Changes in Force Threshold of Single Human Motor Units during Sustained Maximal Voluntary Contraction

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Abstract

Changes in firing patterns of single motor units in fatigue were examined. A force threshold (FT) of a single human motor units was measured before and after sustained maximal voluntary contractions (MVC). Action potentials of single motor units in an abductor digiti minimi muscle were recorded simultaneously with abduction forces of the 5th finger at the proximal interphalangeal joint of a healthy male adult. Thirty motor units were studied. The FT of the motor unit was determined during an ascending and descending force ramp. A sustained MVC for 20 seconds was inserted between the ascending and descending ramps. This set of force development was repeated 10 times without any interval and lasted for 5 minutes totally. The force at the end of 10th sustained contraction decreased to about 30 % of the MVC. The FTs in the ascending and descending ramp were constant in the motor units with the threshold of below 10 % MVC, and decreased in those with above 30 % MVC. The relative ascending FT to the maximal forces at each bout of sustained contraction were constant in the motor units with the FT of below 10 % MVC, and decreased in those with higher FT. On the other hand, the descending FT (% relative to the tension at the end of 20-second sustained contraction) increased in the units with lower FT but was constant with higher FT. In this condition, it might be assumed that the force development of the motor units with the FT of below 10 % MVC did not change, but decreased in those with above 30 % MVC.

KEY WORDS : *Motor unit, Recruitment, Force threshold, Maximal voluntary contraction.*

Introduction

Force exerted is gradually declined while sustaining a maximal voluntary contraction (MVC). It is said that the frequency adaptation and rotation of motor units are more obvious in high frequency firing units than in low frequency ones during MVCs (12). Kurata (5) and Nagatsu et al. (9) observed a continuously firing motor unit with low force threshold (FT) lasting for more than 90 minutes and changes in FT of motor units due to long-lasting tension exertions. It is reported that there are three types of motor units in brachial biceps muscle with short, middle and long continuous firing during sustained force exertions (13). Freund (2) described in his review as "Low-

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threshold motor units recruited during weak efforts had low twitch tension and were fatigue resistant. Motor units recruited at high force levels had higher twitch tensions and faster contraction times and were highly fatigable. During graded voluntary muscle contractions, motor units are recruited in order of increasing contraction strength and diminishing fatigue resistance" (11).

Recently, Bigland-Ritchie et al. (1) reported that the motoneuron firing rates did slow down during voluntary contractions. This result may suggest that the tension decrease may be due to neurogenic frequency fatigue, in another word, due to the decreased firing frequency. However, myogenic factor may not be ignored.

As another possible factor for the decrease in the maximal tension, the current study was carried out to investigate the changes in FT before and after fatigue. The tension produced when the recruitment of a motor unit was began or ended, was named as the FT in each motor unit.

For example, if the % FT in each unit relative to the MVC is constant and also the % FT relative to the maximal force produced, when each FT was measured, increased, the cause of the decline in the maximal tension produced is the decrease in the number of motor units recruited, in another word, neurogenic recruitment effect.

On the other hand, if the % FT relative to the MVC is decreased but the % FT relative to the maximal force produced, when the FT was measured, was constant, the cause of the tension decrease is myogenic and neurogenic frequency, in another word, decrease in the tension production by muscle fibers even though the neurogenic recruitment factor is intact.

However, the firing patterns of single human motor unit in fatigue are still unclear. Therefore, the current study was performed to approach this question.

Methods

The experimental subject was a healthy male adult. Thirty motor units in an abductor digiti minimi muscle were studied. The MVC in the abduction forces of the left little finger was achieved at 5th second and sustained for 20 seconds, and relaxed during the following 5 seconds. Such force development was repeated 10 times lasting for 5 minutes totally without any interval (Fig. 1-A).

Action potentials of single motor units were detected by use of coil-shaped inserted electrodes (6). The action potentials were fed to a biophysical amplifier (AB-620G) of a polygraph (RM-6000). Abduction forces of the little finger at proximal interphalangeal joint were detected by a force-displacement transducer (SB-1T). The output was fed to a carrier amplifier (AP-600G) of the polygraph. These outputs of the polygraph were displayed on a dual-beam memory oscilloscope (VC-10). A continuous recorder (RLG-6101) was used for photographic recordings.

Force thresholds of a motor unit was determined during both an ascending and descending force ramp. The FT relative to the MVC and % relative to the tension produced at that time were calculated in both ascending and descending conditions.

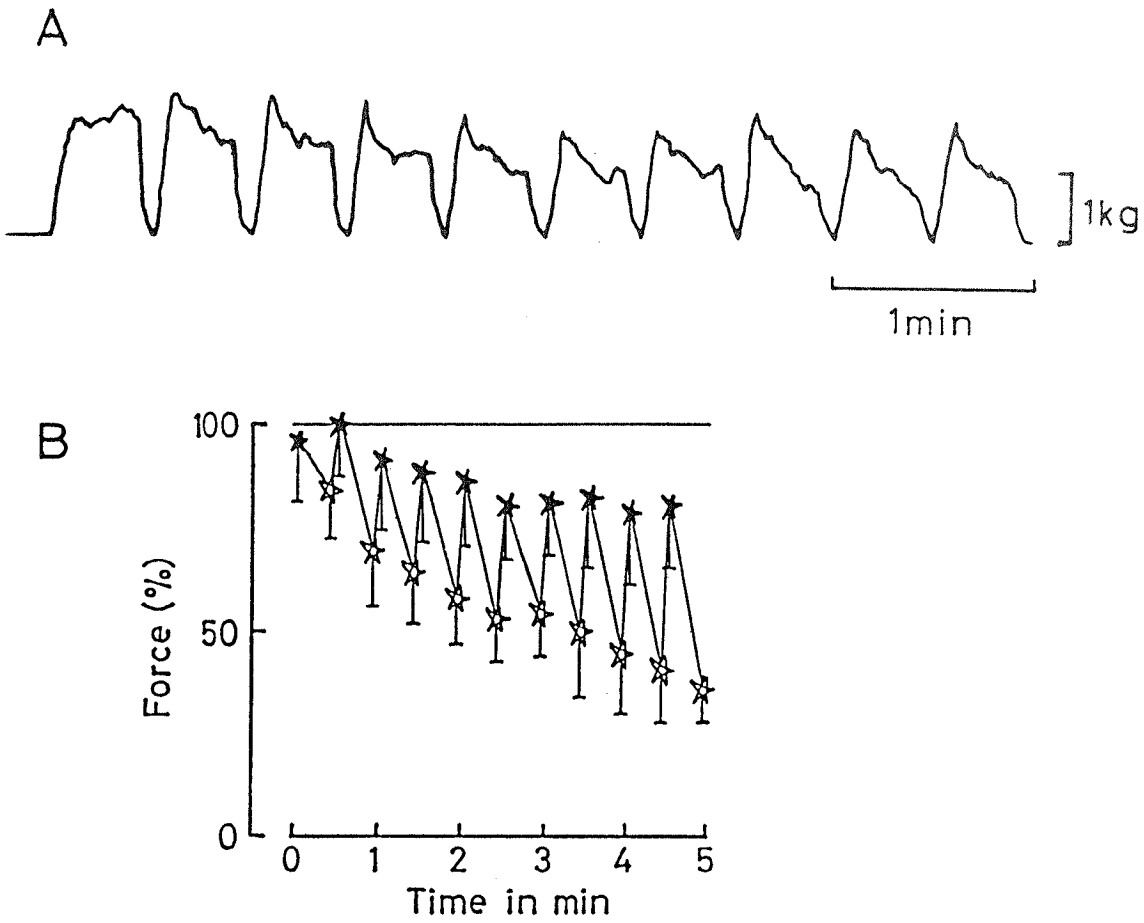

Fig. 1. An example of a force record (A), and mean relative forces (B). The maximal voluntary contraction in the abduction forces of a little finger was performed for 20 seconds after 5-second gradual force increment, and subjects decreased the force gradually during the following 5 seconds. Such force development was repeated 10 times lasting for 5 minutes totally without any interval (A). Such trial was repeated 13 times on different days. Mean values and standard deviations of maximal forces (solid stars) and forces at the end of 20 seconds (open stars) are shown (B).

Firing frequencies of the motor units per second were also calculated.

Twitch tension curves of single motor units were obtained by the spike-triggered force-averaging method (7) using a signal averager (DAT-1100) (Fig. 2-B). Twitch contraction times or time-to-peak tensions and twitch peak tensions were measured.

The tension produced by the direct electrical stimulations of the muscle at 100 Hz, 0.5 ms duration, and 120 V intensity before and after each set of 20-second MVC (Fig. 6-B). An electrical stimulator (SEN-3201) and an isolator (SS-201J) were used for the stimulations. Two silver disks of 10 mm in diameter were placed on the skin above the muscle for the stimulating electrodes. All of the equipments used were

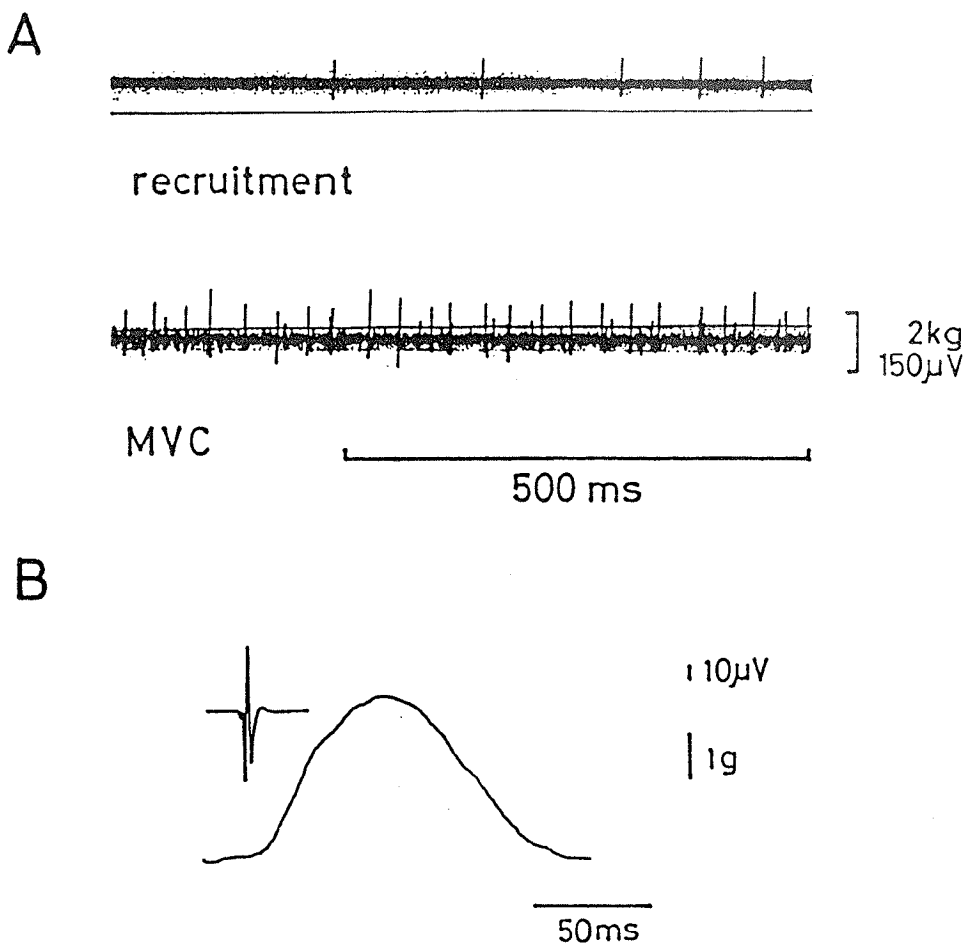

Fig. 2. The records of action potentials in a single motor unit and the abduction force of little finger (A), and the twitch tension curve of this motor unit (B). The upper record was obtained during the recruitment of this motor unit when the force development was increased gradually, and the lower data were recorded during the maximal voluntary contraction (MVC) (A). The twitch tension curve of this motor unit was obtained by spike triggered force averaging method (B).

made by Nihon Kohden Kogyo Company (Tokyo).

Results

Mean values and standard deviations of maximal forces at the beginning and end of 13 sets of 10 MVCs are shown in the figure 1-B. The maximal forces decreased to about 80 % and the forces at the end of 20-second force sustain decreased to about 30 % of the MVC at the 10th final contraction.

Figure 2-A demonstrates the records of action potentials in a single motor unit and the abduction force of little finger. The upper record was obtained during the

recruitment of this motor unit when the force development was increased gradually. The force when the action potential appeared was named the "force threshold (FT)." The lower data were recorded during the MVC. The spikes from each motor unit were well differentiated.

The curve shown in the figure 2-B shows the twitch tension of this motor unit obtained by the spike-triggered force-averaging method. This motor unit has 60-ms of contraction time or time-to-peak tension, 4-g of twitch peak tension and 4% MVC of FT.

The relationship of force produced and FT in the motor unit obtained in the figure 2 was shown in figure 3. These data shown by the circles represent the FT calculated relative to the MVC (A) and % relative to the tension produced at that time (B). The tensions are shown by the stars at the top of the figure. The FT during the force production and reduction are shown by the solid and open circles, respectively. Firing frequencies of this motor unit decreased from 30 Hz at the initial contraction to below 20 Hz at the final contraction.

Figure 4 shows examples of FT obtained during the ascending phase. The unit with lower FT of approximately 10% of the maximum tended to be constant throughout the 5-minute trial. But the units with higher FT of approximately 50% of the maximum initially tended to decrease during the 5 minutes.

During descending phase, these results with either high or low FT initially tended to be unchanged relative to the MVC (Fig. 5). But in the two units, the % FT relative to the maximal force produced, when each FT was measured, increased gradually. In another trials, motor units with the higher % FT initially tended to decrease during the 5 minutes of force production. These decreases were parallel with the decrease in the maximal tension. Therefore, the % FT relative to the maximal tension at each time was unchanged.

The appearance of general trend observed in 30 motor units are shown in table 1. In the units with FT of less than 10% in ascending phase, one case of decrease and seven cases of constant tendency were observed. And nine cases with initial FT of 10-30% and of more than 30% decreased. These tendencies were almost the same between the % FT relative to the MVC and the % FT relative to the maximal force in the ascending phase (Table 1-A and B).

While in the descending phase, no case of decreasing, six cases of constant and two cases of increasing tendencies were observed in the units with FT of less than 10% in the % FT relative to the MVC (Table 1-C). Four cases of decreasing and six cases of constant tendencies with initial FT of 10-30%, and six cases of decreasing, one case of constant and two cases of increasing tendencies with more than 30% were observed.

In the % relative to the maximal force, no case of decreasing tendency was observed in all of the FT. Two cases of constant and six cases of increasing tendencies in the units with FT of less than 10%, five cases of constant and increasing with initial

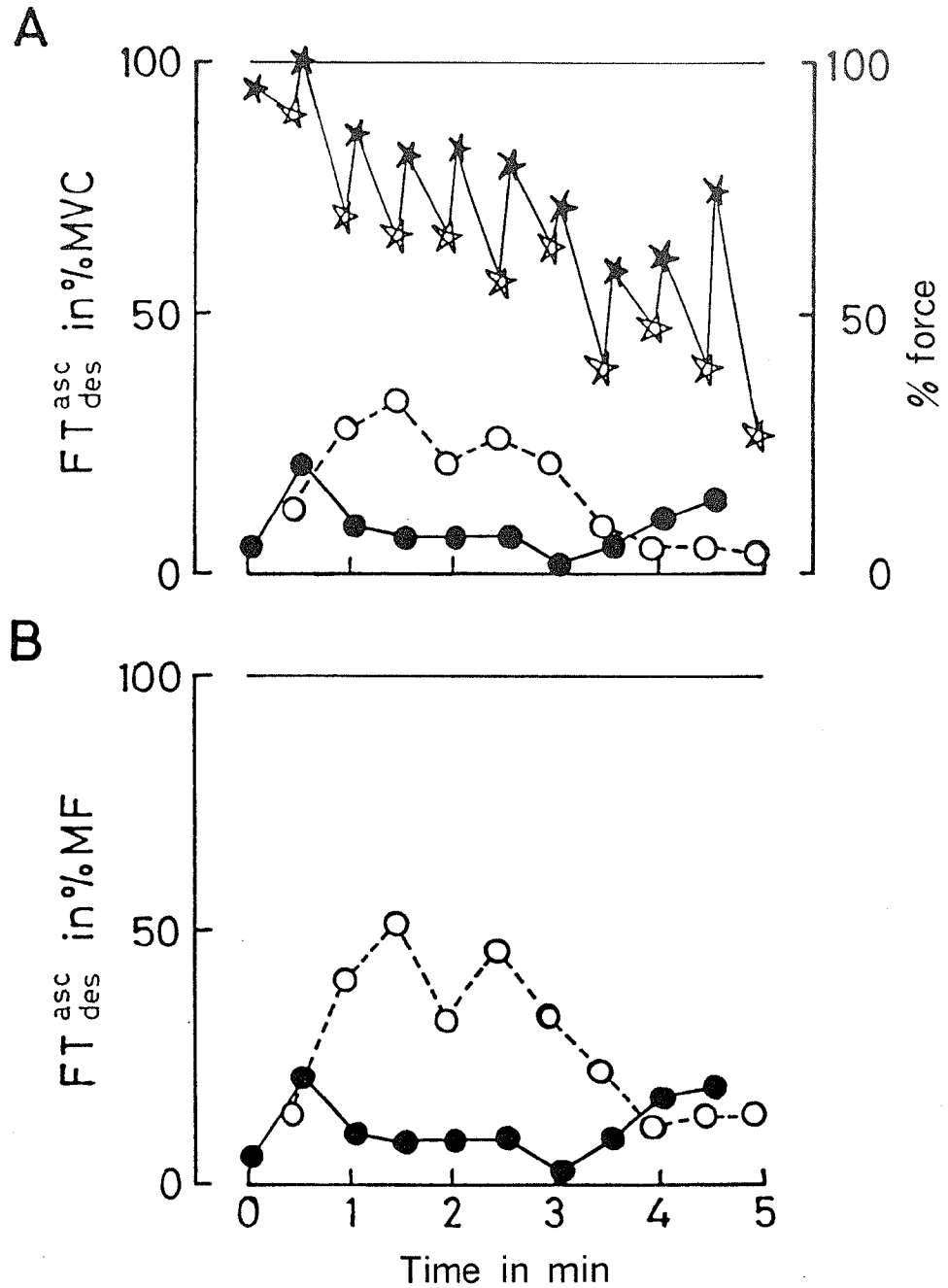

Fig. 3. The relationship of relative force produced and force threshold (FT) in the motor unit obtained in the figure 2. The tensions are shown by the stars at the top of the figure. The data shown by the circles represent the % force threshold calculated relative to the maximal voluntary contraction (MVC) (A). The FTasc in % MF (solid circles) represents the force threshold obtained during the ascending ramp relative to the peak tension gained at the end of the ramp (B). The FTdes in % MF (open circles) is the value obtained during the descending ramp relative to the tension produced immediately before the force decline (B).

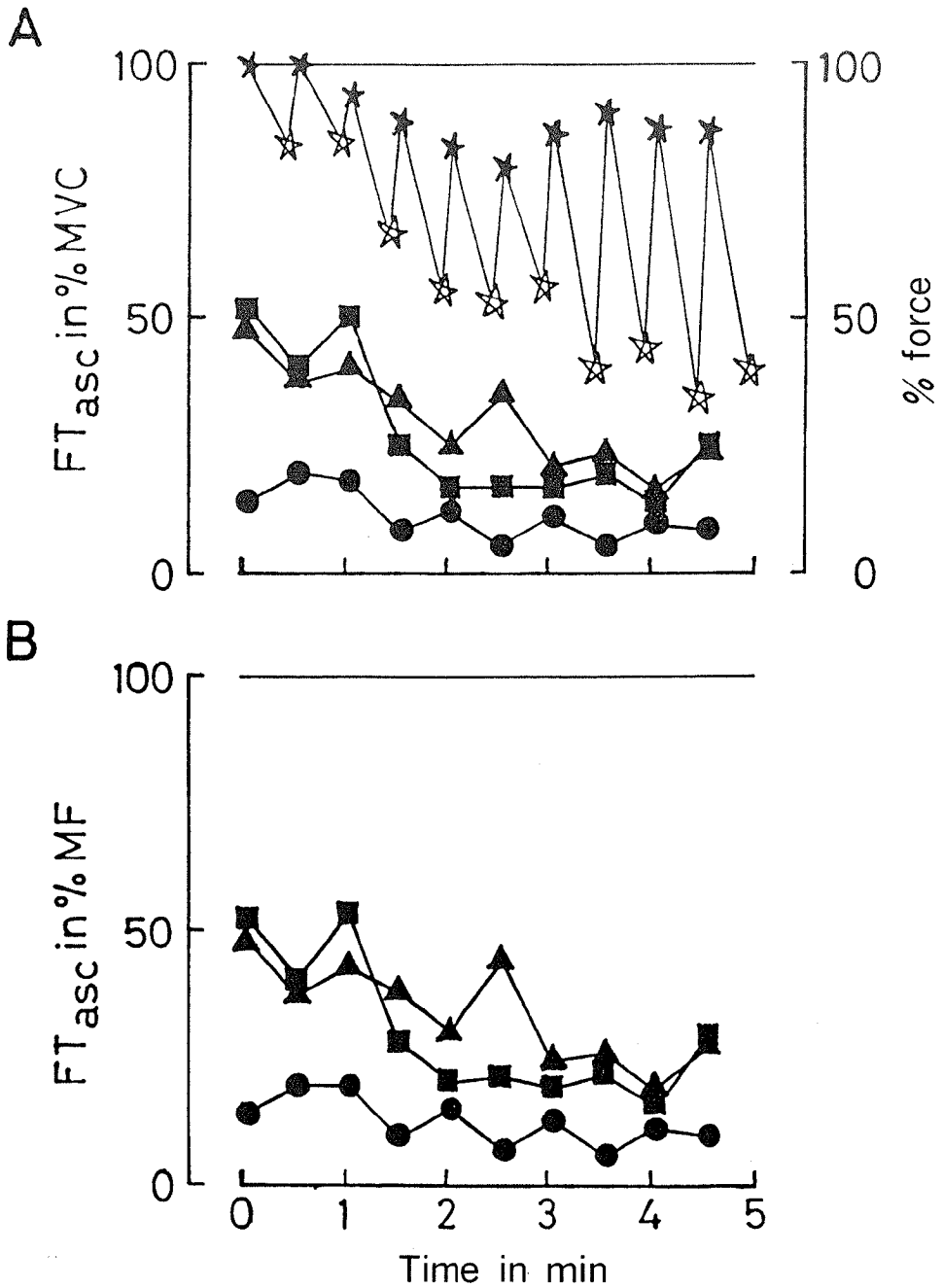

Fig. 4. Examples of % force threshold obtained during the ascending phase (FTasc). The unit with lower force threshold of approximately 10 % of maximum tended to be constant throughout the 5-minute trial. But the units with higher force threshold of approximately 50 % of maximum initially tended to decrease during 5 minutes. See the legend for figure 3 for the meaning of stars.

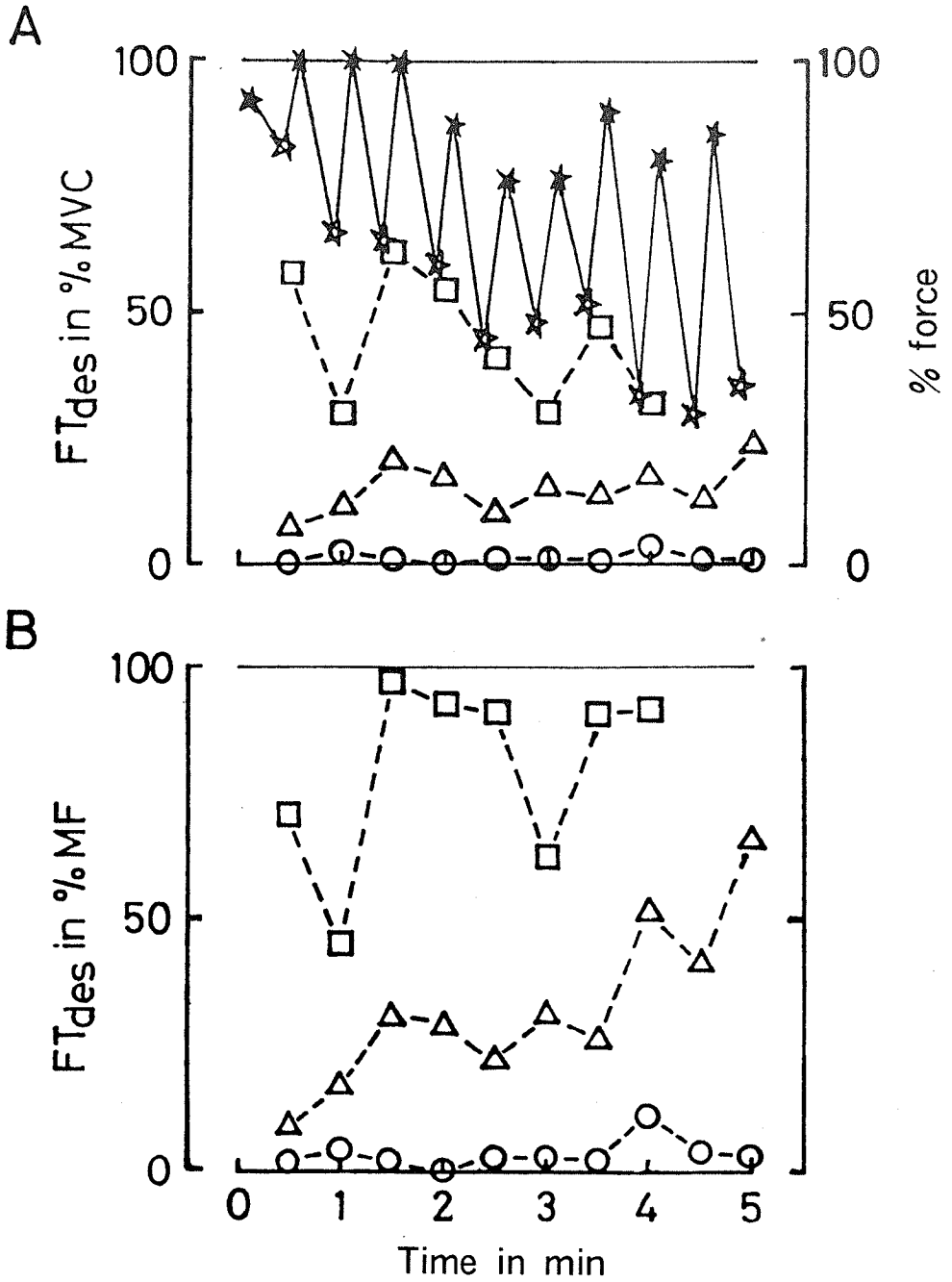

Fig. 5. Examples of % force threshold obtained during the descending phase (FTdes). These results with either high or low force threshold initially tended to be unchanged. But in two units, the % FTdes increased gradually. See the legend for figure 3 for the meaning of stars.

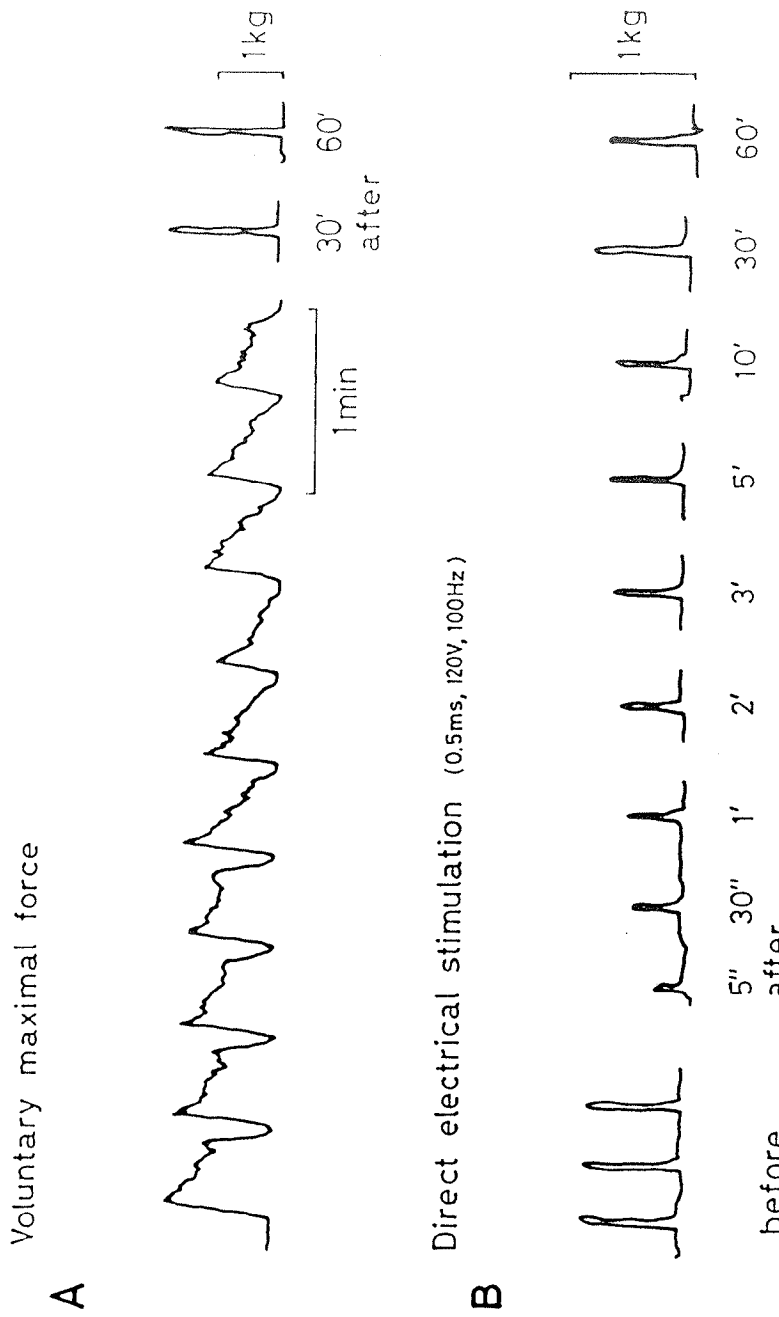

Fig. 6. The tension produced by the electrical stimulations of 0.5 ms duration, 120 V intensity, and 100 Hz frequency (B) before and after 10 bouts of voluntary maximal contraction (A). The force, at 5 seconds after voluntary force exertions, obtained by direct stimulation decreased to about 40 % of the value which was obtained before the set of maximal voluntary contraction. The maximal tensions produced both voluntarily (A) and by electrical stimulation (B) were normalized 30 minites after the series of voluntary contractions.

Table 1. The numbers of general trend observed in 30 motor units. The % force threshold during ascending (FT_{asc}, A and B) and descending phase (FT_{des}, C and D) are shown. The data in A and C are the % force threshold relative to the maximal voluntary contraction (MVC), and the data in B and D represent the % force threshold relative to the maximal force (MF) when each force threshold was measured.

A FT_{asc} in % MVC

	low 0-10%	middle 10-30%	high 30-100%
decrease	1	9	9
constant	7	1	3
increase			
vary			

C FT_{des} in % MVC

	low 0-10%	middle 10-30%	high 30-100%
decrease		4	6
constant	6	6	1
increase	2		2
vary	1		3

B FT_{asc} in % MF

	low 0-10%	middle 10-30%	high 30-100%
decrease	1	9	7
constant	7	1	5
increase			
vary			

D FT_{des} in % MF

	low 0-10%	middle 10-30%	high 30-100%
decrease			
constant	2	5	5
increase	6	5	4
vary	1		2

FT of 10-30 %, and five cases constant and four cases of increasing tendencies with more than 30 % FT were observed (Table 1-D).

Figure 6 shows the tension produced by the direct electrical stimulations at 100 Hz , 0.5 ms duration, and 120 V intensity before and after each set of 20-second MVC. The force, at 5 seconds after voluntary force exertions, obtained by direct stimulation decreased to about 40 % of the value which was obtained before the set of MVC, and recovered to about 60 % at 1 minute after, to about 80 % at 5 minutes after, and returned to the initial value at 30 minutes after.

Discussion

By using the coil-shaped inserted electrodes, the action potentials of single motor units were stably recorded and well differentiated even at the MVC (Fig. 2-A). This type of electrode might be useful to examine voluntary motor control (6).

The twitch tension curve of the motor unit shown in the figure 2-B had 60-ms time-to-peak tension and 4-g of peak tension. The average contraction time of motor units was 75.3 ms, and the average peak tension was 22.8 g in the motor units of human abductor digiti minimi muscle according to the data reported by Ogawa (10). This motor unit had a faster contraction property and a smaller twitch tension. And the unit also had a smaller FT (4 % MVC). It is generally said that the unit with lower FT has slower contraction property and smaller twitch tension (3, 4, 8). But this unit with low FT had a faster contraction property.

The % FT relative to the MVC in this motor unit showed constant tendency in the descending phase. But the % FT showed wide variations in the descending phase. This tendencies were the same in the % FT relative to the maximal force when each FT was measured. This means that the FT of this motor unit may be affected more strongly during sustained force exertions than during repeated force exertions.

As shown in the figure 1-B, differencies between the maximal forces and forces at the end of 20 seconds were obvious. A question was raised by these big differencies whether the muscle itself does not fatigue so much and motor unit recruitment and/or firing frequency decrease, or the muscle contractile ability decrease and the recruitment and/or the frequency are intact. The former is neurogenic recruitment and/or neurogenic frequency factors and the latter is myogenic factor.

As seen in the table 1, in the ascending phase, greater possibilities of constant tendency were observed in the units with FT of less than 10 %. And the FT tended to be increased in the units with more than 10 % FT.

In the descending phase, constant tendency for the units with less than 10 % FT, and decreasing tendency for the units with more than 30 % MVC, were observed. In the FT relative to the maximal force at that time, greater possibilities of increasing tendency were observed in the units with less than 10 %. The tendencies found in the current study that the % FT relative to MVC and to the maximal force in the units with less than 10 % initial FT were unchanged and increased support that these tension decreases may be due to neurogenic recruitment factor. As for the units with initial FT of more than 30 %, the % FT relative to the MVC tended to decrease, and that relative to the maximal

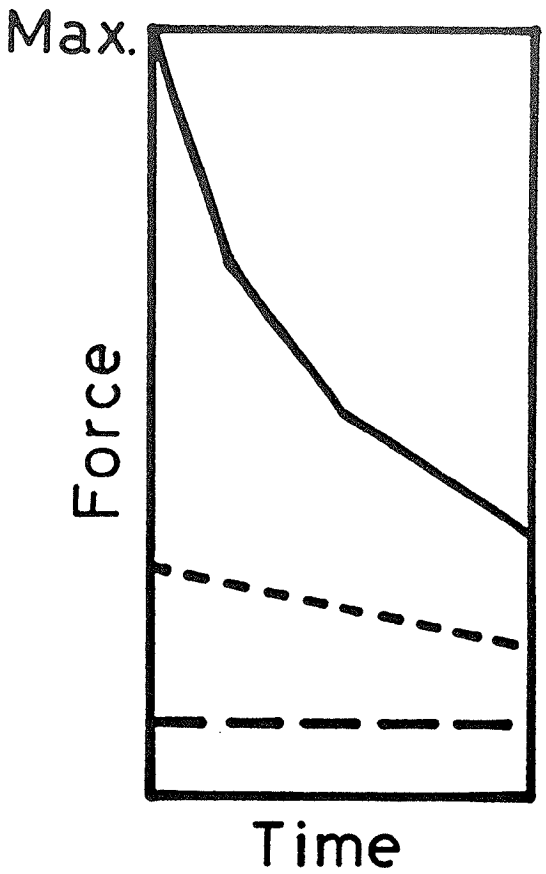

Fig. 7. An assumption from the general results observed in this study. The top solid line represent the mean changes in the maximal tension when the force thresholds were measured. The two broken lines represent the general trend of the changes in the % force threshold. The unit with higher % force threshold initially (----) tended to decrease the force threshold when the maximal tension was lowered. But the % force threshold with lower value initially (——) tended to be constant.

force at that time remained constant. Such results may suggest that these tension decreases were due to neurogenic frequency and/or myogenic factors.

Figure 7 shows an assumption from the general results observed in the present study. The unit with higher % FT initially tended to decrease the FT when the maximal tension was lowered. But the % FT in the unit with lower initial % FT tended to be constant.

The pattern of the changes in the FT were different between the ascending and descending phase. It implies that the FT of motor units may be susceptible to different effects during ascending force development and during force decline after the exertions.

The tension produced by the direct electrical stimulation decreased to approximately 40 % after the 10 consecutive maximal exertion.

In conclusion, it might be assumed that no change in the force development of the motor units with the FT of below 10 % maximal voluntary contraction does occur, but the large decrement in those with above 30 % MVC. It was also suggested that the neurogenic frequency and/or myogenic fectors may play dominant roles in the tension decrease during sustained MVC.

ヒト単一運動単位の閾値張力における持続的最大随意収縮時の変化

倉田　博

最大努力で随意筋収縮を持続している際の運動単位の活動様式に検討を加えた。被験筋は，健康成人男子の小指外転筋であった。小指の等尺性外転張力を近位指節間関節より記録した。単一運動単位の活動電位はコイル状の筋内埋入電極を用いて導出した。最大随意収縮は20秒間づつ，10回繰り返し，その前後を5秒の上行性と下行性のランプ収縮で続けた。各運動単位の活動参加時点および活動停止時点の閾値張力を求めた。各閾値張力を最大随意収縮張力(MVC)に対するパーセンテージで表わし，また，各時点における最大張力(MF)に対する割合も計算した。各回の最大張力は80%に減少し，20秒の各持続収縮終了時点の張力は30%にまで低下した。各運動単位の上行性ランプにおける閾値張力は，10% MVC 以下の低閾値の運動単位では，時間経過に伴う変化の見られないものが多かった。10% MVC 以上の中高閾値の運動単位では，減少傾向を示す運動単位が多かった。下行性ランプにおける MVC に対する閾値張力は，低閾値の運動単位では変化の見られないものが多く，30% MVC 以上の高閾値では，減少傾向を示すものが多く見られた。MF に対する閾値張力は，低閾値で増加傾向を示すものが多く見られた。この条件下では，低閾値の運動単位が発生する張力はほとんど変わらず，高閾値の運動単位の発生する張力が大きく減少して，筋力が低下しているものと考えられた。

References

1) Bigland-Ritchie, B. R., Dawson, N. J., Johansson, R. S. and Lippold, O. C. J.: Reflex origin for the slowing of motoneurone firing rates in fatigue of human voluntary contractions. J. Physiol. 379, 451-459, 1986.
2) Freund, H.-J.: Motor unit and muscle activity in voluntary motor control. Physiol. Rev. 63, 387-436, 1983.
3) Garnett, R. A. F., O'Donovan, M. J., Stephens, J. A. and Taylor, A.: Motor unit organization of human medial gastrocnemius. J. Physiol. 287, 33-43, 1978.
4) Grimby, L., Hannerz, J. and Hedman, B.: Contraction time and voluntary discharge properties of individual short toe extensor motor units in man. J. Physiol. 289, 191-201, 1979.
5) Kurata, H.: The relative threshold of activation of single human motor units in voluntary muscular contraction. Jpn. J. Phys. Fitness 21, 176-182, 1972.
6) Kurata, H., Ogawa, Y. and Masuda, M.: Characteristics of single human motor units during various modes of contractions. Jikeikai Med. J. 27, 191-202, 1980.
7) Milner-Brown, H. S., Stein, R. B. and Yemm, R.: The contractile properties of human motor units during voluntary isometric contractions. J. Physiol. 228, 285-306, 1973.
8) Milner-Brown, H. S., Stein, R. B. and Yemm, R.: The orderly recruitment of human motor units during voluntary isometric contraction. J. Physiol. 230, 359-370, 1973.
9) Nagatsu, H., Ono, M. and Kurata, H.: Changes of threshold of single motor units in the m. vastus medialis by loading of voluntary sustained contraction. Jpn. J. Phys. Fitness 23, 49-50, 1974.
10) Ogawa, Y.: Contractile properties and recruitment threshold of single human motor units. Jikeikai Med. J. 31, 391-400, 1984.
11) Stephens, J. A. and Usherwood, T. P.: The mechanical properties of human motor units with special reference to their fatiguability and recruitment threshold. Brain Res. 125, 91-97, 1977.
12) Tokizane, T. and Tsuyama, N.: Electromyogram (EMG) and its clinical applications. Tokyo J. Med. Sci. 59 (1), 62-87, 1951.
13) Yamamoto, T.: Changes in the frequency of discharge of single motor units during the prolonged voluntary contraction in man. Jpn. J. Phys. Fitness 28, 95-103, 1979.