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van Ingen Schenau, G.J.; Bobbert, M.F.; de Haan, A.

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Does Elastic Energy Enhance Work and Efficiency in the Stretch–Shortening Cycle?

*Gerrit Jan van Ingen Schenau, Maarten F. Bobbert,
and Arnold de Haan*

This target article addresses the role of storage and reutilization of elastic energy in stretch–shortening cycles. It is argued that for discrete movements such as the vertical jump, elastic energy does not explain the work enhancement due to the prestretch. This enhancement seems to occur because the prestretch allows muscles to develop a high level of active state and force before starting to shorten. For cyclic movements in which stretch–shortening cycles occur repetitively, some authors have claimed that elastic energy enhances mechanical efficiency. In the current article it is demonstrated that this claim is often based on disputable concepts such as the efficiency of positive work or absolute work, and it is argued that elastic energy cannot affect mechanical efficiency simply because this energy is not related to the conversion of metabolic energy into mechanical energy. A comparison of work and efficiency measures obtained at different levels of organization reveals that there is in fact no decisive evidence to either support or reject the claim that the stretch–shortening cycle enhances muscle efficiency. These explorations lead to the conclusion that the body of knowledge about the mechanics and energetics of the stretch–shortening cycle is in fact quite lean. A major challenge is to bridge the gap between knowledge obtained at different levels of organization, with the ultimate purpose of understanding how the intrinsic properties of muscles manifest themselves under *in-vivo*-like conditions and how they are exploited in whole-body activities such as running. To achieve this purpose, a close cooperation is required between muscle physiologists and human movement scientists performing inverse and forward dynamic simulation studies of whole-body exercises.

A substantial part of our movement repertoire involves muscle actions in which the concentric phase is immediately preceded by an eccentric phase (prestretch). These muscle actions will be referred to as stretch–shortening cycles (SSCs). In experiments on isolated muscles as well as *in vivo* human arm or leg actions, it has been demonstrated that a prestretch enhances the maximum work output that muscles can produce during the concentric phase. The mechanisms responsible for this enhancement are disputed. For instance, some authors believe that the extra work is due to the release of elastic energy, which has been stored in elastic components of the muscle–tendon complex during the prestretch. Other authors have suggested that nonelastic mechanisms also play a role. Still others even dispute the role of elastic energy.

The authors are with the Institute of Fundamental and Clinical Human Movement Sciences, Free University, Amsterdam, The Netherlands.

In addition to the debate about the mechanisms responsible for enhancing maximum work during the concentric phase by a prestretch, there is a debate as to whether a prestretch affects efficiency. Some authors, for example, suggest that both power output and efficiency are enhanced in the stretch–shortening cycle, while others argue that optimization of one can only be realized at the expense of the other. Participants in this debate have introduced a number of highly controversial definitions and concepts related to work, power, and efficiency.

One would expect that crucial questions could be answered using knowledge obtained at the level of isolated muscles, muscle fibers, and cellular components. However, it turns out that this knowledge cannot be related easily to what is occurring under *in vivo* conditions. Muscle physiologists are often forced to perform their experiments under conditions quite different from those occurring *in vivo* and often use a different set of definitions than biomechanists and exercise physiologists, especially with respect to the issue of efficiency.

The controversies among biomechanists and exercise physiologists, and the difficulties in relating knowledge obtained at different levels of observation, beg for a target article about the SSC. The purpose of this paper is to stimulate the dialogue between the different scientists. In addition to presenting an overview of contrasting views, we shall try to take a position in the controversies, not with the purpose of tackling colleagues but merely to help them shoot at this target. We hope that the dialogue will influence researchers to conduct further studies that will lead to a better understanding of the SSC in particular, and principles underlying control, mechanical output, and efficiency of human movement in general.

Part I: Effects of Prestretch on Maximum Work in the Concentric Phase

There is ample evidence that task performance is improved by making a countermovement, especially in relatively fast, discrete movements (Andersen & Pandy, 1993; Asmussen & Bonde Petersen, 1974a; Bober, Jaskólski, & Nowacki, 1980; Harman, Rosenstein, Frykman, & Rosenstein, 1990; Komi & Bosco, 1978; Svantesson, Ernstoff, Bergh, & Grimby, 1991; Vandewalle, Pérès, & Monod, 1987). For instance, it has been shown that subjects achieve a greater jump height in a so-called countermovement jump (CMJ), where they start from an erect position and make a downward movement before starting to push off, than in a so-called squat jump (SJ), where they start from a semisquatted position and make no countermovement (Asmussen & Bonde-Petersen, 1974a; Komi & Bosco, 1978). This is true even if body configuration at the start of the push-off is the same for both the CMJ and SJ (Anderson & Pandy, 1993; Bobbert, Gerritsen, Litjens, & Soest, 1996). The difference in maximum jump height can be traced to a difference in joint work, especially at the hip joints (Bobbert et al., 1996). In the literature, the following factors have been assumed to contribute to the enhancement of maximum work by a countermovement: the time available for force development, storage and reutilization of elastic energy, potentiation of the contractile machinery, and the contribution of reflexes. The role of each of these factors will be discussed.

The Time Available for Force Development

The first possible explanation for the enhancement of maximum work by a countermovement is that it allows muscles time to develop force. This explanation has been introduced by Asmussen and Sørensen (1971) and repeated by many others (e.g., Bobbert et al., 1996; Chapman & Sanderson, 1990; Ingen Schenau, 1984; Jaric, Gavrilovic, & Ivancevic,

1985; Mungiole & Winters, 1990; Svantesson, Grimby, & Thomée, 1994). Even if subjects are instructed to execute a movement as fast as possible, it takes time before the muscle force reaches its maximum. In leg extension tasks, for instance, it may take 300–500 ms before 90% of the maximal force is reached (Bobbert & Ingen Schenau, 1990; Jaric et al., 1985; Komi, 1979; Thomas, Sagar, White, & Davies, 1988). This is partly due to time constants in the excitation and contraction dynamics of muscle, which in turn depend on muscle fiber type and series elastic compliance (Caldwell, 1995; Hill, 1970; Huxley & Simons, 1971). It is also partly due to limitations in the rate at which the central nervous system generates control signals (Bizzi, Accornero, Chapple, & Hogan, 1984; Winters, 1990). If the concentric contraction starts as soon as the force begins to rise, part of the shortening distance of the muscle–tendon complexes is traveled at submaximal force, and thus the work produced is submaximal. This undesirable effect will be relatively influential in fast arm and leg movements, which typically last only 200–400 ms. The effect can be avoided by allowing the muscles to build up a maximum active state before the start of the concentric contraction, either in an isometric contraction (Bobbert & Harlaar, 1993; Bobbert & Ingen Schenau, 1990) or during a countermovement.

For the argument, it is convenient to illustrate the effect of the countermovement with a forward dynamic simulation model of isolated hip extension (Figure 1). In the model, which is described in detail elsewhere (Bobbert et al., 1996), the trunk rotates about the hip joint. The hip joint torque is determined by the hip extensor muscles only, which are represented by a Hill-type muscle model. Input of the model is the stimulation $STIM(t)$, the dynamics of which are tuned in such a way that the predicted torque–time history matches that observed in subjects performing maximum-height jumps. The initial $STIM$ level was chosen so that the torque exactly balanced the torque due to gravity. In

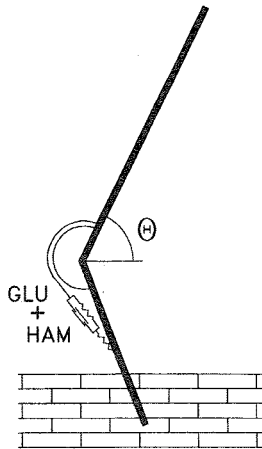


Figure 1 — Schematic drawing of the model of the musculoskeletal system used in forward simulations of a single-joint movement with and without countermovement. The head–arms–trunk segment rotates about the hip joint (H), and the only actuators are the hip extensor muscles (hamstring [HAM] + gluteus [GLU]), represented by Hill-type muscle models. Input of the model is the stimulation of the muscles. From “Why Is Countermovement Jump Height Greater Than Squat Jump Height?” by M.F. Bobbert, K.G.M. Gerritsen, M.C.A. Litjens, & A.J. van Soest, 1996, *Medicine and Science in Sports and Exercise*, 28, pp. 1402-1412. Reprinted with permission of Williams & Wilkins.

a countermovement condition, the head–arms–trunk segment was given an initial angular velocity of -3 rad/s (clockwise) at $t = 0$. The increase in torque developed by the hip extensors caused the angular acceleration to be positive (anticlockwise), so that the angular velocity was reduced to zero at a minimum angle θ_{\min} , and subsequently became positive.

The torque–angle curve obtained in this condition is plotted in Figure 2a. Also plotted is the curve labeled “no countermovement,” obtained when the contraction was started with zero initial angular velocity at angle θ_{\min} . In the no-countermovement condition, less work was produced because it took the torque a certain “angular delay” to catch up with its countermovement companion.

The effect of the time required for force development is entirely consistent with the observation that subjects with a relatively large percentage of slow twitch fibers (Viitasalo & Bosco, 1982), or women with relatively large rise times (Häkkinen, 1991; Komi, 1979), benefit more from a countermovement than subjects with a large percentage of fast twitch fibers. Clearly, the rise time will be closely related to the percentage of fast twitch fibers associated with the high cross-bridge cycle rates of fast twitch fibers in comparison to slow twitch fibers (e.g., Potma, Stienen, Barends, & Elzinga, 1994).

Storage and Reutilization of Elastic Energy

A second explanation offered in the literature for the enhancement of maximum work by a countermovement builds on the role of elastic elements in series with contractile elements. The idea is that during the countermovement, active muscles are prestretched and absorb energy, part of which is temporarily stored in series elastic elements and later reutilized in the phase where the muscles act concentrically. This mechanism is sometimes referred to as “elastic potentiation” (Komi, 1992). Many authors assert that this helps to enhance the maximum work produced during the concentric phase (e.g., Asmussen & Bonde-Petersen, 1974a; Hull & Hawkins, 1990; Komi & Bosco 1978; Svantesson et al., 1991). However, while there is no question that elastic energy is stored and reutilized, the latter assertion seems incorrect. This will be argued below.

First of all, the amount of energy stored in series elastic elements at the start of the concentric phase is not determined by the amount of “negative work” performed but solely by the force at the start of push-off. As explained in the previous section, the countermovement provides the muscles time to build up force prior to shortening. Thus, compared to a condition where no countermovement occurs, more energy is stored in series elastic elements at the start of shortening. However, storage of more energy implies a further elongation of the series elastic elements. At the same origin-to-insertion distance, this elongation occurs at the expense of the length of the contractile elements, and consequently the contractile elements can do less work during the subsequent concentric contraction (e.g., Avis, Ingen Schenau, Toussaint, & Huijing, 1986; Voigt, Simonsen, Dyhre-Poulsen, & Klausen, 1995).

The fact that total work during shortening is not determined by the amount of energy stored in series elastic elements at the start of shortening can easily be illustrated with the simulation model. In the example of the hip extension contraction shown in Figure 2a, the elastic energy stored at the start of the concentric phase was 9.7 J more in the countermovement condition than in the no-countermovement condition. This is a considerable amount compared to the extra 15 J of positive work (the area under the torque–angle relationship for the concentric phase), but the two are not related. This can be demonstrated by increasing the speed of force development. Figure 2b shows that this increases the difference between the conditions in the amount of energy stored, as evidenced by the

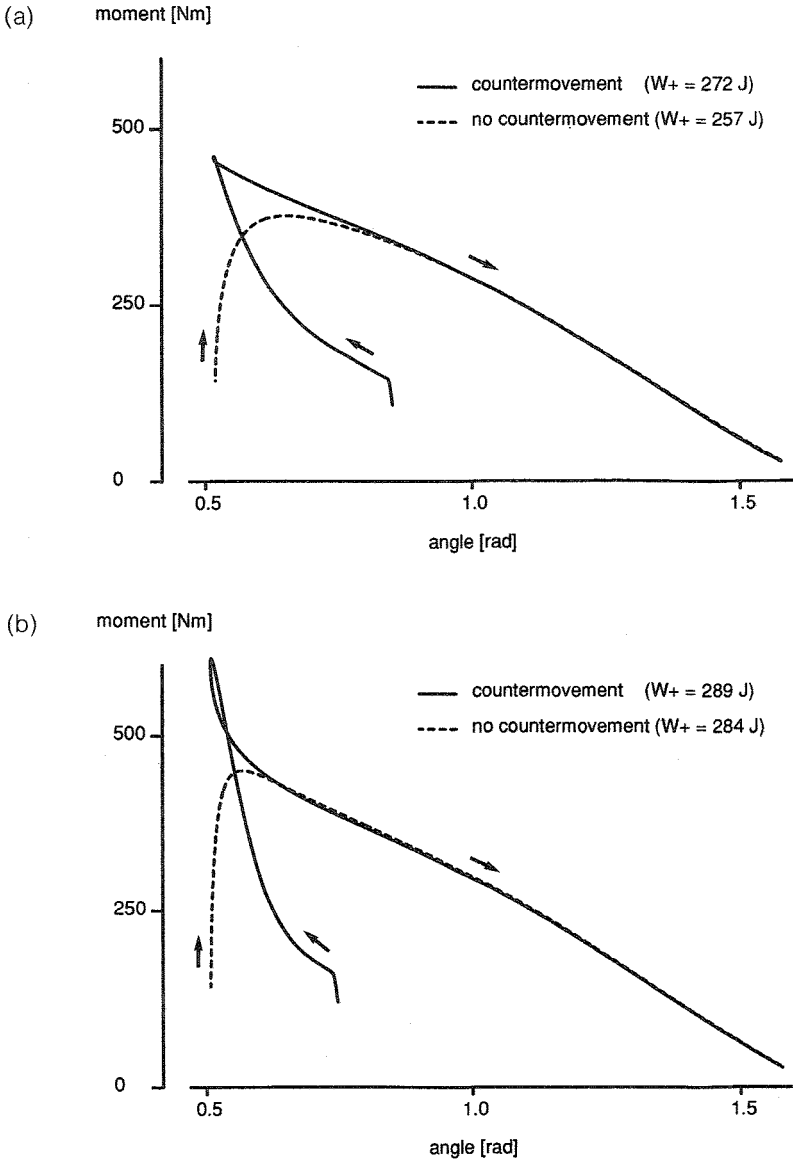


Figure 2 — Moment–angle curves obtained in a forward dynamic simulation, using the model shown in Figure 1. The increase of stimulation of the hip extensors above that required for equilibrium starts at $t = 0$ (start of each curve). In the counter-movement condition, the head–arms–trunk segment is given an initial angular velocity of -2 rad/s at $t = 0$; in the no-counter-movement condition, the angular velocity is zero. (a) Rise of stimulation corresponds approximately to the rise of EMG levels observed in human subjects during vertical jumping. (b) Rise of stimulation and excitation dynamics doubled. From “Why Is Counter-movement Jump Height Greater Than Squat Jump Height?” by M.F. Bobbert, K.G.M. Gerritsen, M.C.A. Litjens, & A.J. van Soest, 1996, *Medicine and Science in Sports and Exercise*, 28, 1402-1412. Reprinted with permission of Williams & Wilkins.

increase of the difference in joint torque at the start of the concentric phase, but it decreases the difference in work produced. Obviously, the dynamics of force development determined the differences in the amount of work produced, not the storage and reutilization of elastic energy!

Mungiole and Winters (1990) arrived at similar conclusions on the basis of comparable simulations. Chapman and Sanderson (1990) referred to simulations which further demonstrated convincingly that work enhancement due to a countermovement is not dependent on elastic energy, since work is enhanced when muscle models are used that do not possess series elastic components at all.

Potential of the Contractile Machinery

A third possible explanation for the enhancement of maximum work by a countermovement is that the prestretch of active muscle alters the properties of the contractile machinery. It is well-documented that the force produced by tetanized isolated muscles may be enhanced by a stretch to values of up to twice the maximum isometric force (Bergel, Brown, Butler, & Zacks, 1972; Cavagna, 1978; Cavagna, Dusman, & Margaria, 1968; Ettema, Huijing, Ingen Schenau, & Haan 1990; Ettema, Soest, & Huijing, 1990; Fenn, 1924; Haan, Ingen Schenau, Ettema, Huijing, & Lodder, 1989), and the same has been found for tetanized single muscle fibers (Edman, Elzinga, & Noble, 1978, 1982). This enhancement, also called potentiation (Hill 1970), has been shown to increase with the speed of stretch (Edman et al., 1978, 1982) and to decrease with the amount of time elapsed after the stretch (Cavagna et al., 1968; Edman et al., 1978, 1982). If the muscle is quickly released after the stretch, it is able to shorten isotonically against its maximum isometric force (Cavagna, Citterio, & Jacini, 1981; Cavagna, Heglund, Harry, & Mantovani, 1994; Cavagna, Mazzanti, Heglund, & Citterio, 1985). Thus, the capacity of the contractile machinery to do work is also enhanced. Woledge and Curtin (1993) suggested that this might be due to strained cross-bridges that are detached to a state which allows them to reattach more rapidly than cross-bridges not subjected to a prestretch. It is questionable, however, whether potentiation plays a role in SSCs occurring *in vivo*, where prestretch speeds are relatively low and the switch from lengthening to shortening occurs gradually. As a matter of fact, it remains to be seen whether the muscle fibers are lengthened at all; several authors (e.g., Alexander & Ker, 1990; Belli & Bosco, 1992; Hof, 1990; Jacobs, Bobbert, & Ingen Schenau, 1993; Rall, 1985; Voigt, Bojsen-Møller, Simonsen, & Dyhre-Poulsen, 1995) have suggested that during SSCs *in vivo*, the knee extensors and plantar flexors are activated in such a way that a concerted contraction occurs, that is, a contraction where the entire muscle-tendon complex is lengthened but the muscle fibers remain isometric or even shorten during the prestretch.

The Contribution of Reflexes

A final possible explanation for the enhancement of maximum work by a countermovement is that the prestretch triggers spinal reflexes (Dietz, Schmidtbleicher, & Noth, 1978) as well as longer latency responses (Melvill Jones & Watt, 1971) that help to increase muscle stimulation during the concentric phase to a supramaximal level. Though many authors assume that especially the H-reflex may play a role in the SSC, the literature that compares movements with and without prestretch does not provide convincing evidence that muscle stimulation is indeed enhanced due to the prestretch (e.g., Bosco, Viitasalo, Komi, & Luhtanen, 1982; Chapman & Sanderson, 1990; Kyroläinen et al., 1990; Svantesson et al., 1991, 1994). Measurements of EMG activity of lower extremity muscles of volley-

ball players during squat jumps (SJ) and countermovement jumps (CMJ) do not indicate enhancement of stimulation during the CMJ (Bobbert et al., 1996). Considering what was said in the previous paragraph, it remains to be seen whether stretch reflexes occur at all. If the contributions during CMJ and other SSCs not requiring absorption of large amounts of mechanical energy are indeed concerted, as suggested by some authors (e.g., Alexander & Ker, 1990; Belli & Bosco, 1992; Hof, 1990; Jacobs et al., 1993; Rall, 1985; Voigt, Boysen-Møller, et al., 1995), there is no lengthening of muscle spindles and thus no trigger for stretch reflexes.

What, Then, Is the Role of Elastic Energy?

A major conclusion from the findings and arguments presented thus far is that the enhanced work output due to a countermovement is not the result of storage and release of elastic energy. Rather, it seems to be largely due to the fact that the muscles can build up force prior to the concentric phase. This conclusion is not only important scientifically but also has implications for training practice. It indicates, for instance, that Wilson et al.'s recommendation (Wilson, Elliot, & Wood, 1992; Wilson, Wood, & Elliot, 1991) that an athlete can improve the capacity to store elastic energy through flexibility training instead of strength training is wrong; an increase in elastic energy will not improve performance in SSCs in discrete movements. As demonstrated in a more recent study (Wilson, Murphy, & Pryor, 1994), the rate of force development seems to be a much more important factor for athletic performance.

By concluding that elastic energy does not explain the enhancement of work during the concentric phase of the SSC, we are in no way trying to suggest that storage and reutilization of elastic energy are of little importance. Apart from playing a role in shock absorption and the generation of high peak power outputs in explosive actions (not exclusively associated with SSCs), elastic energy most certainly plays a role in the conservation of mechanical energy. This is especially important for movements involving repetitive SSCs, where performance is largely limited by the rate at which metabolic energy can be liberated via the anaerobic and aerobic pathways. It is therefore quite understandable that many studies of human and animal locomotion have been focused on possible benefits of the SSC in the transformation of metabolic energy into mechanical energy. This transformation is usually associated with the expression "efficiency." The following discussion is therefore presented under the umbrella of the efficiency of repetitive stretch-shortening cycles.

Part II: Efficiency in Repetitive SSCs

Statement of the Problem

During repetitive movements such as walking, running, and hopping, the sum of the segmental mechanical energies of a subject shows large variations. Since mechanical energy can be conserved in elastic structures during the SSCs, the metabolic costs can be lower than when the required increases of mechanical energy have to be realized entirely by concentric actions of contractile elements of the muscles involved. Storage and reutilization of elastic energy in repetitive SSCs therefore most certainly improve the economy of these movements. Although, for example, running economy can be defined quite unambiguously (e.g., Cavanagh & Kram, 1985a; Daniels, 1985; Williams, 1985), studies based on this concept necessarily remain largely descriptive in nature. In our view, this is unfortunate because interventions in sports as well as medicine and rehabilitation require in-

sight into relationships between performance, technique, and metabolic energy expenditure. Such insight relies on theories that causally relate the generation, degradation, and conservation of mechanical energy to metabolic costs as a function of movement technique.

It is therefore quite understandable that many studies have focused on the concept of efficiency, which is supposed to relate mechanical work to metabolic costs. Application of this concept, however, requires reliable estimates of mechanical work measures as well as related measures of metabolic energy expenditure. Both types of measures are difficult to assess *in vivo*. In hopping and level running, for example, relatively little work is done against the environment, and the energy content of the body returns to about the same value each cycle. The magnitude of the mechanical work done is therefore difficult to assess. Calculation of joint power does not solve this problem, since the time integral over one or more cycles of the summed joint powers results in about zero work also. With respect to *in situ* SSC experiments using isolated muscles, comparable problems exist with respect to the assessment of mechanical work done. Assessing metabolic energy expenditure is also hampered by uncertainties since, for example, little is known about the fraction not associated with the actions of the exercising muscles.

The difficulties mentioned above have led researchers to introduce a variety of work concepts (e.g., net work, positive work, negative work), using various baseline subtractions of metabolic energy in an attempt to estimate efficiency for each concept. As a consequence, the literature presents a bewildering range of power output and efficiency values for whole-body movements, up to quite unworldly extremes. For instance, Kyroläinen and Komi (1995, their Figure 4) reported a power output of their human subjects up to 12,000 W, that is, more than 15 horsepower! Depending on the definitions used, estimates of external power in running appear to vary in many respects (see Aleshinsky, 1986, or Williams & Cavanagh, 1983, for an overview). For running as well as other repetitive SSC exercises, this leads to estimates of efficiency ranging from 0.4 to 0.8 (Cavagna & Kaneko, 1977; Cavagna, Saibene, & Margaria, 1964; Kyroläinen & Komi, 1995; Kyroläinen, Komi, & Belli, 1995; Pierrynowski, Norman, & Winter, 1981). Such values are much greater than the efficiency values of 0.25–0.3 reported in textbooks for contractions of isolated muscles or muscle fibers (e.g., Åstrand & Rodahl, 1977). Though many authors indicate that these high efficiencies point to a contribution of elastic energy in their work estimates, Komi (1992) argued that his results from sledge experiments call into question the definition of efficiency as found in textbooks. Surprisingly, doubts about the textbook values are also raised after a superficial consultation of efficiency studies performed at the level of isolated muscles or muscle fibers, with reported efficiency values fitting quite well in the range of 0.4–0.8 (Buschman, 1995; Woledge, 1968).

In Part II we will argue that the proposed approaches mentioned above do not deepen our understanding of basic principles underlying the benefits of repetitive SSCs. In fact, most of the proposed definitions obscure rather than reveal the relations between mechanical work and metabolic costs and, in some cases, even imply the existence of a *perpetuum mobile*. We further hope to convince the reader that progress will rely on detailed knowledge about the magnitude of mechanical work generated and degraded on the level of the contractile machinery and the associated metabolic costs, as well as about the amount of elastic energy stored and reutilized during the SSCs.

As illustrated in Part I, models of the musculoskeletal system may be helpful in studying the contributions of underlying mechanisms, but for parameter values they rely on results obtained through *in situ* or *in vitro* studies. Unfortunately, it will become clear in Part II that the efficiency measured at the level of isolated muscles or muscle fibers is too low to explain the gross efficiency of whole-body movements. To illustrate this, and

other complicating factors, we are forced to discuss some factors in minute detail. This is inevitable if we are to stimulate future developments that should help fill the gap between knowledge of muscle physiology on the one hand and biomechanics and exercise physiology on the other hand.

Thermodynamic Definition of Efficiency: $W/\Delta G$

In the search for unambiguous relations between mechanical work and metabolic costs, it is inevitable to go back to basics. The concept of efficiency originally stems from thermodynamics, where it is defined as the ratio of actual work done to maximal work attainable (e.g., Rall, 1985). The bonds that hold atoms together in molecules of carbohydrate, fatty acids, and high-energy phosphate compounds (e.g., adenosine triphosphate [ATP] and phosphocreatine [PC]) involved in metabolic processes represent potential energy, or stored energy that can be released to do work. According to the second law of thermodynamics, however, not all of the stored energy can be used; some will always be lost because of the tendency toward disorder (entropy). The maximal amount of energy that can be put to work is called the free energy ΔG (also referred to as Gibbs free energy).

During chemical reactions in a muscle, a certain amount of energy ΔE is released from the reactant molecules. In most textbooks and papers on this subject one will find ΔE replaced by ΔH , the change in enthalpy, which is based on the equation $\Delta H = \Delta E - p\Delta V$, where p is the intramuscular pressure and ΔV the change of muscle volume as a result of the reaction. Since ΔV is about zero in skeletal muscles, ΔH has about the same magnitude as ΔE . The change in free energy that occurs is given by $\Delta G = \Delta H - T\Delta S$, with T the absolute temperature and ΔS the increase in disorder. Thus, in thermodynamics, efficiency (referred to as thermodynamic efficiency) is defined as $e_{therm} = W/\Delta G$. It follows that in our search for an explanation of differences in efficiency values among levels of organization, we need to look at both W and ΔG .

Difficulties in the Assessment or Interpretation of ΔG

How to Compare Measures Across Levels of Organization. With respect to both *in situ* or *in vitro* experiments and whole-body experiments, ΔG can have entirely different meanings depending on the specific aims of research on various levels of organization.

A first important observation is that efficiency measures obtained in, for example, isolated muscles or fibers are often based on measurements of the utilization of immediate energy sources such as ATP and PC. Such measures do not include energy lost in the reactions necessary to resynthesize these immediate sources. Moreover, some measures reflect ATP utilization of the contraction process per se (actomyosin ATP-ase) and do not include the (substantial) amount of ATP required to pump calcium ions back into the sarcoplasmic reticulum. Fortunately, the amount of energy needed for calcium movements is rather constant at around one third of the total isometric energy utilization (Homsher & Kean, 1978). Thus, when necessary, corrections can be made.

A second problem is that ΔG of intermediate reactions is difficult to estimate since it depends strongly on temperature, pH, and concentrations of reactants and products. For this and other reasons, many efficiency calculations are based not on ΔG s but on ΔH s. ΔH equals the sum of heat and mechanical work produced and can be determined using very sensitive instruments (e.g., thermopiles) that register heat production almost instantaneously (e.g., Curtin & Woledge, 1991, 1993). These measures lead to the so-called mechanical efficiency: $e_{mech} = W/\Delta H$. It is important to realize, however, that ΔH can deviate considerably from ΔG when reactions are coupled. ΔG can even be larger than ΔH when an exer-

gonic reaction drives an endergonic reaction, as is the case when hydrolysis of ATP to ADP (adenosine diphosphate) + P_i is coupled to immediate rephosphorylation of ADP to ATP by PC. So values used to express the efficiency of the conversion of ATP-hydrolysis to mechanical work (usually referred to as contraction coupling efficiency e_c) may be based on different measures ($W/\Delta H_{ATP}$ or $W/\Delta G_{ATP}$). Moreover, since the reaction in which ADP is rephosphorylated by PC is an equilibrium reaction, the free energies of ATP and PC are about equal while their enthalpies differ. This should be accounted for when e_c is based on $W/\Delta H_{PC}$ (see discussion following Woledge & Curtin, 1993).

One must further be careful with respect to the precise significance of heat + work measures. Some authors subtract heat released at the very onset of a contraction (usually referred to as labile heat), whereas others cancel its effect by, for example, accounting for only the heat released after a relatively long isometric preload (e.g., Buschman, 1995). Such factors make it almost impossible to derive, from the results of experiments of this last type, estimates of muscle efficiency to be used in models of the musculoskeletal system.

As stated above, e_c , expressed as $e_c = W/\Delta G_{ATP} = W/\Delta G_{PC}$, is a measure for the efficiency of the conversion of immediately available high-energy phosphate compounds to mechanical work. When efficiency measures obtained at different levels of organization are compared, e_c should include the ATP breakdown associated with calcium pumping. To relate this efficiency to, for example, efficiencies calculated on the basis of oxygen consumption, it has to be multiplied by a measure indicating what fraction of the free energy of the substrate oxidized for ATP resynthesis is stored as free energy in ATP. This fraction, referred to as the phosphorylative coupling efficiency e_p , thus equals $e_p = \Delta G_{ATP}/\Delta G_{CHO}$, where ΔG_{CHO} is the free energy of carbohydrate. There seems to be no difference of opinion in the literature that ΔG_{CHO} has a magnitude of about $-2,880$ kJ/mole (Åstrand & Rodahl, 1977; Brooks, Fahey, & White, 1995; Kammermeier, 1993; McArdle, Katch, & Katch, 1991). Though different estimates for ΔG_{ATP} are used in the literature (up to -52 kJ/mole; Haan, Ruiten, Lind, & Sargeant, 1993), the quantity of $\Delta G_{ATP} = -46$ kJ/mole appears most consistent (Brooks et al., 1995; Whipp & Wasserman, 1969; Woledge & Curtin, 1993). Since 1 mole CHO can resynthesize 36 mole ATP, these measures for ΔG lead to an e_p value of 0.575. This e_p value seems largely independent of the metabolic pathway used to capture the energy of the food in the form of ATP (Åstrand & Rodahl, 1977; Gladden & Welch, 1978). For the estimations concerning efficiency elaborated below, literature data about contraction coupling efficiency e_c are multiplied by this e_p to obtain a measure for muscle efficiency. In cases where e_c is defined as $W/\Delta H_{PC}$, the measure is converted to $W/\Delta G_{ATP}$ using $\Delta H_{PC} = -34$ kJ/mole (Woledge & Curtin, 1993).

Whole-Body Movements. For whole-body movements, estimates of the maximal work obtainable from oxidized food are mostly based on measurements of oxygen consumption in steady state. For steady-state conditions, the enthalpy is about equal to the free energy of the food (Di Prampero, 1981; Rall, 1985; Wilkie, 1974; Woledge, 1968). Slightly dependent on the actual foodstuff used (to be deduced from the respiratory quotient), the change in enthalpy of the oxidized foodstuff is calculated. For example, if the respiratory quotient is 1.0, only carbohydrate is oxidized. Oxidation of 1 mole of carbohydrate requires 6 moles of O_2 . If we assume that 1 mole O_2 occupies a space of 22.4 L, 1 L of O_2 is used to combust 0.0075 moles of carbohydrate, and with a free energy for carbohydrate of 2,880 kJ/mole this yields about 21.4 kJ. At an e_p of 0.575, about 12.3 kJ of this is transformed to ΔG_{ATP} . However, as discussed in the following section, this measure does not seem to be really applicable for determining the efficiency of the SSC.

Baseline Subtractions. When working at the level of isolated muscles, physiologists often measure only part of ΔG . Given the specific aims of the studies (e.g., improving

understanding of the basic reactions that drive contraction), this is quite understandable. However, we feel that when the energetics of SSCs are studied, efficiency values should be based on ΔG_{CHO_2} , which includes the energy lost in processes such as calcium pumping in the muscle. Such processes are not directly involved in the tension-generating process, but the free energy lost in this calcium pumping is an integral part of the total metabolic costs involved in generating muscle work.

Some authors have advocated the gross efficiency e_g as the only unambiguous definition of efficiency for the study of whole-body movements. Gross efficiency is the ratio between the external work performed by the system on the environment and the metabolic energy consumption (Cavanagh & Kram, 1985a, 1985b; Ingen Schenau & Cavanagh, 1990; Stainsby, Gladden, Barclay, & Wilson, 1980; Zarrugh, Adams, & Ramey, 1975). However, this approach ignores the fact that energy is required for functions quite different from skeletal muscle contractions. Suppose we calculate ΔG from oxygen consumption in running or cycling and want to relate it to the work of the contractile elements of skeletal muscles involved in moving body segments and in doing work against external forces. In that case, we need to separate the work done by skeletal muscles from the work required for blood circulation, respiration, actions of muscles necessary to maintain posture and generate reaction forces, and ion pumping in the central nervous system and other organs apart from the exercising muscles. The energy required for these processes is referred to as maintenance work (e.g., Cavanagh & Kram, 1985b).

Several different approaches have been advocated to correct for maintenance work. Many authors subtract the oxygen consumption during rest from the oxygen consumption during exercise. Others argue correctly that maintenance work is not constant but increases with workload; heart and respiratory muscles, for instance, require more metabolic energy than during rest. To compensate for the increases in maintenance work, measures such as apparent (or work) efficiency and delta efficiency have been introduced (e.g., Donovan & Brooks, 1977; Gaesser & Brooks, 1975). In these measures, the increase of external work is divided by the energetic equivalent of the corresponding increase in oxygen consumption. Interestingly, apparent work or delta efficiency measures vary greatly among activities in which work is being done against external forces (e.g., wind, gravity). For running, these efficiencies reach values up to 0.69, more than twice those found in cycling (e.g., Asmussen & Bonde-Petersen, 1974b; Lloyd & Zacks, 1972; Pugh, 1971). As argued by Stainsby et al. (1980), apparent, work, and delta efficiency measures are often far in excess of the maximal muscle efficiencies ever published for isolated mammalian muscles. Thus, this type of baseline subtraction leads to incorrect conclusions, unless, of course, we are willing to accept the existence of a *perpetuum mobile* in living systems. A factor that might underlie the relatively high work and delta efficiencies is that, due to the baseline subtraction, part of the tension-independent cost of muscle contraction is not accounted for in the resulting measure of ΔG .

It will be clear from the above that neither gross efficiency nor the baseline subtractions are of any use in assessing a meaningful measure of the efficiency of SSCs. This statement will be further illustrated by our discussion of the assessment of work in the sections to follow.

Difficulties in Determining W and Its Efficiency

In the previous paragraph, we discussed the maximum attainable amount of free energy ΔG . To calculate efficiency, we need to relate this to the mechanical work performed. In mechanics, work and power are based on unambiguous definitions. A force \mathbf{F} exerted by a

system (an explicitly defined free body diagram) does work on the environment according to $W = \int \mathbf{F} \cdot d\mathbf{s} = \int F \cos \alpha ds$, with \mathbf{s} the displacement of its point of application and α the angle between \mathbf{F} and \mathbf{s} . Time differentiation of this equation leads to the definition of power $P = \mathbf{F} \cdot \mathbf{v} = F v \cos \alpha$, with \mathbf{v} the velocity of the point of application of \mathbf{F} . Rotatory equivalents are $W = \int M d\phi$ and $P = M\omega$, with M a torque exerted by the system, ϕ the angular displacement of the system, and ω its angular velocity. Unfortunately, if we want to calculate the efficiency of, for instance, muscle contractions in running, the situation is not so clear-cut. As already indicated, this is associated with the fact that in repetitive movements such as walking, running, and hopping, the work done against the environment is small. Thus, most of the metabolic energy liberated in such movements is related to the necessity to accelerate, lift, and decelerate body segments. After each complete cycle, the energy content of the segments returns to about the same level and, neglecting air friction forces and deformations in the contact between foot and ground, no significant net flow of energy can be established on the basis of external forces (contrary to bicycle ergometry). This means that an approach where the entire organism is taken as a free body diagram is of little use in applying the definitions for mechanical work and power.

Various authors have therefore attempted to deduce measures for work and power from the changes in kinetic-, potential-, and rotational-energy content of all body segments or the body center of gravity, or from joint work measures (e.g., Aleshinsky, 1986; Cavagna et al., 1964; Cavagna, Thijs, & Zamboni, 1976; Fukunaga, Matsuo, & Ichikawa, 1981; Heglund, Cavagna, & Taylor, 1982; Heglund, Fedah, Taylor, & Cavagna, 1982; Kyroläinen et al., 1990; Pierrynowski et al., 1981; Prilutsky, Petrova, & Raitsin, 1996; Winter, 1983). This has led to a bewildering variety of estimates of work and power, attributable to different assumptions with respect to exchange of energy between segments and between forms of energy, and to the way in which decreases of energy (or negative joint work) are dealt with. Since these aspects have been discussed previously (e.g., Aleshinsky, 1986; Cavanagh & Kram, 1985a, 1985b; Ingen Schenau & Cavanagh, 1990; Koning & Ingen Schenau, 1994; Williams, 1985; Williams & Cavanagh, 1983), we will restrict the discussion here to a few major aspects that are relevant for the present purpose: to deepen our understanding of mechanical work in the SSC.

In SSCs there are positive and negative work phases. We concentrate on three different approaches used to estimate work and efficiency: efficiency of positive work, efficiency of negative work, and absolute work and its efficiency.

Efficiency of Positive Work. In this approach, negative work is not accounted for and only positive work is related to metabolic work (e.g., Heglund, Fedah, et al., 1982; Zarrugh, 1981). Conceptually, this approach is comparable to that used in determining positive work and efficiency in isolated muscles or in isolated muscle fibers (e.g., Heglund & Cavagna, 1985, 1987; Potma, Graas, & Stienen, 1994). However, in repetitive movements such as walking, hopping, and running, as well as in SSC contractions measured on isolated muscles *in situ*, the work done during the concentric phase of the SSC is only in part delivered by the contractile machinery. This means that only part of the positive work can be related to metabolic energy according to efficiency as defined in thermodynamics (see Thermodynamic Definition of Efficiency: $W/\Delta G$, in Part II). As long as it is not known what part of the positive work is associated with the conversion of metabolic energy to mechanical energy, the concept of efficiency of positive work in SSCs does not help to reveal basic principles. Rather, we feel that the concepts of positive work and efficiency of positive work in SSC obscure basic processes and therefore are completely meaningless.

Efficiency of Negative Work. In this approach, negative work is assumed to be performed at metabolic costs according to the so-called efficiency of negative work (e.g.,

Belli & Bosco, 1992; Luhtanen, Rahkila, Rusko, & Viitasalo, 1990; Voigt, Bojsen-Møller, et al., 1995; Williams & Cavanagh, 1983). First of all, it seems to make no sense to relate metabolic energy to work conserved in passive elastic structures of the series elastic element (SEE) (remember that part of the SEE is located in the sarcomeres). Since the SEE extension per se is not coupled to ATP breakdown, such a relation is meaningless. What one needs to know is which part of the negative work in an SSC can be related to eccentric actions of the contractile elements (CE). However, even if measures of the true negative work of CE were available, one could dispute the use of the term *efficiency*. After all, in eccentric actions no free energy is converted into work. Rather, mechanical energy is taken from the system and degraded into heat, just as in the operation of a brake. Thus, the question is not which fraction of the free energy is converted into mechanical work, but rather how much metabolic energy is necessary in an action meant to absorb mechanical energy. From a thermodynamic point of view, it is not self-evident that such actions should cost metabolic energy at all. In fact, various machines can convert negative work back into potential energy (even in chemical form), to be used for positive work at a later time. Although, for example, a rephosphorylation of ADP to ATP driven by mechanical work in eccentric actions has never been demonstrated, there are no arguments against an “efficiency” of negative work far in excess of 1.0 (e.g., Stainsby, 1976: ± 8).

Clearly, regardless of the type of contraction, ATP will break down in tension-independent processes. The question arises to what extent this entirely explains the metabolic costs of eccentric contractions. As shown by many authors, the total metabolic costs are considerably lower in eccentric actions than in concentric actions. In fact, in eccentric actions, the costs are even about 3–4 times lower than in isometric actions (Curtin & Davies, 1974; Infante, Klaupiks, & Davies, 1964; Woledge, Curtin, & Nomsher, 1985). The reason seems to be that cross-bridge cycles during (not too fast) eccentric contractions do not require ATP splitting (Curtin & Davies, 1974). Perhaps in SSCs, the metabolic costs of eccentric actions of CE should be related to tension-independent processes only. The question is, however, whether these costs in SSCs can be deduced from experiments comprising eccentric actions only. Many authors account for the metabolic costs of the negative work phases in SSCs by taking “efficiency” measures reported for downhill walking (Margaria, 1968) or for opposing the pedals in backward cycling (Abbott, Bigland, & Ritchie, 1952). For such experiments, efficiency values of -1.2 are reported. It remains to be seen whether such experiments have any relevance for the SSC at all, since it is not known what part of the metabolic costs of the tension-independent processes would also be lost in a concentric action without prestretch.

It seems that the only question truly relevant to the issue of metabolic costs of negative work in SSCs is how large the extra metabolic costs are in contractions including a prestretch compared to contractions without prestretch. The results of recent studies suggest that prestretch does not increase the metabolic costs over those of a concentric contraction without prestretch. Heglund and Cavagna (1987) measured the oxygen consumption in SSC contractions of frog sartorius, rat extensor digitorum longus (EDL), and rat soleus and reported no differences in metabolic requirements between contractions with and without prestretch. Also, Haan et al. (1989) reported similar amounts of energy utilization in contractions with and without a prestretch. The mechanical equivalent of the high-energy phosphate consumption was 981 ± 251 mJ for the concentric actions and 968 ± 127 mJ for the SSCs, with the difference being not statistically significant. These findings support the idea that extra work done during the concentric action is not associated with extra metabolic costs. For the part of the work associated with elastic energy, this is not surprising, but the results suggest that it is also true for the extra work done by the

contractile elements due to muscle potentiation. Curtin and Woledge (1993) and Woledge and Curtin (1993) demonstrated that even the efficiency based on net work measured in muscles that undergo sinusoidal length changes is higher than the efficiencies measured in muscles that contract concentrically from an isometric preload. These results are also consistent with the idea that the eccentric phase of an SSC is not associated with extra ATP breakdown. However, part of the difference in efficiencies may be due to the fact that the stimulation phase was optimized to result in the maximal efficiency in the experiments with the sinusoidal length changes, but not in the earlier ramp shortening experiments.

Woledge and Curtin (1993) argued that strained cross-bridges can detach to a state that allows rapid reattachment without ATP splitting. They suggested that these cross-bridges are capable of much more rapid attachment than detached cross-bridges that have not been subjected to stretch. This might explain the phenomenon of muscle potentiation, although it is not clear yet why a larger number of cross-bridges during shortening would not require more ATP breakdown. Perhaps, as previously suggested (Ingen Schenau, 1984), the SSC helps to avoid a waste of ATP in taking up the slack of muscle fibers, which seems to occur in concentric contractions not preceded by an eccentric phase (Goldspink, 1978).

In conclusion, it seems that the prestretch phase in SSCs does not require metabolic energy in excess of the requirements of a concentric action. According to the results of Heglund and Cavagna (1987), this is even the case in contractions where the negative work of CE is quite substantial. Though following sections will make clear that a translation of *in situ* observations to the *in vivo* situation is not without risk, the low costs of eccentric actions might also explain why the model of Ma and Zahalak (1991), developed to predict the energy consumption in contracting muscles, fails to predict the experimentally observed large drop in energy consumption for slow stretches. Ma and Zahalak qualified this as a major shortcoming of their model.

Absolute Work and Its Efficiency. In this approach, problems with negative work are “solved” by simply adding the absolute value of negative work to the positive work (e.g., Kyroläinen & Komi, 1995; Martin, Heise, & Morgan, 1993; Norman, Sharratt, Pezzach, & Noble, 1976; Prilutsky et al., 1996; Winter, 1979). In this summation, the shortcomings of the above-mentioned measures of positive and negative work are in fact combined: Elastic energy is now not only wrongfully treated as external work but even counted twice. Imagine, for example, a monoarticular SSC as illustrated in Figure 2, where the flexion–extension action is controlled by a muscle in a concerted contraction, that is, a contraction where the CE does not change in length but the SEE lengthens and shortens. If ΔE_{el} is the elastic energy stored and released by the lengthening and shortening SEE, the absolute work approach yields $W = 2\Delta E_{el}$. If this were true, a bouncing ball would be able to solve all our environmental problems in relation to energy requirements, since it would generate work without any input of chemical energy. Clearly, measures of efficiency based on such “work” values have properties of a *perpetuum mobile*. Even in studies where these measures clearly are not meant to be used to determine efficiency in SSCs (e.g., Aleshinsky, 1986; Cavagna et al., 1968; Prilutsky et al., 1996), one wonders why they are proposed. Aleshinsky as well as Prilutsky referred to their work measure as mechanical energy expenditure (MEE), but it is unclear to us how this MEE should help to deepen our understanding of mechanical work in the SSC.

Is Efficiency in SSCs a Relevant Concept?

We have now addressed the difficulties in determining work, and therewith efficiency, in SSC exercises such as running, in which little work is done on the environment. However,

several authors have argued that efficiency is not particularly relevant for running, because conservation of elastic energy plays such an important role. In their view, knee extensor and calf muscle contractile elements do not undergo any (active) lengthening during running but allow their relatively long tendinous tissue to store elastic energy during stretch, with the muscles acting primarily as force generators (Rall, 1985; Taylor, 1980). We are sympathetic with the arguments forwarded in support of this view, which are derived from muscle architecture considerations (e.g., Alexander & Goldspink, 1977; Alexander & Ker, 1990), experimental results (e.g., Hof, 1990; Jacobs et al., 1993; Tidball & Daniel, 1986), and teleological considerations (Winters, 1990). However, we do not subscribe to the view that the muscles merely act as force generators. For that, we feel, the metabolic costs of running are too high: Subjects not specifically trained in either running or cycling always show a larger oxygen consumption during maximal running than during maximal cycling (Matsui, Kitamura, & Miyamura, 1978; McKay & Banister, 1976; McNab, Conger, & Taylor, 1969). It would be hard to explain the high requirement of metabolic energy if running were predominantly driven by isometrically contracting muscles. After all, it is beyond dispute that the metabolic costs of isometric actions are considerably lower than those of concentric actions (e.g., Åstrand & Rodahl, 1977).

Several findings support our conviction that concentric contractile element actions occur in running. First, the metabolic energy input during running is high in the calf muscles (Costill, Sparks, Gregor, & Turner, 1971; Matsui et al., 1978), even though, from an anatomical point of view, these muscles are the most suitable ones to store and release elastic energy (e.g., Alexander & Ker, 1990). Second, joint power data (e.g., Jacobs et al., 1993) as well as muscle force-length data (Komi, 1992, his Figure 6.54) demonstrate that the positive work of the entire muscle-tendon complexes of the calf muscles during plantar flexion is considerably larger than the negative work during dorsiflexion. This is only possible if the contractile elements of the plantar flexors do indeed contribute significantly to positive work. Since little work is done against external forces, the distinct generation of positive work must be counterbalanced by a considerable degradation of mechanical energy as well. It seems, therefore, that even in running, where the joint excursions in the SSCs are relatively small, distinct concentric actions occur. Moreover, the metabolic costs of running are so high that work and efficiency are relevant issues.

At first glance, one would expect that relevant information could easily be tested on the basis of data obtained in experiments performed at lower levels of organization. However, as will be illustrated in the next sections, contemporary data obtained through *in situ* and *in vitro* studies do not seem to throw light upon muscle efficiencies achieved *in vivo*. Even measures for concentric CE work deduced from *in situ* experiments are open to discussion. There is an urgent need for muscle physiology studies aimed at determining the energy cost of muscle actions *in situ* as a function of the types of contraction found in the intact organism.

Is the Whole More Than the Sum of Its Parts?

In this section we will show that muscle efficiency values deduced from *in situ* and *in vitro* experiments are too low to explain muscle efficiency realized during whole-body movements such as cycling *in vivo*, which hardly includes SSCs. A number of differences in conditions will be addressed with the purpose of guiding future studies.

Whole-Body Movements. Some textbooks arrive at a muscle efficiency e_m of about 0.25 by taking the product of phosphorylative coupling efficiency e_p , taken to

be about 0.60, and contraction coupling efficiency e_c , taken to be about 0.40 (e.g., Åstrand & Rodahl, 1977). The value of 0.60 for e_p , which was deduced from the apparent efficiency data of Whipp and Wasserman (1969) disputed earlier, is slightly higher than the value of 0.575, which we derived earlier (How to Compare Measures Across Levels of Organization). The value of e_c , and consequently that of e_m , however, must be too low, as will be argued below.

It seems generally accepted that the maximal gross efficiency e_g in human total body movements, such as ergometer cycling, is about 0.23 (e.g., Åstrand & Rodahl, 1977; Seabury, Adams, & Ramey, 1977). We can estimate from this e_g a measure for muscle efficiency, which in the case of cycling may be equated to the efficiency of concentric CE work. Let us start by assuming that the power lost in the transmission system and in moving the leg segments is 10% of the total mechanical power output of the exercising leg muscles (e.g., Ingen Schenau et al., 1990). Let us further accept the measurements of Poole, Gaesser, Hogan, Knight, and Wagner (1992), indicating that as much as 84% of the total oxygen consumption is used by these muscles (when cycling at 300 W). This leads to an efficiency of the exercising muscles of about 0.30. If we take the e_p value of 0.575 derived earlier, the contraction coupling efficiency e_c should be 0.52 during cycling. During this exercise, however, the muscles contract at varying velocities. This means that at optimal shortening velocity, e_m must be larger than 0.30, and thus e_c must be larger than 0.52!

To a certain extent, these conclusions about e_m are confirmed by data derived more directly from the energy consumption of exercising muscles *in vivo*. With special techniques (e.g., the constant-infusion thermodilution technique), a number of authors have measured the oxygen consumption of arm or leg muscles during exercises from the blood flow through the muscles and the arteriovenous oxygen difference of these muscles. Rowell, Saltin, Kiens, and Christensen (1986), who used a special ergometer for quadriceps muscle exercise, reported a maximal muscle efficiency of 0.195. Poole et al. (1991, 1992) found optimal values of 0.27–0.28 for leg muscles during cycling. Frisk-Holmberg, Jarfeldt, Juhlin-Dannfelt, and Karlsson (1981) reported higher values of up to 0.35 for cycling, whereas Ahlborg and Jensen-Urstad (1991) even mentioned efficiencies of 0.34–0.44 for arm muscles during arm cranking. These values are in concert with our estimate derived from the gross efficiency of cycling, although the calibration of this technique for *in vivo* experiments is not without uncertainty (Poole et al., 1992).

Isolated Muscles and Muscle Fibers. It has been argued that a translation of results obtained at the levels of isolated muscles or muscle fibers is hampered by severe uncertainties. Given our resolute rejection of the concept of efficiency of positive work in SSCs, the only studies that seem relevant are studies of the efficiency of concentric actions and (scarce) studies of the efficiency of net work production. Since this paper is ultimately aimed at human movements, we feel that values obtained from extremely slow muscles such as the tortoise muscle (Woledge, 1968) are irrelevant. In the remaining studies of frog and mammalian muscles, e_c values ranged from about 0.20 to 0.50, with most results concentrated between 0.30 and 0.35 (e.g., Barclay, Constable, & Gibbs, 1993; Curtin & Woledge, 1991; Di Prampero, 1981; Di Prampero, Boutellier, & Morguerat, 1988; Haan et al., 1989, 1993; Infante & Davies, 1965; Lodder, Haan, & Sargeant, 1994; Potma, Graas, & Stienen, 1994; note that, when necessary, the results of these authors were corrected to obtain the value of $e_c = W/\Delta G_{\text{ATP}}$ with $\Delta G_{\text{ATP}} = -46$ kJ/mole). These e_c values correspond to muscle efficiencies $e_m (= e_c \cdot e_p)$ ranging from 0.12 to 0.29, with most values concentrated between 0.17 and 0.20. Such e_m values are in agreement with values obtained on the basis of oxygen consumption measured in animal muscles *in situ*. For instance, Syme (1994),

Stainsby, Peterson, and Barbee (1981), Heglund and Cavagna (1987), and Di Prampero and Margaria (1969) reported muscle efficiencies between 0.19 and 0.21. Thus, so far there seems no reason to call into question our selection of e_c values from the literature or the estimate of e_p proposed earlier in this paper. However, the e_c values are too low to account for muscle efficiencies of more than 0.30 deduced from total body movements in the previous section, and this does present a reason to reconsider the e_c values, or rather the type of contractions upon which they are based.

Efficiency of Isolated Muscles Reconsidered

Experiments Using Skinned Muscle Fibers. One would expect experiments on isolated muscle fibers to provide the ultimate answers to questions raised at higher levels of organization. However, as noticed by Potma (1995), skinned mammalian fibers display a force–velocity relationship that is distinctly different in curvature from that found in intact muscles, fibers, and fiber bundles. For skinned rabbit psoas, the force appears to reach only 2% of the maximal isometric force at 20% of maximal shortening velocity. This is much less than the corresponding force value found in intact mammalian tissues at the same relative velocity. It is unclear to what extent such phenomena influence efficiency measures reported for isolated skinned fibers. One might question, therefore, whether the available results of experiments on skinned fibers have any significance at all for our understanding of the contractile properties of muscles in the intact animal.

Influence of Temperature and Stimulation Frequency. Rall (1985) mentioned two factors cautioning against an extrapolation of *in vitro* and *in situ* data to the *in vivo* situation. The first is that changes in temperature have different effects. Rall raised the muscle temperature of walking lizards by 10 °C. Based on *in vitro* observations, the oxygen consumption was expected to increase by 100%, but in reality it hardly changed at all. The second factor mentioned by Rall is that stimulation frequencies used in most *in situ* experiments are completely different from those generated by the central nervous system of an intact animal. Recent experiments of Buschman (1995) suggest that high stimulation frequencies, often used to obtain a fused tetanus, may have a negative effect on efficiency, especially in slow twitch fibers. Due to asynchronous firing of motor neurons *in vivo*, smooth force responses are achieved at considerably lower stimulation frequencies than during *in situ* experiments.

Efficiency in Fast Versus Slow Twitch Fibers. It appears beyond dispute that the rate of cross-bridge cycling (and ATP turnover) during isometric contraction is considerably higher in fast twitch (FT) fibers than in slow twitch (ST) fibers (e.g., Goldspink, 1978; Potma, Graas, & Stienen, 1994; Potma, Stienen, et al., 1994). This means that the FT fibers may produce higher forces than the ST fibers but are much less economical than ST fibers, with economy being defined here as force–time integral divided by energy consumption. The high cross-bridge turnover rate allows the FT fiber to quickly build up force, produce higher forces at a given shortening velocity, and achieve higher instantaneous power as well as a higher maximal shortening velocity. However, according to Woledge (1968), the development of faster fibers in the course of evolution, which allows more powerful and fast muscle actions, could only be realized at the cost of efficiency. This is convincingly demonstrated by comparing frog or mammalian muscles with the extremely slow tortoise muscle (Woledge, 1968). For instance, the time to maximal tension takes 0.25 s in frog muscle, compared to 4 s in tortoise muscle, but contraction coupling efficiency (in that study measured as $W/\Delta H_{pc}$) is only 0.45 in frog muscle, much lower than the 0.77 of tortoise muscle.

In addition to comparing efficiencies of muscles across species, we may compare efficiencies of fast and slow twitch fibers under *in situ* conditions in one animal. The literature is not unanimous on the outcome of this comparison. Barclay et al. (1993) reported equal efficiencies of 0.30 ($W/\Delta H_{pc}$) for the fast mouse extensor digitorum longus (EDL) and the slow mouse soleus (SOL). However, in a later study the same author showed a clear difference in efficiency between these two muscles: 0.34 in EDL and 0.52 in SOL (Barclay, 1994). The later experiments involved cyclic sinusoidal contractions, whereas those performed in 1993 involved isovelocity shortenings. This seems to support the dependency of efficiency on type of contraction, which will be addressed in the next paragraph. In contrast, Heglund and Cavagna (1987) reported for the rat even lower efficiencies for slow muscles (SOL) in comparison to fast muscles (EDL).

Contradictory findings have also been reported in comparisons across individuals with different fiber composition *in vivo*. Coyle, Sidossis, Horowitz, and Beltz (1992) observed a significant positive correlation between the (gross) efficiency during cycling and percentage of ST fibers of the knee extensors of cyclists. Based on the results of extrapolation of this relationship, they suggested that the FT fibers and ST fibers work at quite different efficiencies, 0.13 and 0.27, respectively. However, Frisk-Holmberg et al. (1981) using blood flow and blood oxygen measurements in subjects ranging widely in fiber composition, could not find such a relationship. Suzuki (1979) even reported a negative correlation between efficiency and the percentage of ST fibers.

In view of all this confusion, we tend to agree with Rall (1985) that it remains to be established unequivocally whether efficiency really differs among fiber types. Perhaps recruitment principles such as the size principle help to reduce effects of differences in cross-bridge cycle rates.

Influence of the Stimulation Protocol. Most results on the efficiency of concentric actions in isolated muscles or muscle fibers have been obtained in contractions at constant velocity or against a constant load, preceded by a relatively long isometric preload. These contractions differ in several respects from real-life contractions and are not specifically designed to prevent a waste of energy. For instance, the isometric preload, which requires metabolic energy, is relatively long, and relaxation is postponed to the end of the contraction, which may also lead to an unnecessary waste of energy (Woledge & Curtin, 1993). In a few studies, it has been shown that efficiency depends on the experimental protocol. From most studies on SSCs in isolated muscles, it can be deduced that, contrary to what occurs *in vivo*, the amount of negative work absorbed by the muscles during prestretch was considerably larger than the amount of positive work done by the muscles during the concentric phase.

Muscles performing SSCs *in vivo* mostly generate positive net work, except in actions such as downhill running and some of the repetitive sledge movements applied by Kyroläinen and Komi (1995). Even in level treadmill running (no air friction), contractile elements need to add work to the system, because not all energy is reutilized. Though one may dispute the amount of energy to be added, it is beyond dispute that the net work output of the muscles must be positive when averaged over a complete running cycle. In the studies on isolated muscles, however, the work done on the muscle during stretch is considerably larger (up to 4 times) than the work done by the muscle; this can easily be deduced from the figures presented in the classic and often cited study by Cavagna et al. (1968) but also from results presented by Bergel et al. (1972) and Heglund and Cavagna, (1985, 1987). Thus, the relevance of these studies in explaining the benefits of SSCs during hopping, walking, and running is questionable.

Fortunately, a number of authors working in the field of isolated muscles have addressed this problem during the past 6 years (Barclay, 1994; Curtin & Woledge, 1993;

Ettema, Huijing, et al., 1990; Ettema, Soest, & Huijing, 1990; Haan et al., 1989; Moon, Altringham, & Johnson, 1991; Syme, 1994; Woledge & Curtin, 1993). To our knowledge, Haan et al. (1989) were among the first who applied stimulation protocols that resemble more closely the stimulations as observed for distal leg muscles during running. For instance, if we account for the phase lag between electromyographic signals and force response (associated with but not equal to the rise-time phenomena discussed above; e.g., Inman, Ralston, Saunders, Feinstein, & Wright, 1952; Vos, Harlaar, & Ingen Schenau, 1991), it appears that the triceps surae muscle-tendon complex is not activated until the very last part of the eccentric phase of the muscle-tendon complex (e.g., Hof, 1990; Jacobs et al., 1993).

Haan et al. (1989) attempted to mimic this situation in SSC contractions of rat gastrocnemius. In their protocol, they started muscle stimulation 150 ms prior to the onset of the concentric phase. They were able to achieve a positive net work output, but the efficiency of net work dropped to about half the value observed in their experiments involving isovelocity shortening contractions preceded by an isometric preload (with the total duration of the stimulation being the same). In this study, however, they did not attempt to optimize net work and efficiency but rather to considerably enhance positive work. Moreover, the total duration of the stimulation was not reduced. In a later study, Haan et al. (1993) showed that when the (active) isometric phase was reduced to 20 ms and stimulation was terminated 30 ms before the end of shortening, contraction coupling efficiency of rat medial gastrocnemius muscle increased from 0.26 to 0.36. By varying the timing of the onset of activation during stretch, Ettema, Huijing, et al. (1990) demonstrated that optimizing net work output is indeed incompatible with optimizing the amount of positive work. These observations indicate that isolated muscle and muscle fiber studies aimed at improving our knowledge about maximal work enhancement in discrete movements (jumping, throwing) require different protocols than studies aimed at helping us to understand maximal performance in repetitive SSCs. Finally, Curtin and Woledge (1993) and Barclay (1994) found distinctly higher efficiencies of net work in their experiments on SSCs than in their previous work on concentric contractions (compare Woledge & Curtin, 1993, and Curtin & Woledge, 1993, with Curtin & Woledge, 1991, or Barclay et al., 1993, with Barclay, 1994).

The findings presented above show that efficiency depends strongly on the experimental protocol used. With proper timing of the onset and termination of stimulation, a prestretch may enhance the CE efficiency of net work in repetitive SSCs compared to that in concentric contractions. The enhancement might be associated with the observation that muscle potentiation due to prestretch does not require metabolic energy. It might also be due to the avoidance of a waste of energy in taking up the slack of the muscle fibers, as suggested by Ingen Schenau (1984). Although this author would be really pleased to have his suggestion confirmed, data of experiments performed to test it were not favorable. As already mentioned, Haan et al. (1989) reported that a prestretch does not seem to affect metabolic energy requirements.

Unfortunately, the attempts, described above, to minimize a waste of energy still lead to e_c values that are too low. The $e_c = 0.36$ of Haan et al. (1993) would correspond to a muscle efficiency of 0.21. Curtin and Woledge (1993) reported a maximal efficiency for fish muscle of $e_c = 0.42$. Barclay (1994) reported e_c values of 0.52 and 0.34 for mouse SOL and EDL, respectively. Accounting for the fact that these values are based on heat + work measures, this corresponds with muscle efficiencies of 0.18 for the fish muscle and 0.22 and 0.15 for the mouse muscles, still substantially lower than the 0.30 estimated from gross efficiency in cycling.

Part III: Summary and Conclusions

Maximum Work in the Concentric Phase

The first major issue addressed in this paper was the effect of a prestretch on the maximum work produced in subsequent concentric action, which has been described for a number of movements *in vivo* such as vertical jumping. This enhancement was attributed to the fact that the prestretch allows the muscles to develop a high level of active state and force before shortening begins. It was concluded that storage and reutilization of elastic energy could be ruled out as an explanation for the enhancement of work and that other mechanisms, such as neural responses and potentiation of the contractile machinery caused by prestretch, play at best a secondary role.

Efficiency of SSCs in Whole-Body Movements

The second major issue addressed was the effect of a prestretch on efficiency. In the literature on whole-body SSC exercises such as running, efficiencies are reported that by far exceed the values found in the literature on concentric actions of isolated muscles and muscle fibers. We attempted to reconcile the efficiency values reported on different levels of organization. As a starting point, we used the thermodynamic definition of efficiency: the ratio $W/\Delta G$ of actual work done (W) to maximal work attainable ΔG , with the latter representing the change in free energy of the food. First, a number of difficulties with the determination and interpretation ΔG were discussed, and we raised the question which part of the total metabolic energy expenditure in total-body movements should be used to calculate efficiency. Several baseline subtractions proposed in the literature were disputed. Subsequently, problems with determining W in whole-body movements were addressed. It was shown that in SSC exercises where work done against the environment is small, W cannot be defined unambiguously. Concepts such as negative work, positive work, and absolute work, introduced in the literature to solve this problem, were debated. It was argued that those concepts of work and its efficiency are of no use for a better understanding of SSCs and the principles underlying control of human movement. It was concluded, therefore, that efficiencies reported for repetitive SSC exercises are questionable and cannot be compared to efficiencies observed in studies of isolated muscles and muscle fibers.

To understand relations between generation, degradation, and conservation of mechanical energy and the associated metabolic costs, we must investigate in detail the types of contraction of the muscles involved, including the precise CE-SEE interactions. The study of these interactions requires muscle models incorporating contractile and series elastic elements. Thus far, such models have only been applied to estimate efficiency of true concentric and eccentric CE work in a few studies on repetitive vertical jumps (Belli & Bosco, 1992; Voigt, Bojsen-Møller, et al., 1995). According to the results of these studies, there is no need to assume any enhanced muscle efficiency due to prestretch. However, the type of muscle contractions present in running will be distinctly different from that in hopping. At first glance, one would expect that the influence of a prestretch on CE efficiency could easily be tested in experiments performed at lower levels of organization. However, as illustrated, contemporary data obtained through *in situ* and *in vitro* studies do not seem to throw much light upon muscle efficiencies achieved *in vivo*.

Efficiency of Isolated Muscles

Efficiencies calculated for whole-body movements (cycling) were compared to efficiencies observed in studies of isolated muscles and muscle fibers. Cycling was selected be-

cause it is a whole-body movement not involving SSC and because more than 90% of the mechanical work is done against the environment. From gross efficiency in cycling, it was deduced that muscle efficiency should be greater than 0.3 and that contraction coupling efficiency should be at least 0.52. These values are much higher than values reported in the literature for isolated muscles and muscle fibers. It was argued that the latter values are too low for several reasons, an important one being the use of energy-wasting experimental protocols. In some studies, it has been shown that efficiency could be increased by changing the stimulation protocol, but not to values sufficient to explain the high efficiencies calculated for cycling. It was concluded that so far, muscle physiologists have been unable to successfully mimic the contraction conditions occurring *in vivo*.

Conclusions

In conclusion, there is no decisive evidence to either support or reject the claim that the SSC enhances efficiency in repetitive movements. The discussion of the various issues has revealed that the body of knowledge about the mechanics and energetics of the SSC is in fact quite lean. A major challenge in the future is to bridge the gap between knowledge on the different levels of organization, with the ultimate purpose of understanding how the intrinsic properties of muscles are exploited in whole-body SSC activities such as running. For this purpose, analysis and simulation of these activities with models of the musculoskeletal system seem indispensable. After all, such models allow unambiguous application of the definitions of work, power, and efficiency. However, the development of models of the musculoskeletal system leans heavily on knowledge acquired at lower levels of organization, and many of the issues at these levels are still debated. Decisive values for the compliance of series elastic elements and contraction coupling efficiencies, to name but a few crucial issues, are still not available. The situation begs for a close cooperation between human movement scientists who perform inverse and forward dynamic simulation studies of whole-body exercises, and muscle physiologists who can perform invasive experiments and test hypotheses generated in these simulation studies.

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