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ABSTRACT

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The present study was planned to demonstrate possible differences in neuromuscular function and mechanical efficiency (ME) between power- and endurance-trained athletes during natural locomotion. Reflex and voluntary functions were studied in isolated conditions and in the maximal and submaximal stretch-shortening cycle (SSC) exercises (jumping and running). In the reflex conditions, the endurance group was more responsive to mechanical stimuli because of obvious dominance of the slow twitch fibers. In the maximal voluntary conditions for knee extensors and plantarflexors, the power athletes produced higher forces with higher rates of force production. However, the respective EMG-time curve did not differ between the subject groups suggesting that the observed differences are primarily of structural origin. In the maximal jumping exercises, the power athletes were also able to produce high preactivation of leg extensor muscles and successive high and smooth eccentric activity. Additionally in the concentric phase of the take-off, they showed rapid EMG recovery. In the submaximal jumping and running, ME was quite similar in all conditions among both subject groups. This might be due to the endurance athletes having more developed oxidative metabolic functions, whereas the power group demonstrated better neuromuscular function. In other words, higher ME could physiologically be achieved by improved economy of the performance or by the better utilization of elasticity. It is therefore suggested that the training background and/or the inherited structures cause differences between the athletic groups in neuromuscular function and in muscle metabolism. However, in many cases these differences were more individual and, therefore, there appeared no influence on ME in group analysis.

Key words: stretch-shortening cycle, mechanical efficiency, stretch reflex, electromyography, muscle strength, jumping, running

CONTENTS

PREFACE

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

I Kyröläinen, H. and Komi, P.V. (1994) Stretch reflex responses following mechanical stimulation in power- and endurance-trained athletes. Int J Sports Med 15: 290-294.

II Kyröläinen, H. and Komi, P.V. (1994) Neuromuscular performance of lower limbs during voluntary and reflex activity in power- and endurance-trained athletes. Eur J Appl Physiol 69: 233-239.

III Kyröläinen, H. and Komi, P.V. (1995) The function of neuromuscular system in maximal stretch-shortening cycle exercises: comparison between power- and endurance-trained athletes. J Electromyogr Kinesiol 5: 15-25.

IV Kyröläinen, H. and Komi, P.V. (1995) Differences in mechanical efficiency between power- and endurance-trained athletes while jumping. Eur J Appl Physiol 70: 36-44.

V Kyröläinen, H., Komi, P.V. and Belli A. (1995) External mechanical efficiency in athletes during running. Scand J Med Sci Sports (in press).

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Jyväskylä, March 1995
Heikki Kyröläinen

1 INTRODUCTION

In most human motions the skeletal muscles are acting through a stretch-shortening cycle (SSC) (Norman and Komi 1979): the eccentric muscular work is followed by the concentric one, and the performance of the muscle during the eccentric phase influences the subsequent concentric action (Cavagna et al. 1965; Komi 1984). The focus of the present series of studies was to investigate SSC related neuromuscular performance of athletes. As an introduction to the existing biomechanical and physiological basis of the problem, a short review of the historical development is given in the following paragraphs.

Marey and Demeny wrote in 1885 as follows: "If we perform two successive vertical jumps exerting each time our maximal effort, it always happens that the second jump is higher than the first one. The storage of work in the tense muscles gives to it, since beginning of the second jump, a very high elastic force which on the contrary was developed only gradually by the muscle during the first jump". Over a hundred years later their observations have been used to evaluate the contribution of elastic energy in jumping (Asmussen and Bonde-Petersen 1974; Cavagna 1977). However, the utilization of muscular elasticity in human motion has been studied since 1923 by Fenn. He observed (1930) that the muscles are unable to keep the energy stored during negative work, but waste it as heat. Later this finding was confirmed by Elftman (1944).

In the beginning of this century, Hoffman (1918) studied reflexes of animals in an isolated condition and introduced the monosynaptic stretch reflex. He utilized EMG for the recordings of the reflexes and described the monosynaptic pathway as the simplest spinal feedback system. The first physiological stretches applied to intact human muscles to study stretch reflex were probably performed by Hammond in 1954. He showed that a sudden stretch of upper limb muscles resulted in two distinct periods of EMG activity at rest. The first electrophysiological recordings during movement were performed by Engberg and Lundberg (1969), and by Grillner (1972) who studied central programming in cats.

In natural human locomotion, the neuromuscular system is acting simultaneously with many other physiological functions. Therefore, biomechanics and exercise physiology have been combined in many studies for obtaining more knowledge about human movement. Since Dickson (1929), who studied how the efficiency of bicycle pedalling was affected by speed and load, many scientists have been interested in the economy of human movement (e.g. Abbott and Aubert 1952; Henry and De Moor 1950; Christensen et al. 1960; Banister and Jackson 1967; Margaria 1968, Whipp and Wasserman 1969). In general, it can be described as mechanical efficiency (ME), which is the amount of the work done related to the net energy expended.

In the present study neuromuscular function and ME were studied during natural SSC exercises (jumping and running) among power- and endurance-trained athletes. The muscle action is continuously regulated by the neural system. Therefore, electromyography (EMG) was recorded during maximal and submaximal exercises as well as in isolated reflex and voluntary conditions. In the analysis, the muscle activity patterns and the integrated EMG (IEMG) were utilized together with other biomechanical and physiological parameters to interpret the ME results. Additional information is given in the review of literature. It consists of the motor control of human movement, as well as the utilization of muscle elasticity and mechanical efficiency in natural human locomotion.

2 REVIEW OF THE LITERATURE

2.1 Motor control of human movement

2.1.1 Motor control theories

The servo control of human movement has been presented in many theories. Historically the first was Merton´s hypothesis (1953) regarding the use of the fusimotor neurons as the primary initiator of muscle contraction. It suggests that the main output of motor command centres are the gamma rather than the alpha motoneurons, and the movement is always preceded by a burst of spindle afferent activity as a result of such fusimotor activity. Later this theory has been disputed. Granit (1975) hypothesized that the alpha and gamma motoneurons are activated simultaneously by the same command signal (alpha-gamma coactivation). The weakness of this theory is that when the intrafusal and extrafusal fibre are acting simultaneously, there will be no change in the state of activity of the spindle afferents and no feedback.

Houk (1979) stated that the spindle feedback is used in concert with the negative feedback from Golgi tendon organs to stabilize the stiffness of the muscle; it is the tendomuscular force related to the change of its length (Nichols and Houk 1976). Houk´s analysis is based on the three major components: 1) a muscular component is purely mechanical, 2) a length-feedback component is mediated by the single pathway and consists of a facilitation of motor output that tends to increase force, and 3) a force-feedback component is mediated by the tendon organ pathway and consists of an inhibition of motor output that tends to decrease the force (Houk 1974).

In SSC-exercises, these proprioceptive reflexes are functioning simultaneously with the voluntary neural system. However, their role

distributions are not well-known. Therefore, further studies are needed to clarify effects of the reflexes on physical performance.

2.1.2 The role of the central nervous system (CNS)

The central nervous system (CNS) can produce organized motor programs without the assistance of sensory feedback. Thus, there is a neural pattern generator residing within the CNS that serves to produce the basic motor program (Wilson 1972). However, sensory information can modify central programs so that the output of the CNS is adaptive to the particular needs of the task. In other words, afferent information influences the central pattern and, conversely, the central pattern generator selects the appropriate afferent information.

Stein (1978) has summarized the principles of motor control as follows: "1) There are command neurons that activate the pattern generator. 2) The pattern generator is composed of a set of local control centres. 3) There are neurons within these centres that coordinate muscular synergies and generate timing signals. 4) Co-ordination among the centres can be produced by centrally derived signals, sensory-derived signals, or both. 5) Sensory signals can measure motor performance and be utilized to improve performance. 6) The pattern and/or the command signals can adjust the properties of sensory pathways during the movement".

2.1.3 Proprioceptive reflex system

In reactive SSC-exercises, such as sprint running and jumping, the fast motor control of human movement is essential for powerful performance. Before the ground contact the extensor muscles are activated under central motor program (Melvill-Jones and Watt 1971; Dietz et al. 1979). The presence and timing of preactivity depend on foot position and on the expectancy of the moment of ground contact. However, in some movements the programmed EMG pattern might be generated on a spinal and/or a brain stem level (Dietz 1992). During the initial ground contact , reflexes from the muscle spindles and tendon organs are thought to play an important role in adjustments to external disturbances. On the whole, many spinal pathways have been identified: Ia excitatory pathways from the muscle spindle's primary endings, pathways of reciprocal Ia inhibition, the circuitry of the recurrent inhibition through Renshaw cells, and the pathways fed by Ib fibre from the Golgi tendon organs (Matthews 1969). If the stretch of the muscle is moderate, it influences the potential of the stretch reflex via Ia-afferent from the muscle spindle (Prochazka et al. 1977), of which primary and secondary endings are more sensitive to small amplitude displacements compared to the larger ones (Matthews and Stein 1969). The pathways that are fed by Ib-afferent fibres from the Golgi tendon organ contribute to the force attainment of limb muscles according to the requirements of a movement (Schomburg 1990).

The primary purpose of the proprioceptive reflex system is to mediate feedback information from the muscles, joints and associated tissues in order to adjust the motor program to irregular movements. Thus, muscle function is continuously regulated by the neural system. Preactivity before the ground contact prepares the neuromuscular system for the eccentric phase (stretching phase) of the muscle action. Therefore, preactivation appears to be a preparatory requirement, both for the enhancement of EMG activity during the eccentric phase of the take-off, and for the timing of muscular action with respect to the ground contact (Moritani et al. 1991). This leads us back to the term tendomuscular stiffness, which can be regulated by the motor servo systems as described earlier. However, the origin of nerve regulators is not well-known.

The investigation of motor control has been focused, to a large extent, on studies of reflex EMG elicited by muscle stretch or electrical stimulation. The short latency stretch reflex (short-latency component) is the monosynaptic reflex mediated by Ia-afferent from the muscle spindle (Lee and Tatton 1975; Jaeger et al. 1982), while the following components (long latency components) may result from different sources of reflex activity: secondary ending activity (Matthews 1984), cutaneous afferent (Darton et al. 1985), long-loop, and transcortical pathways (Phillips 1969; Melvill-Jones and Watt 1971; Marsden et al. 1976). Supraspinal centres may regulate the gain of spinal stretch reflexes and motoneuron excitability during a cyclic movement; according to the demands of force and speed of the motor activity (Moritani et al. 1991). Different latency times of reflexes allows us to conclude that the reflex functions are acting segmentally. However, in voluntary landing the segmented EMG pattern has been suggested to be produced by a central program and any influence of afferent input is little or non-existing (Dyhre-Poulsen et al. 1991).

2.1.4 The effect of motor unit type on its recruitment

The muscle fibre distribution affects the motor function of human movement. The motor unit type has been demonstrated to be a critical factor controlling motor unit recruitment in heterogeneous muscles (Sypert and Munson 1981). The small ST-fibre, which has lower thresholds than FT-fibre, would be recruited first (Calancie and Bawa 1985). Burke (1968) reported that many ST and fatigue-resistant fast twitch (FT_a) units were spontaneously active and were recruited easily with muscle stretch. These same units have been suggested to be very active in movements which involve significant support from the spindle afferent feedback (Burke and Edgerton 1975). In addition, the factors that determine recruitment order are closely related with axonal velocity (Clamann and Henneman 1976; Bawa et al. 1984). In general, the increased motoneuron facilitation and/or the strength of the torque shift causes the EMG to respond with shorter latency (Calancie and Bawa 1985).

2.2 Muscle elasticity and human performance

Elasticity in muscles and tendons play an important role in enhancing both the effectiveness and the efficiency of human performance (Komi, 1984). Stretching an active muscle results in the storage of elastic energy. It can be utilized when the concentric muscular action follows the stretch immediately (the eccentric action) (Cavagna et al. 1965). Classical models (Fenn and Marsh 1935; Hill 1938) describe the behaviour of muscles in three functional components. The contractile and force generating component is characterized by force-velocity and force-length relationships (e.g. Hill 1938; Wilkie 1950). The series elastic component (SEC) and parallel elastic component (PEC) represent elastic structures according to their geometrical relationship with the contractile component. Tendons, along with connective tissues within the contractile proteins, are a major part of the SEC, while the PEC consists of muscle fascia, connective tissue, and sarcolemma. These tissues are passive elastic structures in this three component model of muscle, while cross-bridges and myofibrils are the active components of the SEC. However, it also suggested that the cross-bridges themselves are elastic structures. Especially, the instantaneous elasticity induced by changing the length of the muscle fibre, or at least the greater part of it, might be in the cross-bridges (Huxley and Simmons 1971; Rack and Westbury 1974).

The performance enhancement of the SSC is believed to be due to elastic behaviour of muscle (Komi, 1984). The stretching of activated muscle (eccentric phase) may increase force output in the subsequent shortening (concentric) phase of the muscle. The ability of the muscle to store and utilize the elastic energy is dependent on the stretching velocity, the muscle length (Cavagna et al. 1965), as well as the force attained at the end of the prestretch and the coupling time between the eccentric and concentric phases of the performance (Bosco et al. 1981). A short and rapid stretch with a short coupling time and a high force at the end of prestretch creates a good precondition for utilizing tendomuscular elasticity (Cavagna et al. 1968; Bosco et al. 1982ab). The force attained at the end of the stretching period depends, however, on the amplitude and the velocity of the stretch. During stretching three types of mechanisms may exist in order to explain simultaneous force enhancement: 1) an increase in the number of attached cross-bridges (Colomo et al. 1986), 2) an increase in the force developed by each cross-bridge (Sugi and Tsuchiya 1981), and 3) a recruitment of additional force-bearing elements (Edman et al. 1978).

The phenomenon of elasticity is therefore related to the mechanical structure of the tendomuscular system and to muscle fibre distribution. Subjects with more fast twitch (FT) fibres benefit more from the rapid stretch with small amplitude than their slow type counterparts. On the other hand, slow twitch (ST) fibres have a longer cross-bridge cycle time (Goldspink 1978) which allows them to utilize better long and slow stretches (Bosco et al. 1980).

In-vivo tendon force measurements in humans have given further information about force-length and force-velocity curves during natural locomotion (e.g. Komi et al. 1987; Komi et al. 1992; Fukashiro et al. 1993). In

running, the changes in force-length curve have demonstrated a very sharp increase in force during the stretching phase, which was characterized by a small change in muscle-tendon length. Simultaneously, high potential could be seen in the stretching phase (eccentric action) of the force-velocity curves (Komi 1992). Angular velocity-moment curves have also been used to demonstrate increased performance caused by elastic potential which can be observed as increased power (Huijing 1992). Thus these findings give further information about understanding elasticity and its utilization during the subsequent shortening phase of the muscle.

Special training can modify the tendomuscular elasticity, especially the elastic properties of connective tissue (Suominen et al. 1980, Woo et al. 1981). In the skeletal muscle, these adaptations are manifested by increased tensile strength and stiffness, with the effect being greater in slow contracting muscles compared to fast contracting ones (Kovanen et al. 1984). The stiff material properties in the slow muscle (e.g. soleus) are caused by the relatively high amount of collagen. It is suggested therefore that this kind of collagenous and stiff muscle benefits more the functioning via muscle spindles (Kovanen, 1989), the number of which is higher in slow than in fast muscles (Botterman et al., 1978). However, the mechanisms responsible for the adaptive changes of connective tissues are not clearly understood (Zernicke and Loitz, 1992). In addition, during natural locomotion, elasticity is under motor control all the time. The training has been shown to influence the neural input to the muscle (e.g. Häkkinen and Komi 1986; Kyröläinen et al. 1991). However, there are still many unknown processes of how the tendomuscular system itself and the neuromuscular functions adapt to the different kinds of training.

2.3 Mechanical efficiency (ME) in human locomotion

2.3.1 Methods to calculate ME

ME describes the amount of the work done as a proportion of the energy expenditure. The determination of the mechanical work varies enormously in the literature. The total mechanical work can be divided into two components: 1) external work is the sum of the work required to accelerate the centre of gravity of the whole body and the work done against the gravity, and 2) the internal work is done when moving the limbs around the centre of gravity of the body. However, the methods of defining these two parts of mechanical work have varied. In most cases film analysis was employed to define mechanical work in walking and running (Norman et al. 1976; Cavagna and Kaneko 1977; Pierrynowski et al. 1980; Ito et al. 1983). In calculations the human body has been treated in rigid segments (Winter 1979; Aleshinsky 1986a-e). The film analysis was also used with simultaneously measured force signals for determining the mechanical work (Kaneko et al. 1981). Forces have been time integrated to obtain velocities and positions (Cavagna et al. 1975; Bosco et al. 1981; Kram and Powell 1989). In addition, force measurements

given by a special sledge dynamometer have been combined to the distance the sledge moved to obtain the mechanical work (Kaneko et al. 1984; Aura and Komi 1986ab, Kyröläinen et al. 1990).

The energy expenditure has usually been measured indirectly from the analysis of CO_2 - and O_2 -concentrations in expired air by a manually operated chemical analyser (e.g. Scholander 1947) or by more sophisticated automatic systems.

2.3.2 Earlier findings

After Fenn (1923), many scientists have been interested in the efficiency and/or economy of animal and human locomotion. Margaria et al. (1963a) measured the oxygen consumption in successive knee bending exercises with a variable interval time between flexion and extension of lower limbs. The efficiency was greater when the shortening was immediately followed by the stretching of the muscle. Taylor et al. (1982) have shown that the big red kangaroo becomes more economical as the speed of hopping increases. Bosco et al. (1982a) have demonstrated that ME increases during jumping with higher angular velocities of the knee joint. Therefore, it is possible that implanted mechanical energy may be temporarily stored in the series of elastic components of active muscle for utilization in a subsequent muscle action (Asmussen and Bonde-Petersen 1974). With a good utilization of elastic energy, metabolic demands of muscles may decrease and, subsequently, ME may increase. Training, at least power type strength training, can improve the recoil characteristics of muscles causing increased ME (Kyröläinen et al. 1991).

In jumping, the averaged net ME was 38.7 % in the conditions where the amplitude of knee bending in the braking phase was small (Aura and Komi 1986b). The respective value for jumping with large knee bending was 30.1 %, and without any prestretch of knee extensor muscles the net ME was 19.7 %. In SSC-exercises measured on a sledge apparatus the net ME of positive work was 35.5 ± 6.9 % (Aura and Komi 1986b). This value increased with increased prestretch intensity when the work due to elasticity also increased. However, a recent study indicated that it is not correct to use energy expenditure values of pure negative work in the negative phase of SSC-exercises. In pure negative work EMGs have been much lower than in comparable eccentric phases of SSC exercise. Higher EMG values during SSC exercise would imply higher energy expenditure, while the same mechanical work was being done in both cases. Therefore, the true ME of the eccentric phase in SSC exercise is somewhat different from that of the isolated eccentric exercises. Therefore, the total ME values in SSC exercises have been used in further studies. Its value has been demonstrated to increase due to the power type strength training when the test stretch load was high enough (from 39.5 ± 4.6 % to 46.1 ± 5.0 %, $p < 0.01$) (Kyröläinen et al. 1991). At the same time the displacements of knee and ankle joints as well as muscle activation started earlier. In addition, the training may have modified the reflex control of the eccentric phase during take-off, leading

to obviously more optimal tendomuscular stiffness characteristics in the braking phase (Kyröläinen et al. 1991).

In running, the values of efficiency have varied enormously (from 19 % to 80 %) depending on the methods used to measure and calculate the mechanical work and energy expenditure (e.g. Cavagna et al. 1965; Margaria 1963b, 1968; Pugh 1971; Asmussen and Bonde-Petersen 1974; Norman et al. 1976; Cavagna and Kaneko 1977; Cavagna 1978; Kaneko et al. 1981; Ito et al. 1983). In addition, various other physiological and environmental factors such as age (e.g. Daniels et al. 1978; Krahenbuhl and Pangrazi 1983), sex (e.g. Bransford and Howley 1977), air resistance (e.g. Costill and Fox 1969; Pugh 1970; Pugh 1971), body temperature (e.g. Rowell et al. 1969), body weight (e.g. Cureton et al. 1978; Karen et al. 1981; Bergh et al. 1991), maximal aerobic power (e.g. Mayhew 1977), and muscle fibre distribution (e.g. Bosco et al. 1987) have been noticed to influence running efficiency/economy. Thus, numerous investigations have been published in the physiological aspects of running efficiency/economy. Less research is, however, available concerning how the descriptors of running mechanics affect efficiency/economy. Nevertheless, it has been suggested that biomechanical factors may account for a substantial portion of variations of running efficiency. As compared to a less succesful runner, a faster endurance runner is characterized by less vertical oscillation (Gregor and Kirkendall 1978), longer strides (Hoshikawa et al. 1971; Cavanagh and Williams 1982), less change in velocity during the ground contact (Kaneko et al. 1985), and lower first peak in the vertical component of the ground reaction force associated with a tendency to have smaller anteroposterior peak forces (Williams and Cavanagh 1987). Despite these observations the interaction between the biomechanical and physiological factors is not well-known.

The efficiency/economy of human movement have also been studied in other sport events such as cycling (e.g. Dickson 1929; Henry and De Moor 1950; Christensen et al. 1960; Banister and Jackson 1967; Whipp and Wasserman 1969; Suzuki 1979; Gaesser and Brooks 1975; Bosco et al. 1980) and rowing (e.g. di Prampero et al. 1971; Connors 1974; Cunningham et al. 1975; Hagerman et al. 1978; Secher 1983; Steinacker et al. 1986). On the whole, several cross-sectional studies have been published to determine the efficiency and economy of human locomotion. However, there are not many answers to the following questions: why the efficiency differs between and within the subjects according to the intensity of movement?

3 THE PURPOSE OF THE STUDY

The available knowledge of efficiency/economy of human locomotion is quite extensive. Several studies have also been published in the area of motor control and efficiency of human movement. However, there exist only a few studies combining these research areas. In other words, biomechanical and physiological data have not crossed each other in this respect. In addition, many studies have been done with students or untrained people who are unfamiliar with the movements under research. Therefore, to generalize of those results is difficult. The intensity of a performance has also varied largely in different studies causing difficulty in interpreting the results. Therefore, in the present series of experiments both the training background of subjects and the intensity of performances have been taken into account. The detailed purposes of the present study were:

1) to examine whether there exist differences in stretch reflex responses of the the triceps surae and the quadriceps femoris muscles between the power- and endurance-trained athletes in rest conditions (I and II).

2) to examine whether different training backgrounds and/or inherited factors had modified force production of bilateral leg extension in isometric conditions with maximal, voluntary effort among the power- and endurance-trained athletes (II).

3) to study effects of different impact velocity conditions and therefore different stretching velocities of the leg extensor muscles on the neuromuscular functions in the maximal SSC-exercises among the power- and endurance-trained athletes (III).

4) to compare the mechanical efficiency (ME) between the power- and endurance-trained athletes during submaximal jumping with different stretching velocities of the leg extensor muscles, and with different angular displacements. An additional problem was to find explanations for the expected differences in ME between the subject groups by analysing EMGs, heart rates, blood lactate and other measured variables (IV).

5) to find biomechanical and physiological explanations for obvious differences in ME between the power- and endurance-trained athletes during submaximal running at different speeds, both on the treadmill and on the track (V).

6) to clarify, in general, the role of biomechanical variables as an explanatory factor in the efficiency of natural human locomotion (IV and V).

4 RESEARCH METHODS

4.1 Subjects

A total of 29 athletes who trained and competed regularly volunteered as subjects for this study. 15 of them represented power-trained athletes such as sprinters and jumpers, while 14 endurance runners, cross-country skiers, swimmers and orienteerers formed another group called endurance- trained athletes. The total number of the subjects was 20 (10 + 10) in the first experiment, which was reported in papers I, III and IIIa. 12 of them participated together with 9 new subjects in the second experiment. Thus, in the second experiment the total number of subjects was 21 (11 + 10). Their results are reported in papers I, II and IV. For the last experiment, a total of 10 (5 + 5) subjects were randomly selected from the subjects of the second experiment (reported in a paper V). All the subjects were fully informed of the procedures and appraised of all possible risks involved in this study. Furthermore, according to the instructions, the subjects were not allowed to have any physical exercise in the testing day to prevent influences on the results obtained. Table 1 presents the physical characteristics of the subject groups in these three experimental series.

4.2 Experimental design, testing procedures and analysis

Three separate experiments of the present study were followed by an interval of one year. The first experiment consisted of measurements of anthropometric variables (Table 1), stretch reflexes of the selected plantar- and dorsiflexor muscles and knee extensor muscles, and two types of SSC-exercises (drop

jumps and sledge jumps) with maximal effort. During the second experiment, anthropometric and reflex measurements were repeated as well as some maximal jumps. In addition, maximal voluntary bilateral force of plantarflexors and knee extensors in isometric condition, and two types of SSC-exercises (drop jumps and sledge jumps) with submaximal effort were measured. In the last experiment of the present study, the subjects performed submaximal running on the treadmill and on the track. Their maximal oxygen uptake and maximal running speed were also measured. The measurements of the anthropometry and maximal voluntary isometric force were repeated.

TABLE 1. Mean (± SD) of the physical characteristics of the subject groups. Percentage of the body fat was determined according to Jackson and Pollock (1985). $p < 0.01$, **; $p < 0.05$, *.

EXPERIMENT 1:

Variable	Power group (N = 10)	Endurance group (N = 10)
Age (yr.)	24 ± 5	23 ± 4
Height (cm)	182 ± 5	180 ± 3
Body mass (kg)	76.7 ± 7.9	69.1 ± 3.8 *

EXPERIMENT 2:

Variable	Power group (N = 11)	Endurance group (N = 10)
Age (yr.)	26 ± 6	24 ± 4
Height (cm)	183 ± 6	180 ± 4
Body mass (kg)	76.9 ± 4.3	70.5 ± 4.5 **
Fat %	5.0 ± 1.2	5.3 ± 2.1

EXPERIMENT 3:

Variable	Power group (N = 5)	Endurance group (N = 5)
Age (yr.)	24 ± 5	26 ± 5
Height (cm)	182 ± 6	178 ± 1
Body mass (kg)	77.0 ± 6.2	70.0 ± 5.3
Fat %	4.3 ± 1.6	4.5 ± 0.4

Figure 1 summarizes the experimental design. It also gives a detailed number of performances in each experimental condition. Stretch reflexes for plantarflexors were evoked 5 times in 13 different conditions. Maximal jumps were performed from 10 to 15 times from three predetermined dropping heights. In three submaximal conditions, the number of repetitions of the respective jumps varied between 57 and 62 times . The submaximal running tests consisted of three 5 minutes running at different constant speeds.

4.2.1 Stretch reflexes in rest conditions (I and II)

Patellar reflexes of the right leg were measured with the subjects seated on the dynamometer in a relaxed position. The subjects were blind-folded to prevent them from hearing and thus avoid anticipatory reactions. The lower legs of the

subjects hung vertically with a 90° knee angle. The right leg was fixed tightly to the force transducer. The reflex hammer was dropped from an angle of 90° with respect to the patellar tendon. Upon striking the right patellar tendon, a microswitch embedded in the hammerhead sensed the tap. A total of 6 to 10 patellar reflex measurements were performed for each subject.

EXPERIMENTAL DESIGN

	EXPERIMENT 1	EXPERIMENT 2	EXPERIMENT 3
Anthropometric variables	*	*	*
Stretch reflexes			
- plantarflexors (13 · 5)	*	*	
- knee extensors (6 - 10)	*	*	
Maximal isometric force			
- plantarflexors (2 - 4)		*	*
- knee extensors (2 - 4)		*	*
Maximal SSC-exercises			
- drop jumps (3 · 10 - 15)	*	*	
- sledge jumps (3 · 10 - 15)	*	*	
Submaximal SSC-exercises			
- drop jumps (3 · 57 - 62)		*	
- sledge jumps (3 · 57 - 62)		*	
Running			
- VO_2 max			*
- maximal running speed			*
- on the treadmill (3 · 5 min)			*
- on the track (3 · 5 min)			*

FIGURE 1. Experimental design of the present studies. Numbers describe the number of repetitions or the amount of running time in different test conditions.

Stretch reflexes of the muscles around the right ankle joint were elicited by a special ankle ergometer (Figure 2) similar to that of Gollhofer and Schmidtbleicher (1989; see also Gollhofer and Rapp 1993). It induced different angular displacements and velocities around the ankle joint. The subjects placed both their feet on the pedals, which were driven by two AC-motors connected in series and controlled by a gear system. The maximal torque capacity of the ergometer (150 Nm) is capable of inducing pedal displacements with near constant angular velocities. The subjects sat on a chair that gave 90° at the ankle and knee joints. The foot was placed on the plate so that the axis of rotation of the ankle was aligned with that of the foot plate. The bent right knee was stabilized to prevent extra movements. Angular displacements in the ankle joint were measured by the electrogoniometer attached to the axis of rotation of the ergometer foot plate.

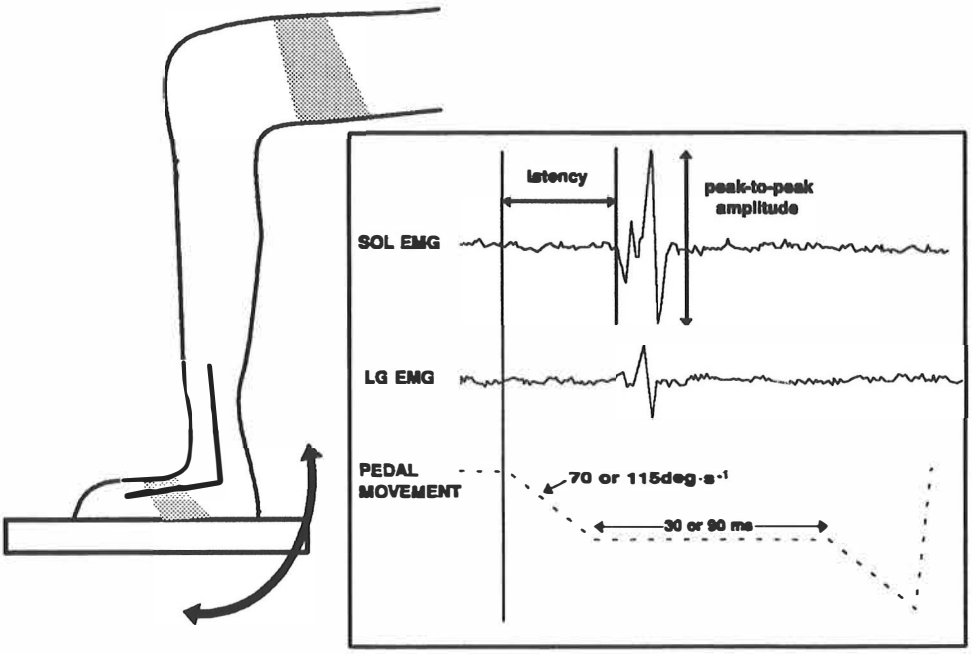

FIGURE 2. Schematic representation of the stretch reflex stimulus and analysis. The stimulus and EMGs are presented as an example of original measured signals (modified from Nicol et al. 1994).

TABLE 2. The mean amplitudes and averaged angular velocities of the measured mechanical stimuli in the present study. In the double stimuli conditions, the neutral position means that the angle of the ankle joint was 90° in the beginning of the stretching, while the second stimulus started from 87° position, respectively.

Stimulus	Delay (ms)	Amplitude (deg)	Velocity ($deg \cdot s^{-1}$)
1. Double 3 deg pos.	50	3	115
2. Double 3 deg pos.	50	3	70
3. Double 3 deg pos.	100	3	115
4. Double 3 deg pos.	100	3	70
5. Double neutral pos.	50	3	70
6. Double neutral pos.	100	3	70
7. Double neutral pos.	50	2	115
8. Double neutral pos.	100	2	115
9. Single	-	3	70
10. Single	-	3	35
11. Single	-	7	70
12. Single	-	3	25
13. Single	-	11	70

Thirteen different mechanical stimuli were selected to evoke stretch reflexes (Table 2). Every stimulus was repeated five times. Single stimuli were always started from the position of 90° in the ankle joint with varied amplitudes, times and velocities. The double stimuli started either from the neutral position (90° in the ankle joint) or from the dorsiflexed position of 87°. The delay between the first and the second stimuli was either 50 or 100 ms. In order to avoid familiarization and fatigue, the various stimuli were applied randomly.

The electromyographic activity (EMG) was measured telemetrically (Glonner) with surface electrodes (Beckman miniature skin electrodes, 650437, Illinois, USA) either from the vastus lateralis (VL), vastus medialis (VM) muscles or soleus (SOL), lateral gastrocnemius (GA) and tibialis anterior (TA) muscles of the right leg. The electrodes were placed longitudinally over the muscle belly. The longitudinal distances between the electrode pairs were at least 10 cm. For quantifying the extent of cross-talk in the present experimental situation, four subjects performed several maximal voluntary muscle actions. Simultaneously measured EMG records of the GA and SOL muscles were then cross-correlated. In maximal drop jumps on the sledge, observations of cross-power spectra and mean cross-correlations ($r_{xy} = 0.18 \pm 0.12$, $p > 0.05$) suggested that the signal cross-talk was negligible. Because the cross-talk analysis is the more reliable the longer the duration of the record length (Winter et al. 1994), this analysis could not be applied to the reflex EMGs. The additional measurements were performed more directly on four subjects in the similar way as reported by Moritani et al. (1990). Near-maximal percutaneous stimulations (Neuropack Four Mini, 50-100V, 50µs rectangular pulse wave) were delivered to evoke compound mass action potentials (M-waves) in GA. The extent of cross-talk was determined by the relative amplitudes of the M-wave recorded from the SOL. In these recordings the mean peak-to-peak M-wave amplitude was 7.39 ± 3.14 mV for the GA and 0.20 ± 0.12 mV for the SOL resulting in the cross-talk of 2.7 ± 0.8%. This value is lower than that of 6% reported by Moritani et al. (1990). Therefore, the distance between the electrode pairs was assumed to cause no significant influence on EMG patterns. Furthermore, it was assumed that the degree of cross-talk would be small or even nonexisting (Moritani et al. 1990; Koh and Grabiner 1993).

The EMG signals of the present study were amplified with a gain of 200 (Glonner Biomes 2000, cut-off frequency 360 Hz/3dB) and recorded simultaneously either with the force and trigger signals (patellar reflexes) or with the angle signal (reflexes of the SOL, GA and TA muscles) on the computer and on the magnetic tape (Racal V-Store, cut-off frequency 2.5 kHz) for further analysis. All data channels had a sampling frequency of 100 Hz.

In the analysis of patellar reflexes, the three best performances which produced the highest reflex forces were chosen for further analysis. The period between the hammer strike and the initial force production (threshold of 1 N) was taken as the total reflex time (TRT). The latency time (LAT) was determined as the time between the hammer strike and the beginning of the EMG response using the threshold of ± 5 µV. The motor time (MT) was determined by subtracting LAT from TRT (Viitasalo et al. 1980; Häkkinen and

Komi 1983). The peak-to-peak reflex amplitudes of the VL and VM muscles were related to the maximal voluntary EMG-values of the same subject, measured during the maximal isometric knee extension (see page 24). The EMG signals were fullwave rectified and the measured signals were averaged for each group. The reproducibility for LAT and MT has been reported to be good (r = .90 - .91, Viitasalo et al. 1980; Häkkinen and Komi 1983).

To measure the TS reflexes, a total of 1300 samples (20 subjects, 13 conditions, 5 performances in each condition) were analysed in the first part of the experiment. In the repetitions one year later, the corresponding values were 1365 (21 subjects, 13 conditions, 5 performances). Each stimulus, and the respective action potential, was analysed separately. The onset of displacements in the angle signal (pedal movement) was used as a trigger for latency times (Figure 2). The threshold for the beginning and for the end of action potentials was set as ± 5 μV.

4.2.2 Maximal voluntary isometric force, force-time and EMG-time (II and V)

Maximal isometric forces and various force-time variables in the bilateral leg extension were measured by a strain-gauge dynamometer. The subjects were instructed to produce their maximal force against the footplate as quickly as possible and to maintain the maximal force for 2-3 s. The angle of the knee joint was kept as 107° for testing the knee extensors and 180° for testing the plantarflexors. The respective value of the ankle joint was 90° in both conditions.

The best performance of each subject was chosen for further analysis. The maximal force and its relative values of 30%, 60% and 90% were calculated for determining the times needed to reach these force levels. On the absolute scale the corresponding time calculations were performed from the levels of 500 N, 1500 N and 2500 N. The maximal rate of force production was also computed. The average force was calculated during the absolute times from the start of the force production. Thus the force was analysed for the following 9 periods: 0 - 100 ms, 50 - 150 ms, 100 - 200 ms, 150 - 250 ms, 200 - 300 ms, 250 - 350 ms, 300 - 400 ms, 350 - 450 ms and 400 - 500 ms.

The EMG activity was simultaneously measured from either the VL and VM muscles or from the SOL and GA muscles. The EMG signals were amplified, fullwave rectified and integrated (IEMG). The maximal voluntary IEMG values were calculated maintaining the maximal force between 500 ms and 1500 ms from the beginning of the force production. The EMG-time curves (EMG was time normalised for 1 s) were analysed in respective time periods as well as the force-time curves. Finally, the measured signals were averaged for each group.

The reproducibility of the measurement of maximal isometric force is reported to be high (r = .98, C.V. = 4.1 %, Viitasalo et al. 1980). The respective values for the rate of force development were: r = .80, C.V. = 17.8% in test-retest comparison (Viitasalo et al. 1980). In the isometric condition, the

reproducibility of IEMG has been reported to be very high as well (r= .88, Komi and Buskirk, 1970; r = .88 - .91, Viitasalo and Komi 1975; r = .95 - .98; C.V. = 3.2 - 6.9 %; Viitasalo et al. 1980).

4.2.3 Maximal jumping performances (III and IV)

Jumping performances of the subjects were tested in two main conditions: drop jumps and SSC-exercises on a sledge (sledge jumps) were utilized. At first, the optimal dropping height was determined individually for each subject in the drop jumps. It means that they were dropped from different heights to find out their best rising height of the centre of the gravity (Komi and Bosco 1978). Thereafter, they performed drop jumps with maximal effort from the three individually predetermined dropping heights: the optimal height (O), the optimum + 40 cm (O+40) and optimum - 40 cm (O-40). Each condition involved about 10 jumps with minimal displacements of the knee joints (reactively).

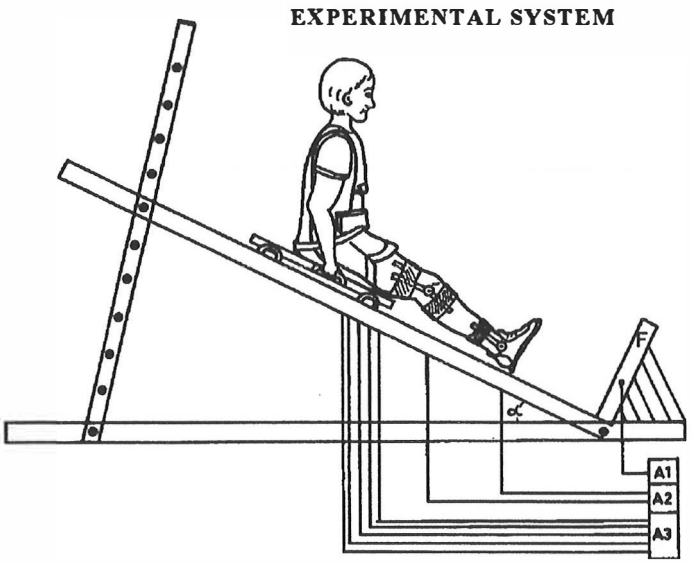

FIGURE 3. Diagram of the experimental system used in the study. The subject was fixed with belts tightly on to the sledge (modified from Kaneko et al. 1984) having an inclination (α) of 22.5°. F and A1, Forceplate and its amplifier; A2, amplifiers of the eletrical goniometers for the knee and for the ankle; A3, electromyographic amplifiers.

Another part of the testing was performed on a special sledge apparatus (Kyröläinen et al. 1990; modified from Kaneko et al. 1984; see Figure 3) for obtaining longer contact times. Furthermore, the testing conditions were more controlled than in the drop jumps. The mass of the sledge was 33.2 kg, and its inclination was 22.5° with respect to the horizontal line. Thus the total weight

(subject+sledge) pointing vertically downward, and the acceleration was even lower than in the drop jumps. The subject sat on the sledge, and he was dropped from different heights for determining the optimal dropping height. Then the assistants returned the subjects to the previous dropping heights: O, O+40 and O-40. Each condition involved about 10 maximal SSC-exercises (sledge jumps), in which the lowest knee angle was about 90°.

In the drop jumps, vertical reaction force (F_Z) was measured with a force platform. On the sledge, the respective force platform was placed perpendicularly to the sliding surface. In both experimental conditions, angular displacements of the knee and ankle joints were measured by electrogoniometers, which were attached to the lateral side of both joints. EMG activity of the VL, VM, GA, SOL and TA muscles were recorded telemetrically with surface electrodes as in the reflex conditions (see page 23). EMGs were digitally recorded simultaneously with records of force and joint angles at a sampling rate of 1 kHz by an on-line computer system. In addition, the measured signals were recorded on a magnetic tape for further analysis.

The six best jumps, determined according to the flight time in the drop jumps and the rising distance of the centre of the gravity in the sledge jumps, were chosen for further analysis. The vertical velocity at take-off was calculated in the drop jumps as follows: $v = 0.5gt$, in which g = the gravity ($9.81\ m \cdot s^{-2}$) and t is the flight time (Bosco et al. 1981). In the SSC exercises on the sledge, the take-off velocity was calculated as has been reported earlier (Kyröläinen et al. 1990).

The raw EMG signals were processed so that they were first fullwave rectified, then integrated (IEMG) and finally time normalized for one second in four different phases: preactivation from 100 ms to 50 ms before the ground contact, preactivation from 50 ms to 0 ms before the contact, eccentric phase and concentric phase. The onset of the ground reaction force of each jump was used as a reference point to identify the beginning and the end of the contact. The electrogoniometer records of the knee joint were used to identify the end of the eccentric phase of the VL and VM muscles, while the SOL and TA muscles were divided into the respective phases according to the ankle joint. The end of the eccentric phase of the GA muscle was identified according to the formula of Grieve et al. (1978).

In addition, the fullwave rectified EMG signals were averaged for obtaining muscle activity patterns both individually and by groups. This phase-dependent averaging method (see Moritani et al. 1991) allows repeated bursts of EMG activity during jumping to be aligned in time with respect to the mechanical data. The averaging was started 200 ms before the onset of the ground reaction force and finished 600 ms (for the drop jumps) or 1300 ms (for the sledge jumps) after that point. However, due to processing limitations of the EMG analysis, this case involved only 5 best performances from each subject. The test-retest reproducibility of the EMG calculated as reliability coefficients has been reported to be relatively high: $r = .94$ for IEMG in jumping (Bosco 1982) and higher than .90 for the most of the parameters in EMG patterns (Gollhofer et al. 1990). These values are quite similar to those reported

in isometric and dynamic actions with controlled movement velocity (r = .88) (Komi and Buskirk, 1970).

4.2.4 Submaximal jumping performances (IV)

The respective jumping performances were utilized as in the maximal jumps. At first, the individual optimal dropping height was again determined. Before the main experiments they performed 3 to 5 maximal drop jumps and sledge jumps. In the submaximal drop jumps (Figure 4), instructions for the subjects were to maximally resist the downward movement during the braking phase, bend the knees minimally, and perform a submaximal push-off phase during the take-off. In all conditions (O, O+40 and O-40), the subjects performed about 60 muscle actions lasting a total of 3 min. The frequency was, therefore, once every 3 s and controlled by an audiosignal. When the subject left the ground contact, two assistants used a rope attached to a vest of the subject and pulled him up to the same energy level by a special pulley system for the next drop. The third assistant took care of the subject's balance during this phase. Recovery times between the exercise sets were as long as it took for oxygen consumption to return to resting level. For studying the physiological loading of the subjects, the heart rate of the subjects was recorded by Sport Tester PE-3000 (Polar, Finland). The metabolic rate of the subjects was also followed by drawing blood samples from a finger tip for lactate analysis (biochemical method, Boehringer Mannheim) in the rest and immediately after every testing condition as well as 3 and 5 min after it.

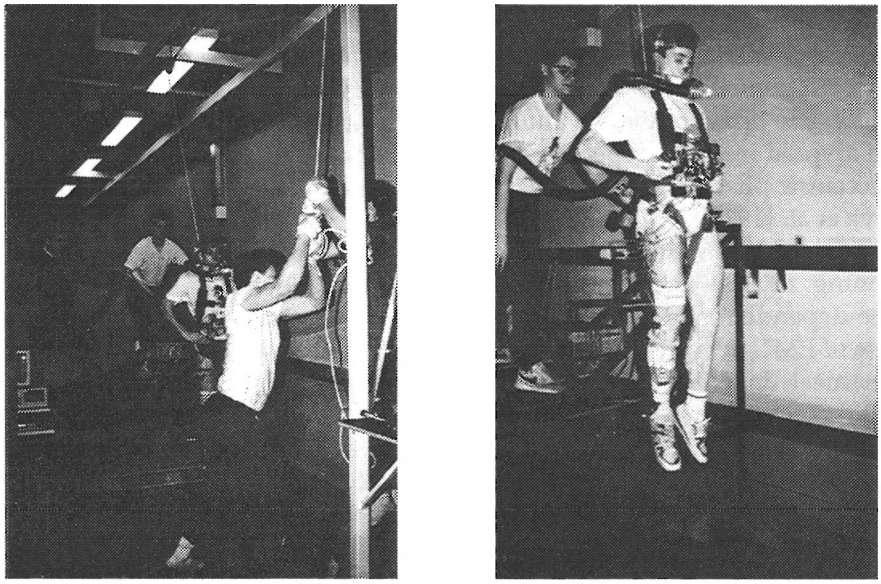

FIGURE 4. A subject performing drop exercises.

The second part of the testing was performed on the same sledge as described earlier (page 25). After determination of the optimal dropping height and maximal sledge jumps, the subjects performed submaximal sledge jumps. Assistants dropped them from the predetermined dropping heights (O, O+40 and O-40). Immediately after the braking phase, followed by the push-off phase of an intensity of 70% of the best single maximal SSC-exercise. The assistants were responsible for the required dropping height, and they also informed the subject of the height that the sledge had been risen to. During the contact with the forceplate, the subject resisted the downward movement and immediately after stopping the sledge (knee angle of 90°), he extended his legs. In all conditions, every subject performed 60 muscle actions lasting a total of 3 min. The recovery times between the exercise sets were determined by the oxygen consumption as in the drop jumps. The heart rate and blood samples were also taken as in the drop jumps.

Both in the drop jumps and in the sledge jumps, reaction forces, angular displacements of the knee and ankle joints, as well as EMGs were measured by the methods described earlier in the present study (pages 23 and 26). Furthermore, during the sledge jumps the distance the sledge moved and its velocity were measured by an optical encoder. The expired gases (sampling flow rate varied from 20 to 40 BR $\cdot$ min^{-1}) were analysed by measuring pulmonary oxygen uptake, the volume of the air, and its concentrations of O_2 and CO_2 by using a semiautomatic system (Oxygon Mijnhardt-4). Their values were averaged and printed out every 30 s. The instrument was regularly calibrated with known gas mixtures. In addition, because of the tube (diameter of 40 mm) from the subject's mouth to the analyser was 3.22 m long, its reliability was tested by comparing the predicted and real values of three tubes of different length. For every measured variable these values behaved highly linearly: e.g. the regression between the tube volume and O_2 (%) was as follows: O_2 (%) = 0.066 $\cdot$ tube volume + 3.047.

Mechanical efficiency (ME) was calculated by dividing the mechanical work (W) by the energy expenditure (ΔE) above the resting level. In the drop jumps, the total mechanical work (external) is the sum of the negative and the positive work calculated as follows:

$$W_{tot} = W_{neg} + W_{pos} = (mgh_1 + \frac{1}{2}mv_1^2) + (mgh_2 + \frac{1}{2}mv_2^2), \text{ where} \qquad (1)$$

m = the body mass,
g = 9.81 m $\cdot$ s^{-2},
h_1 = the displacement of the centre of the gravity during the braking phase,
v_1 = the velocity of the centre of the gravity in the beginning of the ground contact,
h_2 = the displacement of the centre of the gravity during the push-off phase,
v_2 = the velocity of the centre of the gravity in the end of the take-off.

All these factors have been calculated by the ground reaction force when the mass of the subject, the dropping height, and the gravity were known. Thus, the potential energy (mgh_1) was the highest when the subject was lifted up to a starting position of each jump or when the subject achieved the highest position during the flight phase (mgh_2). The turning point (t_4) of the centre of the gravity during the take-off was calculated as follows:

$$\left|\sqrt{2gh}\right| = \left| \frac{1}{m} \int_{t_4}^{t_6} [F(t) - mg]\, dt \right|, \text{ where} \qquad (2)$$

g = 9.81 $m \cdot s^{-2}$,
h = the rising height of the centre of gravity,
m = the body mass,
F = the ground reaction force,
t_4 = the beginning of the push-off phase,
t_6 = the end of the take-off.

In the sledge jump, the mechanical work was calculated by the integral of the function F(x) as follows:

$$W_{tot} = \int_{p_1}^{p_2} F(x)\, dx, \text{ where} \qquad (3)$$

F = the reaction force,
x = the displacement of the sledge,
p_1 = the beginning of the contact,
p_2 = the end of the contact with the force plate.

The power was calculated by dividing the mechanical work by the contact time in both jumping conditions. The net energy expenditure (ΔE) was determined by measuring oxygen uptake ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$), and by calculating respiratory exchange ratio ($R = \dot{V}CO_2 \cdot \dot{V}O_2$) every 30 s. Measurements were made before the exercise (rest $\dot{V}O_2$), during the exercise, and during the recovery period until the $\dot{V}O_2$ returned to the resting level. The resting $\dot{V}O_2$ was subtracted from the total consumption of the oxygen. To calculate the energy expenditure, an energy equivalent of 20180 J per litre of oxygen was applied, when R was 0.82. The change of ± 0.01 in R-value (± 42 J in energy expenditure) of every 30 s was multiplied by the respective value of $\dot{V}O_2$ ($l \cdot min^{-1}$) for getting ΔE. Its mean value (work + recovery) was utilized individually in further calculations.

Finally, the ME of the total work was calculated as follows:

$$ME = \frac{W_{tot}}{\Delta E} \cdot 100\,\% \qquad (4)$$

4.2.5 Running (V)

The submaximal running tests on the treadmill (Figure 5) consisted of measurements of biomechanical and physiological variables. The subjects ran 5 min at the three predetermined constant speeds of 2.50 $m \cdot s^{-1}$, 3.25 $m \cdot s^{-1}$, and 4.00 $m \cdot s^{-1}$ on the treadmill. A week later, the same subjects ran at the same speeds on the track. Recovery times between the running sessions lasted until the oxygen consumption had returned to the resting level. Contact times were measured by special transducers (threshold of 10 N) placed inside the shoes extended under the whole sole. The velocity of the treadmill was measured by means of an optical encoder (Figure 5). The external work of subjects was determined by a kinematic arm, which is a device for three-dimensional recording of human movement. It consisted of four rigid bars linked together by three joints equipped with optical transducers. One end of the kinematic arm was connected to a fixed reference point while the other end, which was fixed to the back of the subject and near the centre of the gravity of the whole body, could move freely in the three spatial directions. For more details of this method, see Belli et al. (1993). Angular displacements of the knee and ankle joints were measured by electrogoniometers, and EMG activity was recorded telemetrically with surface electrodes from the VL, VM, GA, SOL and TA muscles as described detailed on pages 23 and 26.

During running at three submaximal speeds on the track (see Figure 6), the running velocity and the mechanical work were measured by the same method as on the treadmill. The measuring equipment was placed in an electric car, which was driven on the side of the subject. The running speed of the subject was paced by the driver of the car. He drove around the 200 m long track at the predetermined constant speed by following the pointer of a speedometer, which was connected to the optical encoder. The expired air for one minute was collected into the Douglas bag during the period of the steady-state oxygen uptake (from 4 to 5 min or in some cases from 3 to 4 min). The volume of air in the Douglas bag was determined by a gasometer, and its concentrations of O_2 and CO_2 with the same gas analyser as in the treadmill running. Angular displacements of the knee and ankle joints as well as EMGs of the VL, VM, GA, SOL and TA muscles were also measured. In addition, ground reaction forces were measured by a long (13 m) force platform during every lap of 200 m. Figure 7 demonstrates as an example the signals of ground reaction forces, EMGs and electrogoniometers stored simultaneously.

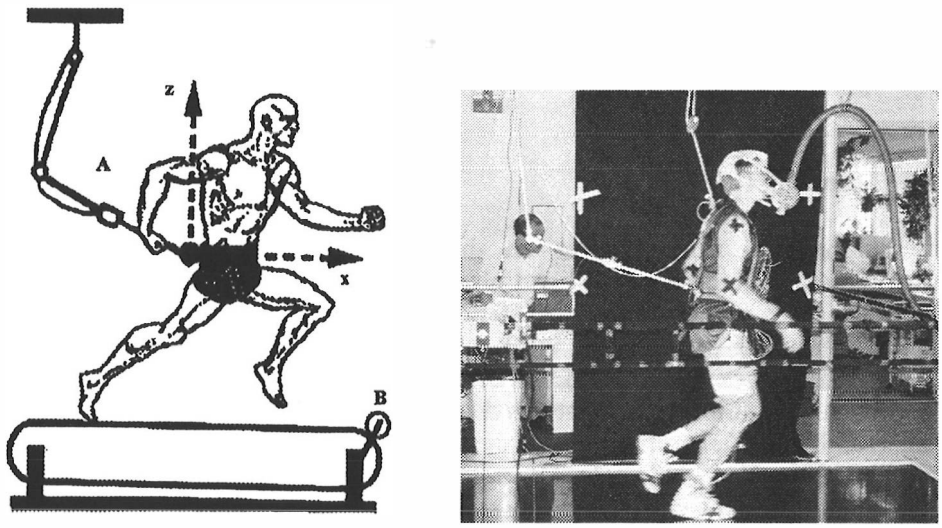

FIGURE 5. Schematic representation of the measurement of the external mechanical work (left). A is the kinematic arm, B is the velocity encoder (Belli et al. 1992). The photo (right) has been taken in the present experiment.

In the analysis of running, forces, angular displacements and EMGs were analysed by dividing the ground contact first into braking and push-off phases according to the orientation of the horizontal force (Mero and Komi 1986). EMG activities were then divided into the different phases and analysed as described earlier in the present study (p. 26).

On the treadmill the oxygen uptake (O_2) and respiratory exchange ratio ($R = \dot{V}CO_2 \cdot \dot{V}O_2^{-1}$) were measured every minute. Measurements were made before the exercise (rest $\dot{V}O_2$ in a sitting position), during the exercise, and during the recovery period. The rest $\dot{V}O_2$ was subtracted from the total oxygen consumption. To calculate the energy expenditure, an energy equivalent of 20180 J per liter of oxygen was applied, when R was 0.82. The change of ± 0.01 in R-value caused the change of ± 42 J in energy expenditure. On the track the energy expenditure was calculated by the respective methods from the expired air of one minute. However, the same individual rest $\dot{V}O_2$ value and respective individual kinetics of energy expenditure were utilized for calculating net energy expenditure as in the test on the treadmill. Increases of lactate level among the power group was ignored in every condition when calculating energy expenditure. This is based on the suggestion that "even large increases of lactate (e.g. 10 mM above resting), in a relatively short time, (e.g. 5 min) in terms of energy equivalent represent rather minor quantities" (di Prampero, 1986). However, contrary results have also been published (e.g. Bangsbo et al. 1990; di Prampero et al. 1993).

The external mechanical work was calculated in z and x directions as follows:

$$PE_{arm} = m \cdot g \cdot z_r \text{ and } KE_{arm} = 0.5 \cdot m \cdot x_r^2, \text{ where} \quad (5)$$

PE_{arm} = the potential energy level,
KE_{arm} = the kinetic energy level,
EE_{arm} = the external energy level,
m = the mass of the subject,
g = the gravity,
z_r = the vertical displacement of the centre of the mass (CM),
x_r = the horizontal velocity of the CM (Belli et al. 1993).)

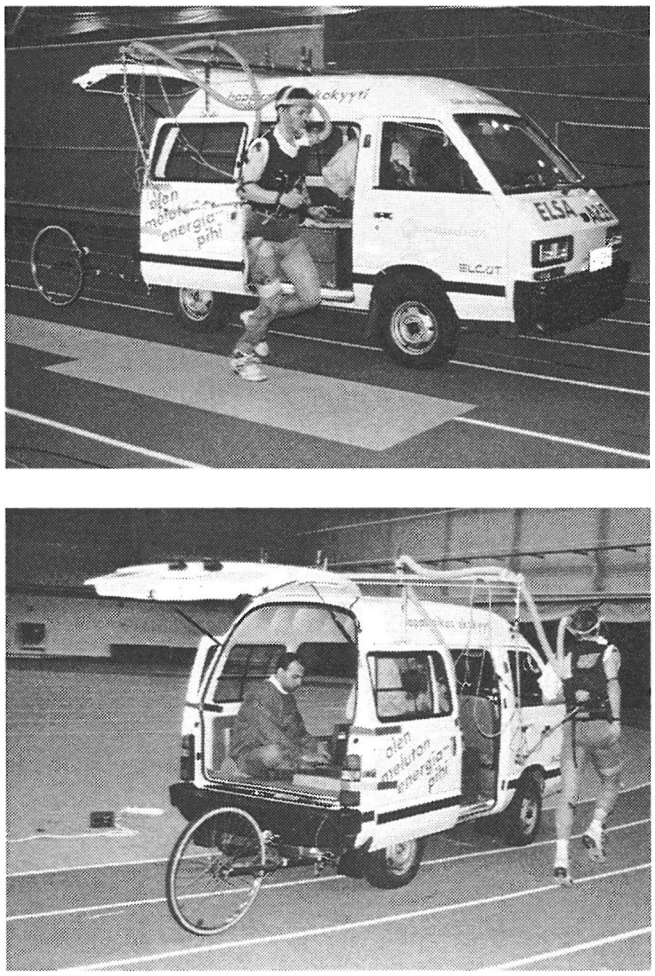

FIGURE 6. The running test on track (see the details in the text).

In contrast to walking, during running the potential and kinetic energy changes of the centre of mass are in the same phase (Cavagna et al. 1976). This was

checked to be the case also in the present study. Therefore, the work is given by the maximal differences between energy levels of each step as follows: W_p = PE, W_k = Δ KE, and $W_{tot} = W_p + W_k$. Thereafter, ME was calculated by dividing the mechanical work (W_{tot}) by the energy expenditure (ΔE) above the resting level.

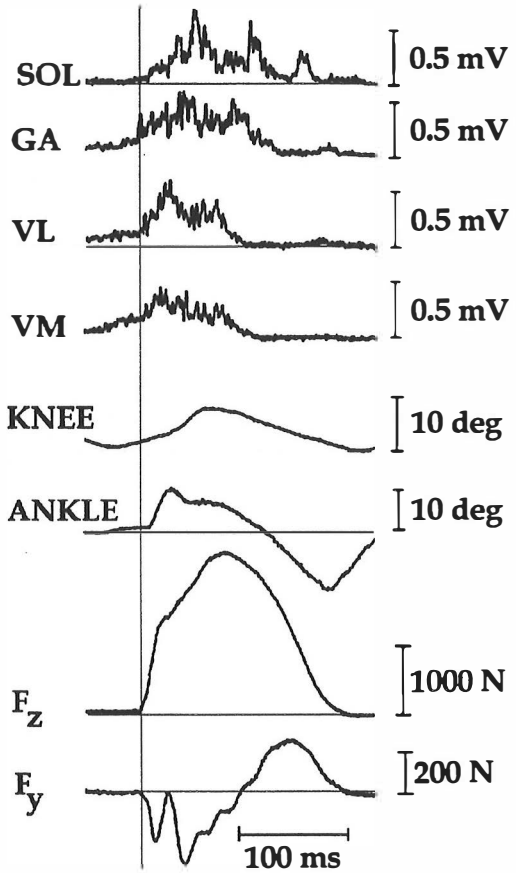

FIGURE 7. The recorded biomechanical variables in running at the speed of 4.00 m · s^{-1} on the track.

Maximal oxygen uptake ($\dot{V}O_2max$) and maximal running speed (v_{max}) were measured for obtaining reference values of physical performances of the subjects. The $\dot{V}O_2max$ test was performed on the treadmill with a progressively increased load. During the first minute of the test the speed was 2.75 m · s^{-1}, and the inclination of the treadmill was 1° in respect to the horizontal line. The subsequent minutes were run at the speeds of 3.25 m · s^{-1}, 3.75 m · s^{-1}, 4.25 m · s^{-1}, and 4.75 m · s^{-1}. Thereafter, the slope of the treadmill was increased (2.3°, 3.5°, 4.2°, 4.9° and 5.6°) until the subject was exhausted. The expired gases were determined by measuring pulmonary oxygen uptake, the volume of the air, and its concentrations of O_2 and CO_2 by using an

semiautomated gas analyser (Oxygon Mijnhardt-4). The instrument was regularly calibrated with known gas mixtures and the measured values were corrected in STPD. The heart rate was determined from the recordings of EKG-signals measured during the running.

The maximal running speed of the subjects was measured on the track. They ran maximally 20 m (flying 20 m) through two photocells having individually chosen acceleration distance, and using the same shoes as in the other parts of the experimental procedure of the present study. Ground reaction forces were measured by a long (13 m) force platform located in the middle of the photocells. Angular displacements of the knee and ankle joints and EMGs of the VL, VM, GA, SOL and TA were measured as well.

4.3 Statistical methods

Mean and standard deviation (SD), and/or standard error (SE) were calculated for all subjects together, and for groups separately (I-V). The experimental conditions were compared to each other by oneway analysis of variance by using the least-significant (LSD) method (I). The statistical significances [$p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*)] between power- and endurance-trained athletes were tested with Student's t-test for independent samples (I-II). Correlation coefficients were utilized to find out relationships between different variables using the relative and/or the measured absolute values. The coefficient of variation was used to find out such variable, which has minimal relative dispersion.

The analysis of variance (ANOVA) was used to test main effects and 2-way interactions of the experimental conditions, and the subject groups in the measured variables (III). In addition, the optimum condition was used as 100 % for relating the conditions of O+40 and O-40 to it. Correlation coefficients between different variables were calculated.

MANOVA for repeated measurements was utilised to test the main effects of repetitions, experimental conditions, and subject groups, as well as their combined effects (interactions) on every measured variable in submaximal jumping (IV). It revealed that the repetition did not have a statistically significant influence on any main variables. Therefore, the repetitions of 41 to 50 were chosen from each subject for further analysis. In addition, all variables were related to their respective values in the maximal jumping exercises. In running (V), MANOVA for repeated measurements was utilized as well. It also revealed that the repetition had no statistically significant influence on any main variables. Therefore, in running on the treadmill, the signals of 30 steps were averaged individually at each running speed. While running on the track, from 9 to 17 contacts were averaged individually.

5 RESULTS

The most important findings obtained from the present series of experiments are presented below. For more details the original papers (I - V) should be consulted.

5.1 Stretch reflex responses

In all conditions the latency times of stretch reflexes in the plantarflexor muscles were shorter (43 $\pm$ 7 ms vs. 45 $\pm$ 7ms, $p < 0.001$ for the SOL muscle, and 40 $\pm$ 8 ms vs. 43 $\pm$ 6 ms, $p < 0.001$ for the GA, n = 499 - 581), and their durations were longer for the SOL and GA muscles among the endurance-trained athletes (N = 10) compared to the power-trained athletes (N = 10). No statistically significant differences in the latency times were observed for the TA muscle between the groups. In the double stimuli conditions, the latency times after the second stimuli were longer for the SOL ($p < 0.05$) muscle among the endurance-trained athletes. No differences were noticed in the durations of the EMG responses.

In the two repeated experiments, negative correlations were noticed between the averaged angular velocity and the latency time of the SOL and GA muscles. After the first stimulus, the correlation coefficients for the SOL muscle were: r = -0.30 ($p<0.001$) in the first experiment and r = -0.41 ($p<0.001$) in the second experiment among power-trained athletes. The respective values were r = -0.18 (ns) and r = -0.33 (ns) among endurance-trained athletes. The same tendency was also observed after the second stimulus. In the double stimuli conditions the second EMG responses were weaker among both groups (Figure 8). As compared to the first response, the reflex amplitude decreased to 40.5 % in power group and to 65.9 % in endurance group. At the same time, the appearance of these cases was only 8.2 % and 16.2 %, respectively.

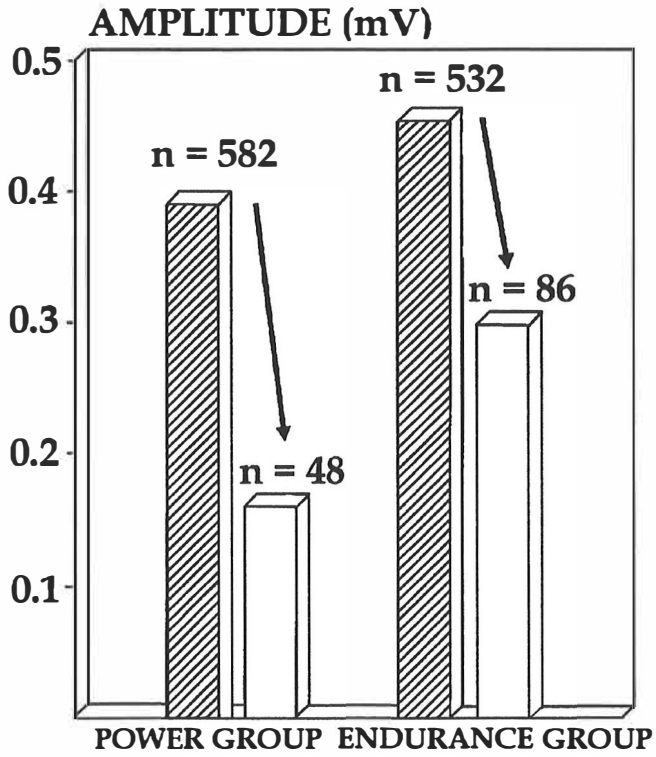

FIGURE 8. The amplitudes of the second EMG response of the SOL muscle decreased and their number diminished drastically among both groups. After the first stimulus the number of existed EMG responses were 582 among power athletes and 532 among endurance-trained athletes. After the second stimulus the respective values were 48 and 86.

TABLE 3. Basic patellar reflex variables for the three best performances of each subject (mean ± SD). The number of reflex responses (n) was between 15 and 21 in both experimental groups, because four subjects in both groups had weak or non-existent reflexes. ***, $p < 0.001$.

Variables	Power athletes (N = 7)	Endurance athletes (N = 6)
Latency time of VL (ms)	24 ± 2	24 ± 2
Latency time of VM (ms)	24 ± 2	24 ± 2
Motor time of VL (ms)	45 ± 9	45 ± 6
Motor time of VM (ms)	43 ± 10	44 ± 6
Total reflex time (ms)	69 ± 10	68 ± 7
Maximal reflex force	27.9 ± 13.9	29.9 ± 17.9
EMG-force ratio of VL (u)	1.81 ± 1.20	2.36 ± 1.70
EMG-force ratio of VM (u)	0.60 ± 0.20	2.25 ± 1.50 ***

The latency and motor times of patellar reflexes for the VL and VM muscles were similar in both groups (Table 3). The relative reflex amplitudes of the VL and VM muscles were higher ($p < 0.01$ - n.s.) among endurance-trained athletes (Figure 9) but the maximal reflex force did not differ between the groups. The relative EMG correlated positively with the maximal reflex force. This relationship was more significant among the endurance-trained athletes ($r = .69$, $p < 0.01$) than among the power-trained athletes ($r = .52$, $p < 0.05$). In addition, the rate of maximal reflex force development (Figure 10) was higher among the endurance athletes (872 ± 362 N x s^{-1} vs. 663 ± 159 N x s^{-1}, $p < 0.01$).

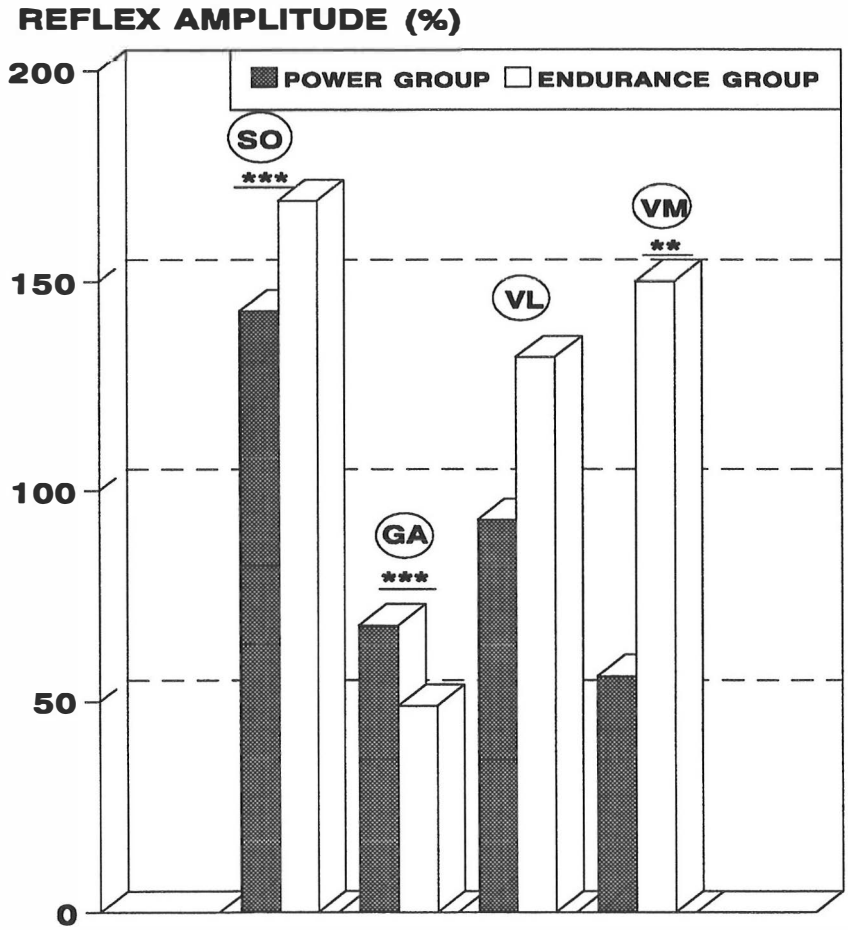

FIGURE 9. Mean of reflex amplitudes related to maximal voluntary amplitudes (MVC) in the leg extensor muscles. The MVC has been determined in the maximal isometric condition to make it possible to compare EMGs of the two different subject groups. The number of reflex responses varied from 15 to 18 for the VL and VM muscles and from 367 to 413 for the SOL and GA muscles. **, $p < 0.001$ and ***, $p < 0.0001$.

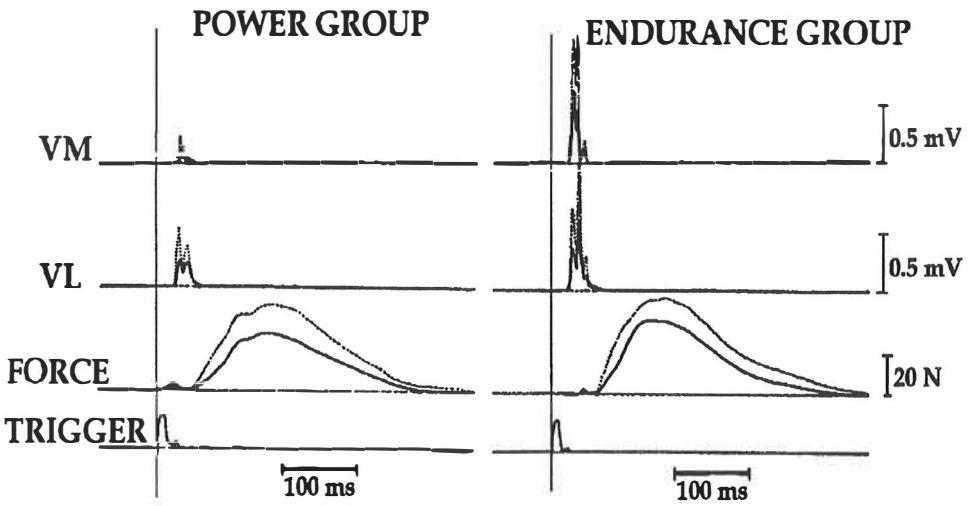

FIGURE 10. Averaged (+ SD) signals of trigger, reflex force and EMGs for 6 power (n = 18) and for 5 endurance (n = 15) athletes.

5.2 Maximal voluntary isometric force, force-time and EMG-time

The power-trained athletes produced higher maximal voluntary forces both by the knee extensor (5416 ± 859 vs. 4085 ± 718, $p < 0.01$) and plantarflexor (3263 ± 547 vs. 2471 ± 330 N, $p < 0.001$) muscles than the endurance-trained athletes. On a relative scale, the times needed to reach the force levels examined did not differ between the two experimental groups. However, on an absolute scale, significant ($p < 0.05$) group differences in the time needed to achieve certain high force levels were observed. In addition, the rate of maximal force development of the knee extensors was significantly higher among the power athletes compared to the endurance athletes (38718 ± 6758 N x s^{-1} vs. 26497 ± 6859 N x s^{-1}, $p<0.001$). The respective value for the plantarflexors did not differ significantly between the groups.

Figure 11 demonstrates that on the absolute scale (above) the average force-time curves of the power group were higher and more to the left than the respective curves of the endurance group. However, on the relative scale (below) no differences were observed. The respective muscle activity patterns were also quite similar among both groups (Figure 12).

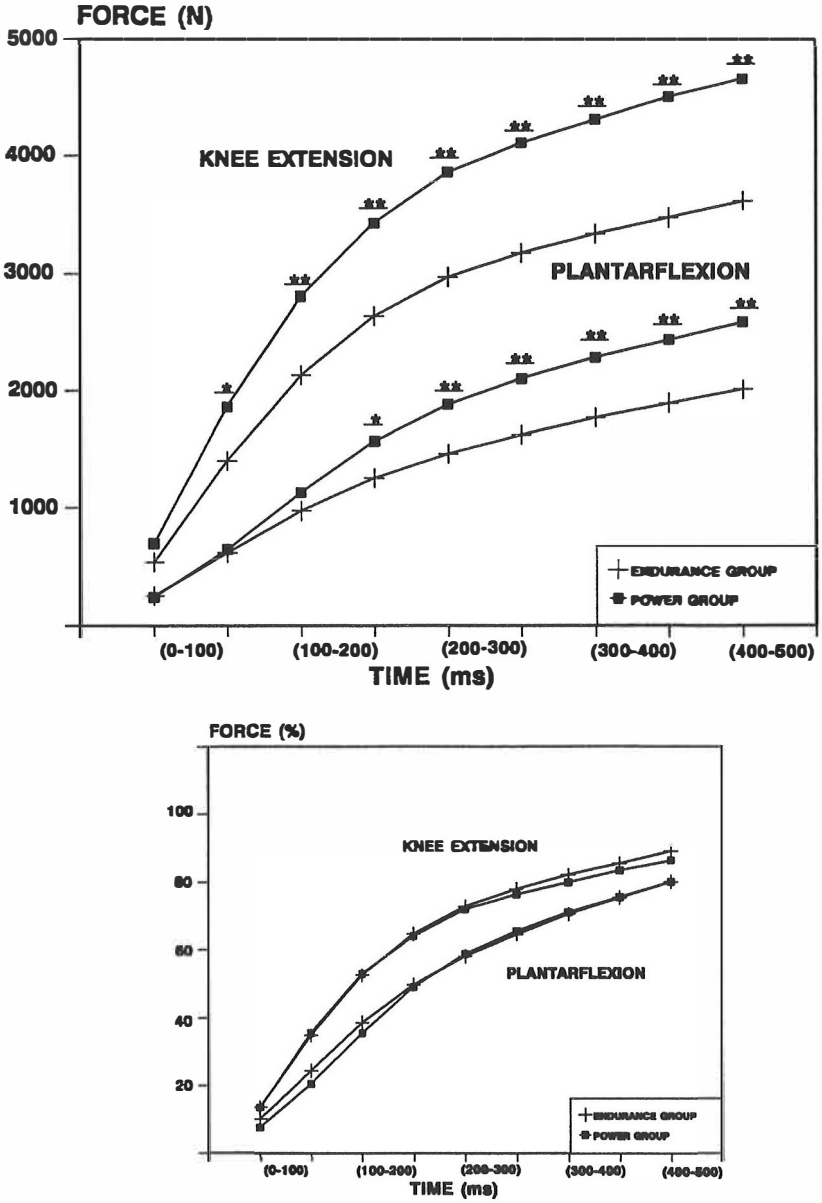

FIGURE 11. Mean absolute (above) and relative (below) force-time curves of the knee extensor and plantarflexor muscles during the maximal rate of force development in voluntary isometric conditions among power- and endurance-trained athletes (N = 11 + 10). *, $p < 0.05$ and **, $p < 0.01$.

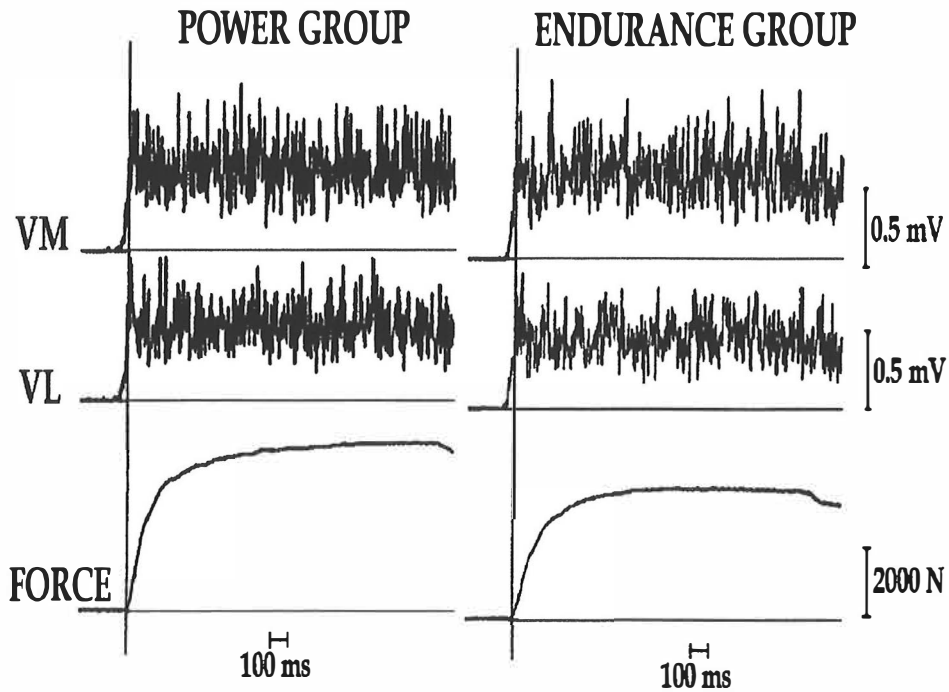

FIGURE 12. Fullwave rectified and group averaged EMG recordings (N = 11 + 10).

5.3 Maximal SSC-exercises

In the drop jump exercises, the optimal dropping height was 0.66 ± 0.15 m for the power group and 0.55 ± 0.08 m for the endurance group. On the sledge the respective values were 0.73 ± 0.08 m and 0.63 ± 0.13 m. However, the average angular velocities of the knee and ankle joints did not differ between the subject groups in the braking phase of the take-off during the drop jumps or the SSC-exercises on the sledge. Otherwise, as the dropping height increased they increased as follows: $F = 131.98$, $p < 0.001$ for the knee joint and $F = 89.51$, $p < 0.01$ for the ankle joint, and $F = 118.50$, $p < 0.001$ and $F = 92.30$, $p < 0.001$ on the sledge, respectively. During the concentric phase of the take-off in the drop jumps, ANOVA revealed a significant group effect on the average angular velocities of the knee and ankle joints (Table 4). Therefore, contact times were shorter ($p < 0.001$)and the take-off velocities were higher ($p < 0.001$) among the power athletes compared to the endurance-trained athletes. On the sledge, the power athletes also had better physical performance ($p < 0.001$) when measured by the respective variables as in the drop jumps.

TABLE 4. Mean contact times, take-off velocities and average angular velocities of the knee and ankle joints in the concentric phase of the take-off. The main group effects (F) varied from 6.16 ($p < 0.05$) to 341.90 ($p < 0.001$) in these different variables.

	POWER GROUP			ENDURANCE GROUP		
Experimental conditions	O-40	O	O+40	O-40	O	O+40
Contact time (s)						
- drop jump	0.159	0.159	0.170	0.188	0.187	0.211
- sledge jump	0.534	0.508	0.519	0.592	0.585	0.617
Take-off velocity ($m \cdot s^{-1}$)						
- drop jump	2.97	3.17	3.06	2.54	2.60	2.52
- sledge jump	3.28	3.15	3.03	2.55	2.62	2.53
Average angular velocity of the knee joint ($deg \cdot s^{-1}$)						
- drop jump	566	565	522	488	469	436
- sledge jump	320	334	330	269	286	281
Average angular velocity of the ankle joint ($deg \cdot s^{-1}$)						
- drop jump	543	560	505	432	388	349
- sledge jump	208	211	204	164	169	165

Figure 13 demonstrates that the amount of muscle activity (IEMG) differed clearly between these two investigated exercises (drop jumps vs. sledge jumps) among both groups. In the drop jumps, EMG activity of the one-joint muscles was higher in the eccentric phase of the take-off as compared to the respective concentric phase while on the sledge it was just the opposite. The GA muscle behaved, however, in a manner different from the other investigated muscles. The TA muscle produced the highest activity just around the touch down to the ground.

The different experimental conditions did not differ clearly in the amount of muscle activities. The group comparison revealed, however, that the rate of EMG development during the preactivity phase was higher among the power athletes (see Figures 13 and 17). Furthermore, during the eccentric phase of the take-off in the drop jumps, the power athletes demonstrated higher EMG activities in the optimal condition ($p < 0.05$ - 0.001 depending on the muscles), as compared to the other conditions. This was not the case among the endurance-trained athletes.

In the drop jumps, the ratio between the eccentric and the concentric EMG showed significant ($p < 0.001$) differences between the groups for the knee extensor muscles (Figure 14). These differences had the same trend in every measured condition. For the SOL muscle the respective ratios were lower (Figure 15): the concentric EMG was almost as dominant in the optimum and O+40 conditions. On the sledge the mean ratio between the eccentric and concentric EMGs of those muscles varied from 0.65 to 0.87 for the power group and from 0.51 to 0.78 for the endurance group. However, the main effects of the subject groups and the experimental conditions were not statistically significant for these variables during the sledge jumps.

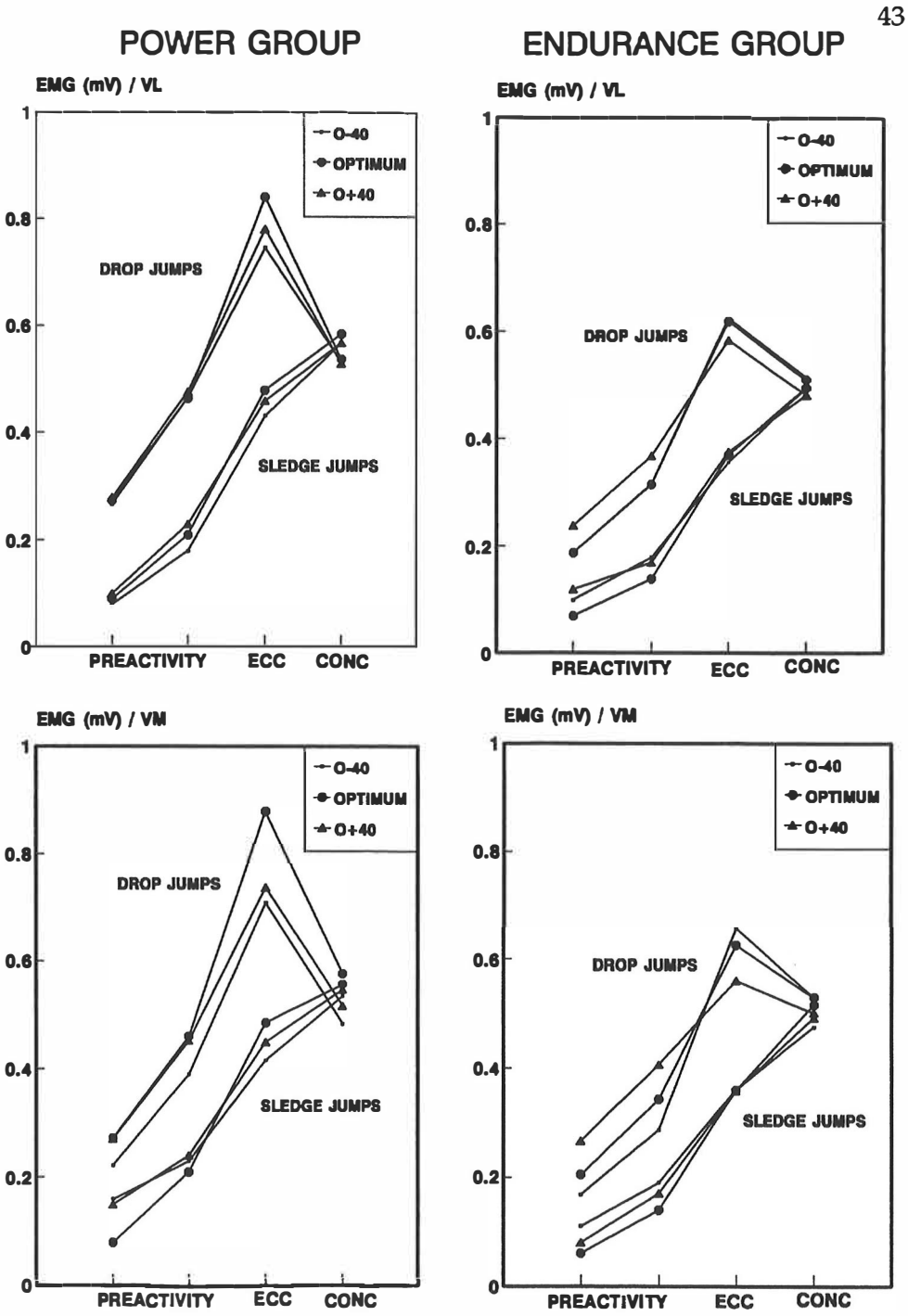

FIGURE 13. Mean of averaged EMG of the VL and VM muscles in four different phases: preactivity (from 0 to -50 ms and from - 50 ms to 100 ms before the ground contact), eccentric activity and concentric activity.

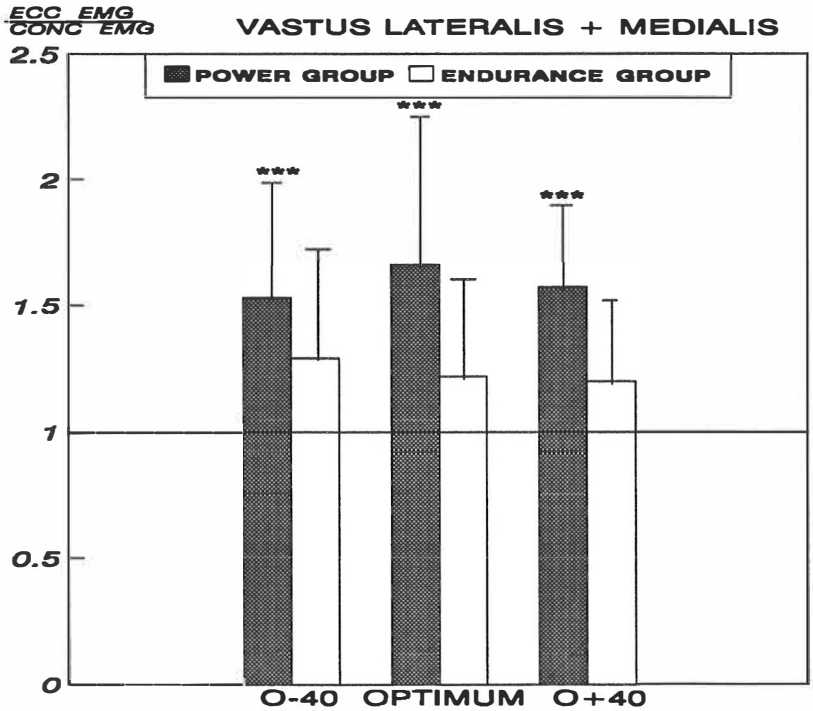

FIGURE 14. Mean (+ SD) of the ratio of eccentric and concentric EMG of the VL and VM muscles in the maximal drop jumps (n = 60 + 60). ***, $p < 0.001$.

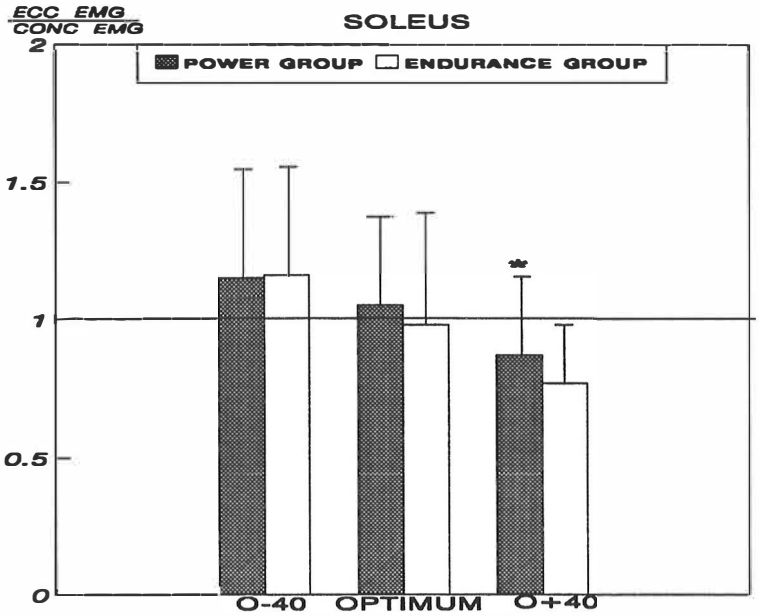

FIGURE 15. Mean (+ SD) of the ratio of eccentric and concentric EMG of the SOL muscles in the maximal drop jumps (n = 60 + 60). *, $p < 0.05$.

The descriptive analysis gave more information about muscle activity patterns (Figures 16 and 17), which seem to differ depending on the conditions and on the subject groups. In the sledge jumps (Figure 16), the EMG amplitudes were lower than in the drop jumps (Figure 17) in every condition among both subject groups. The peak EMG amplitude (stretch reflex) in the SOL muscle can clearly be seen during the eccentric phase of the take-off among both subject groups when the stretching velocity was high enough. The muscle activity patterns of the VL muscle were quite similar among both subject groups, and more oscillation can be observed with increased velocity.

In the drop jumps (Figures 17 and 18) the rate of EMG development was higher among the power group, as compared to their endurance counterparts. In addition, all muscle activity curves were quite smooth in the O and in the O-40 conditions. More oscillation in their muscle activity was noticed when the same subjects were dropped from the height of O+40. Furthermore, one might see that this oscillation was higher among the endurance group as compared to their power type counterparts.

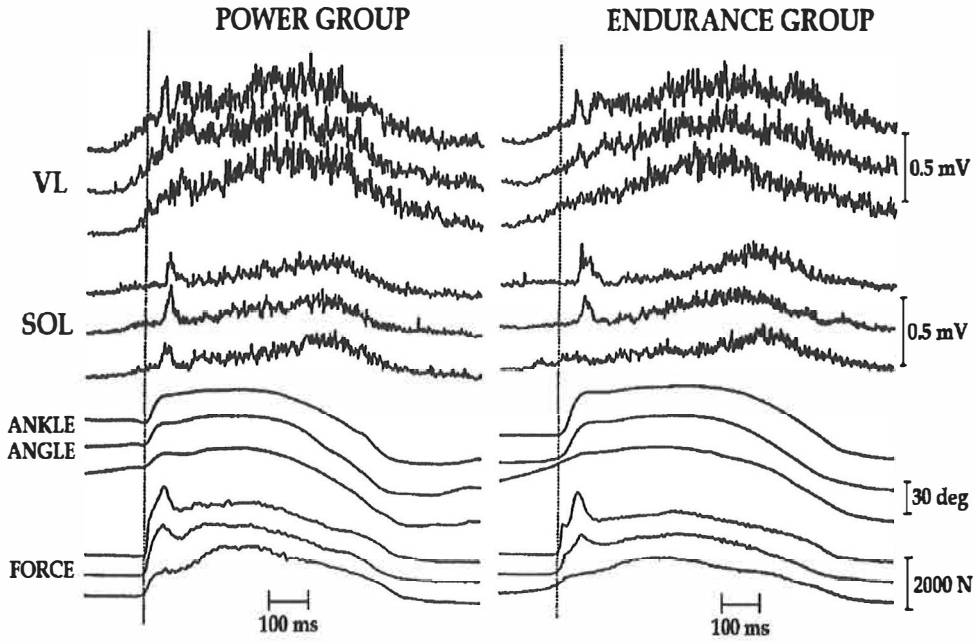

FIGURE 16. Averaged signals of reaction force, ankle angle and rectified EMGs from the SOL and VL muscles from the 5 best performances of each 20 subjects during the sledge jumps. The lowest line for every signal is the condition of O-40, in the middle is the optimum and the highest one is the condition of O+40.

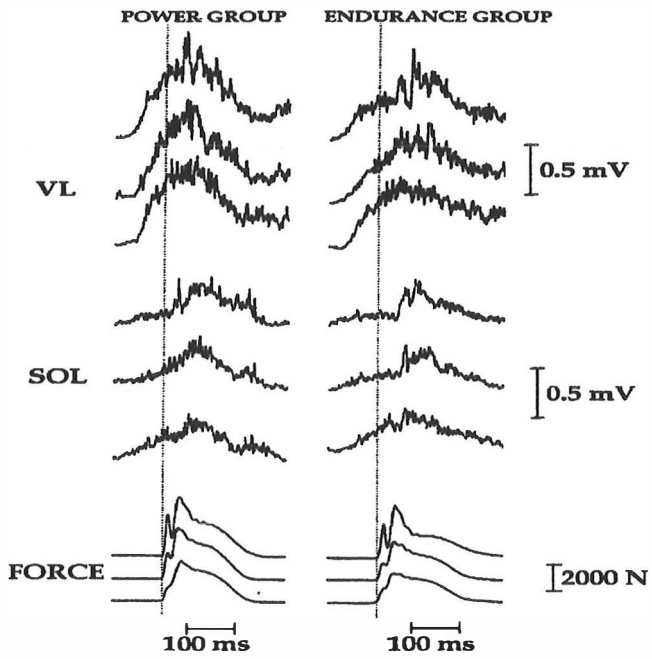

FIGURE 17. Averaged signals of reaction force, ankle angle and rectified EMGs from the SOL and VL muscles from the 5 best performances of each 20 subjects during the drop jumps. The lowest line for every signal is the condition of O-40, in the middle is the optimum and the highest one is the condition of O+40.

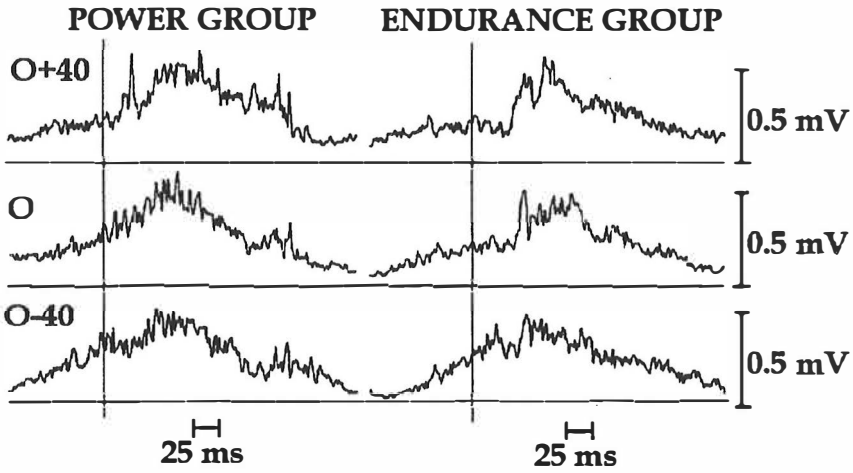

FIGURE 18. Zoomed signals of rectified EMGs from the SOL muscle (see Figure 17) from the 5 best actions of each 20 subjects during the drop jumps (Kyröläinen and Komi, 1993).

5.4 Mechanical efficiency (ME) in jumping

ME did not differ significantly between the subject groups in any of the experimental conditions except in the drop jump condition of O-40. In that particular condition, the mean values of ME were 30.8 ± 6.5 for the power group and 23.8 ± 5.3 for the endurance group ($p < 0.05$). In the present study, these were the lowest mean ME values, while the respective highest ME values were obtained in the sledge jump condition of O+40: 54.9 ± 8.5 for the power athletes and 58.5 ± 5.5 for the endurance athletes. Figure 19 clearly demonstrates that ME increased with inreasing stretching velocity of main working muscles (average angular velocity of the knee joint in the eccentric phase of the take-off), which was different between the experimental conditions ($p < 0.001$). MANOVA also revealed that the ME differed in the sledge jumps ($p < 0.001$) in every condition but, however, in the drop jump conditions of O and O+40 it did not differ significantly within both subject groups.

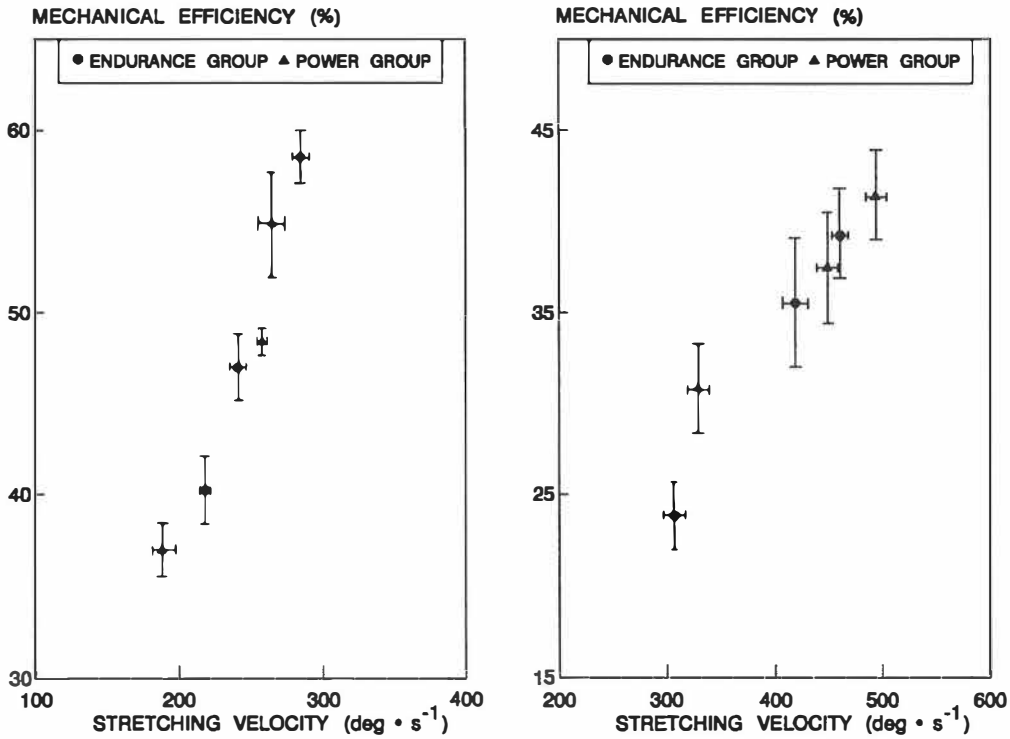

FIGURE 19. The mean (±SE) of ME related to the respective values of the stretching velocity determined indirectly by the angular velocity of the knee joint during the sledge jumps (left) and during the drop jumps (right).

There was only one significant difference in physiological variables between the subject groups in the drop jumps. The mean energy expenditure was 19.2 % higher among the power group. In the sledge jumps, the heart rate and the ventilation were higher ($p < 0.05 - 0.001$) among power athletes as well as the values of the energy expenditure (22.1%). The lactate level of the power athletes was also higher as compared to their endurance counterparts in every measured condition (Figure 20).

In the drop jumps, the mean (± SD) take-off velocities were 79.3 ± 13.9 % (O-40), 74.6 ± 15.4 % (O) and 56.2 ± 14.1% (O+40) from the respective maximal values among the endurance athletes. For the power group these values were 73.6 ± 11.4 %, 71.7 ± 10.8 % and 60.6 ± 10.5 %, respectively. Their average angular velocity of the knee joint in the eccentric phase had a negative correlation with the energy expenditure ($r = -.77$, $p < 0.01$) in the O condition. In the conditions of O-40 and O+40, the respective r-values were also negative: $r = -.32$ (n.s.) and $r = -.53$ (n.s.). However, among their endurance counterparts, these correlation coefficients were positive (from .21 to .57) but nonsignificant. The energy expenditure correlated with the mechanical work in the condition of O+40 among both groups ($r = .59$, $p < 0.05$ for the power group and $r = .68$, $p < 0.05$ for the endurance group). The respective correlations were non-significant in the condition of O for the both groups, and also in the condition of O-40 for the endurance group.

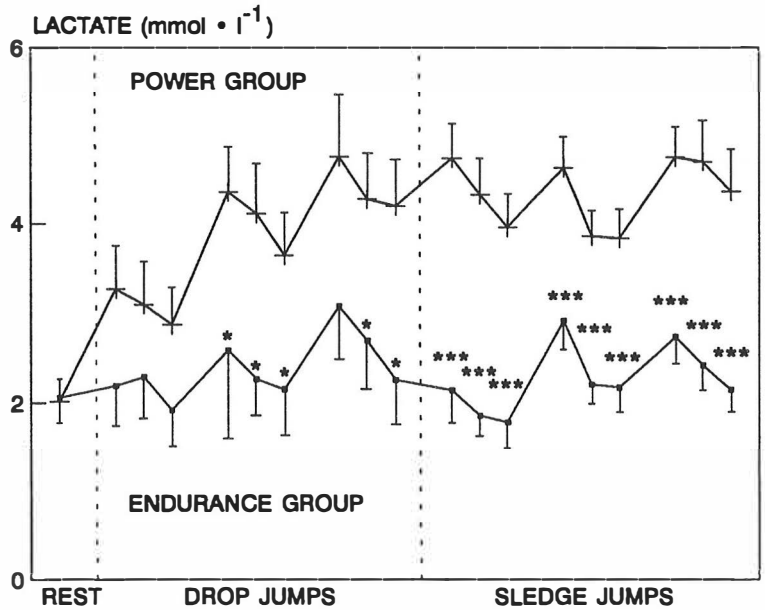

FIGURE 20. The mean (±SE) blood lactate values in the rest and after 0, 3 and 5 min in every testing condition.

In the sledge jumps, the submaximal take-off velocities differed between the subjects because of different individual best maximal SSC. Thus, the higher the negative work (prestretch intensity), the higher the take-off velocity. The correlation coefficients from the lowest dropping height to the highest one for the endurance group were as follows: $r = .88$ ($p < 0.001$), $r = .88$ ($p < 0.001$), and $r = .78$ ($p < 0.01$). For the power group the respective values were $r = .67$ ($p < 0.05$), $r = .67$ ($p < 0.05$), and $r = .95$ ($p < 0.001$).

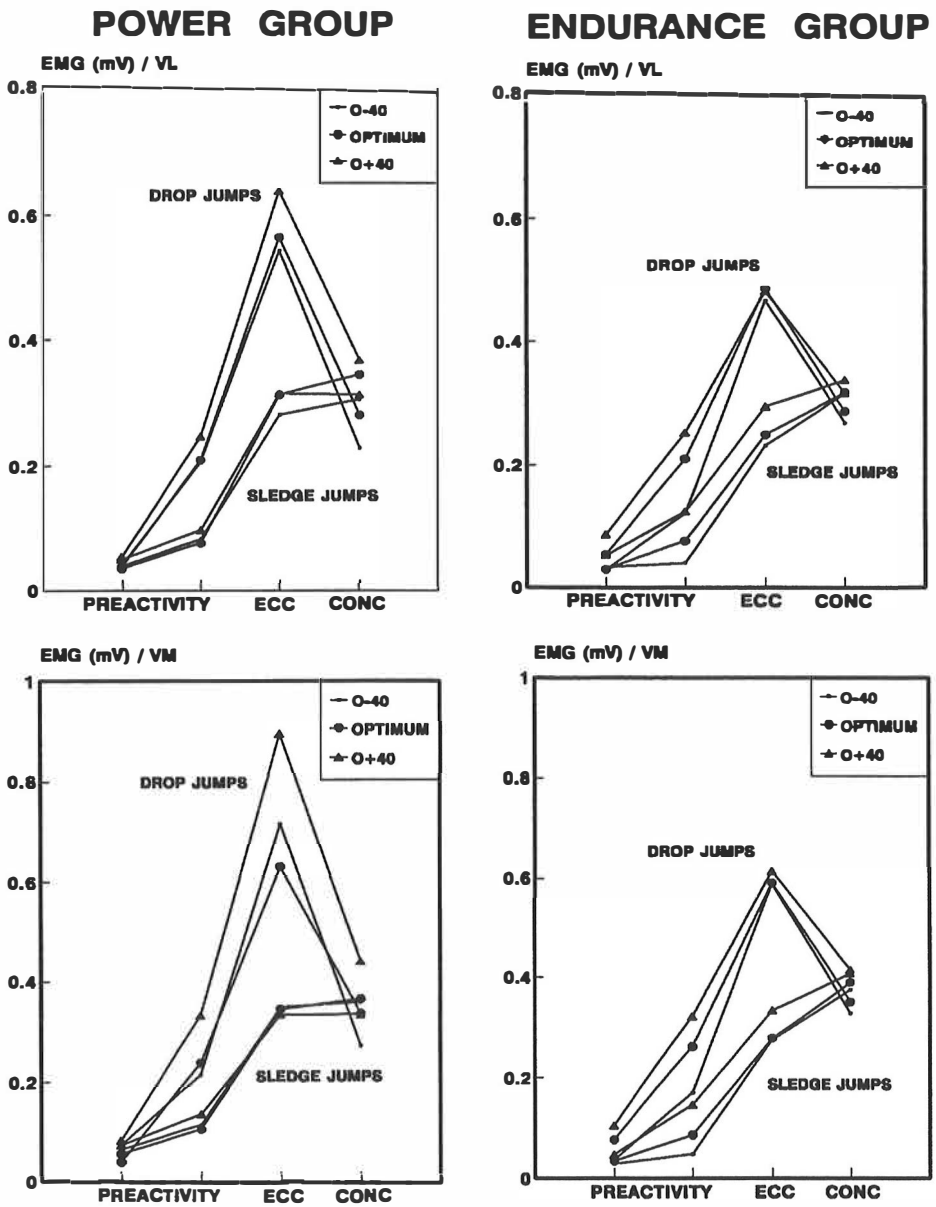

FIGURE 21. Mean of average EMG of the VL and VM muscles in four different phases: preactivity (from -100 to -50 ms and from -50 to 0 ms before the ground contact), eccentric activity and concentric activity.

In every experimental condition, the power values were higher ($p < 0.001$) among power athletes compared to their endurance counterparts, and the drop jumps proved 3 to 4 times more powerful exercises than the sledge jumps. In the case of drop jumps, the eccentric phase dominated the performance (Figure 21) in both subject groups. No statistically significant differences were noticed between the groups with regard to the ratio between the eccentric and concentric IEMGs of the investigated muscles. However, the muscle activity patterns differed quite clearly between the experimental groups both in the drop jumps (Figure 22) and in the sledge jumps (Figure 23). In the lowest stretch load condition (O-40), the muscle activity curves of the knee extensor and the SOL muscles were quite similar between both subject groups but, however, the increased stretch loads caused more oscillation among the endurance group. The endurance athletes had even clear peaks in their muscle activity curves as shown in Figures 22 and 23.

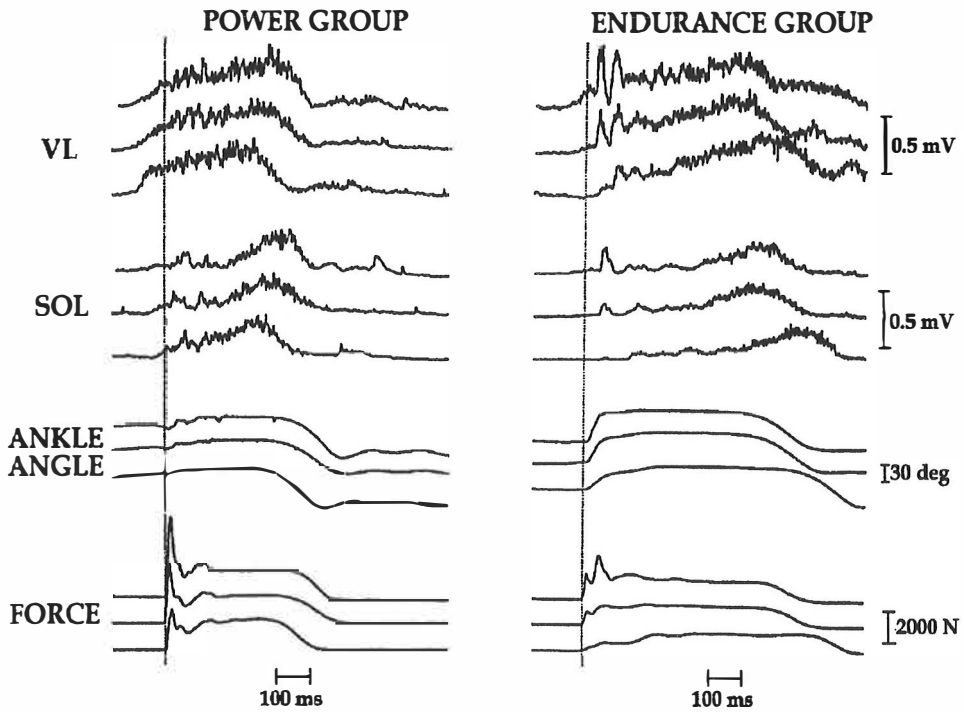

FIGURE 22. Averaged signals of reaction force, ankle angle and rectified EMGs from the SOL and VL during the sledge jumps. The left curves represent a power athlete and on the right hand are the respective curves of an endurance athlete. The lowest line for every group of signals is the condition of O-40, in the middle is the optimum (O) and the highest one is the condition of O+40.

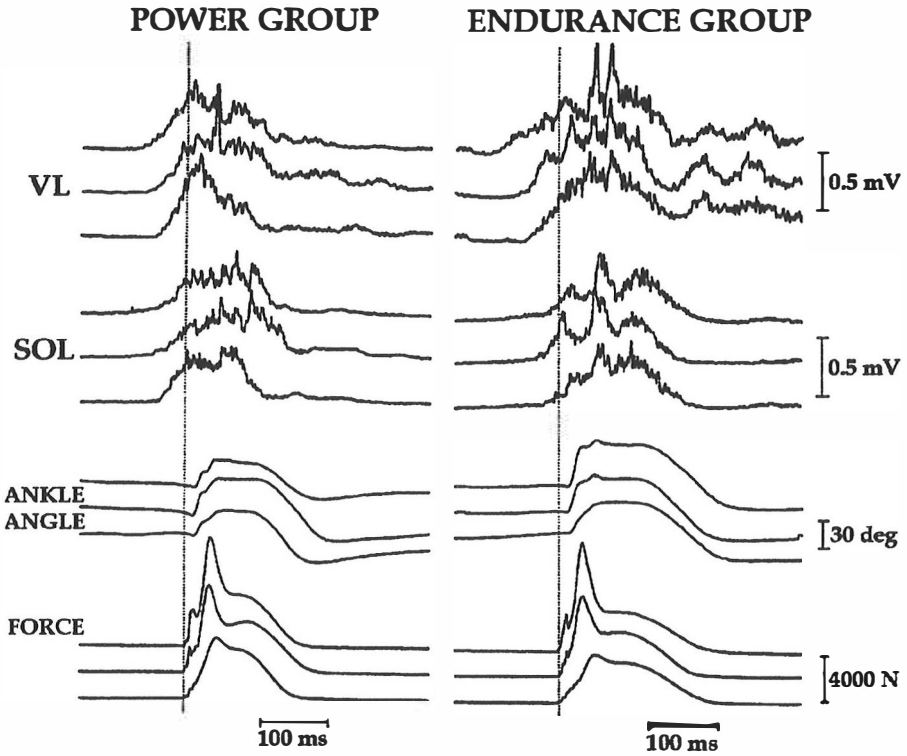

FIGURE 23. Averaged signals of reaction force, ankle angle and rectified EMGs from the SOL and VL during the drop jumps. The left curves represent a power athlete and on the right hand are the respective curves of an endurance athlete. The lowest line for every group of signals is the condition of O-40, in the middle is the optimum (O) and the highest one is the condition of O+40.

5.5 Mechanical efficiency (ME) in running

In any submaximal running conditions, ME did not differ significantly between the subject groups. Figure 24 demonstrates that ME did not changed with increasing running speed on the treadmill among either subject groups. The endurance athletes ran, however, relatively faster and with relatively lower oxygen uptake as compared to their power type counterparts (Figures 24 and 25). Furthermore, among power athletes ME was the higher the shorter the contact time ($r = -.79$, $p < 0.01$) in the treadmill running. The correlation coefficient between the ME and the contact time was -.53 ($p < .05$) for both groups. In addition, the higher the step rate the higher the accumulation of lactate at all three measured speeds ($r = 71$, $r = .67$ and $r = .52$, $p < 0.01 - 0.05$) when power athletes ran on the track.

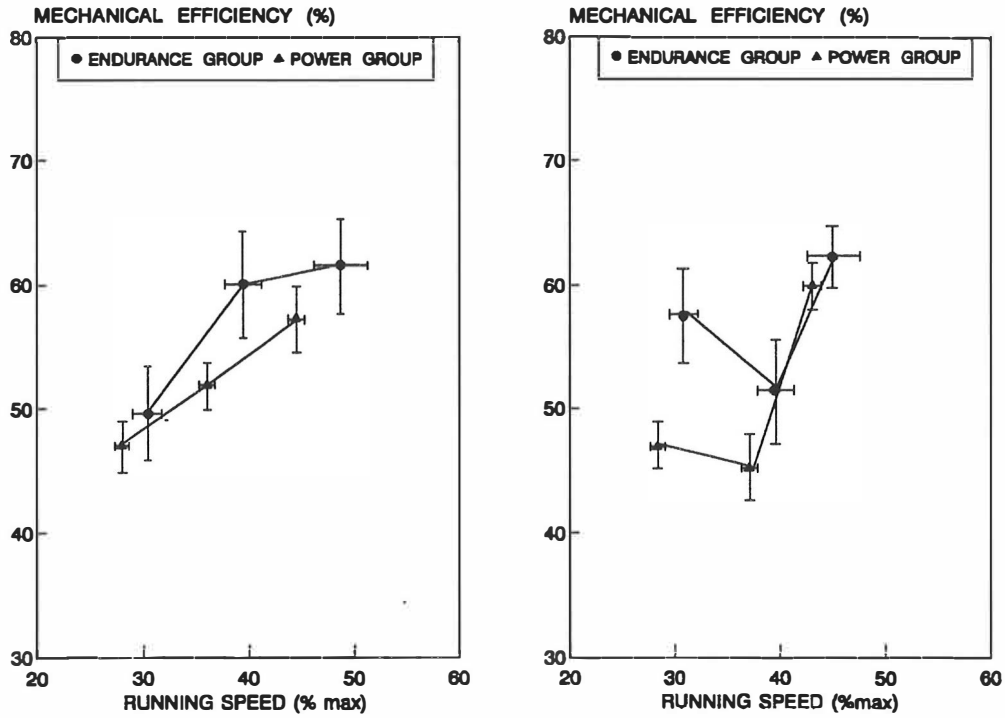

FIGURE 24. The mean (±SE) values of the ME related to the running speed on the treadmill (left) and on the track (right).

Table 5 demonstrates that there were significant ($p < 0.05$ - 0.001) differences in physiological variables between the subject groups. Among the endurance athletes the lactate level was almost the same after every running test. This was not the case among the power group. Their lactate level increased with increasing speed both on the treadmill and on the track. In every test condition the heart rate, pulmonary ventilation, and the oxygen uptake increased more among the power group with increasing running speed as compared to the endurance group. Furthermore, on the average across all conditions the power group used 9.7 % more energy than the endurance-trained athletes. Figure 26 demonstrates this phenomenon when the rate of energy expenditure is expressed per kilogram of body mass.

MANOVA revealed that the subject groups differed significantly ($p < 0.01$) in all force parameters (average and maximal F_z, F_y, and F_r) in the braking phase of the running contact. The power group produced higher braking forces (p varied from n.s. to 0.01) with increasing speed: e.g. for the vertical direction they were 1938 ± 297 N vs. 1716 ± 227 N, 2093 ± 290 N vs. 1909 ± 191 N and 2164 ± 307 N vs. 2048 ± 206 N. However, no differences between the subject groups were noticed when these force values were related to the body weight of the subjects: 2.4 ± 0.2 vs. 2.4 ± 0.2, 2.6± 0.1 vs. 2.5 ± 0.3

and 2.8 ± 0.1 vs. 2.6 ± 0.3, respectively. Neither did the direction of the force production between the groups.

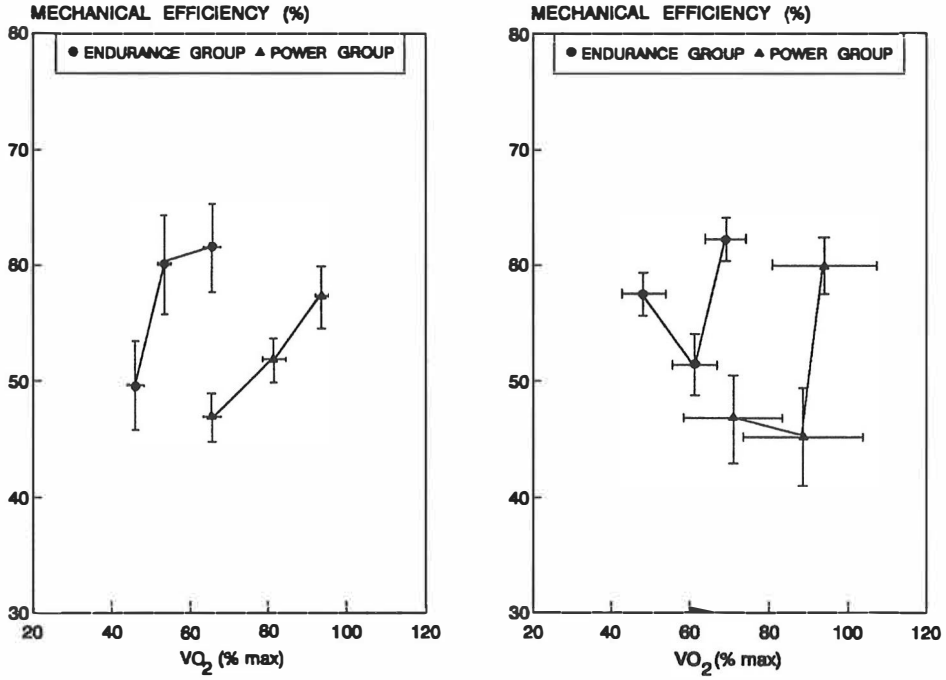

FIGURE 25. The mean (±SE) values of the ME related to the relative oxygen consumption in running speed on the treadmill (left) and on the track (right).

TABLE 5. Mean (± SD) of lactate (La), heart rate, ventilation (VE), relative oxygen uptake (VO_2), and relative speed in running with the three constant speeds on the treadmill (upper table) and on the track (lower table) among the endurance- and power-trained athletes. $p < 0.001$ ***, $p < 0.01$ **, $p < 0.05$ *.

	2.5 m · s^{-1}		3.25 m · s^{-1}		4.0 m · s^{-1}	
	Endurance	Power	Endurance	Power	Endurance	Power
La(mmol·l^{-1})	1.18 ± 0.32	2.14 ± 0.75 *	1.25 ± 0.30	3.05 ± 1.03 *	1.64 ± 0.41	5.70 ± 1.63**
HR (b·min^{-1})	118 ± 10	151 ± 15 **	134 ± 7	172 ± 11 **	153 ± 6	184 ± 8 ***
VE (l·min^{-1})	37.3 ± 4.5	56.8 ± 4.1***	44.3 ± 5.2	80.0 ± 8.5 ***	56.1 ± 6.2	107.3± 3.0***
%VO_2 max	46.2 ± 4.7	65.5 ± 4.6***	53.5 ± 3.5	81.2 ± 6.9 ***	65.7 ± 4.3	93.5 ± 2.9***

La(mmol·l^{-1})	1.12 ± 0.19	2.57 ± 1.10 *	1.10 ± 0.07	4.25 ± 2.26 *	1.46 ± 0.29	6.67 ± 2.88 *
HR (b·min^{-1})	118 ± 9	147 ± 15 *	136 ± 7	165 ± 9 ***	152 ± 7	177 ± 6 ***
VE (l·min^{-1})	42.8 ± 4.5	63.8 ± 7.6 **	56.0 ± 3.3	93.6 ± 15.8 **	67.2 ± 6.9	109.0 ± 14.9**
%VO_2 max	48.2 ± 6.4	70.9 ± 9.7 **	61.3 ± 5.1	88.9 ± 11.4 **	69.0 ± 3.5	94.0 ± 10.1**
% speed max	30.1 ± 2.3	27.7 ± 0.8 *	39.1 ± 2.9	36.1 ± 1.0 *	48.1 ±3.6	44.4 ± 1.2 *

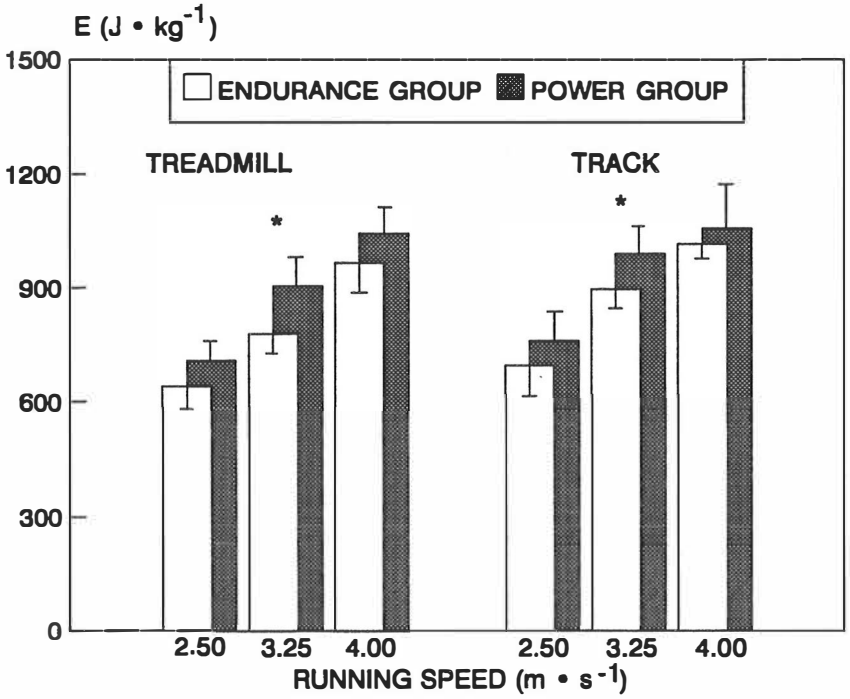

FIGURE 26. The mean energy expenditure divided by the body mass in running at the three different speeds on the treadmill and on the track. The two experimental groups differed partly significantly from each other ($p < 0.05$*).

Further analysis of the present study revealed that in running on the treadmill, the endurance group had slightly shorter contact times than the power group. The difference between the subject groups was significant ($p < 0.05$) in every condition when the contact times were related to their respective values during maximal running These relative values decreased with increasing running speed among both subject groups as follows: 83.8 ± 24.8 % vs. 131.5 ± 18.7 %, 66.9 ± 25.4 % vs. 110.9 ± 4.2 %, and 50.5 ± 21.7 % vs. 92.0 ± 6.0 %. There were no significant differences in step rate, average angular velocity of the ankle joint in the braking phase of the contact, or in vertical displacement of the centre of the gravity of the whole body. In addition, step length, braking time, and most of the angular and force variables were similar between the experimental groups. However, only in a few cases, the endurance group had slightly higher ($p<0.05$) average and maximal angular velocities of the knee joint in the braking phase of the contact.

The muscle activity patterns (Figure 27) and the integrated EMGs did not differ between the subject groups in any conditions . This was the case both on track and treadmill running. Also, the relationship between the eccentric and concentric EMGs did not differ between the experimental groups.

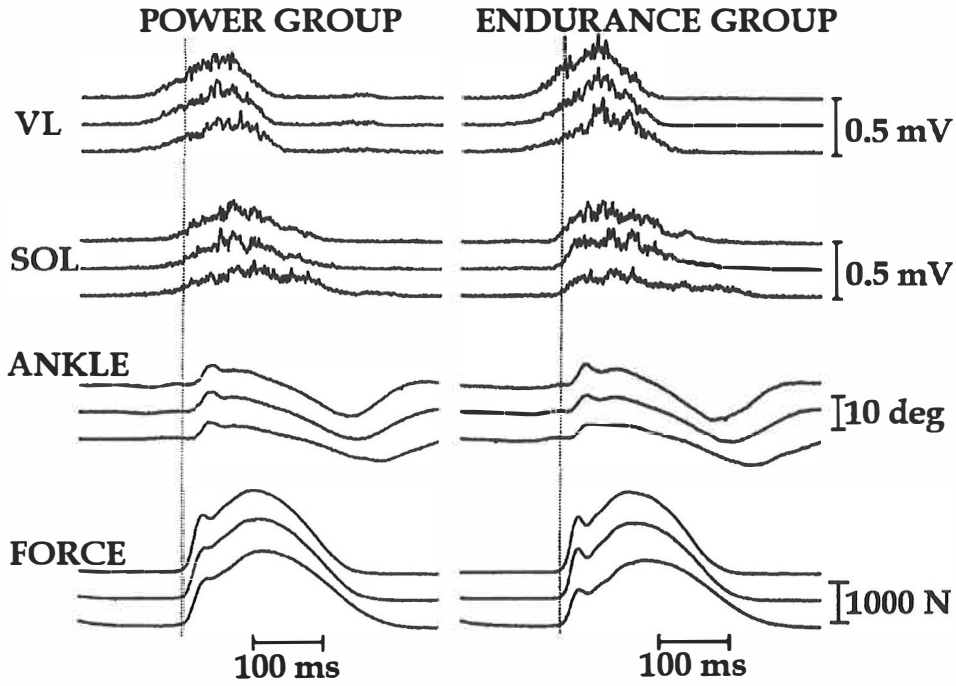

FIGURE 27. Averaged signals of reaction force, ankle angle and rectified EMGs from the soleus (SOL) and vastus lateralis (VL) during the running on the track. The left curves represent a power athlete and on the right hand are the respective curves of an endurance athlete. The lowest line for every group of signals is the speed of 2.50 $m \cdot s^{-1}$, in the middle is the speed of 3.25 $m \cdot s^{-1}$ and the highest one is the speed of 4.00 $m \cdot s^{-1}$.

6 DISCUSSION

The main findings in the present study were as follows:

(1) In the reflex conditions, the endurance athletes possessed higher relative EMG-amplitudes than their power counterparts. Furthermore, these relative EMG-amplitudes correlated clearly with the maximal reflex forces, or with the angular stretching velocities among the subject groups. These correlation coefficients were, however, higher among the endurance athletes.

(2) In the maximal voluntary isometric conditions, the power athletes produced higher forces than their endurance counterparts. However, the respective EMG-time curves of the leg extensor muscles did not differ between the subject groups.

(3) In the maximal SSC exercises, the power group elicited higher preactivity and successive higher eccentric activity related to the concentric one of the leg extensor muscles than their endurance counterparts. In addition, the muscle activity patterns were smoother with the lower dropping heights among both subject groups.

(4) In the total ME during jumping, no differences between the subject groups were noticed in most of the utilized SSC exercises. The endurance group worked with lower heart rate, pulmonary ventilation, and lactate level. On the other hand, the muscle activity patterns differed again between the subject groups, indicating a more powerful braking (eccentric) phase of the take-off among the power group.

(5) The total ME during running did not differ between the subject groups. At the same time, there were only a few biomechanical variables but many physiological variables, which differed between the endurance and power athletes.

6.1 Reflex function in rest

The present study demonstrated that the endurance-trained athletes were more sensitive to mechanical stimuli than the power-trained athletes. Shorter latency times of the SOL and GA muscles, higher relative reflex amplitudes of the VL, VM and SO muscles, and a better recovery of the monosynaptic reflexes among the endurance group suggest this conclusion. Futhermore, the power group had higher and more significant correlation coefficients between the relative EMG and the reflex force of the knee extensor muscles ($p < 0.05$ vs. $p < 0.01$), and between the relative EMG and the averaged angular velocity around the ankle joint ($p < 0.10$ vs. $p < 0.001$) as compared to their endurance counterparts. However, no differences were observed in the reflex latency time, the motor time, and the total reflex time of the knee extensor muscles between the subject groups.

The observed differences between the athletic groups may be explained by musculotendineous properties, and/or nervous system structures, and/or muscle spindle properties, and/or in the lower extremity lengths of subjects. It is well documented that endurance-type athletes are characterized by a high percentage of ST fibers and a high activity of oxidative enzymes, while power athletes could be characterized by a predominance of FT fibres and high activation of glycolytic enzymes in their leg extensor muscles (Saltin et al. 1977; Howald 1982). Thus the higher sensitivity to mechanical stimuli among the endurance-trained athletes observed in the present study could be explained by the fiber-type differences between the groups. Burke (1968) has reported that many ST and fatigue-resistant fast twitch (FT_a) units were spontaneously active and were recruited easily with muscle stretch. These same units have been suggested to be very active in movements which involve significant support from spindle afferent feedback (Burke and Edgerton 1975). Ryushi and his co-workers (1990) confirmed this suggestion by demonstrating that the reflex latency time correlated negatively with the percentage number of FT_a and/or ST fibres. However, the factors that determine recruitment order are closely related with axonal velocity (Clamann and Henneman 1976; Bawa et al. 1984). In this regard, it is interesting to note that the motor units, which are recruited first, have lower axonal conduction velocity (Bawa et al. 1984). Thus, in the present study, the reduced action potential conduction speed may not be powerful enough to cause the lengthening of the latency time over that of the FT-motor units.

The muscles rich in slow-twitch (ST) fibres are known to be more endowed with muscle spindles (Botterman et al. 1978). Proprioceptors in general, such as spindles and tendon organs, might serve as monitors of motor unit activity for controlling reflexes. They are, in addition, largely concerned with the fine control of movements. In the present study, the higher sensitivity of the endurance-trained athletes to mechanical stimuli could partly be explained by more collagenous and stiff material (Kovanen, 1989) and/or by numerical differences in muscle spindles (Botterman et al. 1978). The ability of the primary endings of the neuromuscular spindles to transmit afferent inputs to alpha motoneurons is also controlled by the spinal interneurons, and the

excitability level of the alpha motoneurons determines the reflex response amplitude (Beradelli et al. 1982). It has further been suggested that the amplitude of a monosynaptic reflex be directly propotional to the number of motoneurons activated.

The present findings suggest that the neural control of reflex movements in skeletal muscles may be different in the reflex force production among subjects differing in training background or in neuromuscular structure. An earlier demonstration of electromechanical delay, as defined by time difference between the onset of EMG and onset of force (Cavanagh and Komi 1979), is related to muscle fibre composition in reflex condition, but not in voluntary force production (Viitasalo and Komi 1981). This suggests, however, that the structural differences in muscle and nerve might be at least equally important in this control. H-reflex measurements have been given further support for this suggestion. The ratio between the mean value of maximal reflex response (H_{max}) and the mean value of the direct response (M_{max}) evoked by tibial nerve stimulation is significantly smaller among power-trained athletes as compared to non-trained athletes, which might be due to differences in the length of Ia-afferents on intermediate motoneurons (Casabona et al. 1990).

Earlier studies have shown that the latency times correlated positively with the length of subjects (Ryushi et al. 1990) and with the length of subject's legs (Allum and Mauritz 1984). In the present study, there was statistically not any significant difference between the groups in this regard. Thus the differences in the length of the sensory and/or motor nerves do not explain the observed differences in stretch reflexes of the same muscle between the experimental groups. However, when compared different muscles that explanation is the case. The latency times for the SOL and GA muscles (40-45 ms) were longer than the respective times for the VL and VM muscle (24 ms). Nevertheless, some additional factors have to take into consideration when further studies are done on this problem. For example, the relaxation level of the subjects was not controlled in the present study, and its possible role in influencing the results could not be substantiated. Further studies might also consider measuring H-reflexes parallel with the present approach for possible identification of the selected reflex pathways.

6.2 Maximal voluntary contraction in isometric condition

The power-trained athletes produced higher forces in the voluntary conditions than the endurance-trained athletes. This is in line with previous training studies (e.g. Komi et al. 1982; Häkkinen and Komi 1985ab; Häkkinen et al. 1990). Thus the present cross-sectional study confirms that prolonged power type training with SSC-exercises resulted in improved neuromuscular performance.

Komi (1986) has suggested that explosive-type strength training causes a shift of the force-time curve to the left. The results of the present study support this observation. At the same time, however, the muscle activity

patterns (the EMG-time curves) did not differ between the experimental groups, indicating similar trends in the neural activation of the muscles in the two maximal voluntary isometric conditions. This dissociation between force and EMG might have occurred because the subject groups had different amount of muscle mass measured indirectly as higher (mean 5.3 kg, $p < 0.001$) fat free weight (FFW) value and/or the power athletes had better efficacy in the force transmission from the individual sarcomeres to the skeletal muscle. Earlier studies give additional supports for these interpretations. The maximal voluntary strength of muscles seems to be highly related to the cross-sectional area of the muscle, but, however, different subject groups seem to have the same average force per unit area (e.g. Ikai and Fukunaga 1968; Sale et al. 1987; Ryushi et al. 1988). In addition, there is some evidence that the quality of connective tissue structures is adapted by training (Enoka 1988, Kovanen, 1989). This causes a significant effect on the muscle force transmitted to the tendon (Borg and Caulfield 1980).

The third possible explanation to the present results might again be a possibly different muscle fibre type distribution between the endurance type athletes and the power type athletes (Gollnick et al. 1973; Costill et al. 1976; Saltin et al. 1977). It has been demonstrated that the percentage of FT-fibres of the trained muscle correlated significantly with the improvement of fast force production during the power type training (e.g. Viitasalo and Komi 1978; Häkkinen et al. 1985) as the power athletes demonstrated in the present study.

6.3 Maximal SSC-exercises

The power-trained athletes elicited high preactivity and successive higher eccentric activity of the leg extensor muscles than their endurance type counterparts. In addition, the muscle activity patterns were smoother with the lower dropping heights among both subject groups. These findings were clearer in the drop jumps, which were more reactive movements. On the sledge the subjects had longer contact times and the concentric phase of the take-off was more dominant among both groups. This phenomenon can be confirmed from muscle activity patterns: during the sledge jumps the amount of preactivity was small and the concentric EMG was higher than the eccentric one.

Previous studies, used to clarify neuromuscular adaptations during power type exercises, have examined qualitative and quantitative aspects of the EMG bursts of the leg extensor and arm flexor muscles (e.g. Moritani and deVries 1979; Häkkinen and Komi 1986; Schmidtbleicher et al. 1988). In rapid movements not only has high muscle activation been observed, but also depression or silencing of EMG activity. The results of the present study support these findings (see Figures 17 and 18), which seem to be dependent on the stretching velocity of the muscles and on the training background of the subjects.

The observed differences in an adaptation of the neuromuscular systems between the subject groups can be assumed to take place in many

possible ways. The first available evidence indicates that the critical factor controlling motor unit recruitment in heterogeneous skeletal muscle is a motor unit type (Sypert and Munson 1981). In the present study, the endurance athletes, which have obviously higher percentage of slow twitch fibers (see e.g. Komi et al. 1977) had slightly inclined EMG burst as compared to the power athletes. In other words, the power athletes might have been able to recruit their motor units faster with an increased firing rate of motoneurons (Bigland and Lippold 1954). This suggestion is in line with the findings (Grimby and Hannerz 1977; Nardone et al. 1989) that the high-threshold motor units (FT fibers) were recruited just before the onset of lengthening in brief rapid muscle actions. Thus, for the power athletes, it might be easier to control the timing of the performance and to funnel the targets of excitatory motor commands to the appropriate motor units. Nardone and his co-authors (1989) have earlier suggested this for different muscle types in different muscle actions.

Another explanation for the results of the present study might be that the power-trained athletes had an improved intramuscular coordination, such as a more developed motor unit syncronization (Milner-Brown et al. 1973) associated with both reflex and voluntary function of the neuromuscular system. A support for this allegation can be found in the studies (Schmidtbleicher and Gollhofer 1982; Gollhofer and Schmidtbleicher 1988) which have suggested that better jumpers have also better intramuscular coordination as compared to the poorer ones. The proprioceptors of an active agonist can serve as the main sensors in controlling servomechanism also in jumping exercises. The increase in the EMG activity shortly after ground contact is evoked by proprioceptors via a spinal pathway initiated by primary muscle spindle afferents (Dietz et al. 1979). They play an important role in generating stretch reflexes, being much more sensitive to small amplitude displacements than to large ones (Matthews and Stein 1969).

In general, stretching of a contracting muscle generates large force increments, of which approximately half is due to the stretch reflex which increase the muscle stiffness more than what is predicted from the intrinsic stiffness (Sinkjaer et al. 1988). Hoffer and Andreassen (1981) have demonstrated that for the cat SOL muscle, the force increment due to stretch reflex is even up to three times larger than the intrinsic force increment. In the sledge jumps of the present study, stretch reflexes of the SOL muscle can be seen clearly about 40 ms after the onset of the ground contact among both subject groups. Its magnitude became progressively larger with higher stretching velocity. This supports previous findings that the stretch reflex magnitude increases with more dorsiflexed ankle (Weiss et al. 1986), and that the stretch reflex is velocity dependent (Gottlieb and Agarwall 1979). The magnitude of reflex response increases with the increased stretching velocity because muscle spindle primary ending afferents are velocity sensitive (Matthews and Stein 1969). In the present study, the GA muscle behaved, however, differently when compared to the SOL muscle. The drop in EMG activity between the preactivity and the eccentric activity increased with increased stretching velocity. This might be caused by concurrent increased flexion in the knee joint. Thus, the stretching length of the GA muscle may not change significantly with increased dropping height. One may also speculate

that low GA EMG activity in this phase could be due to Ia inhibition from the TA muscle. Our analysis cannot, however, verify its likelyhood.

Thirdly, learning processes may naturally influence the jumping performances. There were not any great differences in the performance technique between the subject groups, in spite of the fact that the power athletes used drop jumps as a part of their training methods. Anyway, the learning processes can be assumed to occur with the involvement of the cerebellar and cerebrocerebellar communication loops (Ito 1976).

In the present study, the amplitude of displacements of the knee and ankle joints increased with increased dropping height among both subject groups. However, the power athletes had a faster rate of EMG development during the preactivation phase, subsequently a more effective braking phase (more work in shorter time) and a higher EMG-ratio between the eccentric and concentric phases (Figure 15) during the take-off in every condition as compared to their endurance counterparts. Thus, it can be speculated that the power type subjects had higher muscle stiffness than the endurance-trained subjects. Furthermore, it could be assumed that in the jumping exercises, all inputs to the leg extensor muscles are in good balance because hardly any oscillation in the muscle activity patterns was noticed. In other words, smaller drops in EMG activity could be observed between preactivity and eccentric activity when the neuromuscular system is adapted for the used task (Kyröläinen et al. 1991). In this regard, one might see (Figures 17 and 18) that the power athletes had a smoother EMG pattern than their endurance counterparts. It is possible that the centrally determined activation control could smooth muscle activation as a result of adaptation and/or learning processes. However, when the stretching load is too high (the condition of O+40), the reflex peaks become more visible.

In any case, preactivation appears to be a preparatory necessity, both for enhancement of EMG activity during the eccentric phase of the take-off, and for timing muscular action with respect to ground contact (Moritani et al. 1991). Melvill-Jones and Watt (1971) have suggested that this preactivation is preprogrammed and executed from higher centers of the nervous system, on to which the reflex activity is superimposed (Dietz et al. 1979). This statement has not yet been challenged. In the present study, the observed co-activation between the TA and the triceps surae muscle may further increase the stiffness around the ankle joint.

6.4 Submaximal SSC-exercises

6.4.1 Jumping

The power athletes worked more powerfully in jumping performances than their endurance counterparts. At the same time their heart rate, pulmonary ventilation, and lactate level were higher. The EMG patterns, in addition, differed clearly between the subject groups. However, no differences between the groups were noticed in the ratio of the eccentric and the concentric EMGs of

any investigated muscles in any experimental conditions. Furthermore, no differences in the total mechanical efficiency (ME) between the two investigated athletic groups could be observed in most of the utilized SSC exercises. On the other hand, the increased stretch of the muscles measured indirectly by the knee angular velocity increased ME within certain limits in both experiment groups.

Quite similar ME values of jumping among both subject groups indicate that the different training-induced adaptation and/or inherited neuromuscular structure could have no influence on the ME. This conclusion supports some earlier studies measured in bicycle ergometer work (Suzuki 1979; Bosco et al. 1980), which demonstrated that the ME was not related to muscle fibre composition. Neither did Williams and Cavanagh (1987) observe any differences in muscle fibre type among trained male runners who showed good, medium, or poor economy. However, contrary results have recently been published where the %ST fibers correlated positively with efficiency in cycling (Coyle et al. 1992). In the present study, muscle fibre distribution was not determined as mentioned earlier. Nevertheless, it has been demonstrated that endurance type athletes possess a high percentage of ST fibres in their leg extensors as compared to their power type counterparts (Saltin et al. 1977). Thus, obvious differences in muscle fibre distribution between the subject groups in the present study might explain only a part of the similarities of their ME values in every experimental condition.

In general, there might exist two main explanations for similar MEs: 1) The power athletes had more powerful performance associated with more effective function of the neuromuscular system, and a higher muscular strength than their endurance counterparts (Figure 11). This enabled the power athletes to utilize elastic energy better during their jumping performances when the chemical energy was spared. 2) On the other hand, when compared to the power group, the endurance athletes obviously worked on a lower oxygen consumption level as related to their respective maximal values. This implies that the endurance group worked physiologically on a lower loading level even if both groups had the same mechanical work calculated from their individual maximum.

The suggested differences in adaptation of the neuromuscular systems between the subject groups can be assumed to take place in a quite similar way as described in maximal SSC-exercises (pages 58 - 60). The power group might have been able to recruit their motor units faster with an incremental firing rates of motoneurons because the rate of their EMG development seemed to be higher (Figures 22 and 23). The type of a motor unit has been suggested to control motor unit recruitment in heterogeneous skeletal muscle (Sypert and Munson 1981). Thus, it is possible that the power athletes recruited their high-threshold motor units (FT-fibres) just before the onset of lengthening, in brief and rapid muscle actions, as Nardone et al. (1989) has suggested for plantarflexor muscles in dynamic ramp lengthening actions. This, together with other improved function of their neuromuscular system, such as motor unit synchronisation (Milner-Brown et al. 1973), intramuscular coordination (Schmidtbleicher and Gollhofer 1982; Gollhofer and Schmidtbleicher 1988), and preprogrammed preactivation from higher centres of the nervous system

(Melvill-Jones and Watt 1970; Dietz et al. 1979) might create requirements for the neuromuscular system to increase muscle stiffness in a certain physiological range.

Among both subject groups, all inputs to the leg extensor muscles were obviously in good balance under the moderate stretching velocities of the muscles. However, the power group was able to utilize the higher tendomuscular stretches better than their endurance counterparts. Their power increased concurrently with the stretch load, and simultaneously they had less oscillation in their muscle activity. Thus, it is possible that the centrally determined activation control could smooth muscle activation as a result of training-induced adaptation and/or learning processes. However, in the highest stretch load condition (O+40), the reflexes (e.g. Ib inhibition from the Golgi tendon organ) may start to function as a protective mechanism. At the same time, muscle stiffness and the utilization of elastic energy may decrease, metabolic demands increase, and ME decrease. This suggestion is supported by high correlation coefficient values between chemical energy expenditure and the mechanical work in the condition of O+40.

Physiological differences of the metabolism between the subject groups can, on the other hand, explain the observed similarities in ME. The endurance-trained athletes had a lower blood lactate concentration than power-trained athletes after every testing condition (Figure 21). This means that power athletes had a greater lactate production than its removal, which caused lactate accumulation. Endurance training has been shown to cause proliferation of capillaries in the muscle (Andersen and Henriksson 1977) to increase the capacity of the oxidative enzymes (Holloszy 1973) and to increase the number and the size of mitochondria (Kiessling et al. 1971). Thus, these increases, together with a possibly improved O_2 delivery, can be responsible for decreases in blood lactate at a given submaximal work rate among the endurance group in the present study. The power athletes, on the other hand, might have got some of their energy via anaerobic pathways. If so, a part of their energy expenditure was not totally taken into account in our calculations, resulting in an overestimation of their ME values. Especially, this might be true in the sledge jumps because their heart rate and pulmonary ventilation were also significantly higher than their endurance type counterparts. The same could apply to the differences in the lactate values (see Figure 20), although it is possible that both groups in the present study produced the same amount of lactate but the endurance group could have removed it faster than the power group. Endurance training reportedly improves the rates of lactate removal (Donovan and Pagliassotti 1990). In this case, the energy expenditure values are again comparable between the subject groups.

6.4.2 Running

The endurance athletes ran all the time at an aerobic level because they achieved the steady-state metabolic cost and their blood lactate values were stable at each running speed. Therefore, no changes may have happened in

their energy sources during the exercise. The result of the respiratory exchange ratio (R) gives further support for this suggestion. It increased only slightly with increased running speed among the endurance group as follows: 0.79 ± 0.04, 0.81± 0.03 and 0.86 ± 0.03 on the treadmill and 0.81± 0.04, 0.85± 0.02 and 0.88± 0.03 on the track. The power group had higher ($p < 0.05 - 0.01$) R-values compared to their endurance counterparts: 0.88 ± 0.04, 0.97 ± 0.08 and 1.02 ± 0.07 on the treadmill, and 0.88 ± 0.04, 0.95 ± 0.04 and 0.98 ± 0.02 on the track. One power subject had the R-value over 1.00 at the speed of 3.25 $m \cdot s^{-1}$ and three of them at speed of 4.00 $m \cdot s^{-1}$ during running on the treadmill. In general, the conditions of the present study were mostly aerobic. However, for the power group the work at the lowest speed was certainly on an aerobic level and at higher speeds on the treadmill there could have been anaerobic energy expenditure during their running. If so, their true energy cost have been underestimated and, therefore, their ME values are overestimated at the two highest speeds. The recent studies of Bangsbo et al. (1990) and di Prampero et al. (1993) have, however, estimated the value of oxygen debt (lactate production) as an energy yield. In the present study it has been ignored because it would not give the true and exact energy equivalent for anaerobic energy production. Before this general problem of contribution of lactate to energy expenditure can be solved, the present results can be generalized only with caution.

Literature is not uniform regarding ME values at different running speeds. In addition to a more general view that ME increases as running speed increases (Cavagna and Kaneko 1977), there are also contrary results. Kaneko et al. (1985) reported that efficiency values actually could decrease as running speed increases. Later Kaneko (1990) explained that "this discrepancy was not due to physiological factors but rather to an artifactual factor related to net energy cost". More specifically, Kaneko (1990) referred to the problem of the role of the anaerobic energy expenditure. This problem may be relevant for the values of the power group in the present study. In addition, it has to be emphasized that the present methods used did not take the internal work into account. It could be estimated by comparing stride length and stride frequency (Cavagna et al. 1991), which did not, however, differ between the subject groups in the present study. On the other hand, it has been demonstrated that total body mechanical work (external work) explains better aerobic demands in locomotion than segment-based model (external + internal work) (Martin et al. 1993).

In general, endurance runners have shown to have greater ME at relatively low speeds but this relation tended to be reverse at higher speeds (Kaneko et al. 1985). This difference between the two groups of runners may not be due to the calculation of total mechanical power but rather to differences in net energy cost (Kaneko et al. 1985). In the present study the power athletes had a higher lactate accumulation after every running session. During exercise they also had higher metabolic responses indicating that the respiratory- and circulatory systems of the endurance athletes were in a better condition, and/or their oxidative energy supply was more economical, and/or they were able to utilize the elastic energy stored in the tendomuscular system during the

eccentric phase of the contact. Regarding to possible contribution of the storage and recovery of elastic energy, one faces with the problem of estimating its role in the entire running cycle. It is known that ME in pure eccentric exercise increases linearly. However, this phenomenon appears to be individual with the increase of the stretching velocity (Aura and Komi, 1986a). This is due to the contribution of elastic energy. However, the condition is different in the combined stretch-shortening cycle (such as jumping and running), in which the eccentric phase is performed differently compared to the pure eccentric exercise (Kyröläinen et al. 1990).

Furthermore, in the present study, the power athletes were heavier than their endurance counterparts. This was taken into consideration in the calculation of ME. In Figure 26 the energy expenditure has been related to the body mass but there still exist clear differences in the energy expenditure between the subject groups. The other studies have, however, shown that adding or reducing body weight has no effect on oxygen cost ($ml \cdot kg^{-1} \cdot min^{-1}$) of exercise in men (e.g. Davies 1980, Cooke et al. 1991). Cureton et al. (1978) have shown that extra weight has no effect on efficiency. On the other hand, in the recent study of Bergh et al. (1990) reported that the submaximal oxygen uptake and body mass are interrelated during running. According to the results of the present study, it seems, however, that body mass cannot be regarded as a significant factor related to the observed efficiency values.

The measured biomechanical variables gave only a few additional explanations for the observed differences between the subject groups. The shorter contact times and, especially, its shorter braking phase, and high angular velocity in the same phase may increase the utilization of tendomuscular elasticity, and thus may result in greater running economy among the endurance-trained athletes.

The step length had no significant relationship with the other variables among any of the subjects, who had freely chosen their running styles. However, there are studies (e.g. Cavanagh and Williams 1982, Kaneko et al. 1987) which indicate that the aerobic demand of running at a given speed tends to change as the step rate and/or the step length is changing from that which is freely chosen by the runner. In the present study, the step rate was related significantly ($p < 0.001 - 0.05$) to the lactate accumulation among the power group separately in every test condition. In general, the optimal running speed is an individual characteristics which is associated with step length (Cavanagh and Williams 1982, Bhambhani and Singh 1985). Thus, the relationship between economy and biomechanical descriptors were from moderate to low like Williams and Cavanagh (1987) have concluded.

The mean muscle activity patterns and integrated EMGs did not give any further information which could be used to interpret the results of the present study. Therefore, no further EMG analysis was performed

7 PRIMARY FINDINGS AND CONCLUSIONS

The main findings and conclusions of the present study can be summarized as follows:

(1) In the reflex condition, the endurance-trained athletes were more sensitive to the mechanical stimuli used in the present study. Furthermore, their recovery time of the monosynaptic reflex was faster when compared to the power-trained athletes. These results might be explained by the suggestion that obvious differences in the motor unit type and the number of muscle spindles between the subject groups have a powerful effect on the reflex recruitment. It is, however, an open question how much the difference in the training background of the subjects influences the neural control of the reflex movements, including the activities of the present study.

(2) In the voluntary isometric condition, the power-trained athletes produced higher forces than their endurance counterparts. However, the EMG-time curves did not differ between the experimental groups. There seems to exist a dissociation between force and EMG adaptations. The present results can, therefore, be explained by obviously different muscle fibre distribution, by different amount of muscle mass, and by possible differences in the force transmission from individual myofibrils to the skeletal muscle and by specifity of training.

(3) High preactivation of the leg extensor muscles and successive high activation during the braking phase of the take-off result in good physical performance in maximal and submaximal jumping exercises. The power athletes possess an ability to activate their leg extensor muscles faster in the preactivation phase of the stretch-shortening cycle exercises. Correspondingly, they a had rapid rate of EMG recovery in the concentric phase, suggesting efficient recoil characteristics. In addition,

the smooth EMG curves suggest a good balance between facilitatory, inhibitory, and other inputs to the muscle. This might be a necessary condition to create good resistance against high impact forces during powerful jumping exercises.

(4) The relationship between biomechanical and physiological variables during jumping exercises appears to be very complex. In disagreement with the presented hypothesis, both the power group and the endurance group achieved almost the same mean ME values. The power athletes may have a more powerful function of the neuromuscular system associated with higher muscular strength, obviously higher tendomuscular stiffness, and better utilization of elasticity in the tests of the present study. The endurance athletes may have more developed metabolic functions such as oxidative capacity, lactate removal, and mitochondrial system.

(5) ME values did not differ significantly between the subjects groups. This was the case in spite of the fact that the metabolic rsponses were lower among the endurance athletes. On the other hand, only a few biomechanical variables seemed to differ between the subject groups. Therefore, it is assumed that the better understanding of the complex interactions between mechanical and metabolic factors can be achieved through studies emphasizing individuals instead of group comparisons.

(6) The role of the biomechanical variables as an explanatory factor in the efficiency of jumping and running seem to be individual. Physiological and structural differences between subjects create the basis of natural human locomotion which can be modified by enviromental factors such as training. The present study showed that different training may influence the muscle activity patterns as well as muscular mass. These may, on the other hand, produce differences in force and power production as well as in angular velocities around different joints.

8 TIIVISTELMÄ

Tämän tutkimuksen tarkoituksena oli selvittää ihmisen liikkumisen taloudellisuutta ja hermolihasjärjestelmän suorituskykyä. Tutkimuksen koeryhmiksi valittiin teho- ja kestävyyslajien urheilijat, joilla molemmilla on erilaiset harjoitustaustat. Mahdollisia eroja suorituskyvyssä ja liikkumisen taloudellisuudessa pyrittiin selvittämään sekä biomekaanisten että fysiologisten mittareiden avulla. Koehenkilöt testattiin kolme eri kertaa vuoden välein, jolloin mittaukset ajoittuivat samalle harjoituskaudelle.

Ensimmäiseen mittaukseen osallistui 10 tehourheilijaa ja 10 kestävyyslajien edustajaa. Perusrefleksitoimintaa mitattiin levossa sekä polven ojentajalihaksista että plantaarifleksoreista. Lisäksi koehenkilöt suorittivat pudotushyppyjä kolmelta eri korkeudelta, jotka olivat etukäteen määrätyt. Optimikorkeus (O) oli pudotuskorkeus, jolta pudottautumalla koehenkilö saavutti parhaan kehon painopisteen lentoajan. Muut pudotuskorkeudet olivat optimi+40 cm (O+40) ja optimi-40 cm (O-40). Ohjeeksi koehenkilölle annettiin, että hän ponnistaisi mahdollisimman suorin jaloin (reaktiivisesti) kädet tiukasti lantiolla. Kaikki koehenkilöt suorittivat kultakin korkeudelta noin 10 pudotushyppyä, joista 5-6 parasta suoritusta valittiin jatkoanalyyseihin. Vastaavasti koehenkilöt suorittivat maksimaalisia ponnistuksia istuen kelkassa (kelkkahypyt). Suorituksista mitattiin reaktiovoimia, polvi- ja nilkkakulmien muutoksia ja lihasten sähköistä aktiivisuutta (EMG), joka rekisteröitiin pintaelektrodeilla telemetrisesti.

Toiseen mittausvaiheeseen valittiin 11 tehourheilijaa ja 10 kestävyysurheilijaa. Samoin kuin ensimmäisellä mittauskerralla, mitattiin nytkin aluksi lepotilan perusrefleksitoiminnat. Lisäksi koehenkilöiltä mitattiin isometrisesti polven ojentajalihasten ja plantaarifleksoreiden maksimaalinen tahdonalainen voimantuotto. Sen jälkeen määritettiin jälleen kunkin optimaalinen pudotuskorkeus yksilöllisesti sekä pudotus- että kelkkahypyissä. Varsinaisessa mittaustilanteessa koehenkilöt suorittivat noin 60 submaksimaalista ponnistusta kolmen sekunnin välein pudotuskorkeuksilta O-40, O ja O+40. Tämä mahdollisti

steady-state -tilan saavuttamisen kunkin työn aikana. Ponnistuksen jarrutusvaiheen piti olla tehokas, kun taas työntövaiheen submaksimaalinen. Kelkkahypyissä työntövaihe olikin määritetty 70 %:ksi yksittäisestä maksimisuorituksesta. Avustajat antoivat työn aikana koehenkilölle jatkuvaa palautetta kelkan nousukorkeudesta, jotta tehty mekaaninen työmäärä olisi säilynyt vakiona. Reaktiovoiman, polvi- ja nilkkanivelen kulmamuutosten ja EMG-mittausten lisäksi koehenkilöiltä mitattiin hengityskaasuja, sykettä ja veren laktaattipitoisuuden muutoksia. Kelkan nousukorkeus ja nopeus määritettiin matka- ja nopeusmittarilla.

Kolmanteen mittaukseen oli satunnaisesti valittu 5 tehourheilijaa ja 5 kestävyysurheilijaa. Maksimivoiman lisäksi heiltä mitattiin maksimaalinen hapenottokyky juoksumatolla ja maksiminopeus radalla tiettyjen referenssiarvojen määrittämiseksi. Varsinaisen testin aikana koehenkilöt juoksivat aluksi juoksumatolla viisi minuuttia kolmella eri vakionopeudella (2,50m $\cdot$ s^{-1} - 3,25 m $\cdot$ s^{-1} - 4,00m $\cdot$ s^{-1}). Tänä aikana he saavuttivat hapenkulutuksessa steady-state -tilan. Hengityskaasujen lisäksi koehenkilöiltä mitattiin kontaktiaikoja, polven ja nilkan kulmamuutoksia ja EMG:aa. Kinemaattisen varren avulla rekisteröitiin ulkoisen mekaanisen työn laskemisessa tarvittavia arvoja. Viikkoa myöhemmin samat koehenkilöt juoksivat vastaavilla nopeuksilla radalla. Jokaisen juoksukierroksen (200 m) jälkeen koehenkilöiltä mitattiin maahan kohdistuvia reaktiovoimia 13 metriä pitkän voimalevyanturin avulla. Muuten mittaukset olivat samoja kuin juoksumatolla lukuunottamatta hengityskaasuja, jotka kerättiin Douglas-säkkiin minuutin ajalta ja analysoitiin myöhemmin.

Tutkimuksen päätulokset osoittivat, että kestävyysurheilijat olivat tehourheilijoita reflektorisesti herkempiä mekaaniselle stimulukselle. Lisäksi he palautuivat nopeammin monosynaptisesta refleksistä. Kestoryhmän refleksiamplitudit korreloivat tehoryhmää selvemmin refleksivoimaan ja keskimääräiseen nivelen kulmanopeuteen (lihaksen venytysnopeuteen). Isometrisesti mitatuissa maksimaalisissa, voluntaarisissa lihassupistuksissa tehoryhmä tuotti sekä polven ojentajalihaksilla että plantaarifleksoreilla kestoryhmää selvästi suurempia voimia. Myös voimantuottonopeus oli tehoryhmällä selvästi kestoryhmää parempi. Eroja lihasten aktiivisuuden tuotossa ei sen sijaan havaittu.

Lihasten venymis-lyhenemissyklusta hyödyntävissä maksimaalisissa hyppysuorituksissa koeryhmät erosivat toisistaan monella tavalla. Tehourheilijat tuottivat suuremman esiaktiivisuuden, jota seurasi kestoryhmää korkeampi eksentrisen ponnistusvaiheen aktiivisuus. Pudotushypyissä havaittiin lisäksi, että tehoryhmän lihasaktiivisuusmallit ovat tasaisempia kuin kestoryhmällä. Pudotuskorkeuden ollessa riittävän suuri havaittiin myös tehoryhmällä enemmän oskilaatiota lihasaktiivisuusmalleissa. Pudotushypyissä eksentrinen vaihe dominoi konsentriseen vaiheeseen nähden molemmilla ryhmillä, mutta eksentrisen ja konsentrisen aktiivisuuden suhde oli suurempi tehoryhmällä. Kelkkahypyissä ponnistusajat olivat selvästi pudotushyppyjä pitempiä molemmilla koeryhmillä, ja konsentrinen ponnistuvaihe dominoi eksentriseen verrattuna.

Submaksimaalisen liikkumisen taloudellisuudessa hyppien ja juosten koeryhmät erosivat toisistaan vain vähän. Pudotus- ja kelkkahypyissä mekaaninen hyötysuhde vaihteli tehoryhmällä keskimäärin 23,8:sta 54,9 prosenttiin ja kestoryhmällä 30,8:sta 58,5 prosenttiin mittaustilanteesta riippuen. Tehoryh-

män työtehot olivat odotetusti parempia ja lihasaktiivisuusmallit tasaisempia kuin kestoryhmällä, mutta samanaikaisesti heidän sykkeensä, ventilaationsa ja laktaattitasonsa olivat korkeammalla. Mekaaninen hyötysuhde lisääntyi molemmilla ryhmillä polvi- ja nilkkanivelten kulmanopeuksien (jalan ojentajalihasten venytysnopeuksien) lisääntyessä. Submaksimaalisen juoksun aikana mekaanisessa hyötysuhteessa ja useimmissa biomekaanisissa muuttujissa ei havaittu eroja ryhmien välillä. Kestoryhmä juoksi suhteellisesti alemmalla tasolla heidän maksimaalisesta hapenottokyvystään, mutta suuremmalla suhteellisella nopeudella kuin tehoryhmä. Suurimmat ja lähes ainoat merkittävät erot ryhmien välillä havaittiin jälleen fysiologisissa mittareissa. Kestoryhmän urheilijoiden syke, ventilaatio, energiankulutus kehon painokiloa kohti ja laktaattitasot olivat selvästi alempia kuin tehoryhmän urheilijoilla.

Tämän tutkimuksen päätulokset viittaavat siihen, että harjoittelu aiheuttaa muutoksia ihmisen hermolihasjärjestelmän toiminnassa. Täten perittyä geneettistä perustaa voidaan ilmeisesti muokata tietyntyyppisellä harjoittelulla. Levossa mitattujen refleksivasteiden erot koeryhmien välillä voitaneen selittää eroilla motorisen yksikön tyypissä ja lihasspindelien lukumäärässä. Hidas lihassolu sisältää enemmän spindeleitä kuin nopeatyyppinen ja lisäksi hitaalla lihaksella on nopeaa lihasta alempi rekrytointikynnys. Myös aikaisemmista tutkimuksista saadaan tukea edellä esitetylle tulkinnalle kestoryhmän hitaiden lihassolujen hallitsevuudesta. Sen sijaan voluntaarisissa tutkimustilanteissa havaitut koeryhmien väliset erot voimantuotossa voitaneen selittää erilaisen harjoitustaustan lisäksi eroilla lihasmassan ja sidekudoksen määrässä, todennäköisesti erilaisella lihassolujakaumalla sekä eroilla voimansiirrossa yksittäisestä lihassolusta koko luurankolihakseen.

Teholajien urheilijoilla hyppelysuorituksissa havaittu suuri ja nopea esiaktiivisuus, sitä seuraavat korkea ja tasainen eksentrinen aktiivisuus sekä alhainen konsentrinen aktiivisuus mahdollistavat ilmeisesti tehokkaan kimmahduksen. Tämä johtunee siitä, että edellä kuvatuilla tekijöillä pystyttäneen parantamaan lihaksen jäykkyysominaisuuksia, jolloin elastisuuden hyödyntäminen tehostuu. Submaksimaalisissa hyppelysarjoissa tehokkaalla elastisuuden hyödyntämisellä pystyttiin vähentämään kemiallisen energiankulutuksen osuutta, jolloin hyppimisen hyötysuhde parani. Kestävyyslajien urheilijat saavuttivat hyppelyissä kuitenkin samansuuruisia hyötysuhdearvoja kuin tehourheilijat, mikä selittynee heidän kehittyneemmällä hengitys- ja verenkiertoelimistön toiminnalla. Tehoryhmä pystyi siis kompensoimaan heikomman hengitys- ja verenkiertoelimistön toimintansa kestoryhmää paremmalla hermolihasjärjestelmän toiminnalla.

Juoksun taloudellisuuden tutkiminen täytyy ulottaa yksilötasolle saakka. Tässä tutkimuksessa mekaaninen hyötysuhde oli sama molemmilla koeryhmillä huolimatta ryhmien selvistä eroista fyysisen kunnon eri osa-alueilla. Tehoryhmä oli voimakkaampi, tehokkaampi ja nopeampi, kun taas kestoryhmällä oli parempi maksimaalinen hapenottokyky sekä muutenkin kehittyneempi hengitys- ja verenkiertoelimistön toiminta. Sen sijaan biomekaaniset muuttujat eivät eronneet sanottavasti ryhmien välillä. Täten fysiologisten ja biomekaanisten muuttujien välillä vallitsee hyvin monimutkainen suhde, jonka tutkiminen vaatii yksilöllisyyden lisäksi entistä kehittyneempiä menetelmiä etenkin mekaanisen työn määrittämiseksi.

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