We agree with the authors’ views on the fourth point. It is unlikely, largely due to timing considerations, that reflex action contributes significantly to work enhancement in rapid SSCs.

The second part of the target article is much more difficult to follow. The authors point out the difficulty of defining efficiency in a situation such as level locomotion, where essentially no net work is done, and we agree entirely with that. They then dismiss all attempts to overcome this difficulty by calculating the work absorbed and delivered by muscles in the different phases of the cycle, without proposing any better approaches. Although not clearly stated, the thrust of this section seems to be that efficiencies calculated in this way, which are higher than the efficiency calculated from isolated muscles, cannot be taken as evidence for elastic storage. This is because bicycle ergometry shows an efficiency greater than that predicted from measurements on isolated muscle and yet does not involve countermovements.

Although some possible reasons for this are suggested, a number of other factors likely to play a role are not discussed. Thus, cross-species comparisons are involved, with the isolated muscle experiments being carried out mainly on rat muscles. (Energetics experiments on skinned fibers are deservedly treated with caution.) The lower motor unit activation rates involved in cycling compared with the rates of stimulation normally used in isolated muscle experiments are likely to lead to much lower costs in activation (i.e., release and re-uptake of myoplasmic calcium, estimated as 30% of total cost). Recruitment profiles, particularly whether slow (less costly) motor units are predominantly used in cycling compared with running, are important factors to consider.

While we don’t wish to argue against the final conclusion that further work is needed, watching from our office window the hopping wallaby in the animal enclosure below certainly gives us the impression of an efficient, low-effort method of locomotion that makes the concept of energy saving by elastic storage so appealing.

References


The authors are with the Department of Physiology and the Centre for Biomedical Engineering, Monash University, Clayton, Victoria 3168, Australia.

Work, Energy Expenditure, and Efficiency of the Stretch–Shortening Cycle

Boris I. Prilutsky

This response presents a point of view on methods and usefulness of work, mechanical energy expenditure, and efficiency estimations in movements with the stretch–shortening cycle that differs from the point of view of Ingen Schenau et al.
Consider the human or animal body as a closed thermodynamic system; that is, only energy transfer (and no mass transfer) takes place between the body and the environment. Energy is transported between the body and the environment in forms of work and heat. Work done by the body on the environment is positive and work done on the body is negative.

**Mechanical Efficiency**

The conservation-of-energy equation for the body can be written as $\Delta E = W_{net} + H$, where $H$ is energy transported from the system due to heat transfer; $W_{net} = W_{pos} - W_{neg}$, where $W_{pos}$ is positive work done by the system (or energy transported from the system as the result of work done on the environment) and $-W_{neg}$ is negative work done by the system (or energy transported to the system as the result of work done on the system); and $\Delta E$ is chemical energy released. The above equation can be rewritten as $\Delta E + W_{neg} = W_{pos} + H$. The performance of thermodynamic systems is often estimated as the ratio of the desired effect of the system to the energy input required to produce the desired effect. The desired effect of muscle contractions in the stretch–shortening cycle is, typically, the generation of mechanical energy (production of positive work). The energy input to the system (or the maximum obtainable positive work) is the sum of chemical energy released and energy transported to the system as the result of work done on the system ($\Delta E$). Efficiency of positive work can then be defined as $e_{pos} = W_{pos}/(\Delta E + W_{neg})$. This definition of efficiency is consistent with the first and second laws of thermodynamics. Also, it does not equal zero in the stretch–shortening cycle where $W_{pos} = l - W_{neg}$, which is the case for efficiency defined as $W_{net}/\Delta E$ (Curtin & Woledge, 1993; Ingen Schenau et al., 1997). Efficiency $e_{pos}$ defined here seems to discriminate well between animals with and without morphological adaptations for long-distance running (Alexander, 1988; Gambaryan, 1974; Gray, 1968). Distal muscle–tendon complexes of cursorial forms have long, compliant tendons and short fibers. This design allows for reutilization of energy transported to the system in the form of negative work to a greater extent with a smaller contribution of chemical energy released. Coefficient $e_{pos}$ also discriminates well different forms of locomotion (see below), supporting the old suggestion (Cavagna, Saibene, & Margaria, 1964) that positive work is done more efficiently in running than in walking.

**Work**

To calculate efficiency $e_{pos}$, one has to determine $W_{pos}$, $W_{neg}$, and $\Delta E$. As demonstrated by Ingen Schenau et al., the most unambiguous estimate of $\Delta E$ in whole-body movements is the total metabolic energy expenditure without baseline subtractions. Since positive and negative work done by all skeletal muscles in the body cannot be assessed at the present time, muscle work can only be estimated. Among these estimates are “external work” (increase or decrease in total energy of the general center of mass of the system; Cavagna et al., 1964), “total work” (increase or decrease in total energy of the system; Fenn, 1930), and work of joint moments (Elftman, 1939; Winter, 1983). The above estimates of muscle work represent work of different forces and moments (Aleshinsky, 1986; Zatsiorsky, 1994), and it is not surprising that they have different values for the same movement (Williams & Cavanagh, 1983; Zatsiorsky, Aleshinsky, & Yakunin, 1982).

If one assumes that work done by joint moments is the closest estimate of muscle work, then $W_{pos}$ and $-W_{neg}$ can be calculated as $W_{pos} = \Sigma_i W_{pos_i}$ and $-W_{neg} = \Sigma_i -W_{neg_i}$, where $W_{pos_i}$ and $-W_{neg_i}$ are positive and negative work done by the moment at the $i^{th}$ joint. Note that values of positive and negative work calculated using these equations are, typically, higher than those calculated from the summed power of all joint