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OPINION

Efficiency of cycling exercise: misunderstandings of physiology

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Correcting the scientific record

Science, by its very nature, must be self-correcting (Whipp, 2010). Indeed, a primary mechanism for such is the publication of letters to the editor enabling the open criticism of a published paper and, usually, the opportunity for the original authors to respond, as/if they wish (Verkhratsky & Petersen, 2023). Such open debate is central to scientific progress. Denial of this process allows the scientific record to remain in error obfuscating discovery and being antithetical to the progress that science demands. In response to MacDougall et al. (2022) we (Brooks, Gaesser and Poole) wrote a letter to the editor of the *Scandinavian Journal of Medicine and Science in Sports* in February 2023. That letter was duly reviewed and revised and resubmitted to the editorial office of SJMSS on 29 July 2023. Since then we have been unable to obtain any response whatsoever from SJMSS despite multiple emails. We thus recourse to this Opinion article to address the errors introduced into the scientific record by MacDougall et al. (2022).

Ignorance of the seminal paper by Gaesser & Brooks (1975) does not excuse MacDougall et al. (2022) for their misunderstandings of human muscle efficiency. Their paper demonstrates disregard for basic phenomena underlying muscle contraction (Mommaerts, 1969) including the energetics of oxidative phosphorylation, actin–myosin interactions, excitation–contraction coupling and baseline reference points. Moreover, by reproducing data from some of the only studies to have simultaneously measured whole body (pulmonary) and working leg oxygen consumption in response to graded exercise (Friedlander et al. 2007; Poole et al. 1992), in their Fig. 1, MacDougall et al. (2022) demonstrate the implausibility of their position.

Among others, we address the following failings in MacDougall et al. (2022):

1. 'Delta efficiency does not represent muscular efficiency.'
2. 'challenges the notion that the slow component of oxygen uptake represents decreasing efficiency.'
3. '…taking into account the energy cost of ventilation and subtracting that from total V˙O$_2$ will make estimates of efficiency more closely represent muscular efficiency.'

In its purest form efficiency is defined as the ratio of work accomplished/energy required. This necessitates an investigator to parse the separate internal muscle and whole-body support lattices (muscle excitation–coupling, body work and processes of pulmonary/cardiac work) that underlie working locomotory muscles. Consequently, Poole et al. (1991, 1992) and Friedlander et al. (2007) measured simultaneously leg $\dot{V}_{O_2}$ and pulmonary $\dot{V}_{O_2}$ to better isolate skeletal muscle energetics *per se* (see Fig. 1) and net muscle(s) lactate release facilitating assessment of the 'anaerobic' [sic] glycolytic contribution to energetics.

Delta efficiency *does* represent muscular efficiency

MacDougall et al. contend that glycolysis is a major contributor to muscle energetics such that using $\dot{V}_{O_2}$ to calculate efficiency is a major source of error. However, using the data of Poole et al. (1991, 1992) and the ∼ $\dot{V}_{O_2}$ equivalent of lactate of 3 ml O$_2$/mM from di Prampero & Ferretti (1999), as cited by MacDougall et al. (2022), where 2 × leg blood flow = 20 l/min, Δa-v[Lactate] = 0.3 mM, and 2 × leg $\dot{V}_{O_2}$ is 2.8 l/min, the following calculation provides an estimate of the contribution of anaerobic glycolysis to total muscle energy turnover during this exercise task:

Total lactate release = 20 (l/min) × 0.3 mM = 6 mM/min
$\dot{V}_{O_2}$ equivalent of lactate = 6 mM × 3 ml O$_2$ = 18 ml O$_2$/min
% extant $\dot{V}_{O_2}$ = 18/2800 = 0.64%

Thus, the contribution of 'anaerobic [sic] glycolysis' to muscle energy turnover is minimal (i.e. <∼3% based on lactate tracer studies and the example above) because most lactate is removed by oxidation, or converted to glucose that is also oxidized (Bergman et al. 1999; Brooks et al. 1984; Poole et al., 1991, 1992). Consequently, the contention that '…consideration of oxygen uptake alone is an inappropriate means of inferring the energy cost of exercise, and thus efficiency' is moot, reflecting MacDougall et al.'s inability to deal with qualitative or quantitative information.

Furthermore, that pulmonary and leg $\dot{V}_{O_2}$ increase in a nearly parallel fashion (Fig. 1 left panel, from Poole et al. 1992) supports that muscle efficiency can be closely estimated from the slope of work/pulmonary $\dot{V}_{O_2}$.

By equating the 'gross' efficiency rise with incremental exercise intensity to muscle efficiency, MacDougall et al. (2022) appear to have misunderstood the data: to the contrary, perceived effort and physiological stresses increase with exercise intensity. As is well known, and simple mathematics reveals, the apparent gross efficiency increase with power output is an artefact reflecting absence of baseline correction. This was illustrated in the original paper that introduced the delta efficiency concept (Gaesser & Brooks, 1975). In that study, the relationship between $\dot{V}_{O_2}$ and work rate was not perfectly linear, with slightly greater increments in $\dot{V}_{O_2}$ at the highest work rates (see Fig. 1 in Gaesser and Brooks, 1975). This marginally non-linear relationship was precisely captured by the declining delta efficiency at the higher work

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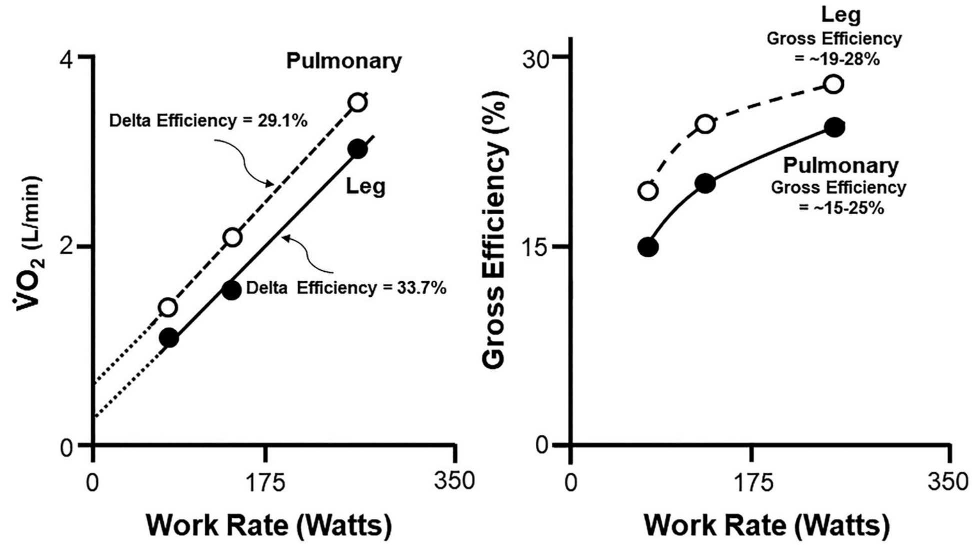

Figure 1. Pulmonary and Leg $\dot{V}_{O_2}$ and Calculated Delta Efficiency (Left) and Gross Efficiency (Right)
Left panel, data from Poole et al. (1992) showing mean $\dot{V}_{O_2}$ at work rates of 83, 146, and 289 watts during 4–6 min bouts of cycle ergometer exercise in 17 male subjects. From the slope of these relationships delta efficiency is calculated at 33.7% across the leg(s) and 29.1% for whole body from pulmonary gas exchange measurements. Right panel, calculated gross efficiency from the same data. Note that the gross efficiency calculated from both leg(s) and pulmonary $\dot{V}_{O_2}$ increases markedly from lowest to highest work rate, not overlapping at all with the delta efficiencies. This behaviour of gross efficiency is wholly artefactual reflecting lack of intercept correction rather than any inherent change or differences in 'muscle efficiency' at higher work rates as best measured by the delta efficiency across the exercising legs. Also contrary to the contentions of MacDougall et al. (2022) delta efficiency measured via pulmonary gas exchange (29.1%) provides a close approximation of that across the exercising legs (33.7%).

rates at all pedalling speeds (see Fig. 2 in Gaesser and Brooks, 1975). By contrast, gross efficiency increased progressively across the entire range of work rates studied (see Fig. 3 in Gaesser and Brooks, 1975), which is entirely at odds with the $\dot{V}_{O_2}$–work rate relationship. More than a century ago, Benedict & Cathcart (1913) used similar experiments in their landmark monograph on muscular work to show that gross efficiency 'indicates little of the potentialities of the human body for severe muscular work, and gives no conception of the possible efficiency of the human body as a machine.' We concur.

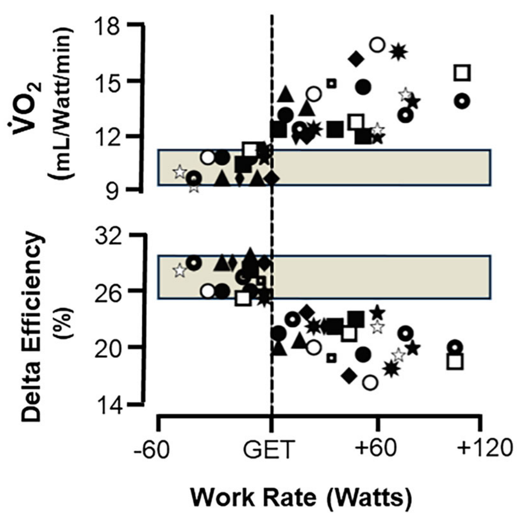

Figure 2. $\dot{V}_{O_2}$ Slow Component Above the Gas Exchange Threshold Increases $\dot{V}_{O_2}$/watt (Top) thus Reducing Delta Efficiency (Bottom).
Top panel, increase in O_2 cost per watt for cycle ergometer exercise (i.e. $\dot{V}_{O_2}$ slow component) above *versus* below the gas exchange threshold (GET). Bottom panel, corresponding reduction in delta efficiency. Different symbols indicate different subjects. Redrawn from the data of Henson et al. (1989).

The slow component of oxygen uptake *does* represent decreasing efficiency

During severe intensity exercise just above critical power when exercise is sustained long enough for the $\dot{V}_{O_2}$ slow component to develop, this additional O_2 cost can reach 1–1.5 litres O_2/min (rev. Gaesser & Poole, 1996). Mammalian muscles are incapable of producing sufficient lactate to substitute for the ATP represented by even a modest $\dot{V}_{O_2}$ slow component. Compare the artefactually *increased* gross efficiency seen in Fig. 1, right panel with the *actual reduction* in delta efficiency in Fig. 2 that results from development of the $\dot{V}_{O_2}$ slow component which increases the $\dot{V}_{O_2}$ per watt for work rates above the gas exchange threshold (GET, heavy and severe intensities) when blood lactate concentration will be rising (Henson et al. 1989). This effect is not only present in humans: Zoladz and colleagues (2008) have demonstrated this reduced efficiency with time during severe intensity muscle contractions in the canine gastrocnemius.

Taking into account the energy cost of ventilation… will, *under most circumstances, have little or no impact on estimates of muscle efficiency*

The ventilatory muscles may account for up to 0.48 litres O_2/min (Aaron et al. 1992). However, an increased ventilation from 96–152 litres/min contributed minimally to the overall $\dot{V}_{O_2}$ slow component (Poole et al. 1991), consistent with Gaesser & Brooks (1975) defining delta efficiency and its measurement.

In summary, the three failures selected above are nestled among a plethora of unsubstantiated pronouncements in MacDougall et al. (2022) that run counter to established wisdom. Whereas Daniel Boorstin (1983) in his epic *The Discoverers* rightly observed that 'The greatest impediment to (scientific) progress is not ignorance but, rather, the illusion of knowledge', MacDougall et al. (2022) in their 'review' have gone to extraordinary lengths to create the illusion of ignorance.

Based upon the above observations in humans and canine muscle we hypothesize that, for short bouts of or ramp/incremental exercise, where there is insufficient time for a $\dot{V}_{O_2}$ slow component to develop, delta efficiency is not a function of work rate or exercise intensity domain but, rather, is unchanged across submaximal exercise intensities (i.e. below the ceiling imposed by the maximal $\dot{V}_{O_2}$). However, for more sustained exercise above GET (or the lactate threshold) where a $\dot{V}_{O_2}$ slow component develops, delta efficiency is reduced commensurately. Whether this behaviour is present in all exercising mammalian muscle(s) remains to be determined, as does its precise mechanistic bases.

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Additional information

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No competing interests declared.

Author contributions

All authors: conception or design of the work; drafting the work or revising it critically for important intellectual content. All authors have read and approved the final version of this manuscript and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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Supporting information

Additional supporting information can be found online in the Supporting Information section at the end of the HTML view of the article. Supporting information files available:

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