in Figure 5) after intramuscular stimulation through the recording electrode. Stimulus frequency (Hz) from bottom to top: 1.0; 8.7; 10.0; 12.5; 15.2

short. Because the lines in Figure 4 are parallel, it is clear that during rapid contractions the higher threshold units start firing earlier although they are not preferentially activated.

The Contractile Properties of Single Motor Units. The timing in the successive recruitment of the motor units of a motoneuron pool is one mechanism for the regulation of the speed of contraction. The other is firing rate modulation. In order to understand the role of recruitment it is necessary to consider its mechanical aspects. For this purpose the contractile events were analyzed analogous to the electrical events. That is, muscle force is measured at the time of the first twitch as it is measured at the time of the first spike. This separate measurement of the electrical and mechanical recruitment of a unit is necessary, because during a change of muscle force, force is different at firing onset and at the subsequent twitch contraction. Since the first twitch contraction is not as short as the first spike, it is, however, necessary to select a distinct part for the correlation to total force. Although the tension development of a single unit starts a few milliseconds after the spike, the peak of the first twitch contraction is the most adequate estimator of the contractile recruitment step. It indicates the time at which the maximal contractile effect of the first spike is added to the force output of the muscle. The relation of this event to total muscle force therefore represents the mechanical counterpart of the electrical threshold force of recruitment.

The twitch contractions of single motor units of human muscles cannot be measured directly during transient contractions. They can either be assessed during steady isometric contractions according to the method described by Milner-Brown et al. [6], or by intramuscular electrical stimulation. We have determined contraction times in both ways. The contractile properties during steady voluntary contractions were recorded from 25 units of the extensor indicis. The firing rates were kept as low as possible while maintaining a continuous discharge. Figure 5A shows such a contraction curve. In the same unit the contraction elicited by stimulation through the recording electrode is shown in Figure 5B. After stimulation the voluntarily activated spike potential was unchanged, indicating that the electrode had not moved. This unit was the only one which could be used for this comparison, since all detectable surrounding units innervated the third finger, so that one unit could be stimulated in isolation. The twitch tension is only slightly different for the two records. The most striking difference was that between the contraction times, which were 19 ms longer in B (64 ms) than in A (45 ms). This difference can be explained by another experiment. The unit was stimulated at various rates as indicated in Figure 6. The partial fusion between subsequent twitches can already be seen at 8.7/s, the contraction time at this rate being 15 ms shorter than at 1/s. The contraction time difference for 1/s and 10/s stimulus rates was 20 ms. The contraction time as well as the relaxation time therefore become shorter with increasing firing or stimulus rates. In addition the twitch tension decreases with increasing rate.

These results explain the differences between the contractile properties measured during voluntary contractions and after stimulation. The unit shown in Figures 5 and 6 could not be continuously activated at rates below 11/s. The mean firing rate of 16 units of the extensor indicis, measured just above the firing threshold during steady isometric contractions of 30 s duration was 11.7 ± 2.0 impulses/s. The lowest firing rates are significantly higher than those reported for the first dorsal interosseus muscle [3, 8]. Slightly lower rates can only be obtained if irregular discharge pattern with lapsing of impulses is accepted. Lapsing causes a change of the next twitch contraction, which in turn alters the average curve.

The contraction time of the unit shown in Figure 5 was similar to the contraction time of the whole muscle elicited by stimulation with a surface electrode fixed to the skin above the endplate zone of the muscle.

For these reasons the contraction times determined by electrical stimulation were considered to be more precise than those measured during voluntary contractions. Since the isolated stimulation of one unit is not possible except in conditions similar to those for the unit shown in Figures 5 and 6, the muscle contraction time after surface stimulation was taken as the best estimator of the mean unitary contraction time.

The Mechanical Recruitment of Motor Units. On the basis of the measurements of the contraction times the change of total muscle force which occurs within that time during a rising contraction can be calculated. Our experiments were confined to conditions in which the RRT remains constant during the contraction time. The results are shown in Figure 7. The change of muscle force during the contraction time is plotted as a function of RRT ($y2$) for the mean contraction time of the extensor indicis (60 ms). In addition the average decrease of the TFR of 12 units of this muscle at increasing RRT is plotted ($y1$). The slope of units with different TFR is similar and can be represented by the regression line (see Fig. 2). As indicated by calculated regression coefficients, the slopes of the two curves are almost equal but of opposite direction. As a result, the sum of the two variables is approximately constant over the range of RRT examined in the course of these experiments.

The decrease of TFR with increasing RRT seems therefore to match the increase of muscle force during the contraction time, so that the mechanical recruitment of a motor unit occurs at approximately the same force level irrespective of the rate of rise of tension.

It is, however, impossible to decide on the basis of our experiments, whether this is really a constant level or whether it is a narrow force range. This uncertainty is due to experimental limitations. The main limitation is the variance of TFR for repetitive measurements. During faster contractions, already small variations of the time of firing onset lead to considerable variations of TFR. Furthermore, the force rises with small irregularities. Because of these inaccuracies, and those involved with measuring twitch contraction times during repetitive firing, no attempt has been made in the present study to match slightly different TFR/RRT slopes of different units (Fig. 2) with their individual contraction times.

The contraction times of the units of the extensor indicis measured during steady isometric contraction are short as a consequence of the high firing rates. The range of the contraction times can however be estimated in this situation. The mean contraction time was 46.4 ± 4.2 ms and the range 39–52 ms. Deviations of the single unit contraction times from the mean contraction time will therefore not exceed 5 ms. The inaccuracy in the calculation of the change of muscle force with RRT during the contraction time introduced by this variance is below 10 g for the whole range of RRT examined (50–2000 g/s).

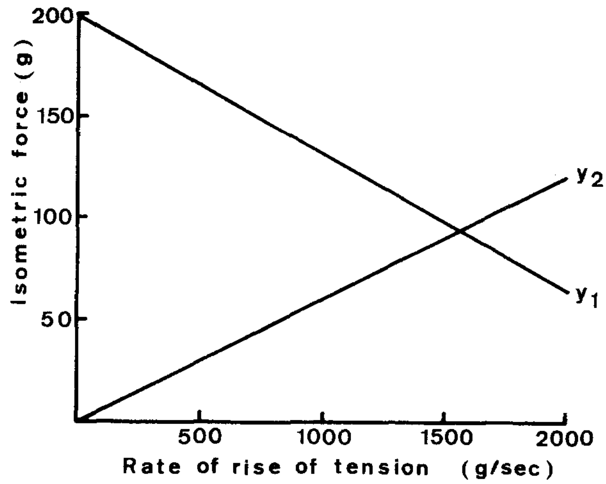


Fig. 7. Regression line of the change of the threshold force of recruitment on the rate of rise of isometric tension ($y_1 = -0.0678\,x + 198.66$) calculated from 12 motor units of the extensor indicis. The increase of muscle force that occurs within the mean contraction time of the muscle is shown for comparison ($y_2 = 0.060\,x$). Further explanation see text

DISCUSSION

In a previous study [4] the firing thresholds of single motor units have been examined during slowly increasing isometric contractions. In this experimental condition, the TFR was closely correlated to the conduction velocity of the corresponding nerve fibre.

The findings reported in this paper extend the former results. They show that the orderly recruitment according to size is preserved if the RRT is systematically varied from very slow to brisk, phasic voluntary contractions. Under these conditions all units show consistent changes of recruitment properties irrespective of unit size. A preferential tonic or phasic mode of activation of small and large units could not be observed, although the muscle recorded has been shown to consist histochemically of about equal numbers of type I and II muscle fibres [5].

The temporal compression of the recruitment domain of the motor units of a muscle at fast contractions leads to an early activation of all units. As shown in Figure 4, the delay between the firing onset of low and high threshold units decreases from 2500 ms during the slowest contractions to less than 100 ms during the fastest contractions tested. This shows that the demands of the movement can also be met if the recruitment of motor units according to size is preserved during brisk contractions. Although the fastest possible contractions were not examined in our experiments, the temporal compression of the recruitment domain during the steepest RRT could be as low as 10 ms.

There are 2 mechanisms underlying the neural regulation of the speed of muscle contraction: the timing in the successive recruitment of motor units and firing rate modulation. This study is solely concerned with the first mechanism. As will be discussed elsewhere the influence of firing rate modulation on RRT is more complex, because it determines not only the rise but also the amplitude of the contraction.

In order to understand how the motoneurone pool organizes the timing in the recruitment of its units to achieve a certain rate of rise of muscle force, it is necessary to consider the mechanical aspects of recruitment. The simplest case is a single discharge and the subsequent twitch contraction. These events are separated by the contraction time. Muscle force will therefore be different at the two events. The size of this difference is a function of the speed of muscle contraction. As a consequence, the mechanical effect of the recruitment of a motor unit would occur at successively higher force levels during increasingly faster contractions if the threshold force of recruitment were constant. In this case more force would have to be generated by firing rate modulation of the earlier recruited units.

Our results show that the timing of firing onset of a unit is so organized that the peak of the first twitch contraction occurs at approximately the same force level irrespective of how fast the contraction is. Since the order of recruitment does not change with RRT this can only be the case if the proportion between the force generated by recruitment and by firing rate modulation of the units activated prior to a particular unit remains unchanged. This demonstrates how precise the tuning is between the recruitment of units and the activity of those already recruited.

In most cases a recruited unit fires more than one spike. The first twitch contraction is therefore fused with subsequent twitches. As shown in Figure 6 the amount of fusion depends on the firing rate. The contractile recruitment step will only be a distinct and distinguishable component of the contraction curve of the unit if the first interspike interval is longer than the contraction time. This is the case for the range of RRT tested in the course of these experiments.

The range of RRT examined does not cover the full range possible. The slowest RRT was chosen at 50 g/s since below that value no measurable change of TFR can be observed. The fastest RRT used was 2000 g/s. The fastest RRT which could be produced by the extensor indicis of 3 male subjects was about 8000 – 10000 g/s. The limitation to only 1/5 of the full range has two reasons:

Firstly, RRT higher than 2000 g/s can only be achieved if the final force is near maximum. This is a consequence of the correlation between maximal RRT and target force (Freund and Büdingen, in preparation). According to this relationship it is impossible to perform contractions of low amplitude with a rise of force as steep as with contractions of high amplitude. The fastest RRT can only be obtained if the target force is near maximum. This would lead to rapid fatigue in the course of the experiment which in turn would influence the results.

Secondly, the performance of strong contractions necessary for the achievement of high RRT is only possible if the onset firing rate exceeds 14/s so that the first contraction is no longer separated from the subsequent contraction. The statement that the contractile recruitment component of a motor unit achieves their maximum at approximately the same force level irrespective of RRT is therefore limited to the range of RRT examined and to linear force increments.

The results demonstrate that the activation of the units in a motoneurone pool is organized to achieve a distinct mechanical result. This result is the stable relation between the force output of the individual motor unit at the time of its mechanical recruitment and the force output of the whole muscle. All the changes of recruitment and firing rate associated with the variation of RRT leave the relationship of the contractile recruitment step of any motor unit almost unchanged with respect to the tension output of all other units of that muscle. This relationship is determined by the excitability of the motor unit within the motoneurone pool.

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