ORIGINAL ARTICLE

H. Kyröläinen · P. V. Komi

Differences in mechanical efficiency between powerand endurance-trained athletes while jumping

Accepted: 29 August 1994

Abstract Mechanical efficiency (ME) of jumping exercises was compared between power-trained (n=11)and endurance-trained athletes (n=10) using both a biomechanical and a physiological approach. In drop jumps and in stretch-shortening cycle exercise on a special sledge (sledge jumps), the subjects performed 60 muscle actions from a dropping height of optimum minus 40 cm (O-40), as well as from dropping heights of optimum (O) and optimum plus 40 cm (O+40). Thus, they were tested in six different tests which lasted for a total of 3 min for each. The mean ME values in the drop jumps from the lowest dropping height upwards were as follows: 23.8 (SD 5.3)%, 35.5 (SD 10.8)% and 39.2 (SD 6.6)% for the power group, and 30.8 (SD 6.5)%, 37.5 (SD 8.7)% and 41.4 (SD 7.0)% for the endurance group. In the sledge jumps the ME values were 37.0 (SD 5.6)%, 48.4 (SD 4.0)% and 54.9 (SD 8.5)% for the power group, and 40.2 (SD 5.9)%, 46.9 (SD 5.7)% and 58.5 (SD 5.5)% for the endurance group. As can be seen, the ME values increased with increasing stretch load. However, the groups did not differ from each other except in the drop jump condition of O-40(P < 0.05). The higher power (P < 0.001) among the power athletes in every measured condition was associated with a faster rate of electromyogram development during the pre-activity, and smoother muscle activity patterns in the ground contact. On the other hand, the endurance athletes had a lower blood lactate concentration after every test, and in addition a lower heart rate and ventilation during the sledge jumps than their power counterparts. Therefore, it would seem that the similar mean ME values between the subject groups could be explained by improved function of the neuromuscular system among the power group and improved metabolism among the endurance group.

H. Kyröläinen (🖾) · P.V. Komi

Department of Biology of Physical Activity,

University of Jyväskylä, FIN-40100 Jyväskylä, Finland

Key words Mechanical efficiency Stretch-shortening cycle · Electromyography · Jumping

Introduction

Mechanical efficiency (ME) describes the amount of the work done as a proportion of the energy expended. After Fenn (1923), many scientists have been interested in the economy of animal and human locomotion. Margaria et al. (1963) have measured the oxygen consumption (VO_2) in successive knee bending exercises with a variable interval of time between flexion and extension of the lower limbs. When shortening of the muscle was immediately followed by stretching, the efficiency was greater. Taylor et al. (1982) have shown that the big red kangaroo becomes more economical as the speed of hopping increases. Bosco et al. (1982) have demonstrated that ME increases during jumping with higher angular velocities of the knee joint. Therefore, it is possible that imparted mechanical energy may be temporarily stored in the series elastic components of active muscle for use in a subsequent muscle action as suggested by Asmussen and Bonde-Petersen (1974). The storage and use of elastic energy of muscles has been shown to depend on stretching velocity and muscle length (Cavagna et al. 1968; Aura and Komi 1986) as well as on the force attained at the end of the prestretch and the coupling time between stretching and shortening phases of muscles (Bosco and Komi 1979; Bosco et al. 1982). As a consequence of a good utilisation of elastic energy, it has been suggested that metabolic demands of muscles may decrease and, therefore, the ME increase (Thys et al. 1972; Aura and Komi 1986; Kyröläinen et al. 1991).

In jumping with stretch-shortening cycle (SSC) exercises, the mean of the net efficiency of positive work has been found to range from 30.1% to 38.7% (Bosco et al. 1982). These authors have, however, used the constant value of 120% introduced by Margaria et al. (1968) for ME of negative work (W_{neg}). This has later been shown to give erroneous values for the calculation of ME of W_{neg} . In fact the difficulty of introducing appropriate values for the negative phase ME has been critically discussed (Oksanen et al. 1990). Therefore, the special sledge apparatus was developed to isolate better different muscle actions, and to enable more accurate calculations of ME (Kaneko et al. 1984). This sledge was also used later to study the combination of eccentric and concentric actions in SSC exercises (Aura and Komi 1986). In their studies the ME of the positive phase of SSC exercise was 35.5 (SD 6.9)%. The ME value of pure eccentric work was used to correlate with the corresponding value of the eccentric phase of the SSC exercise. However, further studies have revealed that the electromyogram (EMG) values of leg extensor muscles during the pure eccentric and the eccentric phase of SSC exercises are different. This has suggested that the two eccentric conditions are not metabolically equal (Kyröläinen et al. 1990).

While the exact determination of the positive work (W_{pos}) ME in SSC exercise seems difficult to achieve, the calculation of total work (W_{tot}) ME seems to give more reliable estimates for SSC ME. Using this approach, it has been shown that, for example, training may modify ME (Kyröläinen et al. 1991). To follow this logic, the present study was designed to examine ME of two groups of athletes, which had clearly different training backgrounds.

Methods

Subjects

A group of 11 power-trained athletes [mean age 26 (SD 6) years, mean height 183 (SD 6) cm, mean body mass 76.9 (SD 4.3) kg] and 10 endurance-trained athletes [mean 24 (SD 4) years, 180 (SD 4) cm, 70.5 (SD 4.5) kg, respectively] volunteered as subjects for this study. All the subjects were highly trained athletes, who had trained systematically and regularly for several years. They were fully informed of the procedures and appraised of all possible risks involved in this study.

Procedure

At first, the optimal dropping height of the subjects was determined individually in the drop jumps with maximal effort. The subjects were dropped from different heights to ascertain for each the best height of rise of the centre of the gravity. Thereafter, they performed drop jumps from the three individually predetermined dropping heights: the optimal drop height (O), the optimum plus 40 cm (O+40) and optimum minus 40 cm (O-40). The subjects were instructed to resist maximally the downward movement during the braking phase, bend their knees minimally, and perform a submaximal push-off during the take-off.

In all conditions, the subjects performed 60 muscle actions lasting a total of 3 min. The frequency was, therefore, once every 3rd s and was controlled by an audio signal. When the subject ceased to be in contact with the ground, two assistants used a rope attached to the vest of the subject and pulled him up to the same energy level by a special pulley system in preparation for the next drop. The third assistant took care of his balance during this phase (Fig. 1). Periods for recovery between the exercise sets were for as long as it took for $\dot{V}O_2$ to return to resting level. To



Fig. 1 The subject performing drop jump exercises

study the physiological strain of subjects, their heart rate was recorded by Sport Tester PE-3000. 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 period and immediately as well as 3 and 5 min after every test.

The second part of the test was performed on a special sledge apparatus (Kyröläinen et al. 1990; modified from Kaneko et al. 1984). The mass of the sledge was 33.2 kg, and its inclination was at 22.5° to the horizontal. For determination of the individual optimal dropping height, the subject sat on the sledge and he was dropped from different heights followed by the maximal take-off phase and the best rising height of the sledge. Thereafter, the subject performed three sets of submaximal SSC exercises (sledge jumps). The assistants dropped him from O, and immediately after the braking phase followed by the push-off phase at an intensity of 70% of his best single maximal SSC exercise. During the next tests, the dropping height was O + 40 and O - 40 followed by the push-off phase with the same intensity as in the first test. The assistants were responsible for the dropping height required and they also informed the subject that the height the sledge had been raised. During contact with the force plate, 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 as in the drop jumps. The recoveries between the exercise sets were determined by $\dot{V}O_2$ as in the drop jumps. The heart rate and blood samples were also taken in the same order as in the drop jumps.

Measurements

In the drop jumps, vertical reaction forces were measured on a force plattform. On the sledge the force plate was placed perpendicularly to the sliding surface. In both jumping conditions, angular displacements in the knee and ankle joints were measured by electrogoniometers (ELGON), which were attached to the lateral side of both joints. The EMG activity of the vastus lateralis (VL), vastus medialis (VM), gastrocnemius (GA), soleus (SOL) and tibialis anterior (TA) muscles was recorded telemetrically (Glonner) with surface electrodes (Beckman miniature skin electrodes,

650437). The electrodes were attached longitudinally over the muscle belly. The EMG signals were amplified simultaneously with the records of force and joint angles at a sampling frequency of 1 kHz. During the sledge jumps, the distance the sledge moved and its velocity were also measured. All the measured signals were recorded both by an on-line computer system, and on a magnetic tape for further analysis.

The expired gases (sampling flow rate varied from 20 to 40 breaths \cdot min⁻¹) were analysed by measuring pulmonary $\dot{V}O_2$, from the volume of the gas, and its concentrations of O_2 and CO_2 by using a semi-automatic system (Oxycon Mijnhardt-4). Their values were averaged and printed out every 30 s. The instrument was regularly calibrated with mixtures of known gas concentrations. In addition, because the tube (diameter 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 in a highly linear manner: e.g. the regression between the tube volume and O_2 (%) was as follows: O_2 (%)=0.066 · tube volume +3.047.

Analysis

The EMG activities were fullwave rectified, integrated (iEMG) and time normalised for 1 s in four different phases: pre-activation from 100 ms to 50 ms before ground contact, pre-activation from 50 ms to 0 ms before the contact, braking phase (eccentric) and push-off phase (concentric). The force signal was used to identify the beginning and the end of the contact. The ELGON 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 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 to obtain individual muscle activity patterns.

Calculations of ME

The ME was calculated by dividing the mechanical work (W) by the energy expenditure (ΔE) above the resting level. In the drop jumps, the mechanical external W_{tot} is the sum of W_{neg} and W_{pos} calculated as follows:

$$W_{\text{tot}} = W_{\text{neg}} + W_{\text{pos}} = \left(mgh_1 + \frac{1}{2} m\nu_1^2 \right) + \left(mgh_2 + \frac{1}{2} m\nu_2^2 \right)$$
(1)

where *m* is the body mass, g is 9.81 m s⁻², h_1 is the displacement of the centre of the gravity during the braking phase, v_1 is the velocity of the centre of the gravity at the beginning of ground contact, h_2 is the displacement of the centre of the gravity during the push-off phase, and v_2 is the velocity of the centre of the gravity at the end of the take-off. All these factors were calculated by using ground reaction force when the mass of the subject, the dropping height and the gravity were known. Thus, the potential energy (mgh_1) was highest when the subject was lifted to the starting position for 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:

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

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

In the sledge jump, the external W_{tot} was calculated by the integral of the function F(x) between the position limits of the sledge p_1 and p_2 as follows:

$$W_{\rm tot} = \int_{p_1}^{p_2} F(x) \,\mathrm{d}x \tag{3}$$

where F is the reaction force, x is the displacement of the sledge, p_1 is the beginning of the contact, p_2 is the end of the contact with the force plate. Thereafter, the power was calculated by dividing W by the contact time in both jumping conditions.

The net ΔE was determined by measuring $\dot{V}O_2$. The $\dot{V}O_2$ and respiratory exchange ratio ($R = \dot{V}CO_2 \cdot \dot{V}O_2^{-1}$ where $\dot{V}CO_2$ is the carbon dioxide production) were measured every 30 s. Measurements were made before exercise (rest $\dot{V}O_2$), during exercise and during the recovery period until $\dot{V}O_2$ returned to resting level. The rest $\dot{V}O_2$ was subtracted from the total $\dot{V}O_2$. To calculate the energy expenditure, an energy equivalent of 20,180 J·1⁻¹ of oxygen was used, when R was 0.82. A change of 0.01 in R caused a change of 42 J in energy expenditure. Thereafter, each R for every 30 s was multiplied by the corresponding value of O_2 (litres per minute) to obtain ΔE . Its mean value (work + recovery) was used in further calculations.

Finally, ME of the W_{tot} was calculated as follows:

$$ME = \frac{W_{\text{tot}}}{\Delta E} \cdot 100\% \tag{4}$$

Due to inaccuracies in the calculation of ME in W_{pos} phase only (see Kyröläinen et al. 1990), the ME analysis included W_{tot} .

Statistical analysis

The MANOVA for repeated measurements was used to test the main effects of repetitions, experimental conditions and subject groups as well as all their combined effects on every measured variable. It revealed that the repetition had no statistically significant influence on any of the main variables. Therefore, the 41st–50th repetitions were chosen from each subject for further analysis. Mean, standard deviation (SD) and standard error of mean (SEM) were calculated by groups by conditions. In addition, all variables were related to their corresponding values in the maximal jumping exercises. Correlation coefficients between different variables were calculated using both the relative as well as the measured absolute values.

Results

The 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 (SD 6.5) for the power group and 23.8 (SD 5.3) for the endurance group (P < 0.05). In the present study, these were the lowest mean ME values, while the corresponding highest ME values were obtained in the sledge jump condition of O + 40: 54.9 (SD 8.5) for the power athletes and 58.5 (SD 5.5) for the endurance athletes. Figure 2 demonstrates clearly that the ME increased with increasing stretching velocity of the main working muscles (average angular velocity of the knee joint in the eccentric phase of the take-off), which was different among the experimental conditions (P < 0.001). The MANOVA revealed also that 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 either subject groups.

Table 1 demonstrates that in the drop jumps, there were nonsignificant differences in physiological varia-

Fig. 2 The mean and SEM values of mechanical efficiency related to the corresponding 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*)



Table 1 Mean (SD) heart rate, ventilation (V_E) and oxygen uptake ($\dot{V}O_2$) during the drop jumps (upper table) and during the sledge jumps (lower table) among endurance- and power-trained athletes

	Optimum -40				Optimum				Optimum +40			
	Endura mean	ance SD	Power mean	SD	Endur mean	ance SD	Power mean	SD	Endur mean	ance SD	Power mean	SD
Heart rate (beats \cdot min ⁻¹)	128	17	143	19	135	15	152	20	143	13	154	16
$\dot{V}_{\rm E}$ (1 \cdot min ⁻¹)	35.3	9.8	40.0	9.0	39.7	7.3	45.3	9.7	42.6	9.1	49.5	8.3
$\dot{V}O_2$ (ml \cdot kg ⁻¹ \cdot min ⁻¹)	23.6	5.9	24.1	3.9	27.8	4.7	27.0	3.4	29.7	4.2	28.2	3.1
Heart rate (beats \cdot min ⁻¹)	130	12	150	16**	128	11	144	11**	133	14	149	13*
$V_{\rm E}$ (1 \cdot min ⁻¹)	34.8	6.2	46.7	8.3***	36.2	4.8	44.3	7.2**	41.6	3.8	48.3	8.5*
$V_{\rm O_2}$ (ml \cdot kg ⁻¹ \cdot min ⁻¹)	23.3	2.6	25.6	2.8	24.8	2.6	23.9	2.7	27.6	2.8	26.3	2.9

P*<0.05, *P*<0.01, ****P*<0.001



Fig. 3 The mean and SEM blood lactate concentration at rest, and after 0, 3 and 5 min of every test *P < 0.05, ***P < 0.001

bles between the subject groups. On the other hand, in the sledge jumps the heart rate and the ventilation were higher (P < 0.05-0.001) among power athletes. Their lactate concentrations were also higher compared to their endurance counterparts in every measured condition (Fig. 3).

In the drop jumps, the mean take-off velocities were 79.3 (SD 13.9)% (O-40), 74.6 (SD 15.4)% (O) and 56.2 (SD 14.1)% (O+40) of the respective maximal values among the endurance athletes. For the power group these values were 73.6 (SD 11.4)%, 71.7 (SD 10.8)% and 60.6 (SD 10.5)%, respectively. Their average angular velocity of the knee joint in the eccentric phase correlated negatively with the energy expenditure (r = -0.77, P < 0.01) in the O condition. In the O - 40 and O + 40 conditions, the *r*-values were also negative: r = -0.32 (n.s.) and r = -0.53 (n.s.) respectively. However, among their endurance counterparts these correlation coefficients were positive (from 0.21 to 0.57) but also nonsignificant. The energy expenditure correlated with the mechanical W in the O + 40 condition among both groups (r=0.59, P<0.05 for the pow-



Fig. 4 The mean and SEM power in the drop jumps and in the sledge jumps. The two experimental groups differed significantly from each other (***P < 0.001). For definition of terms on abscissa see Methods

er group and r=0.68, P<0.05 for the endurance group). The corresponding correlations were nonsignificant in the O condition for both the groups and also in the O-40 condition for the endurance group.

In the sledge jumps, the submaximal take-off velocities differed among the subjects because of individually different best maximal SSC. Thus, the higher the W_{neg} (prestretch intensity) the higher the take-off velocity. The correlation coefficients from the lowest to the highest dropping height were as follows: r=0.88(P<0.001), r=0.88 (P<0.001), and r=0.78 (P<0.01) for the endurance group. For the power group the values were: r=0.67 (P<0.05), r=0.67 (P<0.05), and r=0.95 (P<0.001), respectively.

Figure 4 shows clearly that the power values were significantly higher among power athletes (P < 0.001)compared to their endurance counterparts in every experimental condition, and that the drop jumps were three to four times more powerful exercises than the sledge jumps. In the case of the drop jumps, the eccentric phase dominated the performance (Fig. 5) in both subject groups. No statistically significant differences were noticed between the groups with regard to the ratio between the eccentric and concentric iEMG of the muscles investigated. However, the muscle activity patterns differed quite clearly between the experimental groups both in the drop jumps (Fig. 6) and in the sledge jumps (Fig. 7). In the lowest stretch load condition (O-40), the muscle activity curves of knee extensor and SOL muscles were quite similar between both subject groups but, however, the increased stretch loads caused more oscillation among the endurance subjects. The endurance athletes had clearer peaks in their muscle activity curves as shown in Figs. 6 and 7.

Discussion

The main findings of the present study were:

1. No differences in W_{tot} ME between the two groups of athletes investigated could be observed in most of the SSC exercises performed,

2. As expected the power athletes worked more powerfully than their endurance counterparts but, however, at the same time their heart rate, pulmonary ventilation and lactate concentrations were also higher,

3. While the EMG patterns differed clearly between the subject groups, no differences between the groups were noticed in the ratio of the eccentric and the concentric EMG of any muscles investigated in any experimental conditions,

4. The increased stretch of the muscles measured indirectly by the knee angular velocity increased ME within certain limits in both experimental groups.

The quite similar ME values of jumping between the two subject groups indicated that the different traininginduced adaptation and/or inherited neuromuscular structure could have had no influence on ME. This conclusion supports in part earlier studies where measurements have been made during in cycle ergometer work (Suzuki 1979; Bosco et al. 1980), which demonstrated that ME was not related to muscle fibre composition. Williams and Cavanagh (1987) have also observed no differences in muscle fibre type among trained male runners who exhibited good, medium or poor economy. In the present study, muscle fibre distribution was not determined but, nevertheless, it has been demonstrated earlier that athletes specialising in endurance events have a high percentage of slow twitch fibres and high activities of oxidative enzymes, while power athletes have been shown to have a predominance of fast twitch (FT) fibres and high activation of glycolytic enzymes (Saltin et al. 1977). Thus, obvious differences in muscle fibre distribution between the subject groups in the present study would contribute little to their ME values in every experimental condition.

In general, there might exist two main explanations for similar ME:

1. The power athletes had a more powerful performance associated with a more effective function of the neuromuscular system, and higher muscle strength than their endurance counterparts as has been reported earlier (Kyröläinen and Komi 1994). This enabled power athletes to use elastic energy better during their jumping performances, when the chemical energy was spared.

2. On the other hand, the endurance athletes worked obviously at a lower level of $\dot{V}O_2$ related to their maximal values than the power group. This would seem to imply that the endurance group worked physiologically at a lower loading level even if the both groups performed the same mechanical W calculated from their individual maxima.

The suggested differences in the adaptation of the neuromuscular systems between the subject groups can

Fig. 5 Mean of average electromyogram (EMG) of vastus lateralis (VL) and vastus medialis (VM) muscles in four different phases: preactivity (from -100 to -50 ms and from -50 to 0 ms before ground contact), eccentric (ecc) activity and concentric (conc) activity. For explanation of terms see Methods



be assumed to have taken place in many possible ways. The power group might have been able to recruit their motor units faster with the incremental firing rates of motoneurons, because the rate of development of their EMG seemed to be higher (Figs 6, 7). It has been suggested that the motor unit type is the critical factor controlling 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) have suggested for plantarflexor muscles in dynamic ramp lengthening actions. This, together with other improved functions of their neuromuscular system such as motor unit synchronisation (Milner-Brown et al. 1973), intramuscular co-ordination (Gollhofer and Schmidtbleicher 1988; Schmidtbleicher and Gollhofer 1982), and preprogrammed preactivation

from the higher centres of the nervous system (Melvill-Jones and Watt 1970; Dietz et al. 1979), created requirements for the neuromuscular system to increase muscle stiffness in a certain physiological range.

Between the two subject groups, all inputs to the leg extensor muscles were obviously in good balance under the moderate stretching velocities of muscles. However, the power group was able to use better the higher tendon-muscle stretches 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 have smoothed the muscle activation as a result of a training-induced adaptation and/or learning processes. However, in the highest stretch load condition (O+40), the reflexes (e.g. group Ib fibre inhibition from the Golgi tendon organ) may have started to function as a protec-





Fig. 6 From the bottom panel upwards, averaged signals of reaction force, ankle angle and rectified electromyograms from the soleus and vastus lateralis during the sledge jumps. The *lefthand curves* represent a power athlete and the *right hand ones* are the corresponding curves from an endurance athlete. The *lowest line* for every group of signals is the condition of O-40, *the middle line* is the optimum (O) and *the top line* is the condition of O+40. For definition of these terms see Methods

tive mechanism. At the same time, the muscle stiffness and the use of elastic energy may have decreased, metabolic demands increased, and ME decreased. This suggestion can be supported by the high correlation coefficient values between the chemical energy expenditure and the mechanical W in the O+40 condition.

Physiological differences in metabolism between the subject groups can, on the other hand, explain the similarities observed in ME. The endurance-trained athletes had lower blood lactate concentrations than power-trained athletes after every test (Fig. 3). This means that their lactate production was greater than their lactate removal, which caused lactate accumulation. Endurance training has been shown to cause a proliferation of capillaries in 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 possibly improved O_2 delivery

could have been responsible for decreases in blood lactate concentration at a given submaximal work rate among the endurance group in the present study. The power athletes, on the other hand, might have obtained some of their energy via anaerobic pathways. If so, a part of their energy expenditure was not totally taken into account in our calculation resulting in an overestimation of their ME values. In particular, this might have been true in the sledge jumps, because their heart rates and pulmonary ventilations were also significantly higher (Table 1) than their endurance counterparts. The same could have applied to the differences in the lactate concentrations (see Fig. 3), although it is possible that both groups in the present study produced the same amount of lactate but in the endurance group it may have been removed faster than in the power group. Endurance training has been reported to improve the rates of lactate removal (Donovan and Pagliassotti 1990). In that case, the energy expenditure values would again be comparable between the two subject groups.

From the preceding discussion it is obvious that many improvements have to be made in methodology, and many problems have to be solved before the ME values can be measured very precisely. Firstly, the contribution of elastic energy seems to be difficult to measure. However, some indirect calculations have been made in this regard. In running, the estimated elastic





Fig. 7 From *the bottom panel* upwards averaged signals of reaction force, ankle angle and rectified electromyograms from the soleus and vastus lateralis during the drop jumps. The *left hand curves* represent a power athlete and *the right hand ones* are the respective curves of an endurance athlete. The *lowest line* for every group of signals is the condition of O - 40, the middle line is the optimum (O) and the *top line* is the condition of O + 40. For definition of these terms see Methods

contribution has ranged from 40% to 50% of the total power (Cavagna et al. 1971). Secontly, another big unsolved problem is associated with the calculation of energy expenditure. It is obvious that some anaerobic metabolites such as lactate can be used also as an energy source. Therefore, the measurements of VO_2 and R are in many cases not enough for the determination of the total energy expenditure. The third problem relates more to the area of the biomechanics: how should mechanical energy be determined? The external W is quite easy to measure in many human movements but not the internal W, which was ignored in the present study. In the earlier study, however, the contribution of the rotational energy during the sledge jumps has been assumed to be very low and approximately only 0.1% of the sum of the kinetic and potential energy (Oksanen et al. 1990).

In conclusion, we found that the relationship between biomechanical and physiological variables during jumping exercises was very complex. A better understanding of their interactions can come only through studies of individuals, rather than the mean values for a group. However, both the power group and the endurance group achieved almost the same mean ME. The power athletes may have had a more powerful function of their neuromuscular system associated with higher muscle strength, obviously higher tendon-muscle stiffness and better use of elasticity as seen in the present study. The endurance athletes it appeared may have had more developed metabolic functions such as oxidative capacity, lactate removal, and mitochondrial systems.

Acknowledgements The authors would like to express their gratitude to Mr. Markku Tervakari, Mr. Markku Ruuskanen, Mr. Markku Sillanpää, Ms. Marja-Liisa Romppanen, Ms. Pirkko Puttonen, and Ms. Ursula Salonen for their technical assistance during the measurements and data analysis. Mr. Jouni Mutka and Mr. Timo Ruuskanen are thanked for their advice on the statistical analysis. In addition, Ms. Maria Magdalena Uribe-Martinez and Mr. Pekka Oksanen are thanked for their assistance in some of the calculations. This study was supported in part by grants no. 203/722/90 and 123/722/91 from the Ministry of Education, Finland.

References

Andersen P, Henriksson J (1977) Capillary supply of the quadriceps femoris muscle in man: adaptive response to exercise. J Physiol 270:677-690

- Asmussen E, Bonde-Petersen F (1974) Apparent efficiency and storage of elastic energy in human muscles during exercise. Acta Physiol Scand 92:537–545
- Aura O, Komi PV (1986) The mechanical efficiency of locomotion in men and women with special emphasis on stretchshortening cycle exercises. Eur J Appl Physiol 55:37–43
- Bosco C, Komi PV (1979) Potentiation of the mechanical behavior of the human skeletal muscle through prestretching. Acta Physiol Scand 106:467-472
- Bosco C, Komi PV, Sinkkonen K (1980) Mechanical power, net efficiency and muscle structure in male and female middledistance runners. Scand J Sports Sci 2:47–51
- Bosco C, Ito A, Kokmi PV, Luhtanen P, Rahkila P, Rusko H, Viitasalo JT (1982) Neuromuscular function and mechanical efficiency of human leg extensor muscles during jumping exercises. Acta Physiol Scand 114:543–550
- Cavagna GA, Dusman B, Margaria R (1968) Positive work done by a previously stretched muscle. J Appl Physiol 24:21-32
- Cavagna GA, Komarek L, Citterio G, Margaria R (1971) Power output of the previously stretched muscle. Med Sport 6:159– 167
- Dietz V, Schmidtbleicher D, Noth J (1979) Neuronal mechanisms of human locomotion. J Neurophysiol 42:1212–1222
- Donovan CM, Pagliassotti MJ (1990) Enhanced efficiency of lactate removal after endurance training. J Appl Physiol 68:1053-1058
- Fenn WO (1923) A quantitative comparison between the nergy liberated and the work performed by the isolated sartorius muscle of the frog. J Physiol 58:175-203
- Gollhofer A, Schmidtbleicher D (1988) Muscle activation patterns of human leg extensors and force-time-characteristics in jumping exercises under increased stretching loads. In: de Groot G, Hollander AP, Huijing PA, van Ingen Schenau GJ (eds) Biomechanics XIA. pp 143–147, Free University Press, Amsterdam
- Grieve DW, Pheasant S, Cavanagh PR (1978) Prediction of gastrocnemius length from the knee and ankle joint posture. In: Asmussen E and Jörgensen K (eds) Biomechanics VIA. University Park Press, Baltimore, pp 405-412
- Holloszy JO (1973) Biochemical adaptations to exercise: aerobic metabolism. In: Wilmore JH (ed) Exercise and sport sciences reviews, vol. 1. Academic Press, New York, pp 45–72
- Kaneko M, Komi PV, Aura O (1984) Mechanical efficiency of concentric and eccentric exercises performed with medium to fast contraction rates. Scand J Sports Sci 6:15–20
- Kiessling K-H, Piehl K, Lindquist C-G (1971) Effect of physical training on ultrastructural features in human skeletal muscle.
 In: Pernow P, Saltin B (eds) Muscle metabolism during exercise. Plenum Press, New York, pp 97-101
- Kyröläinen H, Komi PV (1994) Neuromuscular performance of lower limbs under voluntar and reflex conditions in powerand endurance-trained athletes. Eur J Appl Physiol 69:233– 239

- Kyröläinen H, Komi PV, Oksanen P, Häkkinen K, Cheng S, Kim DH (1990) Mechanical efficiency of locomotion in females during different kinds of muscle action. Eur J Appl Physiol 61:446-452
- Kyröläinen H, Komi PV, Kim DH (1991) Effects of power training on neuromuscular performance and mechanical efficiency. Scand J Med Sci Sports 1:78–87
- Margaria R (1968) Positive and negative work performances and their efficiences in human locomotion. Int Z angew Physiol einschl Arbeitsphysiol 25:339–351
- Margaria R, Cavagna GA, Saibene FP (1963) Possibilità di sfruttamento dell'elasticità del muscolo contratto durante l'esercisio muscolare. Boll Soc Ital Biol Sper 34:1815–1816
- Melvill-Jones GM, Watt GD (1971) Observations of the control of stepping and hopping movements in man. J Physiol 219:709-727
- Milner-Brown HS, Stein RB, Yemm R (1973) Changes in firing rate of human motor units during linearly changing voluntary contractions. J Physiol 230:359–370
- Nardone A, Romano C, Schieppati M (1989) Selective recruitment of high-treshold human motor units during voluntary isotonic lengthening of active muscles. J Physiol 409:451-471
- Oksanen P, Kyröläinen H, Komi PV, Aura O (1990) Estimation of errors in the mechanical efficiency. Eur J Appl Physiol 61:473-478
- Saltin B, Henriksson J, Nygård E, Andersen P, Jansson E (1977) Fiber types and metabolic potentials of skeletal muscles in sedentary man and endurance runners. Ann NY Acad Sci 301:3-29
- Schmidtbleicher D, Gollhofer A (1982) Neuromuskuläre Untersuchungen zur Bestimmung individueller Belastungsgrößen für ein Tiefsprungtraining. Leistungssport 12:298–307
- Suzuki Y (1979) Mechanical efficiency of fast and slow twitch muscle fibers in man during the cycling. J Appl Physiol 47:263-267
- Sypert GW, Munson JB (1981) Basis of segmental motor control: motoneuron size or motor unit type? Neurosurgery 8:608-621
- Taylor CR, Heglund NC, Maloiy GMO (1982) Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. J Exp Biol 97:1–21
- Thys H, Faraggiana T, Margaria R (1972) Utilization of muscle elasticity in exercise. J Appl Physiol 32:491–494
- Williams K, Cavanagh P (1987) Relationship between distance running mechanics, running economy, and performance. J Appl Physiol 63:1236–1245