

AUTHORS' RESPONSE

JOURNAL OF APPLIED BIOMECHANICS, 1997, 13, 484-496
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Mechanics and Energetics of the Stretch–Shortening Cycle: A Stimulating Discussion

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Introduction

The target article about stretch–shortening cycles was triggered by controversies on this topic among biomechanists and exercise physiologists and by the difficulties in relating knowledge obtained at different levels of organization. The purpose of the article was to stimulate a dialogue between scientists in different fields. We are therefore very pleased that so many distinguished experts from various disciplines responded with constructive, engaging commentaries. Before reacting to specific points addressed by the commentators, we will attempt to clarify a few points that seem to have caused confusion.

Conceptual Model

Herzog correctly argues that we might have been more careful in explaining the conceptual muscle model used in our reasoning and in defining the series elastic element (SEE) and contractile element (CE). Throughout the paper, we implicitly based our ideas and arguments on a Hill-type muscle model where all elastic structures in, and in series with, the cross-bridges are supposed to be represented by an SEE behaving as a nonlinear passive spring with little viscosity. This means that elasticity associated with the contractile machinery is part of the SEE. The SEE is assumed to lie in series with a contractile element CE, the behavior of which is supposed to be described not only by the force–length–velocity relationship and excitation dynamics but also by functions accounting for history effects due to, for example, potentiation or fatigue.

With respect to distinguishing between SEE in cross-bridges and SEE in tendinous tissue, we expect that at a given muscle force the strain of the cross-bridges is very low compared to the strain of tendinous tissue (e.g., Edman, this issue; Huxley, 1974; Morgan, Proske, & Warren, 1978). Moreover, in intact muscle–tendon complexes, the length of the tendinous tissue in series with each muscle fiber (obtained by subtracting muscle fiber length from origin to insertion distance) is large compared to that in the cross-bridges. For instance, the human *m. gastrocnemius* spans a total origin to insertion distance of about half a meter with muscle fibers of some 6 cm, indicating that each muscle fiber “sees” some 45 cm of tendinous tissue (Bobbert, Huijing, & Ingen Schenau, 1986). Thus, even if the stress–strain relationships of tendinous tissue and cross-bridge series elasticity were the same, the overall SEE behavior would still be dominated by that of tendinous tissue. From this point of view it follows that, in contrast to Goubel, we do not believe that

the stress–strain characteristic of the SEE can be changed significantly during a stretch–shortening cycle (SSC).

Elastic Energy Is Not Insignificant

In the target article we did reject the possibility that the larger work output after a counter-movement is due to storage and reutilization of elastic energy. By no means, however, did we question the significance of storage and reutilization of elastic energy in general, as some commentators seem to have understood (Farley, Minetti et al., Morgan & Proske, Prilutsky, and Zatsiorsky). We stressed explicitly at several places in the target article (e.g., Part I, Storage and Reutilization of Elastic Energy; What, Then, Is the Role of Elastic Energy?; and Part II, Statement of the Problem) that storage and reutilization of elastic energy are highly functional. This is consistent with many of our previous papers, in which we demonstrated the significance of storage and reutilization of elastic energy in throwing (Jöris, Edwards van Muijen, Kemper, & Ingen Schenau, 1985), jumping (Bobbert et al., 1986; Bobbert & Ingen Schenau, 1990), and running and sprinting (Jacobs, Bobbert, & Ingen Schenau, 1993, 1996). As shown in these and many other studies, SEE can play a very distinct role as power amplifier, by storing energy at low rates and releasing it at very high rates (both in movements with and without a prestretch). In fact, this important behavior also largely inspired us in the design of the new skate (the “slapskate”) we developed (Ingen Schenau, Groot, Schreurs, Meester, & Koning, 1996), which has caused quite a revolution in top-level speed skating.

We have also stressed consistently that the role of elastic energy in the conservation of mechanical energy in repetitive SSCs during running is beyond dispute and substantially improves running economy (see Part I, What, Then, Is the Role of Elastic Energy?, and Part II, Statement of the Problem). We did not dispute that the efficiency of positive work during bouncing gait can be larger than 100% (Minetti et al.), since a considerable part of the positive work is due to conservation of mechanical energy. We merely argued that such measures of work and efficiency do not improve our insight in the mechanics and energetics of the SSC, and we disputed the suggestion that the efficiency of the conversion of metabolic energy into mechanical energy is enhanced by a prestretch.

The Origin of Elastic Energy

Three commentaries (Herzog, Morgan & Proske, and Zatsiorsky) question our statement that the amount of elastic energy is determined not by the negative work done by the muscle but by its force. The confusion about this statement may be due to the fact that we did not clearly define SEE and did not add that we used the word *determined* in a mathematical sense. Of course, we agree that in an SSC the elastic energy can largely stem from the negative work, and of course the amount of elastic energy stored in the SEE is about equal to the negative work done on the SEE. It is not, however, equal to the negative work done by the muscle–tendon complex. During a lengthening contraction of a muscle tendon complex, the amount of energy stored in SEE will be smaller than the amount of negative work done on the complex if CE yields (and degrades part of the negative work into heat) or greater if CE shortens (as in concerted actions). What we do know for sure, however, is that the amount of energy stored in SEE is directly related to the current force: At a given characteristic $F = f(l)$, describing the relationship between given force (F) and elongation (l) of SEE, the elastic energy E stored in SEE ($E = \int F dl$) can simply be expressed as a function of l and thus of F .

This basic relationship should also be borne in mind when considering the results of drop jump studies. Zatsiorsky mentions that large changes in dropping height, say from 10 to 100 cm, bring about only small changes (<5 cm) in height of the subsequent jump. From this small "coefficient of restitution," Zatsiorsky concludes that the SEEs are not very elastic. According to us, such a link cannot be made: If drop height is increased more negative work is performed, but if the magnitude of CE force is limited, the extra work is dissipated as heat rather than stored in the SEE. Let us now move to specific points brought forward by the commentators.

Factors Improving Performance in Discrete SSCs

The Time Required for Force Development

In the target article we explained the enhancement of positive work in discrete SSCs by pointing out that the countermovement allows muscles to build up force before shortening begins, so that more force can be produced over the first part of the shortening range compared to a condition where force development must take place during shortening. This explanation, which we did not present as a novel one, as suggested by Bosco, but rather by referring to original sources, is explicitly supported by a number of commentators. However, Zatsiorsky as well as Minetti et al. argue against its significance. Zatsiorsky correctly draws our attention to fast SSCs (e.g., 100 ms in sprinting) and argues that the performance of these SSCs cannot be explained with a time of force development of 300–500 ms, as mentioned in our target article. He feels that we should distinguish between the time courses of active state and force development, with the former being completed earlier than the latter (perhaps even within 20 ms). We fully agree that several processes contribute to slow force development. Generally speaking (see Zandwijk, Bobbert, Baan, & Huijing, 1996, for more details and references), the dynamics of force development depend on (a) stimulation dynamics, that is, the dynamics of the development of muscle stimulation, (b) excitation dynamics, that is, dynamics of developing active state in response to stimulation, and (c) contraction dynamics, that is, the dynamics of developing force in response to active state, which in turn depends on the interaction between the contractile machinery and series elastic structures. The last two processes are often approximated as first-order systems, each with a time constant of about 40–50 ms for leg muscles.

In the target article we restricted ourselves to a comparison between countermovement jumps (CMJ) and squat jumps (SJ), with stimulation dynamics essentially being derived from EMG. In CMJ and SJ, stimulation dynamics play a dominant role in overall force dynamics. The fact that force development occurs during shortening in SJ but is completed before shortening in CMJ sufficiently explains the difference in positive work output between the two jumps, and there is no need to bring in other explanations. However, we agree with Zatsiorsky that in fast SSCs such as drop jumps, muscle stimulation develops in a much shorter time and force reaches much higher values than in CMJ (e.g., Bobbert, Huijing, & Ingen Schenau, 1987). Several mechanisms may contribute. As argued previously (Bobbert, Yeadon, & Nigg, 1992), the muscles may be co-contracted in anticipation of landing so that stimulation dynamics and perhaps even excitation dynamics are less relevant: The joint moment response is dominated by the contraction dynamics of extensors that are forcibly stretched and flexors that are quickly released. During stretching, the force of extensors may increase to very high values in a very short time as a result of the high eccentric velocity, as also pointed out by Zatsiorsky.

If the amplitude of the eccentric movement is small and the transition to shortening takes place in a very short time, the high force and (according to Part I, Potentiation of the Contractile Machinery) the correspondingly large amount of stored elastic energy are still present at the start of shortening (e.g., Bobbert et al., 1987). This means that during shortening more elastic energy will be released. However, the cause lies in not in the series elasticity itself but in the history effect of CE allowing it to produce a greater force at a given length and contraction velocity. In this context, the effect of any mechanism causing individual cross-bridges to produce more force disappears as soon as the cross-bridge detaches, with cross-bridge cycle time being of the order of only 30 ms (Curtin, Gilbert, Kretzmar, & Wilkie, 1974; Stienen, Blange, & Schnerr, 1978).

Minetti et al. propose a charming experiment of an SJ to support our arguments: In the starting position of a squat jump, a jumper should build up force isometrically to the same magnitude as that recorded at joint reversal in the CMJ; subsequently, the jumper should be released. Based on comparable experiments with monoarticular actions (Bobbert & Harlaar, 1993; Bobbert & Ingen Schenau, 1990), we expect that jumpers would indeed jump higher in this "squat jump." Minetti et al. further imply that timing and muscular coordination issues could play a dominant role in explaining the difference in jump height between CMJ and SJ. As they may know, these issues in fact constitute a major area of scientific interest of our group (e.g., Bobbert & Ingen Schenau, 1988; Ingen Schenau et al., 1996). However, as discussed previously (Bobbert, Gerritsen, Litjens, & Soest, 1996), we have found no indication whatsoever that coordination in the two jumps is different; a very important indication of coordination is takeoff position (e.g., Bobbert & Ingen Schenau, 1988), and we have not found this position to be different between CMJ and SJ.

Elastic Energy

The idea that a countermovement is performed primarily to allow the system to add elastic energy in excess of the work capacity of contractile elements was and is, in our perception, the most generally accepted one. We therefore expected that at least some of the commentators would strongly defend the status of this mechanism as the explanation of the work enhancement in CMJ compared to SJ. Surprisingly, our expectation did not come true. Winter mentions elastic energy as a contributing factor next to the rise time of force but does not supply arguments and does not dispute our logic. Farley feels that our discard of storage and reutilization of elastic energy as a mechanism explaining the difference in jump height between CMJ and SJ should not be interpreted to mean that the stretch-shortening cycle does not ever play an important role in enhancing muscle force and power output in explosive movements. In the examples Farley provides in support of this statement, concerning actions both with and without prestretch, extraordinarily high instantaneous peak powers occur. These high power outputs could indeed not be realized without the power amplification by series elastic elements. Again, this is a mechanism to which we fully subscribe (Part I, What, Then, Is the Role of Elastic Energy?). However, it occurs both in CMJ and SJ, although the power input occurs before the pushoff in CMJ and during the pushoff in SJ.

Morgan and Proske feel that we used an inappropriate simulation in the target article to test the role of storage and reutilization as explanation for the difference in work between CMJ and SJ. According to Morgan and Proske the real question is, "What is the source of the stored energy?" We disagree. The source of the energy merely affects the "efficiency of positive work" done during the pushoff. If the force is higher at a given distance between origin and insertion at the start of shortening, more energy is stored in

SEE and less energy is generated by CE, so the “efficiency of positive work” is higher, but this does not mean that more work can be produced. The point we have tried repeatedly to get across (Avis, Ingen Schenau, Toussaint, & Huijing, 1986; Bobbert et al., 1987; Ingen Schenau, 1986) is that at a given distance between origin and insertion at the start of shortening, energy storage in SEE implies extension of SEE, and this extension must occur at the expense of length and potential shortening distance of CE. If the origin to insertion shortening distance is fixed, more work can only be produced if the properties of CE are affected by the prestretch in such a way that CE can produce more force at a given length and contraction velocity. Such changes may be accompanied by a greater contribution of elastic energy, but then the secret still lies in the changed CE properties. Admittedly, our simulations did not enter the range of CE lengths above optimum. It is quite possible that in a concerted contraction, the whole muscle tendon complex is forcibly stretched to a great length while the CE remains at optimal length. This will constitute a favorable situation to start shortening. As suggested by Morgan and Proske and by Herzog, and previously shown by Ettema, Soest, and Huijing (1990), this theoretically could indeed cause a slight improvement in work output during the subsequent shortening. It is questionable, however, whether this same length of the muscle–tendon complex can be reached *in vivo* in a relaxed situation, because now the SEE is no longer stretched and the CE must be lengthened above optimum. We are inclined to assume, with Bizzi, Hogan, Mussa-Ivaldi, and Giszter (1992), that in the normal physiological ranges of motion, muscles act at the ascending limb of their force–length relationship.

Herzog argues that when the SEE is located in cross-bridges, stretching an activated muscle to a target length will allow for an increase in CE work potential compared to a situation where the muscle builds up force isometrically at the target length (Herzog's Example 1). In this case we would tend to conclude that the game ends in a draw: The strained cross-bridges will be able to do more work in their first step but have one attachment site less available than the unstrained cross-bridges at the same shortening distance.

Prilutsky agrees that our arguments apply to CMJ but feels that in locomotion and other types of jumps, such as the high jump, reutilization of elastic energy does enhance positive work. We fully agree of course that a high jump without an SSC would be a disaster. In fact, one would not jump higher than in the squat jump. We feel, however, that the high jump is not a good example because the initial conditions are quite different from those in CMJ and SJ. The reason is that during the run-up, the athlete achieves a considerable amount of kinetic energy. It is difficult to imagine an SJ-type push-off in high jumping with the same high energy content at the onset of the action. The primary purpose of the last push-off is to transfer this energy to effective energy, particularly kinetic energy due to vertical velocity of the center of mass. In fact, it has been shown that, during the final push-off, energy is lost from the system rather than added to it.

Potential

In the target article, we concluded that there was no need to rely on potentiation to explain the greater work produced in a CMJ compared to an SJ. There is no question, however, that stretching an active muscle can induce a force enhancement that lasts after the stretch is completed. As indicated by Edman, the enhancement may be separated into a velocity-dependent and a velocity-independent component, of which the former is by far the greatest. Unfortunately, this component is swiftly released by a minute release (Edman) and is also unable to outlast cross-bridge cycle time, as pointed out before. It is questionable,

therefore, whether it explains the surprisingly high forces observed during the concentric phase of fast SSCs such as drop jumping (Bobbert et al., 1987). The velocity-independent component is a possible candidate, but its amplitude seems too small.

Biewener, however, could be right that force enhancement due to stretch still might constitute an economical type of force development despite the fact that it does not seem to significantly enhance work.

Reflex Contribution in Discrete and Repetitive Movements

First of all, we have to apologize for erroneously calling the short latency stretch reflex an H-reflex, as correctly noted by Komi and Gollhofer and by Zatsiorsky. Fortunately, this caused no confusion given the commentaries on this issue. A crucial question is, of course, whether muscle spindles are stretched at all in the SSCs discussed. Given the arguments presented in the target article and the reactions on this issue by Biewener, Goubel, and Herzog, we feel that this question needs to be at the top of our list of things to investigate, especially for human running but also for other activities and other species.

We fully agree with Komi and Gollhofer that stretch reflexes are more likely to occur faster in movements such as drop jumps, running, and hopping than in the CMJ. These commentators provide convincing evidence that stretch reflexes can indeed occur in such movements.

The remaining topic of discussion is to what extent reflexes as described by Komi and Gollhofer really contribute to force and work enhancement either during the stretch, as hypothesized by Komi and Gollhofer, or during the concentric phase, as indicated by Winter. In fact, this question constitutes a controversial issue in the much broader perspective of the organization of movement in general. In addition to Komi and Gollhofer, many others argue that it is difficult to imagine that peripheral sensory inputs on spinal networks do not play a significant role in the organization of movement on an ongoing basis (e.g., Duysens, Tax, Toppel, & Dietz, 1993). Others, however, such as the first two authors of this paper and obviously also Morgan and Proske, argue that especially in the fast movements as discussed by Komi and Gollhofer, the mechanical effects expressed in force and the resulting velocity and position measures would be simply too late. The supporters of this view argue that these movements must entirely be based on a type of feed-forward control. This controversy is subject to much debate (e.g., the target article of Gandevia and Burke, 1992, and its open peer communications) and deserves considerable further attention. However, since this debate was not explicitly addressed in our target article, we will focus our response on a few major arguments only.

The first key issue in this debate is the time delay between sensor input and force output. The sequence starts with the adaptation of muscle stimulation on the basis of afferent input, which involves a time delay of at least some 40 ms. As indicated above, the transfer function of muscle stimulation to muscle force can be approximated by two first-order systems in series. This means that the electromechanical delay (EMD), defined as the delay between a change in stimulation and the responding change in force, is not a useful measure to account for the actual functional delay of the system since, in theory, it is zero (the step response of the force starts immediately). A more adequate measure, in our view, is the delay found by cross-correlating a varying input (e.g., rectified EMG) with the corresponding varying force. For leg muscles we found this delay to lie in the order of magnitude of 90–100 ms (Ingen Schenau, Dorssers, et al., 1995; Vos, Harlaar, & Ingen Schenau, 1991). In fact, one of the results presented by Komi and Gollhofer fully supports these arguments. In their Figure 2a they present the Achilles tendon force (ATF)

response on the reflex observed in the (relaxed) triceps surae. Clearly, the ATF starts to rise immediately (no EMD) but continues to rise even far beyond the termination of the reflex activity. If we assume a comparable time scale as in Figure 2b, which seems justified considering the pedal curve and the stretch velocity, the lag between peak EMG and peak force is even far greater than the 90–100 ms mentioned above for active muscles.

The neural delay of 40 ms and this 90–100 ms lag mean that if reflexes are to contribute fully to the high forces at the start of shortening in SSCs, the delay between the start of stretch and the start of shortening should be at least 130 ms but most likely even more, since a change in force is not enough to make the reflex a functional action. Forces are usually meant to cause accelerations, which change velocity and (after a second integration) position. These integrations give rise to further phase lags since, for example, an increased force due to a reflex results only in a significant change in velocity (e.g., joint angular velocity, velocity of the center of gravity) after some time in excess of the 130 ms mentioned. Given these phase lags it seems likely that in the fast movements discussed by Komi and Gollhofer, the major effect of the ATF response occurs far after foot contact.

It is a pity that we did not incorporate these arguments in the target article so that Komi and Gollhofer could have responded to them directly. We therefore invite them to continue this discussion in this journal.

In conclusion of this section, it may be said that to explain the difference in jump height between CMJ and SJ, it is sufficient to consider the rise time of force, and there is no need to bring in elastic energy, potentiation, or reflexes. In faster SSCs, force enhancement does seem to occur. This may increase the amount of energy stored in SEE and reutilized, but the ultimate cause remains the fact that CE can produce more force at a given length and shortening velocity. The question to what extent potentiation of the contractile machinery and/or reflexes contribute to the work enhancement during shortening may deserve further attention.

Work and Efficiency in Repetitive SSCs

Measures of Work: Well-Meant But Not Applicable

In the target article, we questioned the applicability of a number of work measures for repetitive SSCs. Two commentators, Prilutsky and Zatsiorsky, took up the gauntlet to defend their choice of such measures. We highly appreciate that these colleagues responded, because their defense provides a good counterbalance for our criticisms of some measures. Prilutsky and Zatsiorsky start out by identifying the problem: Expressions of net power and work are often useless or of minor importance, as illustrated elegantly by Zatsiorsky's antisymmetrical arm movement and tug-of-war examples. Both in the target paper and in previous work (e.g., Ingen Schenau & Cavanagh, 1990) we have explicitly identified this as a major problem. Different, well-meant measures of work and efficiency have been invented in the search for a solution to this problem, such as counting the "mechanical energy expenditure" as external work or using efficiency measures that can exceed 100%. Prilutsky and Zatsiorsky do not explicitly support these excessive applications. On the other hand, however, neither do they explicitly warn that such measures should not be compared to mechanical work actually generated or to the efficiency by which chemical energy is converted into mechanical energy.

In our view, Prilutsky and Zatsiorsky fail to undermine any of our arguments that these measures provide insight into neither the true generation and degradation of mechanical work nor the amount of energy conserved in elastic structures. Zatsiorsky does

state that our bouncing ball example of a perpetuum mobile has no relation with Aleshinsky's model, since storage and reutilization are not permitted in the model. However, he does not follow up with a warning that, as a consequence, the model is unsuitable for application to any human or animal movement including SSCs such as jumping, sprinting, hopping, and running, where storage and reutilization of elastic energy play an important role. We appreciate the intentions of these and previous authors (e.g., Cavagna, Saibene, & Margaria, 1964) to solve the problem identified, even though we feel that their solutions do not improve our insight in the kinetics of mechanical work in SSCs.

Running: Bouncing Ball or Forced Pendulum

Kram and also Minetti et al. express an idea which, as Kram correctly states, is very relevant to the question of whether efficiency in running is a relevant concept. The idea, henceforth referred to as the bouncing ball idea, is that in running the muscles act mainly isometrically, allowing their SEEs to store and release elastic energy. As indicated in the target article, the bouncing ball idea is widely supported and we agree with Kram that our comparison of oxygen consumption between running and cycling is open to discussion since the muscle force levels are quite different. In our view, however, we have supplied strong evidence that the contractile elements of the plantar flexors do add a substantial amount of concentric work (see Part II, Is Efficiency in SSCs a Relevant Concept?). In this response we will explore additional arguments in favor of our position that running does require concentric actions.

In running, two distinct actions of the leg can be distinguished: a decreasing-increasing of the distance between hip and point of foot contact (the bouncing ball action) and a forward and backward rotation of the entire leg relative to the trunk which, to a certain extent, might be compared with a forced pendulum. In the literature there is disagreement about which of these two actions should be judged as the dominant one: In addition to Kram (this issue), see for example Farley and McMahon (1992) and Rall (1985) versus Hildebrand and Hurley (1985) and Mijers and Stendel (1985). In our view, especially the hip flexors and extensors have to shorten considerably and are the main work generators for the required increases in rotational energy of the entire leg relative to the trunk, two times per cycle. These muscles have long fibers and relatively short tendinous structures, which make them especially suitable to generate and absorb work but rather unsuitable to conserve mechanical energy. As argued before (e.g., Ingen Schenau, 1994, and the references therein), this process explains quite convincingly why hooved animals with low moments of inertia (due to their long slender metatarsi and most muscle mass located close to the trunk) run at considerably lower metabolic costs than animals with larger moments of inertia, such as predators and humans. Of course, advocates of the bouncing ball idea will correctly argue that especially in the distal muscles of these species, there is also a distinct difference in the capacity to store elastic energy.

At first sight, the experiments with simulated reduced gravity performed by Farley and McMahon (1992) appeared to provide quite decisive evidence in favor of leg-length variation as the most energy-consuming process in running. If gravity is reduced by 75%, oxygen consumption of running drops by 72%, a finding that led the authors to conclude that the leg rotation process is of minor importance. Of course, we will not deny that the leg-length variation against gravity must be associated with distinct metabolic costs (as for example can be deduced from oxygen consumption required during hopping on the spot). However, we are not convinced that the leg-length variation is the major energy-requiring action, because the authors did not provide information about stride frequency

or angular displacements of the legs. Perhaps the subjects were allowed to run as people on the moon, that is, by increasing the flight duration at a low stride frequency. Since the energy associated with leg rotation will be proportional to the square of the angular velocity, it is not unlikely that the reduced stride frequency in fact had the largest influence on the reduction of metabolic energy. That the authors found a much smaller reduction in energy consumption during walking at low gravity seems to support this suggestion since, due to the absence of a flight phase, reducing gravity will have a much smaller effect on the stride frequency in walking than in running.

Further evidence in favor of the idea that the angular acceleration and deceleration of the leg relative to the trunk constitute the most expensive process during running comes from a comparison of velocities and energy consumption measures in running and speed skating. At equal energy expenditures, speed skaters are able to maintain a velocity more than twice as high as that which runners can maintain. Since in speed skating most of the mechanical work is used to overcome external forces (air and ice friction), the internal losses due to the required leg segment rotations must be enormously reduced in comparison to running. And indeed, a major difference (albeit not the only one) between these sports lies in the necessity to rotate the legs: In speed skating, leg rotation is largely absent since the leg is extended while the skate continues to glide forward. The same phenomenon explains why the skating technique in cross-country skiing is more effective than the diagonal technique. Without claiming to have settled the discussion about the most energy-consuming action in running, we feel that we have provided enough arguments in this section to maintain our statement that efficiency of running is a relevant concept.

Efficiency in Repetitive Movements

The last issue that triggered responses from many of the commentators is the applicability of efficiency measures. Our rejection of the discussed concepts of efficiency of positive work, efficiency of absolute work, and efficiency of negative work received explicit support from a number of commentators. As a matter of fact, no commentator defended such measures, not even commentators who had applied them in their previous work. Since silence means consent, we feel safe to conclude that such measures must be abandoned.

We were pleased to find so many constructive suggestions for alternative measures. In fact, based on the arguments forwarded by a number of commentators (especially Woledge and Prilutsky but also Hof), we admit that with respect to this issue we were perhaps too dogmatic, as Minetti et al. phrased it. Though a certain degree of polarization was deliberately introduced throughout the entire paper in order to provoke discussion, we realize that we were too much focused on accepting only efficiency measures that reveal what fraction of liberated metabolic energy is converted into mechanical energy. We now agree that one can also define efficiency measures as fractions of work from the maximal amount of work attainable, whether it stems from free energy of food or from negative mechanical work done by a system; this is done in many other systems (e.g., technical ones) and in full agreement with the laws of thermodynamics.

We were impressed (not for the first time) by Alexander's application showing how basic principles can be demonstrated using relatively simple models. The applicability of this approach may be perhaps be broadened: In our view, the efficiency value used by Alexander is conceptually equivalent to the definition of gross efficiency since the nominator only accounts for external work.

Barclay mentions the possibility that efficiency values found in muscles of small animals are different from those in larger animals. If this is true, our concern that efficiencies found at the level of isolated muscles (usually from small animals) are far too low to explain gross efficiency in human cycling may be less serious than we thought. Unfortunately, Barclay's suggestion is not supported by the observations discussed by Stienen, so this issue needs to be further explored in future studies. Barclay further suggests that the amount of metabolic energy available in contractions of slow muscles is more or less invariant. Considering energy consumptions measured during various cyclic movements in humans, we do not expect that this suggestion holds in general.

Biewener suggests that while force enhancement does not necessarily lead to work enhancement, one still may expect an advantage in efficiency due to a more economical force potentiation in the SSC. This explanation seems to be associated with our previous suggestion that a prestretch might help to take up the slack of the muscle fibers (Ingen Schenau, 1984). It is difficult to see how this latter explanation fits in with Bosco's suggestion that the shorter the time in which positive work is done, the higher the efficiency in SSCs. In our view, even Bosco's explanation is open to discussion since his Figure 2 is based upon efficiencies of positive work whose significance was so strongly disputed in the target article.

In our target article, we acknowledged that cyclic sinusoidal contractions revealed higher efficiency values compared to isovelocity shortenings in mammalian (Barclay, 1994) and fish muscles (Curtin & Woledge, 1993; Woledge & Curtin, 1993). However, in our further discussion we focused on mammalian muscle. We are grateful for Curtin's overview of the distinct role SSCs play in fish swimming, because it nicely illustrates that efficiency is strongly influenced by timing and also that, indeed, optimization of power can only be realized at the expense of efficiency and vice versa. We hope Curtin is willing to acknowledge that scientists studying human movement are often not in the position to start with fish studies. Considering all the problems discussed in the target article, we do not really share Curtin's optimistic view that a similar approach for the study of human locomotion is possible at present.

Both Hof and Zatsiorsky regard economy-type measures as useful instruments, and Zatsiorsky asks why we judged economy as a measure leading to studies that are largely descriptive in nature. The answer is that while it is possible to study correlations between economy and, for example, aspects of running technique, such correlations are not necessarily causal in nature. On the other hand, as explicitly stated in the target article, economy is an unambiguously defined measure and can be useful in certain applications. Our plea to look for other measures is largely based on our conviction that progress in our understanding of the mechanics and energetics of the SSC relies on the development of predictive models rather than on explorative studies of statistically significant relations.

Hof suggests that due to the action of the SEEs, the velocity of the CEs can remain close to their optimal velocities. We think this is a reasonable idea but would like to note that this is in part also true for movements without prestretch.

In contrast to Morgan and Proske's suggestion, we never stated that the disputed efficiencies cannot be taken as evidence for elastic storage. On the contrary! Of course efficiencies of positive work of 40% or higher (e.g., the 110% mentioned by Minetti et al.) can only be explained by storage and reutilization of elastic energy. What has been stressed, however, is that such a measure neither tells anything about thermodynamically well-defined efficiencies nor constitutes a reliable measure of the amount of elastic energy involved.

Though we appreciate the overview of additional information provided by Stienen, we do not understand where the optimistic tone of his contribution stems from. Stienen

in fact points at several additional complicating factors that obviously need further attention before their implications for human locomotion can be understood. His observation, for example, that in his preparation, low calcium concentration leads to less adenosine triphosphate consumption during shortening than during isometric contractions is fascinating but seems in sharp contrast to energy consumption measured in various whole-body actions as a function of external work.

We agree with Winter that viscosity in the SEE causes mechanical energy to be degraded into heat. Unfortunately, we could not follow his reasoning that this always has a negative effect on efficiency, since it was not clear to us how Winter defined efficiency in his example.

Prilutsky and Woledge and also Hof with his definition of movement efficiency provide convincing arguments that a definition for the total SSC that expresses the positive work done as a fraction of all energy attainable to do this work is thermodynamically correct and certainly meaningful for specific applications. We feel that, apart from sign conventions, the efficiency for the total SSC advocated by Woledge is in fact equal to the definition of the efficiency of positive work advocated by Prilutsky. Note, however, that Prilutsky's definition of positive work is essentially different from the efficiency of positive work disputed in our target article, since it includes all negative work done by the system as a possible source of energy for positive work. Clearly, this measure cannot be related directly to the contraction coupling and phosphorylative coupling efficiencies that were implicated in the target article as important determinants of the conversion of the free energy of carbohydrates to mechanical work. Relations with these measures will require other measures of efficiency. One might think, for example, of the approach advocated in our target article to develop Hill-type models that provide reliable estimates for the amount of elastic energy stored and released in the SEEs and for the amounts of work done on, and absorbed by, the CEs. In such studies, one might investigate the amount of mechanical energy added during the SSC by the CE and express this as a fraction of the free energy liberated. It is equally important to know which fraction of the negative work done by the entire system is reutilized. We feel, therefore, that to improve our knowledge about the mechanics and energetics of SSC, a combination of these measures is indicated.

Acknowledgments

As stated in the introduction of our target article, our major motive to accept the invitation for this enterprise was to stimulate the dialogue among physiologists and biomechanists working at different levels of organization. Given the content of the commentaries, it appears that such a dialogue is not only possible but also really stimulating to guide future research. We feel that the questions concerning the mechanics and energetics of SSCs are not yet solved, but we anticipate that close cooperation between scientists as involved in this discussion will certainly bring us closer to the answers.

We thank the publisher of this journal for devoting an entire issue to this subject, and we are very grateful to the guest editor of this special issue, Dr. Robert J. Gregor, for his enthusiasm, his scholarship, and his dedication to conduct this project.

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