原　著

連続的な筋収縮によって低下する単一運動単位の力閾値

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Successive Muscle Contractions Decrease Recruitment Force Thresholds in Single Motor Units

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Abstract

Preliminary evidence suggests that successive isometric muscle contractions lower the force thresholds (FTs) in single motor units (SMUs). The purpose of the present study was to examine further this observation. FTs of 30 biceps brachii SMUs were recorded from 6 male subjects using fine wire coiled copper electrodes. Subjects rested their upper arm horizontally on a table with their elbow angle set at 90 degrees into flexion. With the forearm in supination, subjects gripped a handle attached to a force transducer to generate isometric flexion forces. Visual force feedback was provided by an oscilloscope. The initial mean FT for 30 SMUs was 20.8 N (range 1.8−54.5 N). FTs were found to decline from <10% to 100% over the course of 5 additional successive contractions or more. The initial mean FT was significantly higher ($p<0.05$) than the mean FT values observed during the final 3 contractions of 5 successive contractions. SMUs exhibiting lower initial FTs generally showed larger percent decreases in FT over successive contractions. Intermittent muscle stretch (90 degrees of extension) reset the SMU FT toward the initial value. This suggests that the source of greater excitatory current in lowering SMU FTs during successive contractions may reside in contraction-induced potentiation of stretch reflex pathways.

Key words： motoneuron, motor units, muscle spindle, stretch reflex, potentiation, human

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Introduction

The muscle force at the time of excitation of a single motor unit (SMU) is called the recruitment force threshold (FT). The FTs in SMUs are known to decrease as the rate of rise in force produce of isometric contraction (contraction speed) increases[3-5]. Preliminary evidence suggests that successive muscle contractions also lower the FT in SMUs[17]. The causal mechanism for this latter acute adaptation has been linked with known contraction-induced potentiation of the stretch reflex[1,6,8-11,14,16]. Previous studies have shown that brief contractions of moderate to maximum intensities produce an enhancement in muscle spindle afferent discharge[1,9-10,14,16], motor neuronal tonic discharge[11,18], electromyographic activity (EMG) and tendon tap reflexes[6,19]. These adaptations have been attributed largely to post-contraction alterations in intrafusal muscle fiber stiffness associated with persistence in binding of actin-myosin contractile proteins[1-2,8-9,14]. Stretch of the muscle beyond the initial length at the time of contraction tends to reset the potentiated stretch reflex pathways to precontraction reflex levels[1,10,14,16]. The purpose of this study was to examine further the effects of successive voluntary muscle contractions on SMU FTs and subsequent muscle stretch in resetting these FTs.

Methods

FTs of 30 biceps brachii SMUs were recorded from 6 male subjects using polyurethane insulated fine wire coiled copper electrodes, 50 micra in diameter[12]. The electrodes were inserted with a 26 gauge hyperdermic needle, 2 mm lateral to midline of the biceps brachii, midway between the proximal and distal attachments. The procedure has been described in detail in a previous article[17]. Briefly, subjects rested their upper arm horizontally on a table with their elbow angle at 90 degrees in flexion. With the forearm in supination, they gripped a handle attached to a force transducer to generate isometric flexion forces. The subject was asked to follow a visual trajectory of a ramp trace with feedback of the voluntary force produce provided by an oscilloscope. An electrogoniometer was attached to the lateral side of elbow. The initial elbow angle and the angle of attachment of the wrist-hand to the force transducer were set at 90 degrees of elbow flexion. An oscilloscope with force feedback and a polygraph recording of SMU activity, muscle flexion force, and elbow angle were used to determine the time of recruitment. Procedures varied among subjects but the major focus was to determine the effects of successive contractions and stretch on recruitment FTs.

Results & Discussion

The effects of contraction speed on recruitment force thresholds (FTs) of 3 biceps brachii single motor units (SMUs) are shown in Figure 1A and B. In Figure 1A, the speeds for two successive contractions were 9.4 N/s and 8.0 N/s, respectively. The SMU FTs were 32 N (large amplitude unit), 25 N (intermediate amplitude unit), and 18 N (small amplitude unit). In Figure 1B, the contraction speeds were 21 N/s to peak throughout. The SMU FTs were now 21 N, 7 N, and 7 N, respectively. These observations are in accord with previous findings reported by Desmedt and Godaux[4-5]. Each series of contractions was preceded by muscle stretch induced by elbow extension of 90 degrees as noted in the lower trace of Figure 1A and B. Interaction effects of speed of muscle contraction and successive contractions on lowering SMU FTs are shown in Figure 2. In

Figure 2A, the FT of the larger unit was 38 N and 34 N for the first and second contractions, respectively. The smaller unit's FT was initially 18 N but a single contraction caused this unit to discharge tonically even after muscle force was returned to baseline. The speeds for two successive contractions were both 11 N/s. In Figure 2B, SMU FTs for ten faster successive contractions (mean=1 contraction/1.2 s) are shown. The initial contractile speed was 41 N/s. The FT of the smaller unit was 2 N and that of the larger unit was 33 N for the first contraction. The FTs shifted forward in time for both units with successive contractions. As observed before (Fig.2A), the smaller unit fired tonically after the initial contraction. The FT of the larger unit, however, decreased to near baseline force levels by the fourth contraction. SMU FTs, therefore, appear to be influenced by both speed of contraction and the previous activation history of the muscle.

The effects of successive muscle contractions on the FT of a SMU at relatively constant rates of force development but with varying temporal-force patterns of sustained isometric force are shown in Figure 3. In Figure 3A, the FT of this unit was lowered over 5 successive contractions from 24 N to 14 N. In Figure 3 B, the FT of the same unit decreased from 22 N to 3 N over 3 successive contractions. It is noted that, in the second contraction, the unit remained tonically active as the muscle force slowly declined past the initial recruitment FT. Since the pattern of a sustained isometric contraction appears to influence the FT at which a SMU remains activated, the pattern of force

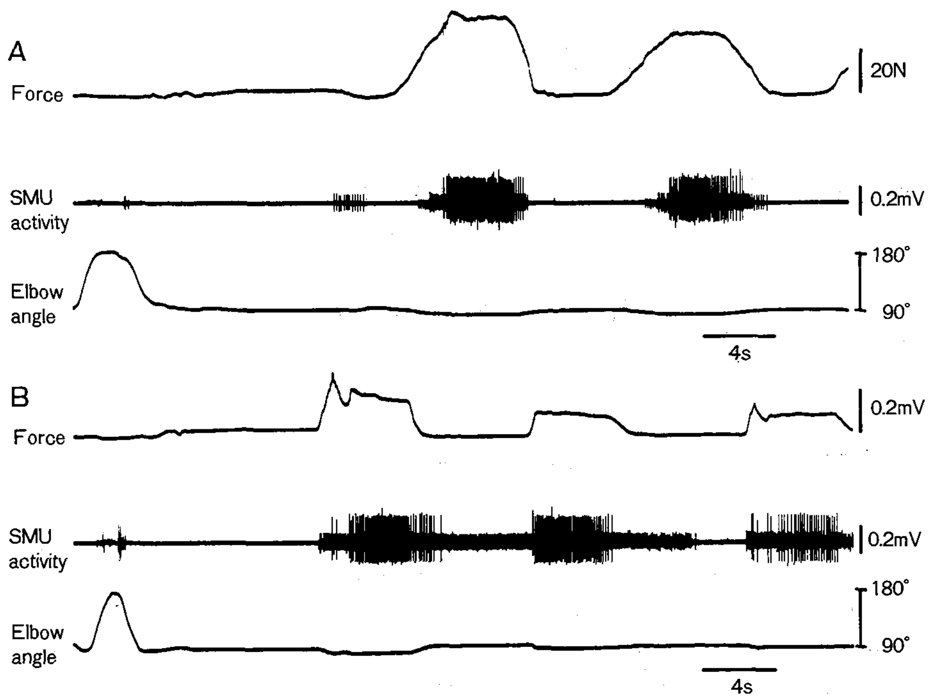

Figure 1. The effects of speed of muscle contraction on recruitment force thresholds (FTs) of 3 Biceps Brachii single motor units (SMUs) are shown. See text for further explanation.

development was also maintained relatively constant in this study.

The temporal latency to SMU recruitment at the respective FT (N) or contraction speed (N/s) is plotted in Figure 4 for 3 SMUs (large, middle, small unit amplitudes) over 8 successive contractions (1–8, upper panel). SMUs with higher FTs were recruited at proportionately longer latencies. SMUs with longer latencies were inversely related to the speed of contraction except for the smaller SMU where no clear relationship was observed.

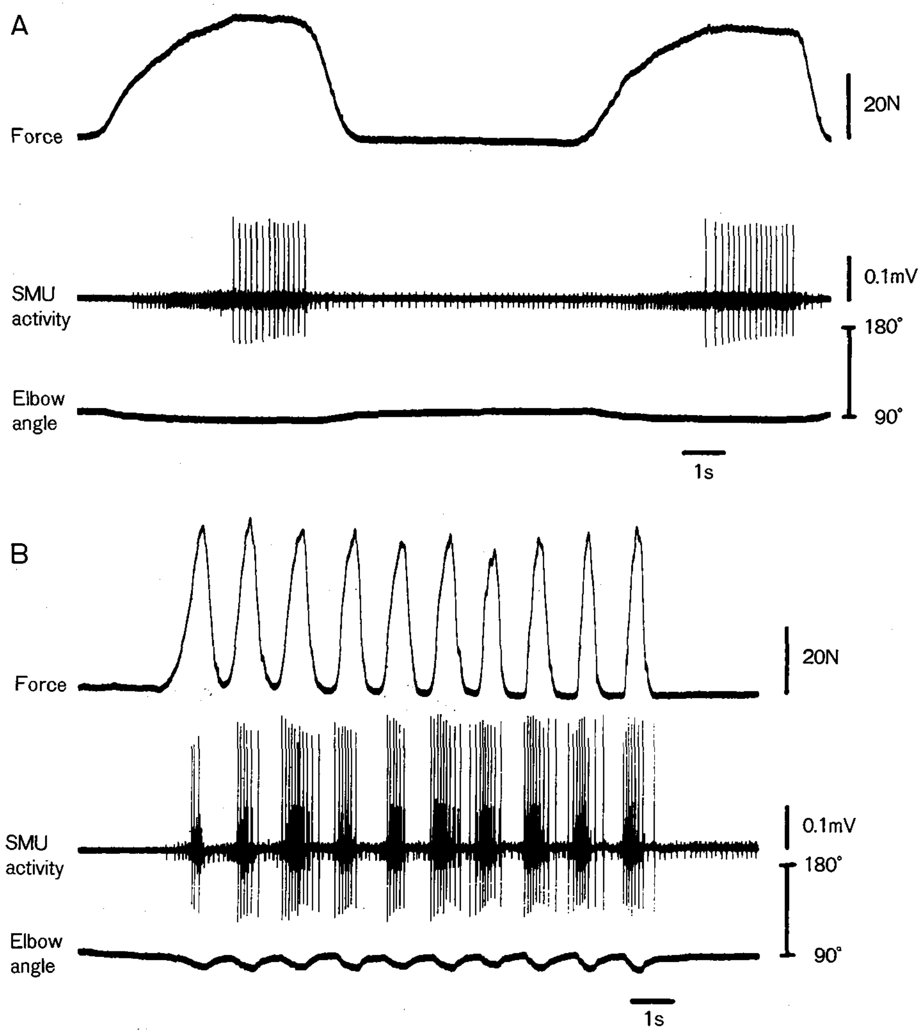

Figure 2. The interaction effects of speed of muscle contraction and successive contractions on lowering SMU FTs are shown. In A, the FT of the larger unit was 38 N and 34 N for the first and second contraction, respectively. A single contraction for the smaller unit (FT = 18 N) caused it to discharge tonically even after the baseline force was resumed. In B, SMU FTs for ten successive contractions (rate mean = 1/1.2 s) was shifted forward in time for both units. As before, the smaller unit fired tonically after the first contraction. The FT of the larger unit decreased to the baseline force by the fourth contraction.

An example of the effects of successive muscle contractions on reduced SMU FTs is shown for 2 SMUs in Figure 5A and 1 SMU in Figure 5B. Muscle stretch at the end of each series reset the respective FTs toward the initial FT levels. In Figure 5C a SMU that did not alter its FT appreciably <10% with successive contractions is shown. This pattern of response was seen in only 2 SMUs out of the total population sampled (n = 30).

A summary of the SMU FTs during 6 successive contractions is shown in Figure 6. Each series of contractions is preceded by muscle stretch induced by elbow extension. The initial mean FT for 30 SMUs was 20.8 N (range 1.8−54.5 N). FTs were found to decline from <10% to 100% over the course of 5 additional successive contractions. The initial mean FT was significantly higher ($p<0.05$) than the mean FT values seen during the final 3 contractions. In Figure 6B the percent decline in FT values for each SMU as a result

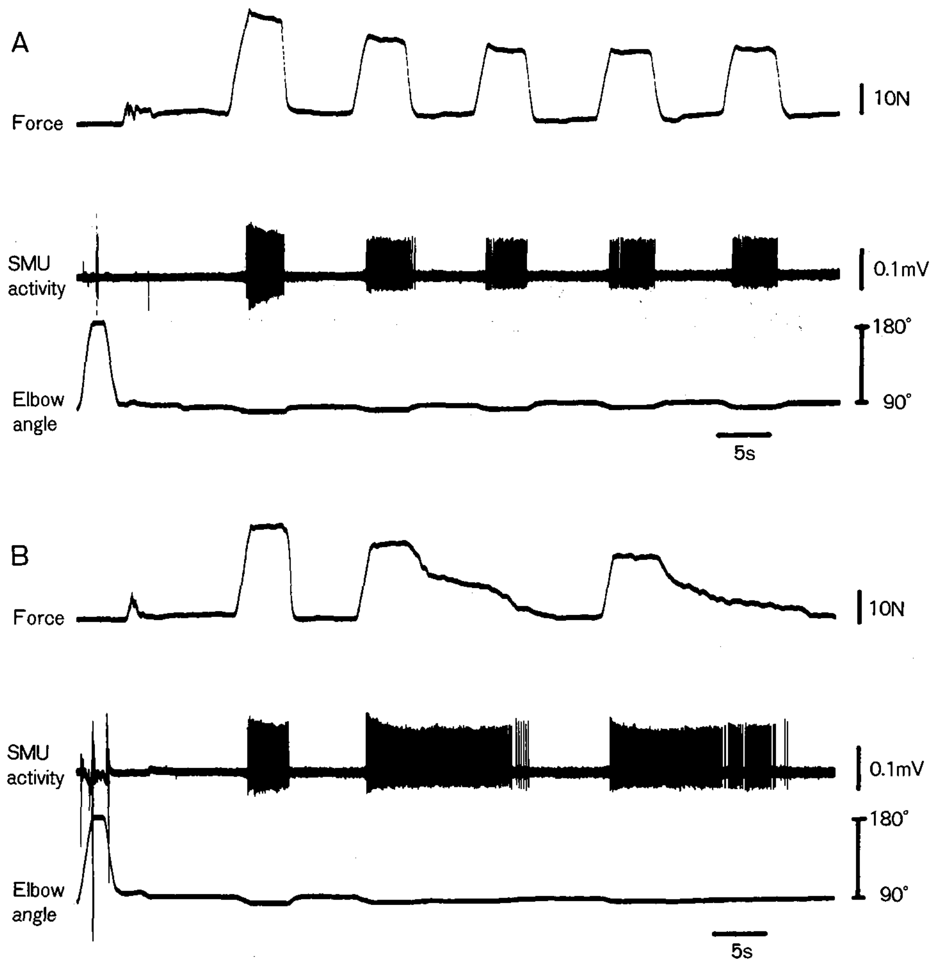

Figure 3. The effect of successive muscle contractions on the FT of a SMU at relatively constant speed but with varying patterns of sustained isometric force is shown. In A, the FT was lowered over 5 successive contractions from 24 N to 14 N. In B, the FT of the same unit decreased from 22 N to 3 N over 3 successive contractions.

of successive contractions is plotted. The percent decrease in FT was greatest in SMUs with smaller action potentials. If the source of potentiation resided in stretch reflex pathways serving the homogenous muscle in which they reside, this would be the predicted outcome and, based on the size principle, this would lower the recruitment force thresholds[7,13].

In view of the present results, it is clear that the acute activation history of skeletal muscle induces a change in the FT of SMUs. This suggests that there is a neuromuscular mechanism that enhances the excitatory current to the alpha motoneuronal pool even under conditions where the contraction speed and the target trajectory force remain relatively constant. Assuming that the voluntary motor command remains unchanged, then the source of this additional excitation likely resides at the spinal segmental level. In light of the existing evidence that stretch reflex pathways can be potentiated in the aftermath of a previous contraction (cf. 8-9, for a review), proposed to be caused by the lingering effects of gamma motor neuronal activation on intrafusal actin-myosin binding[1-2,14], we suggest that the lowering of SMU FTs is caused by potentiation in stretch reflex pathways. This would explain why mus-

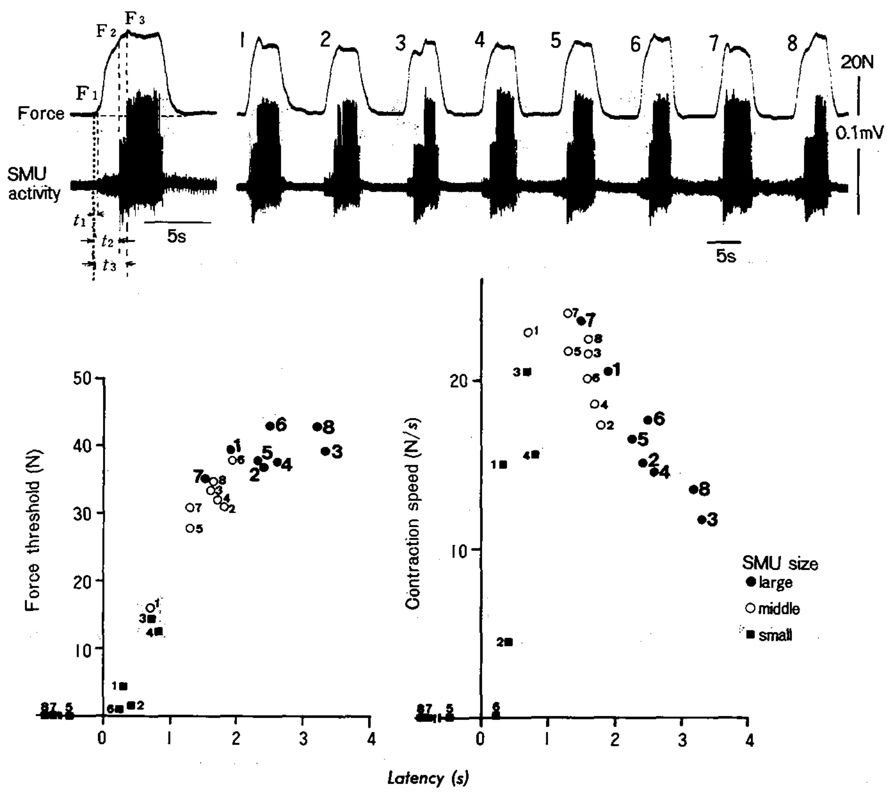

Figure 4. Temporal latencies to SMU recruitment are plotted for 3 SMUs (large, intermediate, and small amplitudes) over 8 successive contractions (upper panel). SMUs with higher FTs were recruited at longer latencies and were inversely related to the speed of contraction (right lower panel). For smaller amplitude and low FT SMUs, no clear relationship was observed. Contraction speeds were measured in Newton per second (N/s).

cle stretch beyond the length at the time of activation attenuates or abolishes the potentiated stretch reflex response (by allowing intrafusal muscle fibers to return to pre-activation passive stiffness levels, involving detachment of persistent actin-myosin bonds) and also resets the SMU FT toward the initial FT as measured during the first contraction[17]. More experimentation will be necessary before the mechanism(s) that alter SMU FTs, due to succcessive contractions, can be elucidated. Nevertheless, it can be concluded that many factors need to be considered, including 'short term activation history,' in determining the FT of SMUs, and that the measurement of a SMU FT is far more complex than previously assumed (cf. 15).

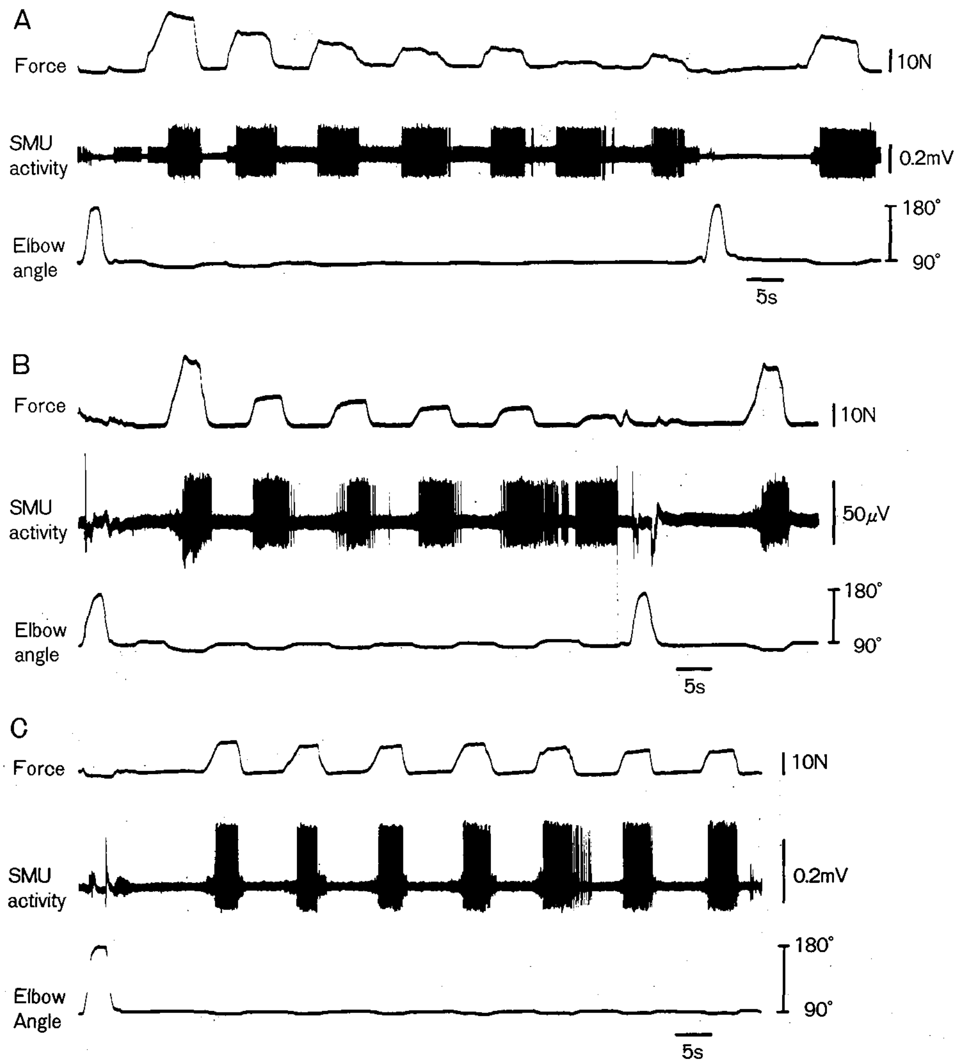

Figure 5. The effects of muscle stretch on resetting the FT of 2 SMUs after successive contractions are shown in A and B. In C, the FT of this SMU was not appreciably altered (<10%) by successive contractions.

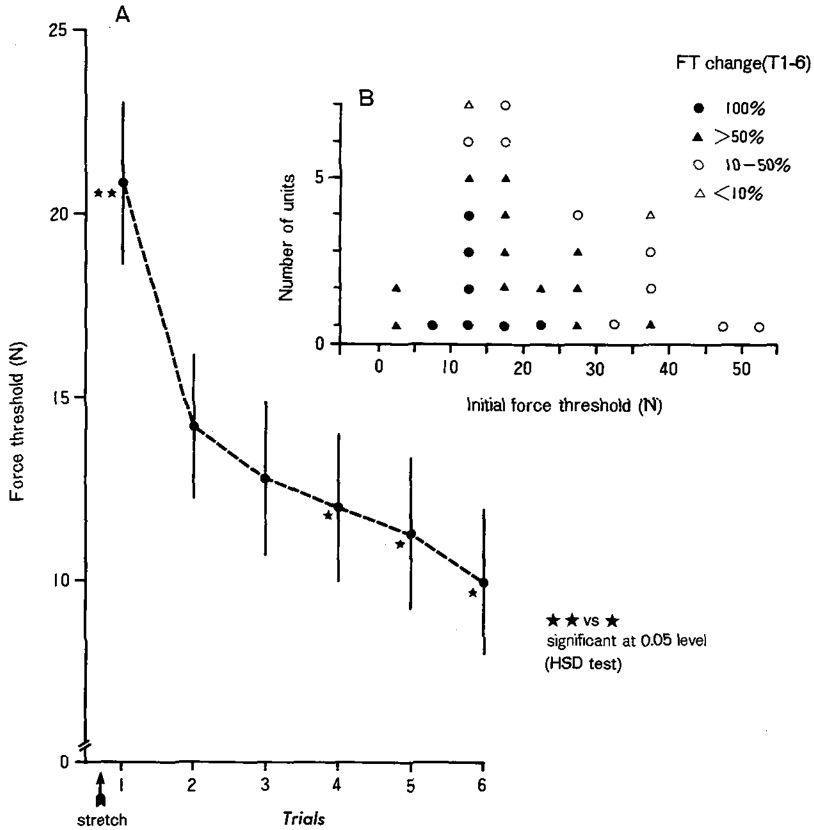

Figure 6. The changes in FTs of a population of 30 SMUs during 6 successive contractions are summarized. See text for details.

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