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Comments on Point:Counterpoint: Skeletal muscle mechanical efficiency does/does not increase with age

HETEROGENEOUS EFFECT OF AGING ON MUSCLE EFFICIENCY

TO THE EDITOR: There is little doubt that the cost of locomotion is impaired with age as it is evident that centenarians, due to their exceptional longevity, present unique adaptations in their skeletal muscle efficiency to compensate for their extremely low $\dot{V}O_{2\max}$. However, the underlying question of whether skeletal muscle efficiency is altered with age is unsettled (4, 6). In fact, both opponents present compelling evidence in support of their opinion, and the reason for this disagreement is likely that both authors are looking at different muscles. Indeed, there is accumulating evidence that age-related alterations in skeletal muscle efficiency vary among muscle group. For instance, a selective atrophy, independent of the fiber type, has been documented in skeletal muscles with age (5). It is therefore likely that a similar phenomenon occurs for muscle energetics properties. The suggestion that ATP cost of contraction is improved with age (6) is based on examinations of the tibialis anterior. Interestingly, this muscle also exhibits preserved features with age in terms of mitochondrial efficiency (1) and oxidative capacity (3). In contrast, reduced oxidative capacity (3), in conjunction with impaired mitochondrial and contractile efficiency (2), has been documented in the quadriceps, which would, at least partially, explain the increased cost of locomotion with age as this muscle group is a major contributor to force production during these activities. The reasons for the heterogeneous effect of aging on skeletal muscle efficiency remain unclear, but likely stem from differences in fiber type and chronic load associated with locomotion.

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THE MEASUREMENT OF EXERCISE EFFICIENCY

TO THE EDITOR: It is important to consider the conceptual validity of measuring skeletal muscle mechanical efficiency from

whole body $\dot{V}O_2$ measured at the mouth, as conducted by Venturelli et al. (4). $\dot{V}O_2$ measured at the mouth incorporates contribution of nonpropulsive factors (e.g., basal metabolism and moving the legs), and so the oxygen cost exercise cannot be solely attributed to the working muscle (3). Therefore, the use of the term “skeletal muscle mechanical efficiency” in this context (4, 5) is a misnomer.

We agree with Ortega (2) that the use of a ramp protocol by Venturelli et al. (4) did not allow sufficient time for steady state to be achieved (at least 2–3 min is required at low to moderate intensities), which is critical for assessing exercise efficiency. As can be seen from the error bars of Fig. 2C of Venturelli et al. (4), the RER of a number of centenarians was considerably greater 1.00 for the majority of work rates they assessed. This indicates energy release from anaerobic energy pathways that is not reflected in the $\dot{V}O_2$ at the mouth and may result in overestimated efficiency values. Additionally, Venturelli et al. (4) used an online gas analysis system to determine $\dot{V}O_2$ in their study. Online breath-by-breath systems process expired gases in real time, and so gas volume measurement errors may occur with every breath, particularly at low and high flow rates (6). Thus, we propose that Douglas bags and steady-state exercise intensities should be used when assessing exercise efficiency (1).

[Due to reference restrictions, we apologize to authors who we could not cite in this letter.]

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REDUCED WORK EFFICIENCY WITH AGE WITHOUT CHANGE IN FIBER TYPE

TO THE EDITOR: Venturelli and Richardson (5) contend that selective loss of type II muscle fibers combined with greater metabolic efficiency of type I fibers contribute to an increased work efficiency in older adults. Our direct measurements reveal the opposite finding: reduced work efficiency with age

without change in fiber type composition but rather the result of lower mitochondrial efficiency with aging.

Data from our study of older adults ($n = 35$, 65–80 yr) with a wide range of muscle fiber composition (10–90% type I) found no relationship between delta (work) efficiency on a cycle ergometer and percent type I fiber content ($r^2 = 0.03$, $P = 0.33$) (4). The lower delta efficiency with aging occurred concomitantly with lower mitochondrial efficiency but not contractile-coupling efficiency (3). In an independent study, we demonstrated that lower mitochondrial efficiency and reduced aerobic capacity together are important factors in slower walking speed in older adults (1).

Another key factor that mediates work efficiency with aging is exercise training. A 6-mo endurance-training program in older adults (65–80 yr) improved leg energy coupling (mitochondrial efficiency) and work efficiency without a change in fiber type composition (2, 4). Together, these data suggest that the loss of mitochondrial efficiency is central to the physiology of reduced work efficiency and walking speed with age. These mitochondrial and work changes occur independent of age-related changes in muscle fiber type composition.

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VIEWPOINT “ON THE HYSTERESIS IN THE HUMAN ACHILLES TENDON”

TO THE EDITOR: A number of factors probably influence exercise efficiency: task, measurement technique, biomechanics, and body composition. Ortega (3) suggests that phosphorylation efficiency may decrease in older muscle due to an increase in uncoupled phosphorylation, whereas Venturelli and Richardson (4) emphasize that age-related loss of inefficient type II muscle cross-sectional area and a proportional increase in efficient type I muscle area contribute to muscle contraction coupling efficiency. However, others have found no association between uncoupling and muscle fiber type distribution, but

rather decreased mitochondrial efficiency associated with greater adiposity (2). It is possible age-related increase in body fat may primarily be responsible for the decrease in mitochondrial efficiency during aging. However, overall muscle efficiency is the product of phosphorylation and contraction coupling efficiencies, which are determined by both ATP demand and O₂ consumption, which is difficult to measure simultaneously.

Additionally, biomechanical factors should be considered when measuring whole body efficiency during locomotion. It is likely that an increase in activation of stabilization/balance muscles while walking can impair locomotion efficiency in frail older adults. Lastly, tissue elasticity decreases with age, therefore older adults may not use elastic energy during locomotion as well as younger adults. Despite showing a positive relationship between age and muscle economy and walking economy in older women (1), we have also shown a negative relationship between age and elastic energy potentiation and walking economy in older women (unpublished). In conclusion, we feel that the problem is too complex to make a blanket statement concerning the relationship between economy and age.

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A FEW OTHER THINGS TO THROW INTO THE “POT” THAT IS MECHANICAL EFFICIENCY

TO THE EDITOR: The two protagonists (4, 6) present convincing arguments, despite the acknowledged differences in exercise tasks that underpin each of their arguments. Notwithstanding the usual factors that must be considered when measuring mechanical efficiency during human activity, i.e., baseline subtractions to provide the precise definition of efficiency used (gross, net, work, delta) (5) and the influence contraction speed and muscle temperature has on these measures (1), there are other aspects to considered.

Both sides consider the impact of changing phenotype with aging as a shift to a predominance of type I muscle fibers. However, the pattern of motor unit/muscle fiber recruitment must be considered alongside the age-related changes in muscle size and phenotype. In line with the size principle, low intensities would favor type I recruitment, with higher intensities requiring a greater contribution from type II, although a component of rate coding also probably exists. Although the precise recruitment patterns are not known during exercise in older people, it is likely that even at the very low external

workloads performed they will be working closer to their maximal muscle capacity and will thus rely more on the available type II fibers. Furthermore, the switch to an aerobic phenotype that is thought to contribute to the increased efficiency must be considered in light of observations that mechanical efficiency is higher when the majority of energy is provided from anaerobic sources than when provided from aerobic sources (3). These observations corroborate in vitro measurements of different efficiencies of the various metabolic pathways (2).

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TO THE EDITOR: I have read with great interest this Point: Counterpoint discussion on whether the muscle mechanical efficiency increases with age. In favor of the counterpoint argument (3), I have questioned the fiber-type difference in mechanical efficiency (i.e., slow-twitch fibers are more efficient than fast-twitch fibers). In my opinion, an approximately linear relationship between oxygen uptake and exercise intensity despite the hierarchical order of muscle fiber recruitment (the size principle) supports the view that mechanical efficiency does not critically depend on the fiber type. In fact, several studies, including He et al. (2) cited by Venturelli and Richardson (5), have provided evidence that the fiber-type difference is not in the fraction of ATP energy converted into mechanical work, but in the rate at which the energy conversion occurs.

In a recent paper, Venturelli et al. (6) demonstrated that oxygen uptake during cycling at a given absolute work rate was consistently lower in centenarians than in young subjects. It should be noted, however, that maximal work rate in the centenarians corresponded to less than 20% of that in their younger counterparts, where predominant recruitment of slow-twitch fibers can be assumed (1, 4). Therefore, it is unlikely that the higher metabolic demand in young subjects can be explained by their faster muscle phenotype. It is also unlikely that the muscle fibers recruited during daily activities (e.g., walking) are influenced by age or fiber composition, because most of daily activities are mainly achieved by activation of slow-twitch fibers even in young subjects.

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STIFFNESS AND HYSTERESIS OF HUMAN TENDONS

TO THE EDITOR: Venturelli et al. (4, 5) showed greater mechanical efficiency during cycling in centenarians than in young counterparts. This may be associated with the age-related increase in the proportion of type I muscle fibers (4, 5) that have a greater metabolic efficiency compared with type II fibers.

However, a large body of evidence supports the contention that mechanical efficiency during exercise does not increase with age (1–3). Moreover, no correlations were observed between myosin heavy chain composition and mechanical efficiency of cycling in elderly individuals (1). We concur with Ortega (3) that using a ramp test with step durations of 1 min may likely overestimate mechanical efficiency in elderly individuals. This may be due to their slower oxygen uptake but also to their higher relative effort, compared with young subjects pedaling at the same power output [e.g., 35 W represents ~30% and ~100% of maximal oxygen uptake in young and elderly individuals, respectively (5)]. As more metabolic energy via anaerobic pathways has to be generated at the same work rate in elderly than in young subjects, assessment of metabolic energy through oxygen uptake ($\dot{V}O_2$) measurement underestimates actual metabolic energy. This may contribute to overestimate mechanical efficiency in elderly individuals: delta efficiency and the slope of $\dot{V}O_2$ -power output relationship were ~80% and ~3.9 ml·min⁻¹·W⁻¹, respectively! [Estimated from Fig. 3 (5).] Estimation of mechanical efficiency from ramp tests should be restricted to the moderate intensity domain (below gas exchange threshold) for which the linearity of the $\dot{V}O_2$ -power output relationship can be reasonably assured (6).

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STIFFNESS AND HYSTERESIS OF HUMAN TENDONS

TO THE EDITOR: Efficiency is a ratio: the experimental measure of the denominator is pretty safe, while mechanical work (in absence of other biases) depends on the considered components: external, internal work, and, within the latter, friction and other dissipations inside and outside the body. For instance, the internal mechanical work depends on pedaling frequency (2, 4). This should be taken into account when comparing studies about bicycling. Metabolic consumption, though, could include some unpredictable energy used to coactivate antagonist muscles (for the same mechanical work produced) and to generate isometric muscle contraction (with no work at all). These components could remarkably bias the estimate of “just” (working) muscle efficiency. Also, we need to remind that the Global efficiency referred to in the commented papers (5, 6) is the product of transmission and muscle efficiency (3). Joint-stabilizing cocontractions could be responsible for the lower global efficiency in elderly walking (1). The relationship between metabolic cost of transport and speed, although higher in old people, shows an age invariant optimal speed (at which the cost is minimum). Although there are clues supporting the role of the pendulumlike paradigm in determining that speed, the proposed shift in fiber types should have caused a lower optimum speed in elderly. It seems counterintuitive that older muscles become more efficient than young ones, which should have evolved to best perform in the demanding phase of their life span (vehicle mechanics and engines become less efficient with age).

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TASK INFLUENCES MECHANICAL EFFICIENCY IN OLD AGE

TO THE EDITOR: Although perhaps not stated explicitly in these Point:Counterpoint arguments (4, 6), one feature to emerge is that a change of mechanical or muscle efficiency in relation to adult ageing is dependent on the type of contraction performed or the task being studied. For example, during rather artificial protocols that use only isometric contractions, older adults seem to be less fatigable or may not differ during intermittent isometric contractions (1). However, during dynamic shortening contractions, older adults are more fatigable (3), especially at faster velocities (2). In addition, during repetitive lengthening contractions, power loss is greater in old compared with young adults (5). Thus the improved efficiency attributed to fiber type changes and enhanced oxidative capacity does not seem to provide a functional benefit during repetitive shortening or lengthening contractions in muscles of older adults. Arguments have been put forth that age-related slowing of contractile capacity is advantageous (6) and sometimes matches with age-related lower motor unit firing rates, although importantly this is not always observed (discussed in 2) and may be muscle dependent. During dynamic contractions, however, slower contractile kinetics are not advantageous because of impaired power output, which is dependent on the combination of contractile velocity and torque. Sarcopenia and the associated losses of strength and power occur with healthy adult aging, but the key feature for muscle efficiency, at least when framed during the stress of fatigue, may be related to the limitations in shortening velocity when the task is dynamic.

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COMMENT: CONSIDER MECHANICAL EFFICIENCY AND COMORBIDITY

TO THE EDITOR: The debate regarding age-related changes in mechanical and muscle efficiency should consider the impact of comorbidity. Although several of the physiological studies mentioned by Drs. Venturelli, Richardson, and Ortega (5, 6) are excellently designed; the potential impact of comorbid conditions is not well considered. Approximately 90% of adults over 65 years old have at least one disease, and over

70% have two or more conditions (3). Therefore, participants in these previous studies might not be generalizable to the population as a whole. Additionally, many older adults have mobility impairments due to a combination of the aging processes and specific disease conditions. As we have demonstrated in our previous work, older adults who report mobility impairments have a higher metabolic cost of movement (4). There is a large literature demonstrating that common comorbid conditions that are closely connected with aging (e.g., arterial diseases, osteoarthritis lung disease, stroke, neurological conditions) result in a high level of output energy for a given workload (1, 2). It is extremely difficult to tease out these conditions from natural aging and the effect they may have on mechanical efficiency. Considering the effect of comorbid conditions could simultaneously support the point and counterpoint of this argument. Despite a transition to a higher proportion of type I fibers that increases muscle efficiency, comorbid conditions that contribute to gait alterations would at the same time reduce mechanical efficiency. Additional research is needed to consider whether underlying disease con-

ditions modify muscle and mechanical efficiency to an extent that influences healthy aging.

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