

## Relationship between the efficiency of muscular work during jumping and the energetics of running

C. Bosco<sup>1,2</sup>, G. Montanari<sup>2</sup>, R. Ribacchi<sup>3</sup>, P. Giovenali<sup>3</sup>, F. Latteri<sup>4</sup>, G. Iachelli<sup>4</sup>, M. Faina<sup>5</sup>, R. Colli<sup>5</sup>, A. Dal Monte<sup>5</sup>, M. La Rosa<sup>6</sup>, G. Cortili<sup>7</sup>, and F. Saibene<sup>7</sup>

<sup>1</sup> Laboratory of Sports Biomechanics and Exercise Physiology, Kuortane Sport Institute, Finland

<sup>2</sup> Centro Studi e Ricerche — FIDAL, Via Po, 50 — Roma

<sup>3</sup> Istituto Anatomia Patologia — Università di Perugia

<sup>4</sup> Facoltà di Medicina e Chirurgia — Università di Catania

<sup>5</sup> Dipartimento di Fisiologia e Biomeccanica dello Sport, Istituto di Scienze dello Sport — Roma

<sup>6</sup> Facoltà di Medicina e Chirurgia — Università Cattolica, Roma

<sup>7</sup> Centro Studi di Fisiologia del Lavoro Muscolare del CNR — Milano, Italy

**Summary.** The running economy of seventeen athletes was studied during running at a low speed ( $3.3 \text{ m} \cdot \text{s}^{-1}$ ) on a motor-driven treadmill. The net energetic cost during running expressed in  $\text{kJ} \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$  was on average 4.06. As expected, a positive relationship was found between the energetic cost and the percentage of fast twitch fibres ( $r=0.60$ ,  $n=17$ ,  $p<0.01$ ). In addition, the mechanical efficiency during two different series of jumps performed with and without prestretch was measured in thirteen subjects. The effect of prestretch on muscle economy was represented by the ratio between the efficiency of muscular work performed during prestretch jumps and the corresponding value calculated in no prestretch conditions. This ratio demonstrated a statistically significant relationship with energy expenditure during running ( $r=-0.66$ ,  $n=13$ ,  $P<0.01$ ), suggesting that the elastic behaviour of leg extensor muscles is similar in running and jumping if the speeds of muscular contraction during eccentric and concentric work are of similar magnitudes.

**Key words:** Muscle mechanics — Muscle efficiency — Stretch-shortening cycle — Muscle elasticity — Fibre types

### Introduction

It has been shown that stretching an active muscle temporarily modifies its elastic characteristics, causing the muscle to work more efficiently during the subsequent positive work phase (Cavagna

and Citterio 1974). The potentiation of muscular performance observed after prestretch has been attributed to the storage and re-use of elastic energy. It has also been observed that net and apparent mechanical efficiency, estimated in a large variety of exercises performed with a stretch-shortening cycle pattern, have been found to be greater than those to be expected from what is known of the maximal efficiency of transformation of chemical energy into mechanical work (e.g. Asmussen and Bonde-Petersen 1974; Bosco et al. 1982b). Thus, part of the positive work measured has been assumed to be delivered, free of cost, from the recoil of previously stretched elastic elements. It is likely, however, that both the storage and the re-use of elastic energy change markedly according to the mechanical behaviour of a muscle during stretching. In fact the amount of elastic energy re-used has been shown to be a function of both muscle length and rate of prestretch (Bosco et al. 1981; Cavagna et al. 1968), provided that the transient period between stretching and shortening (coupling time) is favourable. In this connection Bosco (1982) suggested that the elastic behaviour of muscle is related to its mechanical and morphological structure. Thus the coupling time of a muscle and the stretching speed may affect the re-use of elastic energy differently according to whether slow or fast twitch fibres are activated (Bosco 1982). These observations suggest that some of the differences observed in muscle economy between individuals may lie in differences in the ability to store and re-use elastic energy. The present study was designed to examine how running economy is related to different muscle fibre compositions of leg extensor muscles. In addition, the energy expenditure during a stretch-shortening cycle of muscular activation as occurs in running was compared with that calculated from the same

Offprint requests to: C. Bosco, Laboratory of Sports Biomechanics and Exercise Physiology, Kuortane Sport Institute, SF-63170 Kuortane OP, Finland

muscle group loaded at a working speed similar to that found during running. The working speed was obtained in series of jumps executed with and without prestretch conditions. The ratio between the mechanical efficiencies of jumps performed with and without prestretch was used to evaluate the effect of prestretch on muscle efficiency.

## Methods

Seventeen track and field athletes participated in this study. Their mean age, height and weight ( $\pm$ SD) were  $22.8 \pm 6.0$  years,  $177.0 \pm 5.1$  cm and  $66.0 \pm 6.2$  kg. Their muscle fibre distribution was  $40.6 \pm 12.1\%$  fast twitch (FT) fibres. After being informed of the purpose and possible discomfort, all subjects were required to run on a motor-driven treadmill for 4.5 min at  $3.33 \text{ m} \cdot \text{s}^{-1}$ . During running, step frequency was calculated by counting the number of steps executed in 30 s.

At rest and during the exercise and recovery periods, oxygen uptake ( $\dot{V}_{O_2}$ ) was measured over every 15-s time period using an automated system (Ergo-Pneumotest-Jaeger OM/05-A/EDV/80) which was calibrated before and after each test against known gas concentrations. After exercise gas collection continued until  $\dot{V}_{O_2}$  reached the base line. Of the 17 subjects tested on the treadmill, 13 volunteered to perform two additional exercises. These exercises consisted of rhythmical vertical jumps at such a frequency and height that the performance in each series could be carried out for a period of 1 min. The first series (I) was performed in the rebound condition. The second series (II) was executed in the no rebound condition, the subjects maintaining  $\approx 1$  s isometric period between the eccentric and concentric phases. Both series were executed with large knee angular displacements ( $\approx 90^\circ$ ).

$\dot{V}_{O_2}$  was measured with the same procedure utilized during the running test. The net oxygen cost of each jumping series (net  $\dot{V}_{O_2}$ ) was calculated by adding the oxygen uptake during the 1 min jumping exercise to that of the recovery period, and subtracting the resting oxygen consumption from both periods. The respiratory exchange ratios during jumping were  $> 1.0$ .

The jumps were performed on a force-platform (Kistler 24852/C) sensitive to vertical ground reaction forces.

Mechanical work was calculated by integration of the acceleration from the force-time curve recorded from the force-platform. Each series of jumps was also filmed with a JVC-HR 2650 EG video cassette system including camera JVC-GXN 70 E and an electron marker ( $\pm 0.01$  s). The total mechanical work (positive and negative) performed was calculated through the potential energy change. However, no marked ( $\pm 3.7\%$ ) difference has been found between the two methods (Bosco et al. 1982b). In both rebound and no rebound jumping exercises, during the transition period between the eccentric and concentric work phases, the leg extensors are working isometrically. Nevertheless, during the calculation of the mechanical work this phase was not included, in spite of the fact that maintenance of this position required expenditure of metabolic energy. Since the energetic cost of isometric work in similar conditions has been measured previously (Bosco et al. 1982b) and its influence has been reported to be very small, it was neglected in the calculation of mechanical efficiency. Similarly, during the no-rebound jumps, even if the eccentric-concentric transition period (coupling time) was voluntarily prolonged to about 1 s, its effect on the net mechanical efficiency

has been calculated to be less than 1% (Bosco et al. 1982b); therefore this period was also excluded.

The work from the lowest point during contact to the highest point during flight (peak-to-peak vertical displacement of centre of gravity) was assumed to be positive ( $W_{\text{pos}}$ ). The negative work ( $W_{\text{neg}}$ ) was assumed to be numerically equal to  $W_{\text{pos}}$  and to have the energetic efficiency of  $-1.2$  (e.g. Asmussen 1952; Davies and Barnes 1972; Margaria 1938). Thus the energetic cost of positive work ( $E_{\text{pos}}$ ) was calculated according to the following formula:

$$E_{\text{pos}} (\text{kJ}) = \text{NET } \dot{V}_{O_2} \times 20.93 - \frac{W_{\text{neg}}}{1.2} \quad (1)$$

where 20.93 is the constant to change  $\dot{V}_{O_2}$  into work units.

The mechanical efficiency computed for the vertical jump series I and II was defined as the ratio of the output to the input energy. In the present study, input energy was taken as the net chemical energy expended and output energy as the mechanical work to move the mass of the body upwards ( $W_{\text{pos}}$ ). Thus, the net mechanical efficiency ( $\eta$ ) was obtained as follows:

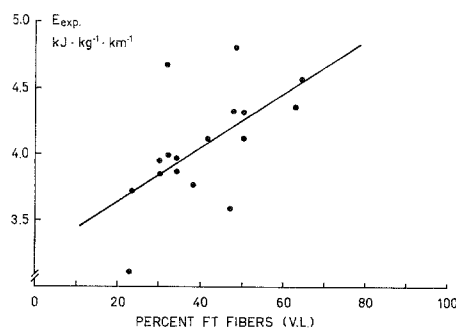
$$\eta = W_{\text{pos}} \times E_{\text{pos}}^{-1} \times 100 \quad (2)$$

where  $E_{\text{pos}}$  = energetic cost of positive work calculated according to Eq. 1.

*Determination of fibre composition.* The needle biopsy technique introduced by Bergström (1962) was used to obtain samples from vastus lateralis. The cryostat-cut samples were stained for myofibrillar ATPase (adenosine triphosphatase) (Padykula and Herman 1955) for classification of the fibres as FT or ST according to Gollnick et al. (1972).

## Results

The net energetic cost during running on a treadmill at  $3.3 \text{ m} \cdot \text{s}^{-1}$  expressed in  $\text{kJ} \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$  was on average  $4.06 \pm 0.4$  (SD). As expected the net energetic cost during running demonstrated a significant negative relationship with the percentage of fast twitch fibres present in vastus lateralis (Fig. 1). In contrast, no significant relationship was found between the net energetic cost of run-



**Fig. 1.** Relationship between energy expenditure ( $E_{\text{exp}}$ ) per kilogram and per kilometre and the percentage of fast twitch fibres in vastus lateralis.  $y = 3.24 + 0.02x$ ;  $r = 0.60$ ,  $n = 17$

**Table 1.** Mean ( $\pm$ SD) physical characteristics and selected parameters studied during running

Group	Percentage FT fibres (m. vastus lateralis)	$E_{\text{exp}}$ (kJ · kg <sup>-1</sup> · km <sup>-1</sup> )	Leg length (cm)	Stride length (cm)	Stride rate (cm)
Fast (6)	54.1 7.7	4.42 0.24	93.83 2.77	127.17 4.96	2.62 0.09
Slow (11)	33.24 7.15 ***	3.87 0.38 **	91.18 3.16 ns	123.18 5.34 ns	2.70 0.12 ns

The asterisks denote the statistical significance (Student's *t*-test) between the two groups (\*\*  $P < 0.005$ , \*\*\*  $P < 0.001$ , ns = not significant)

ning and height, weight, leg length, stride length and frequency in any subject. Neither could a significant difference be demonstrated between slow twitch and fast twitch groups in respect of any variable measured during running other than energy expenditure (Table 1).

The net  $\dot{V}_{O_2}$  and  $W_{\text{pos}}$  for each series of jumps are shown in Table 2. The same table also presents the average net efficiency and the values for selected mechanical parameters calculated for both rebound and no-rebound exercises.

The effect of prestretch on muscle efficiency was represented by the ratio between the efficiency of muscular work performed during rebound jumps and the corresponding value calculated in no-rebound exercises ( $\eta_r \times \eta_{\text{nr}}^{-1}$ ). This ratio demonstrated a statistically significant relationship with energy expenditure during running in the thirteen subjects examined (Fig. 2).

## Discussion

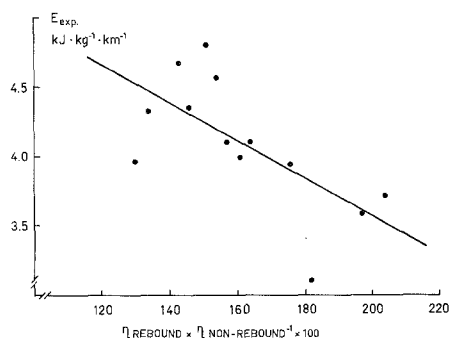
In agreement with early studies (e.g. Cavagna et al. 1964; di Prampero et al. 1979) the energy expenditure during running on a treadmill at a constant speed of 3.3 m · s<sup>-1</sup> was on average 4.06 kJ · kg<sup>-1</sup> · km<sup>-1</sup>. However, despite the re-

sults of many authors (e.g. Costill et al. 1973; Margaria et al. 1975), who observed a lack of statistical difference in running economy between groups of runners, in the present experiment a positive relationship has been observed between energy expenditure and the percentage of fast twitch fibres (Fig. 1). Although running economy has been associated with a variety of kinetic and kinematic parameters (e.g. stride length; Cavanagh and Williams 1982), in the present study such an association could not be found when stride length, stride rate, leg length, and leg length/height ratio were examined, nor could a statistical difference be found between these parameters in sprinters and middle-distance runners (Table 1). To avoid the possible effect of training on running economy (Passmore and Durnin 1955), the running speed chosen for the treadmill test was too slow to have been currently utilized by any member of either group during their annual training programme.

The present results, on the other hand, agree with the findings of Kaneko et al. (1983), who noted that the mechanical efficiency of distance runners was appreciably higher (72%) than that observed in sprinters (47%) when running slowly (3.66 m · s<sup>-1</sup>). These authors assume that the distance runners had a higher percentage of ST fi-

**Table 2.** Oxygen consumption, net efficiency and some mechanical variables studied in thirteen subjects during jumping exercises (mean  $\pm$ SD)

Jumping condition	Jumping frequency	Peak-to-peak vertical displacement of C.G. (cm)	Mechanical work of positive phase (kJ)	Net $\dot{V}_{O_2}$ (litres)	Net efficiency of positive work (%)
Rebound	59.2	78.5	32.1	6.72	27.3
	3.2	12.1	7.1	1.82	4.3
No rebound	40.1	74.7	20.7	6.11	18.7
	4.1	8.8	4.6	1.32	2.7



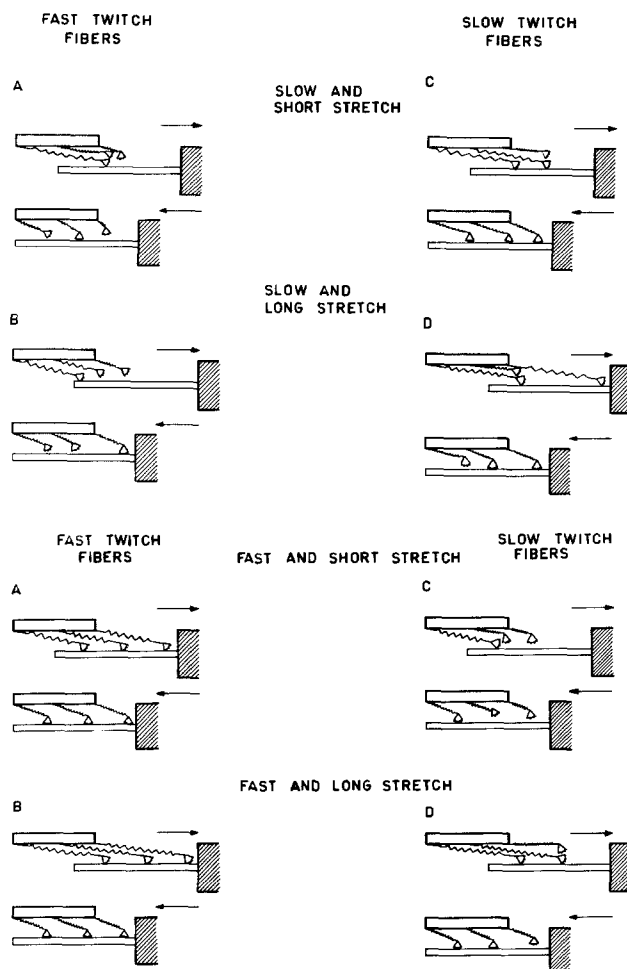
**Fig. 2.** Energy expenditure ( $E_{exp.}$ ) when running on a treadmill is shown as a function of the net efficiency ratio between rebound and no-rebound jumping exercises ( $\eta_{rebound} \cdot \eta_{no\ rebound}^{-1}$ ).  $y = 6.30 - 0.01x$ ;  $r = 0.66$ ,  $n = 13$

bres, and explained their findings on the basis of the metabolic response of slow fibres. Evidence has been presented that slow fibres showed higher efficiency than fast fibres when the contraction rate was low (Awan and Goldspink 1972; Wendt and Gibbs 1974). In addition Kaneko et al. (1983) argued that the higher efficiency observed in distance runners, as compared to sprinters, could not explain differences in the recoil of elastic energy.

The present findings, however, are not likely to be explained by the relationship between the efficiency of slow and fast muscles and the shortening velocity. If this were the case, the mechanical efficiency calculated during the jumping experiment should have shown a relationship to FT fibres composition similar to that found for energy expenditure during running. Such relationships were not observed, even though the knee angular velocity of leg extensor muscles, during identical jumping exercises, has been previously reported to be similar to or even slower than that reached during running at  $3.3 \text{ m} \cdot \text{s}^{-1}$  ( $5.0 \text{ rad} \cdot \text{s}^{-1}$  and  $5.5 \text{ rad} \cdot \text{s}^{-1}$  respectively for jumping and running; Bosco et al. 1982a; Bates et al. 1978). In the light of the above observations it is likely that elastic energy is one candidate factor which can be responsible for the low energy expenditure measured during running. This concept is substantiated by the fact that, using the equation presented by Cavagna and Kaneko (1977) for the estimation of mechanical work during running, the value of 52% is found for mechanical efficiency. This value is much higher than the corresponding one calculated during the no-rebound jumping series (18%) (Table 2), which reflects therefore only the transformation of biochemical energy into mechanical work. Although the recoil of elastic energy contributes notably to mechani-

cal efficiency during the positive work performed immediately after prestretch, Bosco et al. (unpublished work) have presented evidence that the elastic phenomenon cannot account alone for the total extra work delivered free of cost during the stretch-shortening cycle. In fact, it was found that the magnitude of the potential elastic energy which could be stored within the muscles was lower than the extra work performed as a consequence of the prestretching activity. The finding of Bosco et al. (1986) corroborates the suggestion of Cavagna (1977) and Bosco (1982), who pointed out that the enhanced efficiency observed during a stretch-shortening cycle is also due to the fact that previous stretching decreases the time in which positive work is done during the subsequent shortening. However, the decrease in the time to perform positive work in running, as a consequence of prestretch, should not affect slow and fast subjects differently. This is supported by the study of Bosco (1985), who found no difference in the time to execute positive work after prestretch activity between slow and fast subjects. Consequently, the effect of the recoil of elastic energy seems to contribute markedly to running economy, even if it is likely that fast subjects were not able to benefit as much as slow ones. This occurred in spite of the fact that a similar or even lower magnitude of elastic energy has been calculated as being stored within the leg muscles of distance runners compared to sprinters running at the same velocity as that of the present study (Kaneko et al. 1983).

It should be pointed out that the re-use of elastic energy during positive work has been shown to rely on both the amount of elastic energy stored during eccentric work and the duration of the coupling time (Bosco et al. 1981; Cavagna et al. 1968). Therefore, considering that an increase of 1 ms in coupling time may correspond to a decrease in the potentiation effect due to a prestretch of 20 N (Bosco et al. 1981), and taking into account that the coupling time during running at speeds similar to that used in the present study has been found to be about 8 ms (Ito et al. 1983), the finding that the energy expenditure during running was lower in slow subjects than in sprinters can be explained using the hypothesis of Bosco (1982) (see Fig. 3), who suggested that a long coupling time makes it easier for slow muscle fibres to retain their elastic energy longer without detachment of the cross-bridge. In this connection, evidence has been presented that the stretch-shortening cycle of leg muscles during foot contact on the ground and the relative length



**Fig. 3.** A schematic model to suggest the attachment and detachment cycle of actomyosin cross-bridges in fast twitch (*left*) and slow twitch (*right*) fibres, working at different speeds and with different lengths of stretch. In rapid and short stretch, fast twitch fibres are more able to store and re-use elastic energy than slow fibres. In contrast, in short or long stretches performed at a slow speed, and a long stretch executed at a fast speed, slow twitch fibres retain the cross-bridge attachment for a longer period and therefore can re-use more elastic energy than fast twitch fibres (Redrawn from Bosco 1982)

of the coupling time is too short to be a limiting factor for the recoil of elastic energy in slow subjects when running (Bosco and Rusko 1983). On the other hand, it has been suggested that the limiting effect of the coupling time on the recoil of elastic energy is relevant in fast twitch fibres during running (Bosco and Rusko 1983). This is consistent with the fact that the cross-bridge life time in FT fibres is shorter than in ST fibres (Barany 1967; Goldspink et al. 1979; Lännergren 1976). Therefore, if the coupling time is longer than a few milliseconds, some of the cross-bridges in the FT fibres will be detached and their elastic poten-

tial lost. This is probably the reason why the economy of running is higher in slow subjects than fast ones when running at slow and moderate speed (e.g. Kaneko et al. 1983).

Although substantial effort is currently being put into developing a better understanding of the influence of elastic recoil, it has been claimed that studies of jumping or knee bends have not produced any data applicable to running. In this connection Cavanagh and Kram (1985) found a poor correlation between running economy and the recoil of elastic energy during sit-stand-sit exercise. It is likely, however, that the latter exercise was performed at a muscle rate slower than that which occurs during running. In addition, Cavanagh and Kram (1985) have pointed out that there is not, at present, an adequate test to measure the ability of a subject to utilize stored elastic energy under realistic locomotor conditions. Even if these observations are correct, it should be remembered that in the present study a positive relationship was observed between running economy and the ratio between the mechanical efficiency during jumps performed with and without rebound (Fig. 2). This is perhaps one of the most interesting findings of the present experiment, suggesting that it might be possible to get accurate information about the recoil of elastic energy from jumping exercises when the stretch-shortening cycle is performed at a rate similar to that in running.

## References

- Asmussen E (1952) Positive and negative muscular work. *Acta Physiol Scand* 28:364–382
- Asmussen E, Bonde-Petersen F (1974) Storage of elastic energy in skeletal muscle in man. *Acta Physiol Scand* 91:385–392
- Awan MZ, Goldspink G (1972) Energetics of the development and maintenance of isometric tension by mammalian fast and slow muscles. *J Mechanochem Cell Motil* 1:97–108
- Barany M (1967) ATPase activity and myosin correlated with speed of muscle shortening. *J Gen Physiol [Suppl 2]* 50:197–218
- Bates BT, Osterning LR, Mason BR (1978) Lower extremity function during the support phase of running. In: Asmussen E, Jørgensen K (eds) *Biomechanics VI-B*. University Park Press, Baltimore pp 30–39
- Bergström J (1962) Muscle electrolytes in man. *Scand J Clin Lab Invest Suppl* 68
- Bosco C (1982) Stretch-shortening cycle in skeletal muscle function, with special reference to elastic energy and potentiation of myoelectrical activity. *Studies in Sport, Physical Education and Health* 15. University of Jyväskylä
- Bosco C (1985) Mechanical delay and recoil of elastic energy in slow and fast types of human skeletal muscle. Abstract, X International Congress of Biomechanics. *Arbete och hälsa* 14:35

- Bosco C, Rusko H (1983) The effect of prolonged skeletal muscle stretch-shortening cycle on recoil of elastic energy and on energy expenditure. *Acta Physiol Scand* 119:219—224
- Bosco C, Komi PV, Ito A (1981) Prestretch potentiation of human skeletal muscle during ballistic movement. *Acta Physiol Scand* 111:135—140
- Bosco C, Viitasalo JT, Komi PV, Luhtanen P (1982a) Combined effect of elastic energy and myoelectrical potentiation during stretch-shortening cycle. *Acta Physiol Scand* 114:557—565
- Bosco C, Ito A, Komi PV, Luhtanen P, Rahkila P, Rusko H, Viitasalo J (1982b) Neuromuscular function and mechanical efficiency of human leg extensor muscles during jumping exercises. *Acta Physiol Scand* 114:543—550
- Cavagna GA (1977) Storage and utilization of elastic energy in skeletal muscle. In: Hutton RS (ed) *Exercise and sport sciences reviews*. Journal Publ, Santa Barbara, pp 89—129
- Cavagna GA, Citterio G (1974) Effect of stretching on the elastic characteristics and the contractile component of frog striated muscle. *J Physiol (Lond)* 239:1—14
- Cavagna GA, Kaneko M (1977) Mechanical work and efficiency in level walking and running. *J Physiol (Lond)* 268:467—481
- Cavagna GA, Saibene FP, Margaria R (1964) Mechanical work in running. *J Appl Physiol* 19:249—256
- Cavagna GA, Dusma B, Margaria R (1968) Positive work done by a previously stretched muscle. *J Appl Physiol* 24:21—32
- Cavanagh PR, Kram R (1985) The efficiency of human movement — a statement of the problem. *Med Sci Sports Exerc* 17:304—308
- Cavanagh PR, Williams KR (1982) The effect of stride length variation on oxygen uptake during distance running. *Med Sci Sports Exerc* 14:30—35
- Costill DL, Thomason H, Roberts E (1973) Fractional utilization of the aerobic capacity during distance running. *Med Sci Sports* 5:248—252
- Davies CTM, Barnes C (1972) Negative (eccentric) work. Physiological responses to walking uphill and downhill on a motor-driven treadmill. *Ergonomics* 15:121—131
- di Prampero PE, Cortili G, Mognoni P, Saibene FP (1979) Equation of motion of a cyclist. *J Appl Physiol* 47:201—206
- Goldspink G, Larson RE, Davies RE (1970) The immediate energy supply and the cost of maintenance of isometric tension for different muscles in the hamster. *Z Vgl Physiol* 66:389—397
- Gollnick PD, Armstrong RB, Saubert IV CW, Piehl K, Saltin B (1972) Enzyme activity and their composition in skeletal muscle of untrained and trained men. *J Appl Physiol* 33:312—319
- Huxley AF, Simmons RM (1971) Mechanical properties of the cross-bridges of frog striated muscle. *J Physiol (Lond)* 218:59—60P
- Ito A, Komi PV, Sjödin B, Bosco C, Karlsson J (1983) Mechanical efficiency of positive work in running at different speeds. *Med Sci Sports Exerc* 15:299—308
- Kaneko M, Fuchimoto T, Ito A, Toyooka J (1983) Mechanical efficiency of sprinters and distance runners during constant speed running. In: Matsui H, Kobayashi K (eds) *Biomechanics VIII-B*. Human Kinetics Publishers, Champaign, Ill, pp 754—761
- Lännergren A (1976) Force-velocity relation of isolated twitch and slow muscle fibres. XV Scandinavian Congress of Physiology and Pharmacology, Århus. *Acta Physiol Scand [Suppl]* 404:87
- Margaria R (1938) Sulla fisiologia e specialmente il consumo energetico della marcia a della corsa a varia velocità ed inclinazione del terreno. *Atti della R Accademia Nazionale dei Lincei (Rendiconti)* 7:299—368
- Margaria R, Aghemo P, Pinera Limas F (1975) A simple relation between performance in running and maximal aerobic power. *J Appl Physiol* 38:351—352
- Padykula R, Herman E (1955) The specificity of the histochemical method of adenosine triphosphatase. *J Histochem Cytochem.* 3:170—195
- Passmore R, Durnin JVGA (1955) Human energy expenditure. *Physiol Rev* 35:801—836
- Wendt IR, Gibbs OL (1974) Energy production of mammalian fast and slow twitch muscle during development. *Am J Physiol* 226:642—647