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NEUROMUSCULAR PERFORMANCE IN VOLUNTARY AND REFLEX CONTRACTION

WITH SPECIAL REFERENCE TO MUSCLE STRUCTURE AND FATIGUE

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ACADEMIC DISSERTATION TO BE PUBLICLY DISCUSSED,
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CONTENTS

PREFACE

This thesis is based on the following papers, which will be referred to by their Roman numerals:

I   VIITASALO, J. T., and P. V. KOMI. Force-time characteristics and fiber composition in human leg extensor muscle. Eur. J. Appl. Physiol. 40: 7-15, 1978.
https://doi.org/10.1007/BF00420984

II   VIITASALO, J. T., S. SAUKKONEN, and P. V. KOMI. Reproducibility of measurements of selected neuro-muscular performance variables in man. Accepted for publication in Electromyography and Clinical Neurophysiology. 1980.
https://pubmed.ncbi.nlm.nih.gov/7250028/

III VIITASALO, J. T., and P. V. KOMI. Interrelationships between electromyographic, mechanical, muscle structure and reflex time measurements in man. Accepted for publication in Acta Physiol. Scand. 1980.
https://doi.org/10.1111/j.1748-1716.1981.tb06710.x

IV   VIITASALO, J. T., and P. V. KOMI. Effects of fatigue on isometric force and relaxation-time characteristics in human muscle. Accepted for publication in Acta Physiol. Scand. 1980.
https://doi.org/10.1111/j.1748-1716.1981.tb06709.x

V   VIITASALO, J. T., and P. V. KOMI. EMG, reflex and reaction time components, muscle structure and fatigue during intermittent isometric contractions in man. Accepted for publication in International Journal of Sport Medicine. 1980.
https://doi.org/10.1055/s-2008-1034657

1. INTRODUCTION

The time cource of skeletal muscle contraction is composed of
several delays both in force production and in relaxation. On-
set of EMG activity on a muscle has been used as a timing mark
to divide the delays into central and peripheral ones. In the
central part the time interval between a stimulus and change of
electrical activity (EMG) in a reacting muscle has been desig-
nated as premotor time in voluntary contraction (Weiss 1965) and
as latency in reflex induced contraction (Hayes 1972).

   In the peripheral part of the neuro-muscular system a delay
exists between the change of electrical activity in the muscle
and the early change of muscle force or movement. In voluntari-
ly induced reaction movement this delay has been called "reac-
tion motor time" (Weiss 1965) and in reflex movement "reflex
motor time" (Hayes 1972). These delays have also been referred
to as electro-mechanical delays in the literature. In addition
there is a time interval from the early change of muscle force
to the point where a pre set level of force or velocity of move-
ment has been reached. In isometric contraction this force
production part of the force curve has been called the force-
time (f-t) curve. The respective part of the force curve during
relaxation is named relaxation-time (r-t) curve in this thesis.
Theoretically it can be thought that these peripheral delays
and time intervals are under the influence of structure,
training status and fatigue of the neuro-muscular system.

   There are two different sites in the neuro-muscular system
which affect the contraction characteristics of a muscle;
firstly the contraction properties of single motor units (MU)
including their firing frequencies, and secondly the recruitment
pattern of the MU population of a particular muscle, which are
under the control of the proprioceptive feedback mechanisms and
higher centers of the nervous system.

Human skeletal muscles are composed of fast and slow motor units which have functionally and structurally different kinds of α -motoneurons and muscle fibers (eg. see Edgerton 1976). Fast and slow skeletal muscle fibers differ eg. in respect of their twitch mechanograms (Eberstein and Goodgold 1968, Lännergren 1974) so that fast twitch fibers (FT) can produce their force faster and relax quicker than the slow twitch fibers (ST). Because motor units have been shown to be composed of a uniform type of muscle cells (Brandstater and Lambert 1969, Burke et al. 1973), it is logical that there are differences in force production and relaxation also at the motor unit level according to the type of the unit (fast or slow) (Steg 1964, Buchthal and Schmalbruch 1970a, Burke et al. 1973, Gydikov et al. 1976).

The contraction characteristics of a muscle fiber have been shown to be under the influence of its innervation so that eg. the sharp mechanogram of a fast muscle or fast motor unit changed to a slower one when its fast α -motoneuron was replaced by a slow one (Buller et al. 1960, 1971, Mommaerts et al. 1969). This suggests that if the firing characteristics of a α -moto-neuron could be changed eg. by training as suggested by Cracroft and Petajan (1977), it would change also the contraction characteristics and mechanogram of the respective MU. This idea has received some support in some recent studies, which have shown that muscle fiber distribution could be affected by training and age (Larsson et al. 1978a, Jansson et al. 1978, Tesch et al. 1979) although a strong genetic basis has been substantiated (Komi et al. 1977a). The contraction characteristics of MUs have been shown to be sensitive also to fatigue so that muscular fatigue lengthens both the force production and relaxation of MU. These changes have been proved to be more pronounced in FT than in ST units both in animals (eg. Steg 1964) and in man (eg. Gydikov et al. 1976).

The contraction characteristics of individual MUs most probably have an effect on the electromechanical delay, on f-t and on r-t properties of a whole muscle. However, in this connec-

tion the firing frequency and recruitment pattern of MUs may also be important. Motor units have been shown to differ in respect of their firing frequencies so that fast MUs are able to fire at higher frequency than the slow ones (Gydikov and Kosarov 1973, Hannerz 1974, Steg 1964). In consequence slow units begin to fuse at a lower firing rate than the fast units as shown by Steg (1964). The recruitment pattern differs most probably according to the velocity of contraction so that eg. during slow isometric tension development MUs recruit according to the so called size principle (Henneman et al. 1965) so that small slow MUs recruit at low tension levels and big fast MUs at higher levels. However, during rapid isometric force production the fast MUs have been thought to be the ones that start the contraction (Gydikov and Kosarov 1974). The recruitment order may also be different in reflex-induced contraction as compared to a fast voluntary contraction (see eg. Buchthal and Schmalbruch 1970b, Burke 1973). However, experiments are lacking to demonstrate conclusively a normal reversal of the order of MU recruitment from tonic to phasic units. Moreover, the firing rate and recruitment pattern are influenced by fatigue (Person and Kudina 1972, Gydikov and Kosarov 1973, 1974). The effects of fatigue are also in this connection related to the type of MUs so that fast MUs become fatigued and stop firing earlier and they decrease their firing frequency more than their slow counterparts (Gydikov and Kosarov 1973, 1974).

Thus according to the results referred to above it can be thought that the electromechanical delay, f-t and r-t of a whole muscle or muscle group could be under the influence of the fiber distribution of the respective muscle/muscles. To support this Nilsson et al. (1977) found in humans a significant dependency between muscle fiber composition and the time interval from the onset of EMG activity to the point where a pre set velocity was reached in voluntary concentric contraction so that the delay was shorter in subjects with high percentage of fast twitch muscle cells (FT%). However, the delays reported by Nilsson et al. (1977) were relatively long (95 ms) as compared to those

(26-60 ms) reported by Corser (1974), Ralston et al. (1976),
Cavanagh and Komi (1979) and Norman and Komi (1979). So it is
not clear if the muscle structure correlated with the "true"
electromechanical delay or with the delay in force production
prior to the pre set velocity. The results of Norman and Komi
(1979) give support to the hypothesis that EMD in voluntary con-
traction could be related to muscle structure. They found a
shorter delay (26 ms) in m. triceps brachii, which they assumed
to be a faster muscle than m. biceps brachii, which, in fact,
had a longer delay of 41 ms. The hypothesis that the f-t or r-t
characteristics of a muscle are related to its structure is
supported by Buller et al. (1960) who show a difference between
the mechanograms of isolated cat fast and slow muscles and by
McComas and Thomas (1968) and Gatev et al. (1977) who stimulated
human fast and slow muscles and found the rate of force produc-
tion and the relaxation of fast muscles to be greater than those
of slow ones. However, the effects of muscle structure on EMD
either in reflex or in voluntary contractions, on isometric
force-time as well as on relaxation-time variables have not been
investigated extensively using subjects with different muscular
structure.

Fatigue has been shown to impair the contraction character-
istics of MUs, decrease their firing frequency and change the
recruitment pattern in relation to the type of MU as described
above. At the muscle or muscle group level the percentage
distribution of different fiber types has been shown to be re-
lated to the amount of force decrease both in dynamic
(Thorstensson and Karlsson 1976, Nilsson et al. 1977) and in
isometric (Viitasalo and Komi 1978a) fatigue contractions. The
selective fatiguing of the neuro-muscular system according to
the muscular structure has also been verified eg. using the
integral of myoelectrical activity (Ochs et al. 1977, Komi and
Tesch 1979) or the EMG frequency spectrum (Viitasalo and Komi
1978a, Larsson et al. 1978b, Komi and Tesch 1979) as indicator.

Following the changes in MU mechanogram, in firing frequency
and in recruitment, an increase can be assumed to happen during

fatigue in EMD and slowing in f-t and r-t characteristics at individual muscle or muscle group level. Moreover, these changes could be in relation to muscle structure. In support of this Nilsson et al. (1977) and Klimovitch (1977) reported the time delay between muscle EMG activity and muscle contraction to increase during fatigue and Nilsson et al. (1977) found the increase to be more pronounced in a "fast" than in a "slow" subject. However, as discussed previously, these authors reported so long values of EMD as compared to the values found in the literature that it is not clear if fatigue increased EMD or if it slowed the early part of force production. The f-t and r-t curves of a whole muscle as such have been proved to slow during fatigue (eg. Boulange et al. 1979).

The present series of experiments were designed to investigate in pre-fatigue and fatigue conditions the values and inter-relationships of selected neuro-muscular performance variables and especially their association with muscle structure. The variables included electromechanical delay in reflex and voluntary contraction, isometric force, force-time and relaxation-time, EMG integral and mean power frequency of the power spectral density function and blood lactate.

2. METHODOLOGICAL ASPECTS

2.1. Subjects

Eight subject groups volunteered for the first study (I): ski-
jumpers, male and female skiers, speed skaters, volley-ball
players, monozygous and dizygous twins and untrained policemen.
Many of the athletes had participated in the Olympic Games, in
World Championships and in European Championships between 1972
and 1976 as members of the Finnish national teams.

The subjects for the four other studies (II, III, IV and V)
were healthy male students in physical education. Table 1 sum-
marizes the number of subjects, their age, height, weight and
muscle fiber distribution (ST %) in m. vastus lateralis of each
subject group. The determination of ST % has been described in
section 2.4.5.

2.2. Statistical methods

Conventional statistical methods were employed to calculate the
mean ($\bar{x}$), standard deviation (SD), standard error of the mean
(SE) and linear correlation coefficient (r). Coefficient of va-
riation (C.V.) was determined according to the following formu-
las

$$C.V. = SD/\bar{x} \times 100$$

$$\text{where} \quad SD = \sqrt{\frac{\Sigma (x_1-x_2)^2}{N}}$$

in which x_1-x_2 = intraindividual differences between two succes-
sive measurements (A and B)

        N = number of subjects

        $\bar{x}$ = average of all subjects across measurements
A and B   Hyvärinen et al. (1972)

Table 1. Means (+SD) of the physical characteristics and age of the subject groups.

Subject groups	n	Age (years)	Height (cm)	Weight (kg)	Fiber distribution in m. VL (%ST)
Study I					
Skijumpers, ♂	8	24.0 + 3.3	173.9 + 5.4	70.3 + 7.2	54.4 + 7.7
Cross-country skiers, ♂	9	24.6 + 3.2	174.9 + 4.2	68.6 + 7.2	65.2 + 7.2
Cross-country skiers, ♀	7	22.7 + 4.9	164.9 + 6.0	58.7 + 9.1	62.1 + 7.7
Speed skaters, ♂	5	23.6 + 2.9	180.9 + 3.8	76.2 + 1.8	71.6 + 12.0
Volley-ball players, ♂	9	23.8 + 2.5	187.1 + 5.9	82.9 + 7.6	53.1 + 11.3
Policemen, ♂	8	34.0 + 4.1	172.9 + 8.4	74.1 + 12.8	46.2 + 17.6
Monozygous twins, ♂	5+5	16.6 + 1.8	172.4 + 6.7	55.3 + 9.7	58.8 + 10.3
Dizygous twins, ♂	10+10	18.5 + 3.3	177.5 + 6.6	65.9 + 12.7	54.6 + 12.6
Studies II, III, IV and V					
Students in physical education, ♂	29	22.5 + 2.3	179.7 + 5.9	71.6 + 6.3	47.9 + 13.2

The differences between mean values were tested for significance using dependent and independent Student's t-test.

2.3. Dynamometers and experimental design

In the first study (I) the isometric both leg extension force-time curve was measured with a knee angle of 107 degrees and a hip angle of 120 degrees on an electromechanical dynamometer shown in Figure 1. The subjects were told to produce on command a maximum force against the footplate as quickly as possible. After a few warm-up contractions three trials were registered. Two best contractions on the basis of the maximum force level were included for further analysis. The subjects were biopsied after the measurement for determination of muscle fiber composition.

Data for the studies II - V was collected in the same measurement situation. The subjects were familiarized with the dynamometer (shown in Figure 2) and test contractions one week before the measurements, which consisted of isometric right leg knee extensions as response to visual and auditory stimulus with the knee and hip angles of 90° and 120°, respectively, and of patellar reflexes measured on the same dynamometer and measurement position as the reaction contractions. During the reflex measurements the position of the dynamometer was changed with a hydraulic pump so that the lower leg of a subject could hang freely in vertical position as shown on the upper part of Figure 2.

The measurements in studies II - V were started with 14-16 warm-up contractions. After five minutes six patellar reflexes were measured in sequence during one minute. This was followed by a blood sample and 100 maximal isometric knee extensions as reactions to simultaneous auditory (73 dB) and light (a lamp, Ø 7 cm, 1 W) signals. The subjects were instructed to react to the signals as quickly and as strongly as possible by extending the leg against a cuff fixed to a strain gauge system, to maintain the maximal force as long as the signals were on (2.5 s)
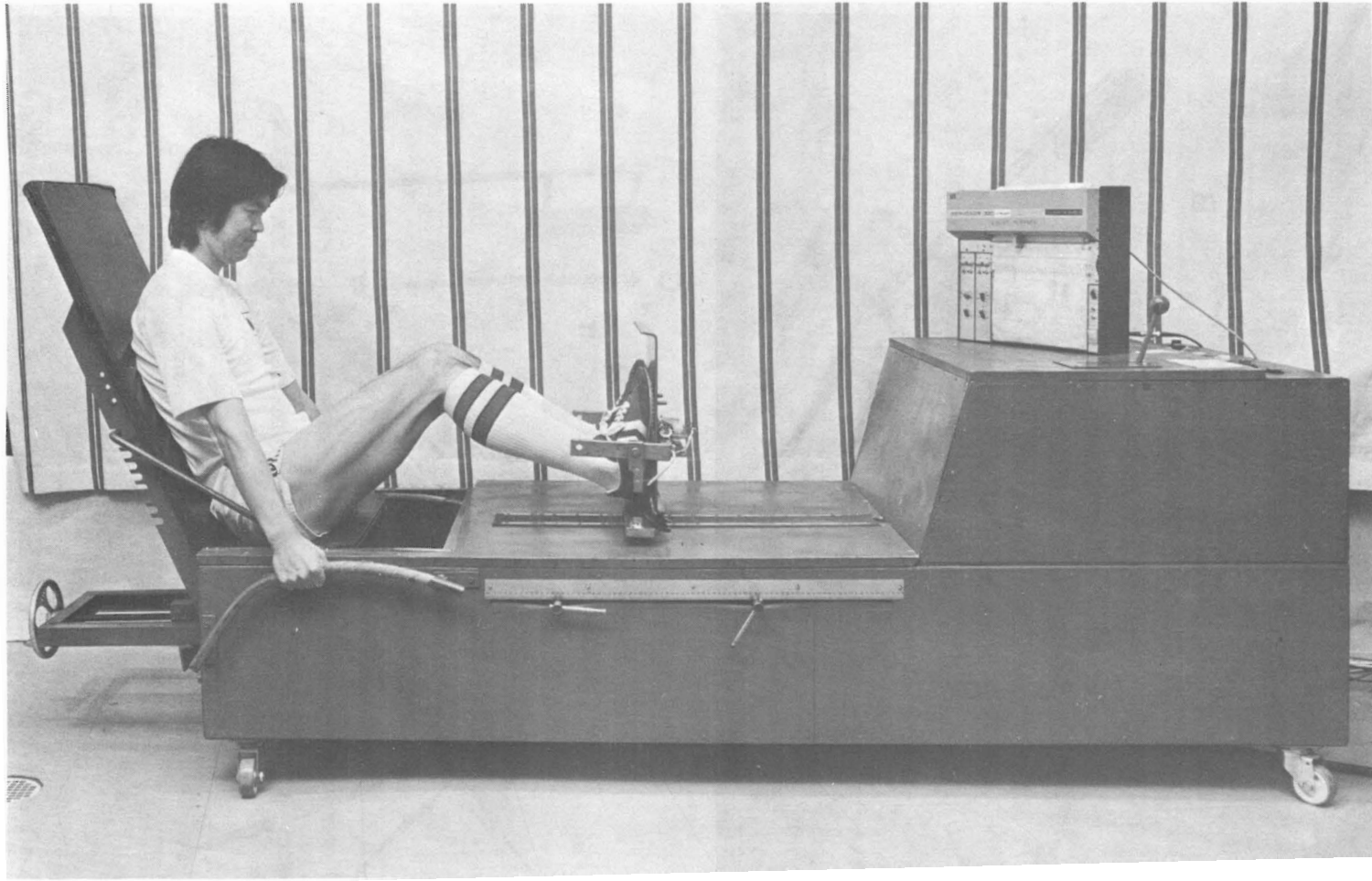
Figure 1. Dynamometer for the both leg isometric force-time measurements (Komi 1973).
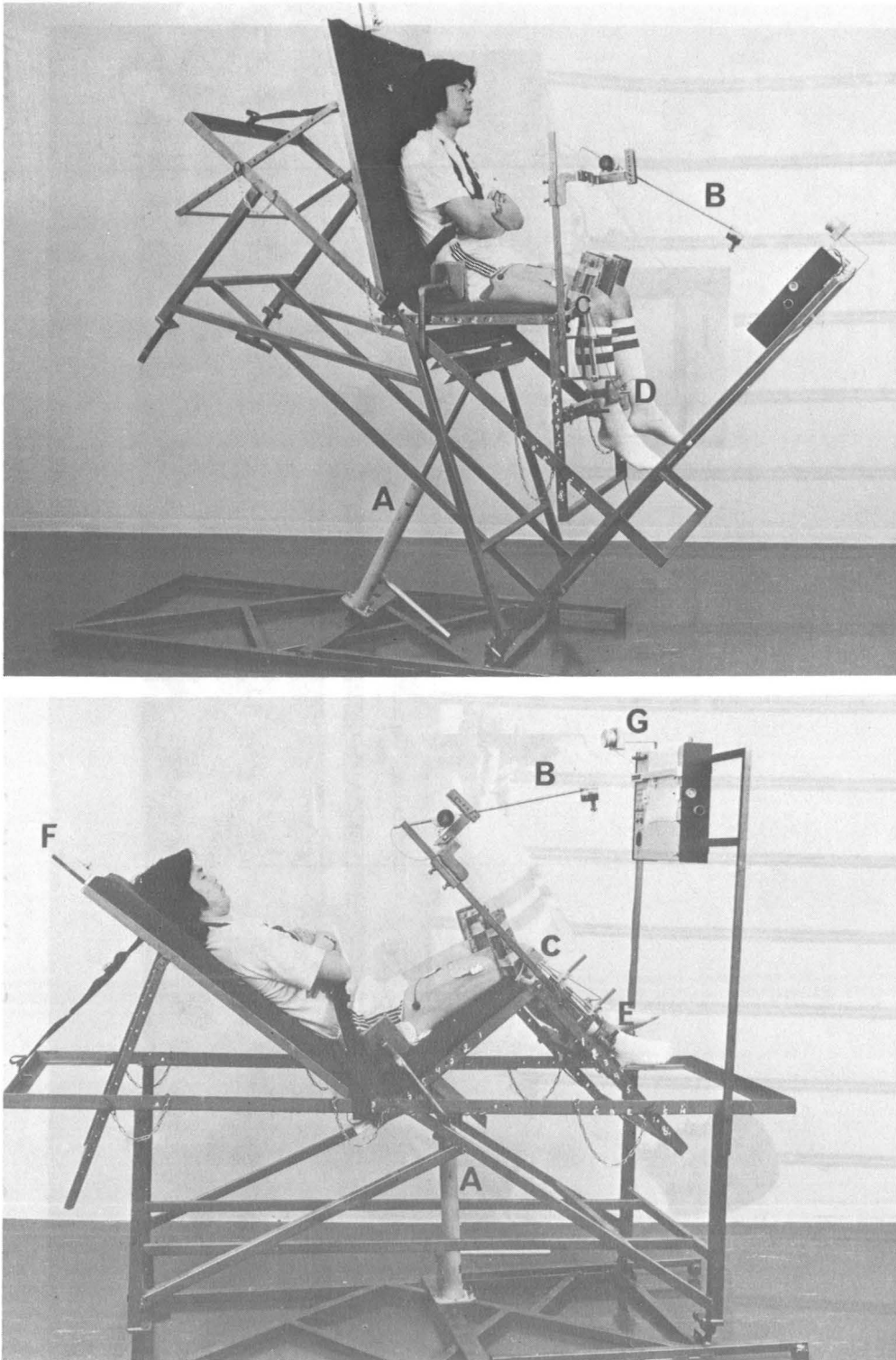
Figure 2. Dynamometer for the patellar reflex (upper) and vol-
untary isometric extension (lower) measurements. A:
hydraulic lifting mechanisms; B: reflex hammer; C:
electrical goniometer; D: accelerometer; E: cuff;
F: loudspeaker for auditory signal; G: lamp for
visual signal.

and to relax the muscles suddenly after the disappearance of the
signals. The signals were given by an electrical timing unit
with random interpauses between 1.4 - 4.0 s. The recovery after
the 100 contractions was registered during ten minutes. One
recovery measurement including one reaction and three reflex
contractions was taken at the beginning of each recovery minute.
Blood samples were also taken at the end of the work - between
90'th and 95'th contractions - and at the beginning of each
recovery minute. The subjects were biopsied one week before the
first measurement from the right vastus lateralis muscle as de-
scribed in 2.4.5.

2.4. Variables, analytical methods and their reproducibility

Most of the reproducibility values presented in this chapter are
based on study II, where they were calculated between the aver-
ages of the first and third, and second and fourth successive
contractions. These averages were designated as A and B, re-
spectively. For reflex parameters the respective means were
calculated using the four first reflexes measured prior to the
fatigue contractions. The reproducibilies of biopsy measure-
ments were established using two different samples taken from
the same insertion site one after another.

     In the first study (I) the reproducibilities of f-t para-
meters were determined between two different contractions taken
during.the same test session and for day-to-day comparison be-
tween two measurements taken at an interval of 3 to 9 days.

2.4.1. Electromechanical delay in reflex measurements

Patellar reflex time (TRT) was fractionated into latency (LAT)
and motor time (RfMT) by the onset of EMG as described by Hayes
(1972). The motor time has also been called reflex electro-
mechanical delay (EMD) in this thesis.

Patellar tendon was tapped by a reflex hammer with a constant impact energy of 0.63 Nm when the subjects sat relaxed and blindfolded on the dynamometer (see upper part of Figure 2). The impact was sensed by an piezoelectric accelerometer fixed to the anterior and distal part of the leg as shown in Figure 3. EMG activity was registered for the determination of LAT and RfMT as described in Chapter 2.4.4. The moment when the leg started to move was established using an electrical goniometer (see Figure 3). Acceleration, EMG activity and change of angle were stored on magnetic tape (Racal, Store 7) with a timing signal of 1 kHz (Exact Model 126 VCF/Sweep Generator) and played back on a Honeywell Visicorder Type 2106 with a speed reduction of 16 times. The calculation of LAT and RfMT was performed with the accuracy of 0.5 ms and using the thresholds of 17 μV and 0.03° for EMG and angle, respectively.

The correlation coefficient and coefficient of variation between the two averages (A and B) of two measurements for reflex motor time were found to be satisfactory (r = .90, C.V. = 13.1 %). Even though the absolute value of RfMT in this study due to the low thresholds was shorter than in most studies reported earlier (discussed in study II) the reproducibility of RfMT was of the same order as reported in literature (Travis and Young 1930, Tipton and Karpovich 1966, Hayes 1972, Kroll 1973).

2.4.2. Electromechanical delay in voluntary reaction measurements

Maximal isometric force during the 100 contractions in studies II - V was produced as reaction to simultaneous auditory and light signals.

Total reaction time (TRT) was fractionated into premotor (PMT) and motor times (MT) by the onset of EMG activity according to Weiss (1965). MT is also called voluntary electromechanical delay (EMD) in this thesis. For the calculation of PMT and MT the reaction signal was stored together with EMGs and force
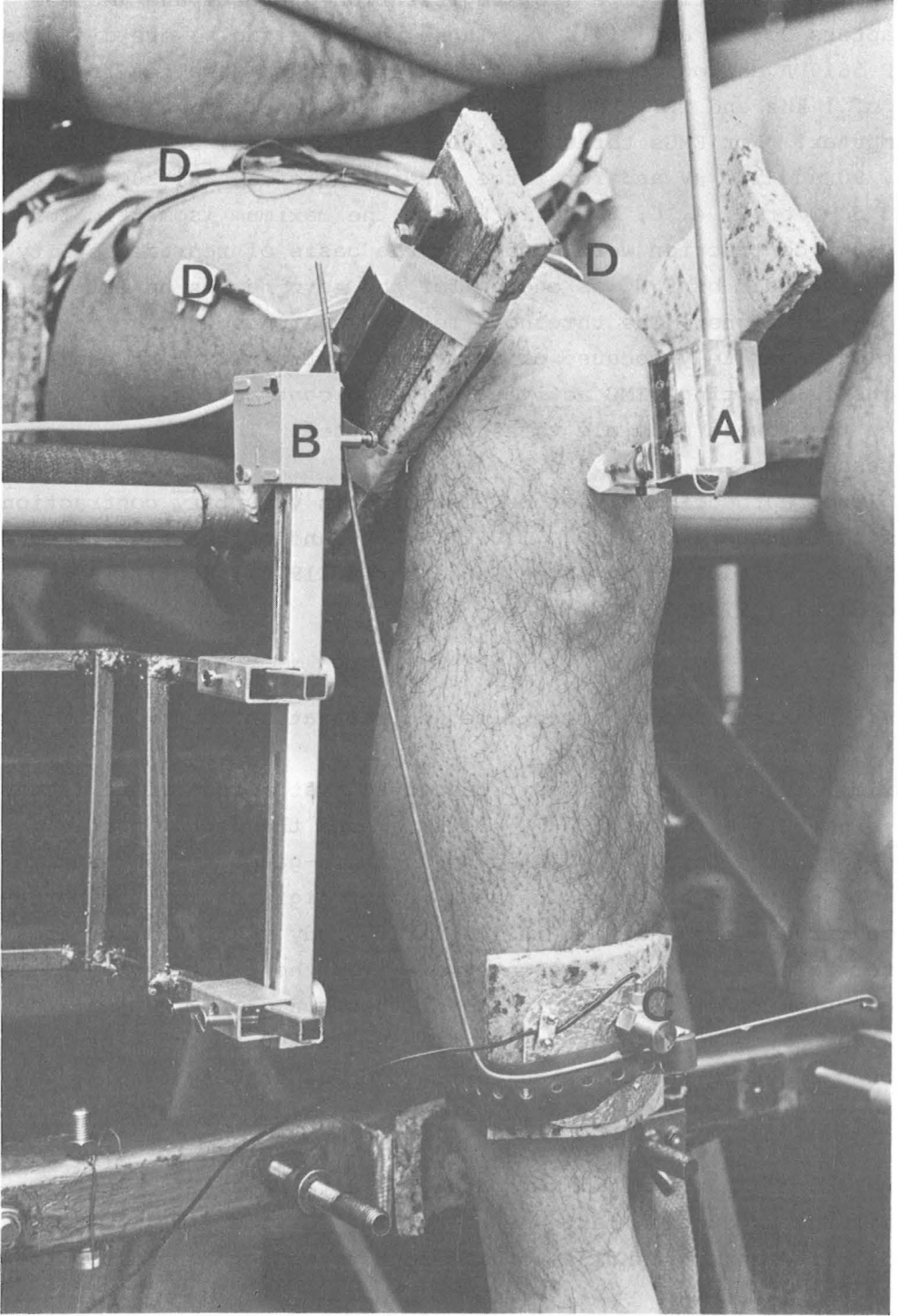
Figure 3.   The experimental setup for patellar reflex measure-
ments. A: reflex hammer; B: electrical goniometer;
C: accelerometer; D: EMG electrodes.

signal on magnetic tape (for registration of force and EMG see
Chapters 2.4.3. and 2.4.4.). These analog signals were digitized
(HP 5610 A analog to digital converter) with a sampling frequen-
cy of 1 kHz and TRT, PMT and MT were calculated using HP 21-MX
computer. For EMGs thresholds of 10, 20, 30, 40, 50, 60, 70,
80, 90 and 100 µV and for force thresholds of 5, 10, 20, 30, 40
and 50 N or 2, 4, 6, 8 and 10 % from the maximum isometric force
of each contraction were used. On the basis of reproducibility
the threshold of 5 N was chosen for the termination of TRT and
MT calculations. The threshold for EMG was chosen for each re-
action separately because of inter- and intraindividual varia-
tions in "resting" EMG activity prior to contraction. In each
case the lowest possible threshold was used. The mean EMG
threshold was 36.1 + 9.1 µV.

The reproducibility of EMD measured in voluntary contraction
was satisfactory (r = .93, C.V. = 8.2 %) and of the same order
as reported earlier by Laine Santa Maria (1970), Kroll (1973)
and Hayes (1975).

2.4.3. Maximal force, force-time and relaxation

Maximal isometric force was produced against a foot plate (study
I) or a cuff (studies II - V) fixed around the distal part of
the leg. The force was sensed by a strain-gauge system, ampli-
fied and stored on magnetic tape. After digitization the force-
time curves were analyzed in the first study with HP 2116C com-
puter calculating the time intervals from the beginning of force
production to different force levels between 5 and 100 % of the
maximum force at 5 % intervals. The beginning of force produc-
tion was determined for each contraction separately finding the
flexion point of the force curve from the digitized data.

In the following four studies (II - V) maximal force, force-
time and relaxation-time were analyzed with HP 21-MX computer.
The force production part was calculated for the time intervals
from different thresholds to different force levels and for the

time taken to increase the force a given increment expressed
both in absolute and in relative force scales (study II). The
relaxation part of force curve was also analyzed in the same way
using the level of 85 % as the starting point for calculations
(study II). On the basis of these analyses the best reproduci-
ble relative and absolute increments and decrements (20 % and
100 N) were selected for studies III - V. Thus in force produc-
tion the time intervals were calculated to increase the force
between the following relative and absolute force levels: 5-
25 %, 25-45 %, 45-65 %, 65-85 %, 25-125 N, 125-225 N and 225-
325 N. The respective force levels for relaxation were 75-55 %,
55-35 %, 35-15 %, 275-175 N and 175-75 N. The level of 75 % in
the relaxation part was selected for the starting point of
calculations to ensure the beginning of the relaxation phase in
all subjects. In addition, the f-t and r-t curve were analyzed
for their steepest point finding the highest value of a slope
coefficient (N/s) calculated during five milliseconds. These
were called maximal rate of force development (RFD) and rate of
relaxation (RR). Maximal force was calculated finding the
highest mean of five successive digital points (5 ms) during
contraction.

   The reproducibility of force-time measurements expressed as
correlation coefficients between two successive trials (study I)
was found to be .80 or higher for force levels below $0.9 \times P_O$.
The day-to-day comparison showed correlation coefficients of
.66-.76 for the respective force levels. Times taken to produce
P_O were not reproducible (study I). In study II correlation
coefficients between means of two measurements were .72-.87 for
relative force increments of 20 % and .76-.92 for absolute in-
crements of 100 N. The respective values for relative force
decrements in relaxation were .77-.80 and for absolute decre-
ments .59-.78. The reproducibility of rate of force development
and rate of relaxation were of the same order (r = .84, C.V. =
17.8 % and r = .90, C.V. = 20.7 %, respectively).

   Maximal force proved to be more reliable than force-time and
relaxation-time variables (r = .98, C.V. = 4.1 %, study II) and

of the same order as reported previously by us for one leg iso-
metric knee extension (Viitasalo and Komi 1975, Viitasalo et al.
1977).

2.4.4. Electromyographic characteristics

EMG was recorded in studies II - V from m. vastus lateralis,
vastus medialis and rectus femoris during reflex and reaction
contractions. Beckman miniature skin electrodes were fixed bi-
polarly over the motor point area of each muscle (for details
see study II and Viitasalo and Komi 1975). EMG signals were
amplified with Brookdeal 9432 preamplifiers (60 dB, 1 Hz - 1
kHz) and stored on magnetic tape simultaneously with accelera-
tion and signal from goniometer in reflex measurements, and with
stimulus signal and force in reaction measurements. EMGs were
used to determine the initiation of muscle activity for calcula-
tion of electromechanical delay in reflex and in reaction meas-
urements as described in Chapters 2.4.1. and 2.4.2. In addi-
tion, at the maximal force level in reaction contractions EMGs
were analyzed during 2 s for their integrals (IEMG) and mean
power frequencies (MPF) of power spectral density function (see
Kwatny et al. 1970, Viitasalo and Komi 1975).

   The reproducibilities of IEMG and MPF calculated between the
means of the first and third, and second and fourth contractions
were satisfactory (r = .98, C.V. = 6.9 % and r = .95, C.V.
3.2 %, respectively) and higher than in our earlier report (Vii-
tasalo and Komi 1975).

2.4.5. Biopsy variables and blood lactate

One week before the first measurement (studies II - V) or imme-
diately after the tests (study I) two muscle biopsies were taken
from the right m. vastus lateralis of the subjects from the same
insertion site using the standardized technique of Bergström

(1962). The myosin ATPase method (Padykula and Herman 1955) was used for identification of the fast (FT) and slow twitch (ST) fibers. Fiber distribution was calculated using the number of both cell types in the sample and it was expressed as per cent of slow twitch fibers (ST %). In studies II - V the relative areas of FT and ST fibers and their area ratio (FT/ST) were determined by optical planimetry. Using the ST % and FT/ST values the relative area occupied by the ST cells in the total fiber area was calculated. This was called corrected ST % (CST%). The planimetry and calculations are described in detail in study II.

The reproducibilities of the biopsy variables calculated between the two samples were not so high as those of the other variables described earlier. The reproducibility of CST% (r = .83, C.V. = 16.6 %) was better than that of FT/ST (r = .73, C.V. = 17.6 %) or ST % (r = .66, C.V. = 17.8 %). The coefficients of variation reported earlier for ST % or FT % by Thorstensson (1976), Suominen (1978) and Tesch (1980) (10 %, 13.1 % and 6.2 %, respectively) were lower than in this study. Thorstensson (1976) reported the coefficient of variation between two different muscle samples for absolute ST and FT areas to be 16-17 % and for FT/ST ratio 9 %. Halkjaer-Kristensen and Ingemann-Hansen (1979) studied variation of FT and ST cell absolute sizes using repeated biopsies. They reported the coefficient of variation to be in the order of 15-20 % and concluded the variation in fiber size and distribution between repeated needle biopsies to be mainly due to biological inhomogeneity in the muscle. In Tesch's study (1980) the coefficient of variation for FT/ST ratio was 7.5 % and for muscle fiber area, which equals the CST% in this study, 10.5 %. The optical planimetry method itself used in study II has been proved to be more reliable (r = .99, C.V. = 5.0 %) than eg. weighting method (r = .95, C.V. = 6.0 %) or calculation of the transverse axis (r = .77, C.V. = 11.5 %) (Viitasalo and Mäkinen 1980). The fact that the C.V. for FT/ST ratio in study II was higher than in most of the studies cited is probably due to a larger number of cells

($\bar{x}$ = 173) included for analysis of each sample without any pre-
determined selection of fibers for analysis. Tesch (1980) and
Thorstensson (1976) selected from both ST and FT population 10
largest, right angle orientated fibers. However, when the rep-
resentativeness of a sample of ten cells to the whole population
of cells in a biopsy sample was analyzed, the correlations be-
tween these two measurements of the FT/ST ratio were found to
be relative low (r = .55 - .88) (Viitasalo and Mäkinen 1980).

The reproducibilities of biopsy measurements found in this
study (II) are not quite comparable to those of the other vari-
ables used because in further calculations the average of two
biopsies was used and the reproducibility was calculated for two
separate samples. So to determine the real comparable reproduc-
ibility of the biopsy variables four different samples should be
taken.

Blood samples were taken from the finger tip in studies IV
and V before the 100 contractions, between the 90'th and 95'th
contractions as well as at the beginning of each of the ten re-
covery minutes. The samples were analyzed for the lactate
using the standardized method of Biochemica Boehringer.

3. RESULTS

3.1. Electromechanical delay

Electromechanical delays were calculated separately for m.
rectus femoris, vastus lateralis and vastus medialis. Further
analyses were performed using the average of these three values.
Table 2 summarizes the means and standard deviations for each
main variable in prefatigue, fatigue and recovery conditions.
Electromechanical delay was found to be significantly shorter
in voluntary contraction (MT = 38.3 $\pm$ 8.3 ms) ($p < .01$) than in
reflex contraction (RfMT   45.4 $\pm$ 9.0 ms) (study III).

     Intermittent isometric fatigue effected a significant de-
crease in voluntary and reflex electromechanical delay (ΔMT =
7.0 ms, $p < .05$, ΔRfMT = 4.5 ms, $p < .01$) when the first fatigue
contraction was compared to the first recovery measurement
(study IV). Reaction MT recovered to the prefatigue level or
above it in two minutes. On the other hand reflex MT did not
reach the prefatigue level during the ten minutes recovery peri-
od.

3.2. Isometric force, force-time and relaxation

One leg isometric maximal force was shown (study II) to be
666.0 $\pm$ 133.7 N or when expressed per body weight 9.3 $\pm$ 1.6
N/kg. During the first nine isometric fatigue contractions
maximal force declined to 620.5 $\pm$ 123.0 N (6 %, n.s.) and
further to 504.1 $\pm$ 113.5 N level (24 %, $p < .001$) during the 100
contractions (study IV). The recovery of force was complete in
about five minutes (see Table 2).

     Fatigue effected a slowing in f-t and r-t curves as shown in
Figure 4 (study IV). Maximal rate of force development (RFD)
declined from the prevalue of 7721 $\pm$ 2569 N/s to 4941 $\pm$ 2078 N/s
(36 %, $p < .001$), and rate of relaxation (RR) from 5943 $\pm$ 2154

Table 2. Means and standard deviations for each main variable in prefatigue, fatigue and recovery conditions (studies II – V). MT = reaction motor time, RfMT = reflex motor time, RFD = maximal rate of isometric force production, RR = maximal rate of relaxation, IEMG = integrated EMG, MPF = mean power frequency of EMG power spectral density function.

	Prefatigue	Fatigue After 9 contractions	Fatigue After 98 contractions	Recovery (minutes) I	II	III	IV	IX
MT (ms)	38.3 + 8.3	35.9 + 12.2	36.6 + 9.9	31.3 + 15.8	41.4 + 10.9	42.0 + 11.7	40.3 + 10.3	44.2 + 11.5
RfMT (ms)	45.4 + 9.0			40.9 + 5.2	42.9 + 7.2	45.7 + 10.6	46.8 + 10.7	46.1 + 9.6
Max force (N)	666.0 + 133.7	620.5 + 123.0	504.1 + 113.5	584.2 + 95.7	574.1 + 107.8	600.8 + 110.7	638.1 + 114.3	644.9 + 120.9
RFD (N/s)	7721 + 2569	7266 + 2565	4941 + 2078	5828 + 1657	5859 + 1730	5879 + 1611	6410 + 2212	6521 + 2389
RR (N/s)	5943 + 2154	4862 + 1553	3744 + 1096	6014 + 1581	5700 + 1801	5969 + 1844	6017 + 1659	5769 + 2182
IEMG (µV∗s)	319.7 + 93.9	300.4 + 85.1	305.6 + 92.6	326.1 + 97.4	315.4 + 87.2	328.5 + 98.6	344.2 + 98.4	343.3 + 100.8
MPF (Hz)	97.6 + 10.0	92.8 + 10.5	90.5 + 15.1	95.8 + 12.8	97.3 + 12.9	99.2 + 12.7	101.4 + 12.4	100.7 + 12.3
Blood lactate (mmol/1)	1.5 + 0.5		4.5 + 2.0	4.6 + 2.0	4.4 + 2.0	4.2 + 2.0	3.6 + 2.0	3.1 + 1.8

N/s to 3744 $\pm$ 1096 N/s (37 %, p < .001) during fatigue. When the force curve was studied using constant or relative increments or decrements the changes during fatigue were found to be greater at higher force levels. During recovery the relaxation varia- bles returned within one minute back to the prefatigue level or even below it showing an increased rate of force relaxation. However, the ten minute period was too short for f-t variables to demonstrate complete recovery.
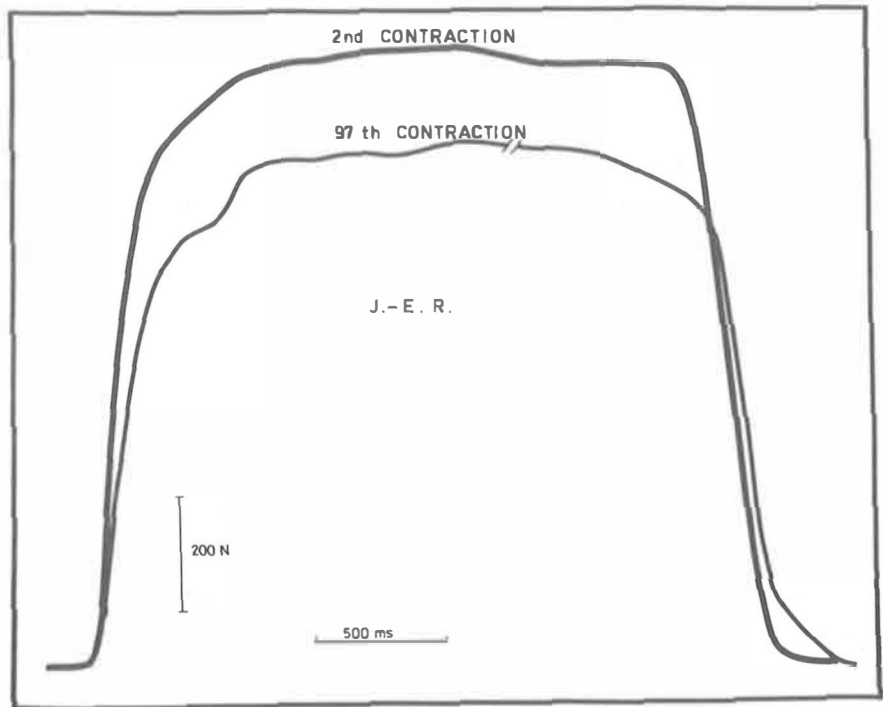
Figure 4. Example of the force curves of the 2nd and 97th fatigue contraction.

3.3. Electromyographic variables

EMG variables (IEMG and MPF) were calculated for each muscle -
m. rectus femoris, vastus lateralis, vastus medialis - separate-
ly. For further analysis they were averaged (studies II - V).
   Isometric fatigue did not change the average IEMG signifi-
cantly from the prevalue of 319.7 $\pm$ 93.9 mV∗s (study V). MPF,
however, decreased significantly (from 97.6 $\pm$ 10.0 Hz to 90.5 $\pm$
15.1 Hz, 7.3 %, p < .05) during the 100 contractions. It recov-
ered to the prefatigue level in about two minutes (see Table 2).

3.4. Blood lactate

Blood lactate measured before, during and after the 100 fatigue
contractions (studies IV and V) increased from the prevalue of
1.5 $\pm$ 0.5 mmol/l to the maximum value of 4.6 $\pm$ 2.0 mmol/l
(310.5 %) which was measured one minute after the work. It re-
covered during nine minutes to the level of 3.1 $\pm$ 1.8 mmol/l
(see Table 2).

3.5. Interrelationships between neuromuscular performance
variables before, during and after fatigue

The absolute values of all variables were correlated in pre-
fatigue conditions (studies I and III). Table 3 summarizes some
of the correlations measured in study III.
   Electromechanical delay measured in voluntary contraction
(MT) had significant correlations with the rate or force devel-
opment (r = -.64, p < .001), maximum force (r = -.62, p < .001)
and muscle structure expressed either as ST % or CST% (r = .58,
p < .001 and r = .51, p < .01, respectively) so that shorter MT
was associated with greater force development, greater maximum
force and higher number or total area of fast twitch muscle
cells in a biopsy sample. Correlation coefficients between MT

Table 3. Intercorrelation coefficients between the main variables in prefatigue condition (study III). For abbreviations see Table 2. ST % = percent of slow twitch fibers in m. vastus lateralis, CST% = the relative area occupied by the ST cells in the total fiber area.

		1	2	3	4	5	6	7	8
Max force	1							r .57	p < .001
IEMG	2	.51						r = .46	p < .01
MPF	3	.16	.06					r = .36	p < .05
RFD	4	.60	.11	.06					
RR	5	.55	.42	−.08	−.53				
MT	6	−.62	−.19	−.16	−.64	−.41			
RfMT	7	.12	−.14	−.23	.30	.03	−.16		
ST %	8	−.14	−.09	.01	−.09	−.03	.58	−.04	
CST%	9	−.18	−.14	−.08	−.03	.02	.51	−.13	.94

and EMG variables were not significant.

Electromechanical delay measured in reflex contraction (RfMT) did not correlate significantly with any of the variables included in this thesis. The correlation coefficient between MT and RfMT was -.16 (n.s.).

Maximal force was found to correlate significantly with RFD ($r = .60$, $p < .001$) and with times taken to increase the force a constant absolute increment of 100 N ($r = -.46 - -.53$, $p < .01$) It was also significantly related to RR ($r = .55$, $p < .01$), MT ($r = -.62$, $p < .001$) and IEMG ($r = .51$, $p < .01$) but not to ST % ($r = -.14$, n.s.) or CST% ($r = -.18$, n.s.).

FT variables expressed as time taken to reach a certain force level were found to correlate significantly ($p < .05 - .01$) with muscle fiber distribution (ST %) up to the force level of $0.9 * P_O$ in study I. The highest coefficient of correlation was between ST % and the time taken to reach the level of $0.4 * P_O$ ($r = .50$, $p < .01$). However, the correlation coefficients between ST % or CST% and different f-t variables in study III failed to reach the level of statistical significance. In addition to the significant relations with maximal force and MT, RFD and the absolute increments of f-t were found to correlate significantly with RR and some relative and absolute decrements of relaxation (study III).

The subjects were found to have different abilities to cessate the neural activity at the beginning of relaxation (study III) so that a steep relaxation curve was connected with a sudden decrease of EMG activity.

Relative changes of the variables were intercorrelated also in _fatigue_ and _recovery_ conditions (studies IV and V). The changes of electromechanical delay measured either in voluntary or in reflex contraction did not correlate significantly with the muscle structure of other variables measured.

The relative decrease of maximal force during fatigue was significantly greater in subjects with low ST % or CST% after nine ($r = .36$, $p < .05$; $r = .40$, $p < .05$, respectively) and after 98 contractions ($r = .46$, $p < .01$; $r = .41$, $p < .05$, respective-

ly). The relative values during recovery were also lower in
subjects with low ST or CST% (r = .37 - .51, p < .05 - .01; r =
.36 - .49, p < .05 - .01, respectively).

The changes of RFD were significantly related to muscle
structure during fatigue but not during recovery so that sub-
jects with low ST % or CST% decreased their RFD more after nine
(r = .36, p < .05; r = .11, n.s., respectively) and after 98
contractions (r = .45, p < .05; r = .39, p < .05, respectively)
than the "slow" subjects. The amount of blood lactate was found
to be related to muscle structure so that it was higher during
and after fatigue (r = -.39 - -.41, p < .05) in subjects with low
CST%.

The changes of relaxation variables during fatigue did not
correlate significantly with muscle structure. By contrast, the
slowing of r-t curve during fatigue was related to weakened
ability to cessate neural activity (EMG) suddenly.

The change of EMG integral after nine contractions was sig-
nificantly related to muscle structure expressed either in ST %
or CST% (r = .45, p < .05; r = .42, p < .05, respectively) and
also to respective changes of maximal force (r = .46, p < .01).
After the 98 fatigue contractions these correlations did not
reach the level of statistical significance. The changes of MPF
of the power spectral density function did not correlate signif-
icantly with the muscle structure variables.

4. DISCUSSION AND CONCLUSIONS

Selected neuro-muscular performance variables and their inter-
relationships were studied in reflex and voluntary contractions
before, during and after fatigue. This discussion will concen-
trate on electromechanical delay measured both in reflex and
voluntary contraction, on isometric force-time and relaxation-
time variables, and on maximal force, EMG integral, EMG frequen-
cy spectrum, muscle structure and blood lactate. The results
will be discussed for prefatigue and fatigue situations sepa-
rately.

Electromechanical delay, force-time variables and maximal
force in voluntary maximal isometric contraction were found to
be interrelated as shown schematically in Figure 5. This sug-
gests that these variables are determined partly by the same
neuro-muscular factors such as eg. muscle structure or level of
training.

In voluntary force production there can be distinguished at
least two different mechanisms which affect the electromechani-
cal delay and f-t variables; contraction behavior of a single
motor unit including its firing frequency, and recruitment pat-
tern of MUs of the whole muscle. Each firing MU can be thought
to have an EMD of its own which is composed of conduction of ac-
tion potential along the muscle fibers and into the T-system, re-
lease of Ca^{2+} by the sarcoplasmic reticulum, formation of cross-
bridges between actin and myosin filaments and stretching of the
series elastic component by the contractile component. Fast and
slow MUs have been shown to differ in respect of action poten-
tial conduction velocity on the muscle fibers (Buller et al.
1965, Eberstein and Goodgold 1968) and in terms of the structure
of the t-tubules system (Luff and Atwood 1972). The shapes of
MU mechanograms differ also so that an FT MU can produce its
force and relax quicker than an ST unit (Steg 1964, Gydikov et
al. 1976). These have been suggested to be related to differ-
ences in myosin ATPase activity between FT and ST muscle fibers

(Barany 1967, Gutmann et al. 1969, Barnard et al. 1971, Close 1972) and/or most probably to the differences in the ability of sarcoplasmic reticulum of FT and ST fibers to release and uptake Ca^{2+} (Mommaerts et al. 1969, Brody 1976, Briggs et al. 1977). FT and ST fibers have been thought to differ also in respect of their rate of cross-bridge cycling so that this rate and following this the rate of rise of isometric tension is slower in ST than in FT fibers (Lännergren 1976). Thus, for these reasons a slow MU is likely to have a longer EMD than a fast MU.

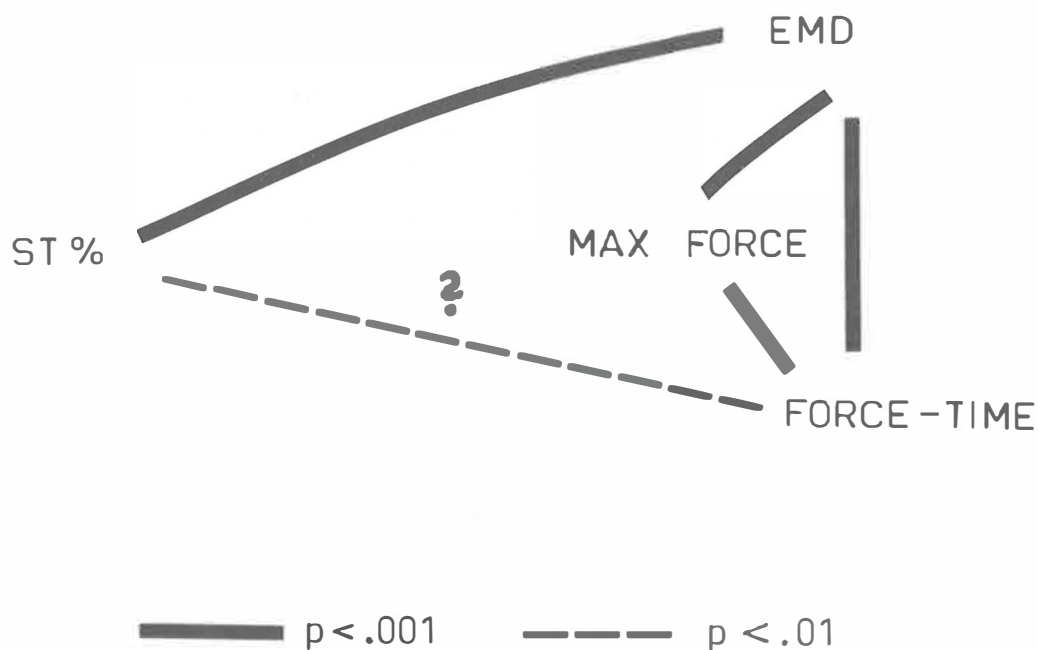Figure 5. Relationships between muscle fiber composition (ST %), electromechanical delay (EMD) in voluntary contraction, maximal force and force-time.

The possible differences between elasticity of FT and ST muscle fibers may likewise have had some effects on EMD and also on f-t and r-t variables. However, because studies concerning interrelationships between elasticity and muscle structure on

one hand, and the effect of fatigue on elasticity on the other
hand are lacking, this discussion concentrates only on the con-
tractile part of the neuro-muscular system.

Fast and slow motor units have been shown to differ in vol-
untary contraction with respect to their firing frequency and
recruitment pattern. In slow isometric contractions it has been
suggested that there operates a so called size principle, ac-
cording to which smaller motoneurons are recruited first
(Henneman et al. 1965). However, in voluntary movements or con-
tractions where high acceleration or high rate of force develop-
ment is needed, FT units, which fire at higher frequency, have
been reported to be very active (Grimby and Hannerz 1968, 1977,
Gydikov and Kosarov 1974). In reflex contraction, however, the
ST units have been thought to be of more importance than the
fast ones (Buchthal and Schmalbruch 1970, Burke 1973). This
probably explains why EMD measured in reflex contraction was
longer than voluntary EMD (study II) and why reflex EMD did not
correlate with muscle structure or the values of other neuro-
muscular variables measured during a voluntary contraction
(study III). This explanation may be valid at low and constant
stimulation level of the reflex loop as used in the present
study. However, McIlwain and Hayes (1977) were able to show the
mechanical values and temporal data of the H-reflex to be de-
pendent on the intensity of stimulation, which suggests the size
principle to work also in reflex contractions. Thus in the
further studies of EMD in patellar reflex condition the inten-
sity of stimulation should be included as a controlled variable.

According to the mechanical behavior and recruitment model
described above the interdependency between voluntary EMD,
force-time and muscle structure are in line with current know-
ledge about the function of the neuro-muscular system. The cor-
relation between ST % and EMD is also in line with the results
reported by McIlwain and Hayes (1977) and by Nilsson et al.
(1977), and support the hypothesis of Norman and Komi (1979)
However, the interdependency between muscle structure and f-t
variables according to the results in studies I and III is not

so clear; in study I a significant relationship existed but in
study III the correlation coefficients did not reach the level
of statistical significance. One explanation for the discrep-
ancy could be found in differences in the testing procedures;
in study I the test contractions were isometric both leg exten-
sions but in study III isometric one leg knee extensions were
used. However, most probably the discrepancy can be explained
by differences in the training status of the subjects. In study
I the subjects were very heterogeneous with respect to their
training level and habits; sportsmen of high quality (skiers,
skijumpers, volley-ballplayers, skaters), untrained policemen
and normal school children. In study III the subject group was
more homogeneous - students in physical education. Thus it
seems that the significant correlations found in the first study
(I) may be explained by either selection of subjects to differ-
ent types of sport events according to their muscle structure or
by the effects of training on muscle structure. The selection
model is supported by those studies that have not found any ef-
fects of training on muscle structure (Gollnick et al. 1973,
Thorstensson et al. 1975, 1976a) or which have emphasized the
effects of heredity on it (Komi et al. 1977a). On the other
hand there is also evidence that muscle structure may change
during training (Tesch et al. 1979, Jansson et al. 1978) or as a
function of age (Larsson et al. 1978). However, no matter why
the subject groups in study I differed in respect of their mus-
cle structure we can assume that the endurance trained subjects,
who also had higher mean ST % than the power event subjects,
differed greatly in their every-day and every-year training and
this could have influenced the differences in their f-t para-
meters. In cross-innervation studies it has been shown that
neural drive has an important effect on the shape of MU mechano-
gram (Buller et al. 1960, 1971, Close 1969, Mommaerts et al.
1969) The change of innervation has been thought to change the
ability of sarcoplasmic reticulum to release and uptake Ca^{2+}
(Mommaerts et al. 1969), which in turn changes the mechanogram.
Thus the type of prolonged training (eg. skiing vs. skijumping)

may have had a pronounced effect on isometric f-t characteristics, thus modifying the basic f-t characteristics given by the muscle structure. The possible effects of training can be seen, when f-t curves of the untrained policemen and the well-trained skijumpers were compared. The average of ST % and maximal relative force for both of these subject groups did not differ significantly but their f-t curves differed greatly as shown in Figure 6. Sensitivity of the f-t curve to training has been also verified in the studies of Sukop and Nelson (1974), Thorstensson et al. (1976b), Häkkinen et al. (1980) and Viitasalo (1980).
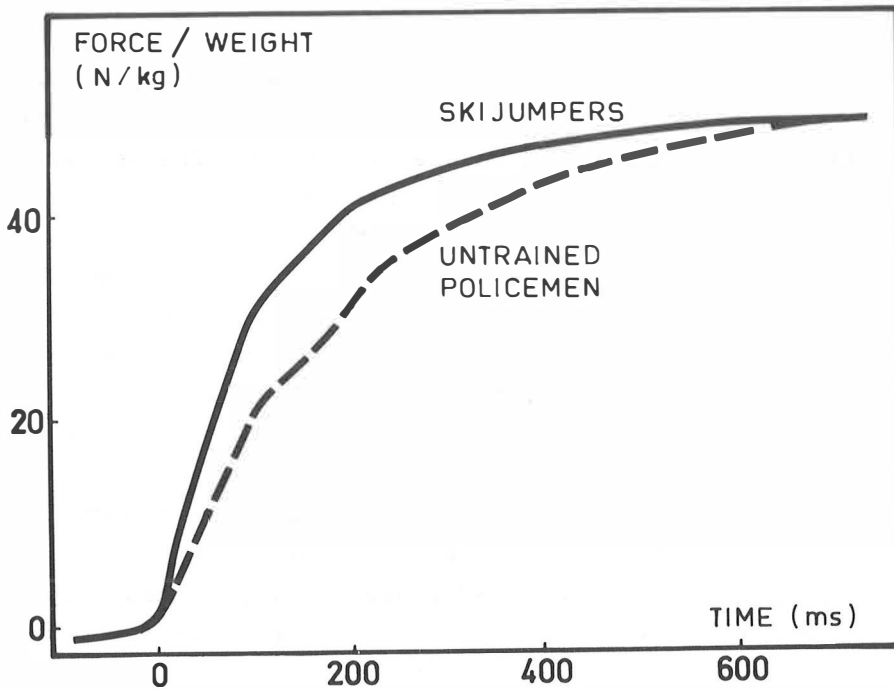
Figure 6. Average force-time curves of the skijumpers and untrained policemen.

Fast MUs have been shown to produce higher tensions than the slow ones (see Wuerker et al. 1965, Burke 1967, Burke et al. 1971, Karlsson 1980). Following this it can be theorized that the subjects with high FT percentage may also have greater maximal force as compared to the slow ones. This has been proved in some studies (Komi et al. 1977b, Tesch and Karlsson 1978) but there exists also data (Hulten et al. 1975, Thorstensson 1976) which support the result in study III that the dependency is very weak or that it is lacking. One explanation for the discrepancy between results of the different studies may, like in connection with f-t characteristics, be in the training status of subjects. For example Tesch and Karlsson (1978) found a significant correlation between isometric force and FT percentage. They reported the one leg isometric knee extension force for their subjects to be 1160 N or 16 N/kg. These values are almost twice those found in physical education students (666 N, 9.3 N/kg) in study III, where we did not find any significant correlations between muscle structure variables and maximal isometric force.

The relaxation part of isometric force curve was not significantly related to muscle structure (study III). Thus the interindividual differences could not be explained by the reported differences of FT and ST motor unit mechanograms (Steg 1964, Gydikov et al. 1976). According to study III the interindividual differences might be due to differences in the ability of the subjects to cessate the neural activity suddenly. This suggests that some neural mechanisms are involved. However, the experimental designs used do not warrant any detailed discussion whether these mechanisms are central or whether they have some connection with proprioceptive feedback systems.

100 maximal isometric contractions caused reduction in maximal isometric force, slowing of force production and relaxation, increase of blood lactate and decrease of EMG mean power frequency (studies IV and V). Changes of EMG integral, maximal force, force-time and blood lactate were significantly related to muscle structure (Figure 7) so that subjects rich in FT fi-

bers showed a greater reduction of maximal force, of rate of
force development and of EMG integral after nine contractions,
and greater reduction of maximal force and rate of force devel-
opment and higher blood lactate after 98 contractions. During
recovery the maximal force, force-time and blood lactate values
of "fast" subjects showed greater deviation from the prefatigue
level than the values of "slow" subjects.
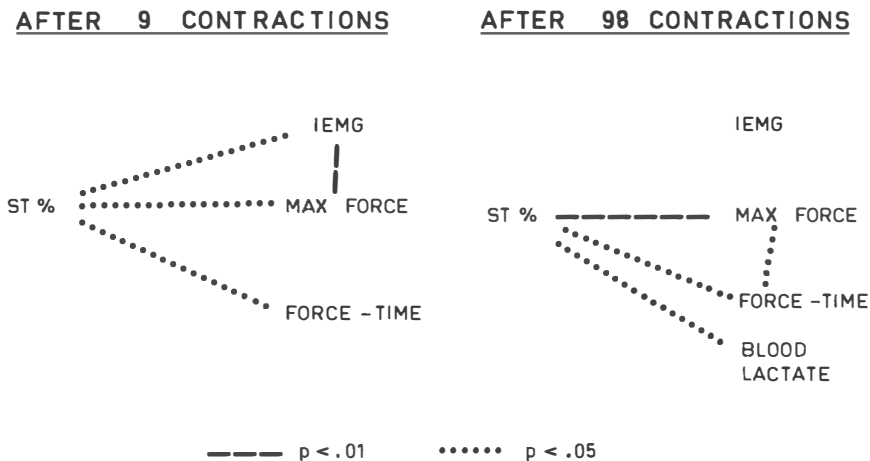
Figure 7.   Relationships between muscle fiber composition (ST %)
            and relative changes of integrated EMG activity
            (IEMG), maximal force, force-time and blood lactate
            after 9 (left) and 98 (right) contractions.

    The term "muscular fatigue" has been suggested to mean the
failure to generate the required or anticipated force during
muscular exercise (Karlsson 1980). Muscular fatigue can be di-
vided into central and peripheral fatigue according to whether
the effects concentrate in the central nervous system or whether
the fatigue appears in the neuro-muscular junction or in the
muscle fiber itself. However, these two sites of the neuro-
muscular system may be closely interrelated during fatigue as
discussed by Asmussen and Mazin (1978a, b).

Muscular fatigue has been shown to change the motor unit mechanogram so that the force production and relaxation part became slower and maximal force level lower (Steg 1964, Gydikov et al. 1976). Fatigue tends also to decrease the firing frequency of MUs (Gydikov and Kosarov 1973). These changes may be the main reasons for the decrease of isometric force production, maximal force and relaxation found in study IV. The changes of MU mechanogram and its firing frequency have been shown to be more remarkable in fast than in slow motor units (Steg 1964, Gydikov and Kosarov 1973, Gydikov et al. 1976). Fatigue produced during high intensity contractions has also been thought to effect the dropping out of primary fast MUs (Gydikov et al. 1976). Thus most probably the selective changes in MU mechanograms, in their firing frequencies as well as in MU recruitment pattern explain the interdependency between muscle structure and relative changes of force-time and maximal force (study IV, Figure 7). The greater force decline during fatigue in subjects with high FT percentage as compared with those with high ST percentage is in agreement with results reported by eg. Thorstensson and Karlsson (1976), Nilsson et al. (1977), Tesch et al. (1978a) and Viitasalo and Komi (1978a).

The 100 fatigue contractions led to a significantly higher rise of blood lactate in subjects with high FT percentage (study IV). This most probably reflects also higher intramuscular lactate value in "fast" subjects. The result is in agreement with those of Essen and Häggmark (1975), Tesch et al. (1978b) and Bonen et al. (1979) and according to Karlsson (1979) is due to greater potential of ST fibers to utilize lactate as fuel. Accumulation of lactate has been shown to decrease intramuscular pH (Mayerhof 1925, Sahlin 1978) which has been thought to reduce the capacity of the sarcoplasmic reticulum to release and uptake Ca^{2+} (Sreter 1969, Dunnett and Nayler 1978, Kentish and Nayler 1978, Robertson and Kerrick 1979) and to reduce the sensitivity of the contractile elements to Ca^{2+} (Schadler 1967, Portzehl et al. 1969, Fuchs et al. 1970) and following these to weaken muscle fiber force production.

Due to the differences in the amount of blood lactate these negative effects of lactate on muscle contraction in study IV were most probably more pronounced in subjects with high FT percentage. Thus the amount of lactate explains partly the changes of muscle contraction capacity during fatigue, which in turn is related to interrelationships between muscle structure and relative changes of force-time and maximal force (study IV). However, lactate may not be the only variable to explain changes of force variables. It has been also suggested that high H^+ concentrations may be connected with impaired muscle function (Fuchs et al. 1970, Nakamaru and Schwartz 1972). In this connection the correlation coefficients between relative change of maximal force and that of blood lactate on one hand and between relative change of RFD and blood lactate on the other hand did not reach the level of significance (study IV). This suggests that here may be some mechanisms other than blood lactate that can also influence the selective effect of fatigue on the "fast subjects". These mechanisms may also be more central and be related to selective decrease of firing frequency and dropping out of MUs as discussed above.

The accumulation of lactate has been assumed to effect a decrease of action potential conduction velocity on muscle fiber (Mortimer et al. 1970). This has been suggested to change the EMG frequency spectrum to lower frequencies during fatigue (Kadefors et al. 1968, Mortimer et al. 1970, Lindström et al. 1970). Viitasalo and Komi (1978a) were able to show these changes during isometric contraction at .7 * P_O force level to be greater in subjects rich in FT muscle fibers. This finding was supported by Larsson et al. (1978b). These results are explainable by the differences in the accumulation of lactic acid between "fast" and "slow" subjects as described above. However, in study IV, we were not able to confirm the result of Viitasalo and Komi (1978a). The explanation for the discrepancy may be in differences of work and rest relations between these two studies. In our previous study (Viitasalo and Komi 1978a) the high intensity static isometric contraction most probably

decreased the intramuscular circulation and washout of metabolic
by-products during the contraction. This was followed by
ischemia and greater decrease of MPF   25 %) than in study IV
(7.3 %), where the 100 fatigue contractions were separated by
relatively long interpauses (from 1.4 to 4.0 s, $\bar{x}$ = 3.08 $\pm$ 0.86
s). Effects of fatigue on MPF may also be partly "neutralized"
by the rise of intramuscular temperature, which has been shown
to change the spectrum to higher frequencies (Petrofsky 1979).
Moreover, according to Bolstad and Ersland (1978) the rise of
intramuscular temperature is likely to be higher in muscles rich
in FT fibers than in the "slow" muscles. Thus, due to the rela-
tive long interpauses in study IV decreasing effects of fatigue
(lactate?) on MPF were probably not so great as during a static
contraction and at the same time elevated intramuscular tempera-
ture possibly tended to increase MPF selectively more in "fast"
than in "slow" subjects. Following this the decrease of MPF was
not related to muscle structure as reported previously (Viita-
salo and Komi 1978b, Larsson et al. 1978b, Komi and Tesch 1979)

Literature is not in full agreement concerning the effects
of fatigue on EMG integral or on its amplitude at maximal force
level. Merton (1954) found no changes in EMG during maximal
isometric contraction. Stephens and Taylor (1972), Komi and
Rusko (1974), Ochs et al. (1977) and Viitasalo and Komi (1980)
reported maximal IEMG to decrease during fatigue but
Thorstensson and Karlsson (1976) and Nilsson et al. (1977) re-
ported a tendency for EMG output to even increase with repeated
maximal voluntary concentric contractions. Komi and Viitasalo
(1977) found the changes of IEMG during fatigue to vary accord-
ing to muscle and type of contraction (eccentric-concentric)
and Bigland-Ritchie et al. (1975) showed the ability of a sub-
ject to increase the decreased EMG activity back to prefatigue
level in brief "super efforts" during fatigue. In study V IEMG
did not change significantly during the 100 extensions. How-
ever, during the first nine contractions the small changes of
IEMG correlated significantly with fiber distribution and with
relative change of maximal force (Figure 7) so that "fast" sub-

jects showed the greatest decrease of IEMG and force. The re-
sults could be explained by selective fatigue and dropping out
of fast motor units. The result is in line with those reported
by Ochs et al. (1977) and Komi and Tesch (1979).

The dependency between muscle structure and change of IEMG,
however, was not significant after the 100 contractions. Mi-
gration of electrical activity from one muscle to another has
been suggested to happen during fatigue (Lippold 1955, Viitasalo
and Komi 1977) and it could also be the reason for the disap-
pearance of significance after the 98 fatigue contractions.
However, in study IV IEMG was measured and averaged from three
of the four knee extensor muscles. So there is no reason to be-
lieve that m. vastus intermedius has such a function to compen-
sate the fatigue effects found in other parts of m. quadriceps
femoris. Thus there must be some other mechanisms like synchro-
nization of MUs (Scherrer and Bourguignon 1959, Lippold et al.
1960, Missiuro et al. 1962, Sloan 1965, Person and Kudina 1968,
Kwatny et al. 1970, Person and Libkind 1970) involved, which
affected the EMG integral. However, these mechanisms need more
investigation.

Electromechanical delay measured either in reflex or in vol-
untary contraction decreased significantly during fatigue (study
 IV). The results are contrary to those reported by Nilsson
et al. (1977), Klimovitch (1977) and Wood (1979), who found vol-
untary EMD to increase during fatigue. However, EMDs reported
by these authors were so long as compared to those reported eg.
by Corser (1974), Ralston et al. (1976), Cavanagh and Komi
(1979) and Norman and Komi (1979) or to those found in studies
II and IV that there is reason to believe that because of the
relative high threshold used by Nilsson et al. (1977) and
Klimovitch (1977) the increases of EMD were due to slowing of
early force-time curve during fatigue, which was also shown in
study IV and discussed above. This may likewise explain the
significant correlation that Nilsson et al. (1977) found between
muscle fiber distribution and change of EMD during fatigue. The
decrease of voluntary EMD during fatigue is in line with the

results by Hayes (1975) and Viitasalo and Komi (1980). The latter study reported a slight but not significant decrease of EMD after 85 kilometer long ski race. They did not find any significant correlations between the change of EMD and muscle structure, which is in line with the results obtained in study V. Thus it seems that some other mechanisms are more responsible for changes of EMD during fatigue than muscle structure. Increase of muscle temperature may explain partly the decrease of EMD so that elevated temperature increased the propagation velocity of action potential on and inside the muscle fiber (see Buchthal et al. 1954) and speeded chemical reactions inside the muscle, eg. rate of Ca^{2+} release by the sarcoplasmic reticulum (Harigaya and Schwartz 1969) and excitation-contraction coupling. This explanation concerning the effects of elevated temperature on the propagation velocity of action potential on muscle fiber is in line with the effects of fatigue on MPF of EMG and its connections with elevated temperature as discussed above.

Relaxation variables were the most sensitive to fatigue but they also recovered from fatigue very quickly - in about one minute (study IV). These changes during and after fatigue were not significantly related to muscle structure. Instead ability to cessate neural activity quickly was seen to lengthen during fatigue (study IV). Thus some neural mechanism is assumed to be responsible for the slowing down of relaxation during fatigue together with the slowing down or relaxation of individual MUs. However, the possible central mechanisms need more investigation. At MU level the reason for the change of mechanogram during fatigue was probably changes of intramuscular lactate and pH, which in turn may inhibit resynthesis of ATP (see Sahlin 1978). Diminished amount of ATP may have slowed the function of Ca^{2+} pump, removal of Ca^{2+} from contractile material and following this the relaxation of MU took more time.

The r-t variables recovered in one minute below the pre-fatigue level showing the subject to be able to relax faster after fatigue than before it. This could be explained by possi-

bly elevated intramuscular temperature (eg. Edman and Flitney 1978) which speeded chemical reactions, eg. in this case rate of Ca^{2+} removal from the contractile material (eg. Harigaya and Schwartz 1969, Sreter 1969). The one minute recovery period after the 100th contraction can be thought to have been long enough for resynthesis of ATP to allow a full operation of Ca^{2+} pump and thereby for effective removal of Ca^{2+} from contractile material (see Fitts and Holloszy 1976). The effect of temperature on relaxation is partly supported also by Westerman and Gerbrandy (1969), who found shortening of Half Relaxation Time of the ankle jerk with increasing of muscle temperature.

In conclusion, some neuro-muscular performance variables like electromechanical delay, force-time, maximal force and EMG integral were found to depend on muscle structure either in pre-fatigue, fatigue or postfatigue situations. However, possible effects of training or habitual type of physical activity, inaccuracy in the determination of muscle fiber distribution or fiber area using one or two biopsies, and uncertainty of representativeness of muscle samples taken from one of the four working muscles did not allow any high correlations between muscle structure and the variables studied. Therefore, in further studies it seems important to examine in more detail how training influences neuro-muscular performance variables taking into account muscle structure. Moreover, when knee extensions are used, the relative contribution of each head of m. quadriceps femoris to force production and dependency between the structure of m. vastus lateralis and the three other knee extensors should be investigated. In addition, it would seem to be important to combine measurements of intramuscular lactate, pH and temperature with the parameters described in the present report.

TIIVISTELMÄ

Tutkimuksessa selvitettiin hermolihasjärjestelmän toimintaa ref-
lektorisessa ja isometrisessa tahdonalaisessa lihassupistuksessa
ennen väsytystä, väsymyksen aikana sekä palauduttaessa väsymyk-
sestä. Tähän yhteenvetoon on sisällytetty tutkituista muuttu-
jista reflektorinen ja tahdonalainen elektromekaaninen viive,
isometriseen voimantuottoon ja relaksaationopeuteen liittyvät
muuttujat, maksimaalinen isometrinen voima, maksimaalisella jän-
nitystasolla mitattu lihaksen EMG-aktiviteetin integraali ja te-
hotiheysspektrin painopiste, veren maitohappopitoisuus sekä li-
haksen lukumääräinen ja pinta-alaan perustuva solusuhde.

Tutkimuksen ensimmäisessä (I) osajulkaisussa selvitettiin 38
urheilijalla ja 38 ei-urheilijalla molempien jalkojen isometri-
sella ojennuksella tuotetun voima-aika käyrän muuttujien tois-
tettavuutta sekä voimantuottonopeuden riippuvuuksia neulabiop-
siatekniikalla m. vastus lateraliksesta määritettyyn solusuhtee-
seen. Osajulkaisuissa II - V tutkittiin edellä mainittujen her-
molihasjärjestelmän toimintaa kuvaavien muuttujien mittausten
toistettavuutta, muuttujien keskeisiä riippuvuuksia sekä yhteyk-
siä lihaksen rakenteeseen. Raporttien II - V aineisto kerättiin
samassa testaustilanteessa 29 liikunnanopiskelijalla siten, että
mittaukset aloitettiin l4-l6:lla isometrisella verryttelysupis-
tuksella, jonka jälkeen rekisteröitiin kuusi patellaarirefleksiä
koehenkilön oikeasta jalasta tämän ollessa istuma-asennossa sekä
otettiin lepoverinäyte sormenpäästä. Tätä seurasi sata l.4
4.0 s välein toistettua maksimaalista oikean jalan isometristä
ojennusta reaktiona samanaikaisiin ääni- ja valosignaaleihin.
Palautumista sadan supistuksen aiheuttamasta väsytyksestä seu-
rattiin kymmenen minuutin ajan rekisteröimällä kunkin palautu-
misminuutin alussa kolme patellaarirefleksiä ja yksi maksimaali-
nen isometrinen ojennus. Verinäyte otettiin lisäksi 90-95 su-
pistuksen välillä sekä kunkin palautumisminuutin alussa. Patel-
laarirefleksiä käytettiin reflektorisen elektromekaanisen vii-
veen laskemiseen. Isometrisistä maksimaalisista ojennuksista

puolestaan laskettiin tahdonalainen elektromekaaninen viive,
voimantuotto- ja relaksaationopeus, maksimaalinen voima sekä EMG
muuttujat. Koehenkilöiden m. vastus lateraliksen rakenne määri-
teltiin kaksi viikkoa ennen testauksia suoritetulla neulabiop-
sialla.

Tahdonalaisessa lihassupistuksessa mitattu elektromekaaninen
viive korreloi merkitsevästi lihaksen solusuhteeseen siten, että
nopean solusuhteen omaavien koehenkilöiden viive oli lyhempi
kuin "hitaiden" koehenkilöiden viive. Tuloksen oletettiin joh-
tuvan toisaalta hitaan ja nopean motorisen yksikön supistumis-
ominaisuuksien ja syttymisfrekvenssien eroista, ja toisaalta yk-
siköiden selektiivisestä rekrytoitumisesta nopeaa voimantuottoa
vaativassa supistuksessa. Nämä tekijät oletettiin vaikuttavan
myös tutkittuihin voima-aika ja relaksaatio-ominaisuuksiin. En-
simmäisessä (I) osajulkaisussa, jossa koehenkilöinä oli eri la-
jien huippu-urheilijoita sekä ei-urheilijoita, molempien jalko-
jen isometrinen voima-aika käyrä havaittiin riippuvan lihaksen
solusuhteesta siten, että "nopeiden" koehenkilöiden voimantuot-
toajat olivat "hitaita" lyhyempiä. Tätä tulosta ei kuitenkaan
voitu varmentaa kolmannessa (III) osajulkaisussa, jossa koehen-
kilöinä oli liikunnanopiskelijoita. Tulosten eroavuus oletet-
tiin osoittavan voima-aika käyrän olevan enemmän riippuvainen
harjoituksesta kuin lihaksen rakenteesta. Yksilöiden väliset
relaksaatio-ominaisuuksien erot liittyivät interindividuaali-
siin eroihin kyvyssä lopettaa neuraalinen aktiviteetti äkilli-
sesti. Sen sijaan lihaksen solusuhteella tai solujen pinta-
alalla ei ollut merkitseviä yhteyksiä relaksaatioon vastoin kir-
jallisuuden perusteella tehtyä oletusta. Reflektorisessa lihas-
supistuksessa mitattu elektromekaaninen viive oli merkitsevästi
pidempi kuin tahdonalaisen supistuksen viive. Reflektorinen
viive ei korreloinut merkitsevästi maksimaaliseen voimaan eikä
voima-aika muuttujiin kuten tahdonalainen viive. Näiden teki-
jöiden yhdessä kirjallisuudesta saatujen viitteiden kanssa pää-
teltiin tukevan käsitystä, että monosynaptinen refleksikaari
toimisi pääasiassa hitaiden motoristen yksiköiden kautta.

Sata maksimaalista väsytyssupistusta aiheutti voimantuotto-
ja relaksaationopeuden hidastumisen, reflektorisen ja tahdon-
alaisen elektromekaanisen viiveen lyhenemisen, maksimaalisen
voiman ja EMG:n tehotiheysspektrin painopisteen pienenemisen se-
kä veren laktaatin kasvun. Nämä muutokset kytkeytyivät lihaksen
rakenteeseen siten, että väsymyksen aikaiset maksimaalisen voi-
man, voima-aika muuttujien ja veren laktaatin muutokset olivat
suurempia nopean solusuhteen omaavilla koehenkilöillä. Integ-
roidun EMG-aktiivisuuden muutokset kymmenen ensimmäisen supis-
tuksen aikana liittyivät maksimaalisen voiman muutoksiin ja li-
haksen solusuhteeseen siten, että nopean solusuhteen omaavien
koehenkilöiden IEMG ja voima pienenivät enemmän kuin "hitaiden"
koehenkilöiden vastaavat arvot. Väsymyksen aikaiset muutokset
ja niiden riippuvuudet tai riippumattomuudet lihaksen rakentees-
ta selitettiin laktaattipitoisuuksien, lihaksen lämpötilan, rek-
rytointimallin, motoristen yksiköiden syttymisfrekvenssien sekä
syttymisen synkronisaation muutosten avulla.

Vastaisissa hermolihasjärjestelmän toimintaan liittyvissä
tutkimuksissa tulisi selvittää mm. m. vastus lateraliksesta mi-
tatun lihaksen solurakenteen edustavuus koko polviniveltä ojen-
tavaan lihasryhmään (m. quadriceps femoris) nähden sekä toisaal-
ta tämän lihasryhmän neljän eri osan keskinäinen "työnjako" vä-
symyksen, lihasjännityksen, supistumisnopeuden ja raajan nivel-
kulmien funktiona. Samoin antanee intramuskulaarisen laktaatin,
pH:n ja lämpötilan mittaaminen mahdollisuuden selittää tarkemmin
mekanismeja, jotka liittyvät väsymyksen aikaisiin hermolihasjär-
jestelmän toiminnan muutoksiin.

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