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REVIEW-SYMPOSIUM

The fourth dimension: physiological resilience as an independent determinant of endurance exercise performance

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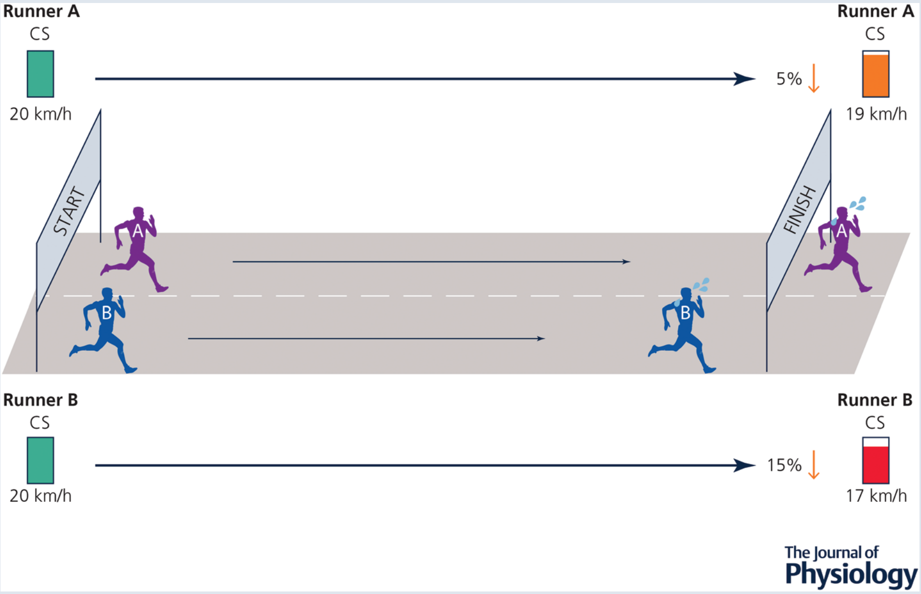

Abstract Endurance exercise performance is known to be closely associated with the three physiological pillars of maximal O_2 uptake ($\dot{V}_{O_2max}$), economy or efficiency during sub-maximal exercise, and the fractional utilisation of $\dot{V}_{O_2max}$ (linked to metabolic/lactate threshold phenomena). However, while 'start line' values of these variables are collectively useful in predicting performance in endurance events such as the marathon, it is not widely appreciated that

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these variables are not static but are prone to significant deterioration as fatiguing endurance exercise proceeds. For example, the 'critical power' (CP), which is a composite of the highest achievable steady-state oxidative metabolic rate and efficiency (O_2 cost per watt), may fall by an average of 10% following 2 h of heavy intensity cycle exercise. Even more striking is that the extent of this deterioration displays appreciable inter-individual variability, with changes in CP ranging from <1% to ∼32%. The mechanistic basis for such differences in fatigue resistance or 'physiological resilience' are not resolved. However, resilience may be important in explaining superlative endurance performance and it has implications for the physiological evaluation of athletes and the design of interventions to enhance performance. This article presents new information concerning the dynamic plasticity of the three 'traditional' physiological variables and argues that physiological resilience should be considered as an additional component, or fourth dimension, in models of endurance exercise performance.

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Abstract figure legend Illustration of the concept of 'physiological resilience'. Two athletes might have similar physiological characteristics ($\dot{V}_{\mathrm{O_2max}}$, lactate threshold, running economy or, in the example given, critical speed (CS)) at the start of a race but these may deteriorate more with time elapsed or distance covered in one athlete compared to the other (e.g. 5% *vs*. 15% decline in CS). This property of resilience, or durability, should therefore be considered as an additional component (the '4th dimension') in physiological models of endurance exercise performance.

> *Who speaks of conquering? To endure is everything.* (Rainer Maria Rilker).

Introduction

In 1991, Dr Michael Joyner presented a model of the physiological determinants of endurance exercise performance that has proved to be highly influential (Joyner, 1991). In his paper, Joyner argued that the speed sustained during endurance events, such as the marathon, was a function of an athlete's 'performance $\dot{V}_{\mathrm{O_2}}$' (i.e. the mean $\dot{V}_{\mathrm{O_2}}$ sustained during the event) and their running economy (i.e. the steady-state O_2 cost of running) (Fig. 1). In this model, the performance $\dot{V}_{\mathrm{O_2}}$ is determined by the maximal O_2 uptake ($\dot{V}_{\mathrm{O_2max}}$) and the 'lactate threshold' (LT), variables which, together, determine the fractional utilisation of the $\dot{V}_{\mathrm{O_2max}}$ that is sustainable for the competition distance. Running economy (in ml O_2 per kg body mass per km of distance covered) is important in translating the performance $\dot{V}_{\mathrm{O_2}}$ into running speed. Using hypothetical but realistic values for $\dot{V}_{\mathrm{O_2max}}$ (84 ml/kg/min), LT (85% $\dot{V}_{\mathrm{O_2max}}$) and

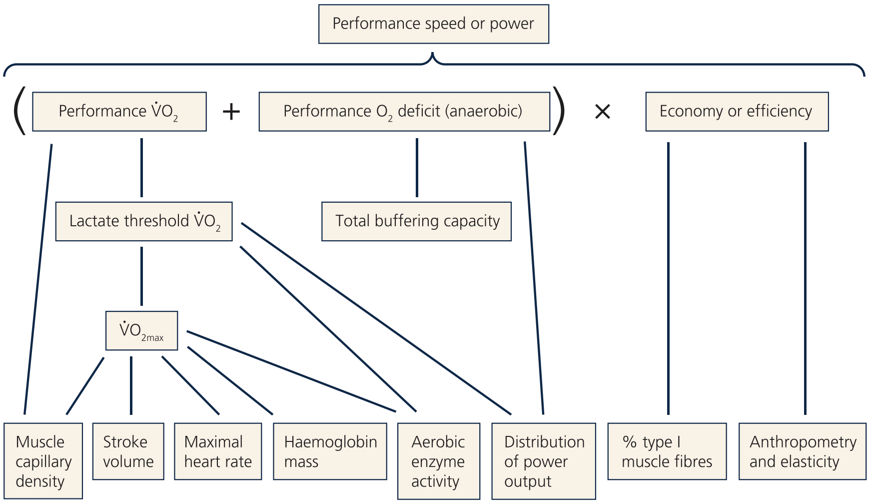

Figure 1. The 'classical' model describing the physiological determinants of endurance exercise performance
Redrawn from Joyner and Coyle (2008).

running economy (∼200 ml/kg/km) in elite male distance runners, Joyner used this model to predict a theoretical best possible marathon performance of 1:57:58.

At the time that Joyner's paper was published, the men's marathon world record stood at 2:06:50 and the prediction of a sub-2 h marathon seemed outlandish. However, some 30 years later, at the time of writing, the unofficial men's marathon world record stands at 1:59:40 (achieved at the Ineos 1:59 Challenge exhibition event, held in Vienna in 2019) while the official world record is 2:01:09 (achieved at the Berlin mass participation marathon in 2022), with both records being held by the Kenyan Olympic champion, Eliud Kipchoge. While these values are clearly much closer to Joyner's forecast, even the 1:59:40 performance, during which several variables important to performance were optimised, including pacing and drafting, environmental conditions and the use of neoteric footwear (Hoogkamer, Snyder et al., 2018; Senefeld et al., 2021; Snyder et al., 2021), is 1 min and 42 s slower than Joyner's prediction. As Joyner himself concluded, this shortfall suggests that 'current concepts regarding limiting factors in endurance running need additional refinement and empirical testing' (Joyner, 1991).

It is possible to update the inputs into the Joyner model using data collected as part of Nike's 2017 'Breaking 2' marathon project, which culminated in a 2:00:25 performance, again by Kipchoge. In the Breaking 2 project, 16 of the world's very best male distance runners had their $\dot{V}_{\mathrm{O_2max}}$, blood lactate responses and running economy determined during physiological tests performed both on the treadmill and in the field (Jones et al., 2021). The results were interesting in that they showed that elite-level marathon performance could be achieved through a variety of different combinations of $\dot{V}_{\mathrm{O_2max}}$, sustainable fraction of $\dot{V}_{\mathrm{O_2max}}$ and running economy. It was notable that the mean $\dot{V}_{\mathrm{O_2max}}$ for the cohort (∼75 ml/kg/min when the highest value achieved by an individual during either treadmill or field testing was selected, and with a range of ∼64–84 ml/kg/min) was somewhat lower than might have been anticipated. However, the highest intensity at which a physiological steady-state could still be achieved, as estimated from the lactate turnpoint (LTP) during an incremental exercise protocol (Caen et al., 2021; Jones & Doust, 1998; Smith & Jones, 2001), was an impressive 92% $\dot{V}_{\mathrm{O_2max}}$, while the group mean running economy was 191 ml/kg/km. Overall, $\dot{V}_{\mathrm{O_2max}}$ was lower but fractional utilisation and running economy were better than the values employed by Joyner when predicting best possible marathon performance (Joyner, 1991). Using data from Jones et al. (2021) and inserting realistic values for a hypothetical world's best athlete into Joyner's model (i.e. 80 ml/kg/min for $\dot{V}_{\mathrm{O_2max}}$, 88% $\dot{V}_{\mathrm{O_2max}}$ for sustainable fraction, and 192 ml/kg/min for running economy) produces a theoretical best possible men's marathon performance of 1:55:05, which is clearly considerably faster than the current world's best performance. While it is possible that, in a further ∼30 years' time, a performance akin to this might be achieved, this startling prediction appears to confirm that the Joyner model lacks an important variable or requires refinement.

Critical speed

An alternative, but related, way to evaluate the determinants and limitations to endurance exercise performance is through the critical power (CP) or, for running, critical speed (CS) concept (Jones et al., 2019). The hyperbolic relationship between a given running speed and the duration it can be sustained was first reported by A. V. Hill for world record performances (Hill, 1925). This relationship, which has been shown to exist in many different species (Burnley, 2023) and in a wide variety of exercise modalities in humans (Jones et al., 2010), has an asymptote (i.e. CS, expressed in units of speed, m/s) and a curvature constant (termed D', with the units of distance, m). In other exercise modalities such as cycling, the asymptote is termed critical power (CP, W) and the curvature constant is termed W' (kJ), representing a fixed amount of available energy above CP. The CS and D' can explain differences in exercise tolerance across a range of human populations (Burnley & Jones, 2018) and are sensitive to several interventions including training (Poole et al., 1990; Jones & Carter, 2000; Vanhatalo, Jones & Burnley et al., 2011).

As an aside, it is noteworthy that, of all the individual physiological variables measured in the elite athletes who took part in the 'Breaking 2' marathon project, it was only the phase II time constant describing the dynamic $\dot{V}_{\mathrm{O_2}}$ response across the transition from standing rest to submaximal exercise that was significantly correlated with personal best marathon performance (Jones et al., 2021). It might be speculated that this is secondary to the relationship between fast $\dot{V}_{\mathrm{O_2}}$ kinetics and a high CP or CS (Goulding et al., 2021; Murgatroyd et al., 2011) with a high muscle oxidative capacity, mitochondrial function, type I fibre proportion and capillarity being important underpinning factors (Christensen et al., 2016; Mitchell et al., 2018; Pringle et al., 2003; Vanhatalo et al., 2016).

The importance of CS to endurance exercise performance is that it separates speeds that are sustainable in a physiological steady-state (i.e. stable pulmonary $\dot{V}_{\mathrm{O_2}}$, blood [lactate], muscle [phosphocreatine] and pH, muscle O_2 saturation) from those wherein substrate-level phosphorylation makes a sustained contribution to energy turnover and physiological homeostasis cannot be attained (Jones et al., 2008; Matthews et al., 2023; Poole et al., 1988; Vanhatalo et al., 2016). When exercise is performed above CS, exercise tolerance is constrained and this is explained by the size of the difference between the speed being sustained and the CS, since this will dictate the rate of D' utilisation. When D' is exhausted, which corresponds with the attainment of $\dot{V}_{O_2\max}$ and with muscle metabolic variables reaching their respective peak ([inorganic phosphate]) or nadir (pH, [phosphocreatine]) values (Black et al., 2017; Jones et al., 2008; Vanhatalo et al., 2016), the individual cannot continue to exercise at the same speed and will be obligated to slow down or stop. Practically, CS represents a speed that is fractionally higher than the highest aerobic performance speed, and has parallels with the product of performance $\dot{V}_{O_2}$ and running economy as presented in the Joyner model. Indeed, it might be argued that 'critical $\dot{V}_{O_2}$' could be usefully substituted for 'lactate threshold $\dot{V}_{O_2}$' in the Joyner model (Fig. 1) since it is the former that will dictate the sustainable $\dot{V}_{O_2}$ for the majority of competitive endurance events.

In elite distance runners, some endurance events, for example the 5000 m, are performed in the so-called severe intensity domain (i.e. above CS) such that performance is a function of both CS and D' (Kirby et al., 2021; Nixon et al., 2021). Ultra-endurance events lasting many hours, on the other hand, are performed in the moderate intensity domain, that is below the LT, when blood [lactate] first increases above baseline values. All other events, including the marathon (at least when this is completed in 2.0–2.5 h), are performed in the heavy intensity domain – above the LT but below CS. It should be noted here that CS or maximal lactate steady state can be approximated during an incremental step treadmill test by the LTP, which can be observed when the rate of blood lactate accumulation accelerates beyond ∼3–5 mM (Jones & Doust, 1998; Smith & Jones, 2001). That the marathon is performed in the heavy intensity domain is intuitive given that physiological factors associated with fatigue development exhibit distinctly different profiles for exercise performed below compared to above CS (Black et al., 2017; Burnley et al., 2012; Poole et al., 2016). Indeed, it has been estimated that elite male marathon runners sustained approximately 96% of their CS (as calculated from their personal best performances over shorter distances) when running their best marathon time (Jones & Vanhatalo, 2017). It should be emphasised that both the LT and CS occur at high fractions of $\dot{V}_{O_2\max}$ in elite endurance athletes such that both the heavy and the severe exercise intensity domains are compressed and are relatively narrow compared to less well-trained cohorts (Jones & Poole, 2008).

Physiological 'resilience' during endurance exercise

If it is accepted that staying close to CS, but not exceeding it except for perhaps in a finishing sprint, is important for high-level endurance events such as the marathon, then both the absolute CS and its stability over time are likely to be crucial performance determinants. Recently, a series of studies by Clark and colleagues (Clark et al., 2018, 2019a, 2019b) addressed the latter point. In their studies, Clark et al. used a 3-min all-out cycle test protocol (Vanhatalo et al., 2007) to expeditiously estimate CP both in a fresh condition (i.e. when participants attended the lab in a rested condition) and immediately following the completion of 2 h of cycling in the heavy intensity domain (Fig. 2). The results showed that group mean CP and W' were reduced by 8—11% and 17—22%, respectively, following the 2 h exercise bout (Clark et al., 2018, 2019a, 2019b). The ∼10% fall in CP indicates a substantial decrement in the power output at which a metabolic steady-state can be attained and clearly has profound implications for endurance performance and the physiological limitations which underpin such performance. These results suggest that an absolute power output that is in the heavy intensity domain (<CP) and which should be sustainable in relative comfort in the early part of an endurance sports event would eventually approach, and then exceed, CP such that the same absolute power output may reside in the severe domain by the end of the event. If this were to occur, then fatigue would develop rapidly and the power output (or speed) may need to drop to enable the athlete to complete the event. In reality, it is likely that the athlete would perceive their proximity to the (declining) CP and that the power or speed sustained in the race would decline in parallel with CP. These scenarios are consistent with the experience of 'hitting the wall' during events such as a marathon, which is the perception of extreme fatigue and a rather sudden and irresistible reduction in speed. A recent study has also demonstrated that prolonged endurance exercise, specifically 2 h of moderate intensity cycle exercise, reduces the LT and gas exchange threshold (GET) (Stevenson et al., 2022), such that a specific moderate domain exercise prescription might drift into the heavy domain if the exercise bout is protracted, with the likelihood of a faster rate of fatigue development (Brownstein et al., 2022b).

While the group mean reduction in CP of ∼10% in the studies of Clark et al. (2018, 2019a, 2019b) was striking, the inter-individual variability in response was even more remarkable, with the range being 0.4–32%. The decrease in LT and GET following 2 h of heavy intensity cycling was also found to be of the order of 10% at the group mean level but with appreciable differences between individual participants (Stevenson et al., 2022).

As stated by Clark et al. (2018), the novel demonstration of considerable between-participant differences in fatigue resistance during heavy intensity exercise which impacted the magnitude of fall in CP indicates that endurance exercise performance ‘might depend not only on the value of key physiological variables at baseline but also on the extent to which these variables deteriorate as exercise proceeds’. Recognising that the three physiological variables described by Joyner (1991) are not fixed but may change over time *during* endurance exercise gives rise to the notion that an additional, temporal, factor influences endurance performance, that is there is a ‘fourth dimension’ which might be termed *resilience* or durability. Dictionary definitions of resilience refer to the ability of an individual to withstand functional decline following acute and/or chronic stressors. When applied to endurance exercise, resilience might therefore be understood to represent the ability to resist fatigue and maintain performance.

Possible determinants of physiological resilience

A candidate explanation for the fall in CP following 2 h of heavy exercise is a loss of efficiency such that a given power output requires a higher $\dot{V}_{\mathrm{O}_2}$ in the fatigued state. Indeed, consistent with earlier studies for both cycling (Hagberg et al., 1978; Passfield & Doust, 2000) and running (Brueckner et al., 1991; Xu & Montgomery, 1995), the relative $\dot{V}_{\mathrm{O}_2}$ in the studies of Clark et al. increased significantly over the 2 h heavy intensity exercise bout, from 64% to 68% $\dot{V}_{\mathrm{O}_2\mathrm{max}}$ (Clark et al., 2018) and from 65% to 72% $\dot{V}_{\mathrm{O}_2\mathrm{max}}$ (Clark et al., 2019b), alongside a fall in respiratory exchange ratio (RER) from ∼0.86 to 0.79, which would be expected to increase $\dot{V}_{\mathrm{O}_2}$ by ∼1.7%. Such a rise in O_2 cost during long-duration exercise is to be expected based upon known changes in muscle fibre recruitment profiles and metabolic substrate utilisation (Gollnick et al., 1973; Vollestad & Blom, 1985). However, in individual studies, Clark et al. (2018, 2019a) found no significant correlation between the increased $\dot{V}_{\mathrm{O}_2}$ during the 2 h exercise bout and the fall in CP. Interestingly, when participants completed a maximal 3-min all-out test immediately following 2 h of heavy exercise, the peak $\dot{V}_{\mathrm{O}_2}$ attained was not different from that attained in a fresh condition (Clark et al., 2018, 2019a). Moreover, when participants completed constant-power-output tests to the limit of tolerance, ostensibly in the severe domain, immediately following 2 h of heavy exercise, the peak $\dot{V}_{\mathrm{O}_2}$ was not consistently lower than that attained in a fresh condition, being lower in Clark et al. (2018) but not different in Clark et al. (2019a). From these studies, the decrease in CP does not appear to be directly related to decrements in either metabolic efficiency or $\dot{V}_{\mathrm{O}_2\mathrm{max}}$.

Collating the data sets from the three studies published by Clark et al. to provide 43 individual responses provides some additional insight. The change in CP following 2 h of heavy exercise was not significantly correlated with baseline values for $\dot{V}_{\mathrm{O}_2\mathrm{max}}$ ($r = 0.03$), GET ($r = -0.25$), CP ($r = -0.11$) or W' ($r = 0.25$). However, while the change in CP was not significantly correlated with the change in $\dot{V}_{\mathrm{O}_2}$ ($r = -0.10$), it was correlated with the % $\dot{V}_{\mathrm{O}_2\mathrm{max}}$ achieved at the end of the 2 h exercise bout ($r = -0.42$; $P < 0.01$). These results imply that, at least when exercise intensity is normalised: (1) high aerobic fitness does not necessarily afford additional physiological resilience, and (2) the increase in O_2 cost during endurance exercise *per se* is less important than the relative intensity of the exercise bout. It should be noted here that the change in relative exercise intensity during an endurance exercise bout is a function of both an increase in O_2 cost and a potential fall in $\dot{V}_{\mathrm{O}_2\mathrm{max}}$ (Clark et al., 2018; cf. Clark et al., 2019a).

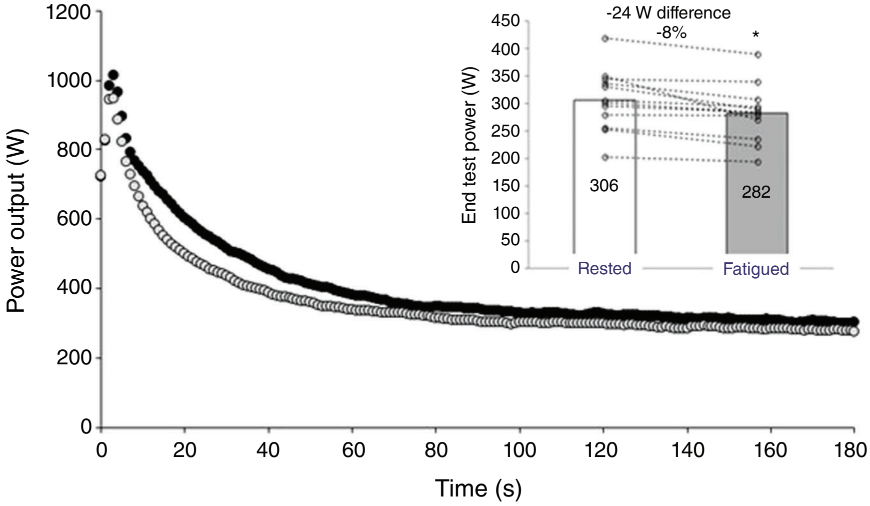

Figure 2. Power–time relationship during a 3-min all-out cycle test for the estimation of critical power (CP) in competitive cyclists

Filled circles show the response in a rested condition and open circles show the response immediately following 2 h of heavy intensity exercise in a representative participant. Note the lower asymptote in the fatigued condition, consistent with a reduced CP, and the lower work done above the end-test power, consistent with a reduced *W*′. The inset shows the group mean and individual participant changes in CP. Data from Clark et al. (2018).

As emphasised earlier, such changes create the risk of an athlete traversing their CP, with consequences for the ability to sustain power output.

To provide insight into the time course of changes in CP during endurance exercise, Clark et al. (2019b) asked participants to complete a 3-min all-out cycle test following 40 min, 80 min and 2 h of heavy intensity cycle exercise. The results clearly showed that the fall in CP was not linear. Rather, CP was not different from that measured in a fresh condition at either 40 min or 80 min but was 9% lower at 2 h, indicating a rather rapid deterioration in endurance capacity later on in endurance exercise and providing clues as to potential underlying physiological mechanisms (Fig. 3*A*). Changes in W' exhibited a different time course from changes in CP, with a significant fall compared to the fresh condition being evident at both 80 min and 2 h. These results are consistent with earlier reports of an inverse relationship between W' remaining and the magnitude of the developing $\dot{V}_{O_2}$ slow component during shorter bouts of heavy and severe exercise (Jones et al., 2011). The reduced ability to complete work above CP, which will also have important implications for performance (Fukuba & Whipp, 1999; Kirby et al., 2021), is most likely explained by glycogen depletion, including of type II muscle fibres (Miura et al., 2000) and effects on sarcoplasmic reticulum calcium release (Ortenblad et al., 2013). Muscle biopsy samples obtained before and after the 2 h exercise bouts indicated that glycogen depletion was substantial (65–70%; Clark et al., 2019a, 2019b).

The importance of carbohydrate (CHO) availability to the maintenance of CP during endurance exercise was also investigated by Clark et al. (2019b), who asked study participants to consume CHO-rich sports drinks (delivering 60 g CHO/h) or placebo during 2 h heavy intensity exercise bouts. Compared to placebo, the CHO intervention resulted in an elevated RER and rate of carbohydrate oxidation as well as greater blood glucose concentration over the final ∼60 min of the exercise bout. Moreover, muscle glycogen concentration was higher at 2 h in the CHO-supplemented condition compared to placebo. This coincided with significantly better preserved CP in the CHO condition compared to the placebo condition (Fig. 3*B*). Remarkably, in the CHO-supplemented condition, CP was not different following 2 h of heavy exercise compared to the value measured without prior exercise. When data from two similar studies were combined, muscle glycogen concentration was significantly correlated with CP when both were measured following 2 h of exercise (Clark et al., 2019a, 2019b). These results are consistent with a recent report that preservation of CP following fatiguing exercise in professional cyclists was related to a lower rate of CHO oxidation (and a higher rate of fat oxidation) during submaximal exercise when measured in a fresh condition, responses that would be expected to spare muscle glycogen utilisation (Spragg et al., 2023a). Although muscle glycogen concentration was spared by CHO ingestion compared to placebo in Clark et al. (2019b), it still fell substantially from the pre-exercise value, and it is therefore interesting that CP was well maintained whereas W' declined to the same extent in the CHO-supplemented and placebo conditions. One explanation for this is that additional muscle fibre recruitment was necessary and sufficient to maintain the $\dot{V}_{O_2}$ associated with CP whereas there was insufficient glycogen to support glycolysis during severe intensity or all-out exercise (consistent with the observed blunting of the blood lactate response) when more or most fibres must be recruited (Vanhatalo, Poole et al., 2011).

The importance of adequate CHO availability during endurance exercise to the maintenance of CP, and therefore performance, is likely linked to differences in the O_2 cost of ATP production for CHO compared to fat (Krogh & Lindhard, 1920). Theoretically, provided there is sufficient glycogen availability, maintaining a higher RER and therefore a higher rate of CHO oxidation will require a lower $\dot{V}_{O_2}$ for a given power output and would be expected to enhance performance (Burke et al., 2019). This is illustrated by the work of Passfield & Doust (2000) who showed that the reduction in the total work that could be done during a 5-min maximal exercise bout following

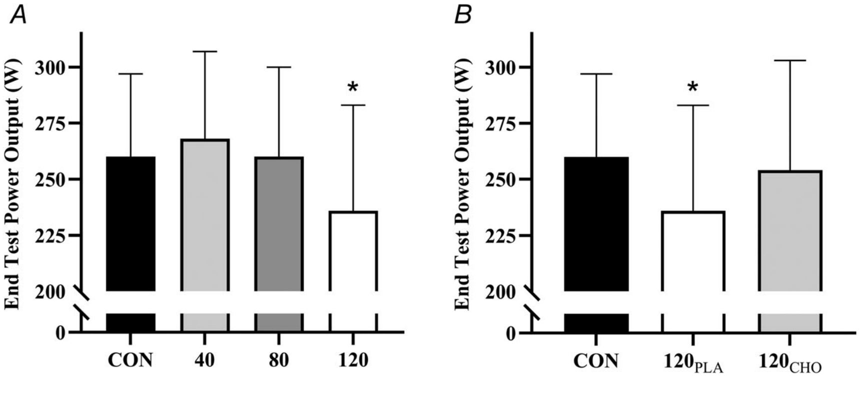

Figure 3. Effects of exercise duration and carbohydrate ingestion on critical power

A, time course for the reduction in estimated critical power (CP) during 2 h of heavy intensity exercise. There was no significant change compared to the value measured in a fresh condition before 80 min of exercise but a substantial fall was observed at 120 min. *B*, influence of 60 g/h carbohydrate (CHO) ingestion on estimated CP. The decrease in CP was markedly attenuated compared to the placebo condition when CHO was ingested. Data from Clark et al. (2019a).

60 min cycling at ∼60% $\dot{V}_{O_2}$ peak was strongly correlated with a reduction in gross efficiency.

Field-based evaluation of physiological resilience

Several recent studies have explored the ability of athletes to maintain or reproduce performance during or following the completion of bouts of endurance exercise in training or competition. For example, Maunder et al. (2021) reported field data from 11 well-trained marathon runners who self-reported their running speed as a fraction of ‘threshold’ and their heart rate (HR) as a fraction of its maximum at each 10% of marathon race distance. Similar to the results of Clark et al. (2019b), the athletes were able to sustain ∼92% of threshold pace until around 70% of the race distance (∼18 miles) after which speed fell progressively, reaching around 89% of threshold pace in the final decile. Simultaneously, HR increased from ∼88% of maximum at around 60% of the race distance to reach ∼91% of maximum by the end. Maunder et al. (2021) calculated the ratio of changes in HR to changes in speed to provide a more sensitive index of the ‘decoupling’ of internal to external work, a metric that may be especially useful in a field context. However, it should be recognised that HR does not necessarily reflect changes in O_2 cost or energy cost due to cardiovascular drift (Billat et al., 2022), which may be linked to hypovolaemia if sweat losses are not replaced (Coyle, 1998).

Decoupling of heart rate and speed (i.e. an increase in HR for a given speed, a fall in speed for the same HR, or a concurrent increase in HR and decrease in speed) appears to occur at around two-thirds of marathon distance (Maunder et al., 2021; Smyth et al., 2022). Smyth et al. (2022) analysed the characteristics of decoupling in >82,000 recreational marathon runners and reported that the ratio of internal to external work was, on average, 16% higher at 35–40 km than at 5–10 km (Fig. 4). Notably, there was substantial inter-individual variability with those expressing low decoupling (<10%) having faster marathon performances than those expressing high decoupling (>20%). Both the magnitude and the time of onset of decoupling were associated with marathon performance, and the inclusion of a decoupling metric improved the prediction of marathon performance compared to a model using CS alone (Smyth et al., 2022). Intriguingly, females decoupled less than males, although whether this is a function of physiological differences or use of a more realistic pacing strategy by females remains to be resolved.

The ability to resist fatigue has also been shown to be a characteristic of successful competitive road cyclists. From an analysis of training and racing data, Gallo et al. (2022b) found that the mean power produced during maximal efforts of 1, 5 and 20 min was barely altered in professional riders even after the accumulation of up to 50 kJ/kg of work (Fig. 5). In contrast, mean power outputs declined substantially and progressively with accumulated work done in elite under-23 riders. Indeed, record power outputs in a fresh condition were similar in the two groups and it was only superior fatigue resistance (i.e. resilience) that differentiated the professionals from the under-23 riders. Similarly, van Erp et al. (2021) reported that higher standard (category 1) cyclists expressed superior ability to reproduce high mean power outputs over fixed durations following the accumulation of up to 50 kJ/kg work done compared to category 2 cyclists. Moreover, despite producing similar power profiles over a range of durations in a non-fatigued (no prior exercise) situation, compared to WorldTour cyclists, ProTeam cyclists expressed a greater deterioration of mean power over the same durations (especially those ≥5 min) with accumulating work done (Mateo-March et al., 2022). The superior resilience of the WorldTour cyclists is amplified between the first and third week of a Grand Tour event (Muriel et al., 2022), underlining the importance of this physiological characteristic to performance outcomes. Consistent with the findings of Clark et al. for changes in CP during heavy intensity cycling, Valenzuela et al. (2022) reported that the deterioration of 20 min time trial performance in professional cyclists following a 4 h training ride compared to a fresh condition was variable between

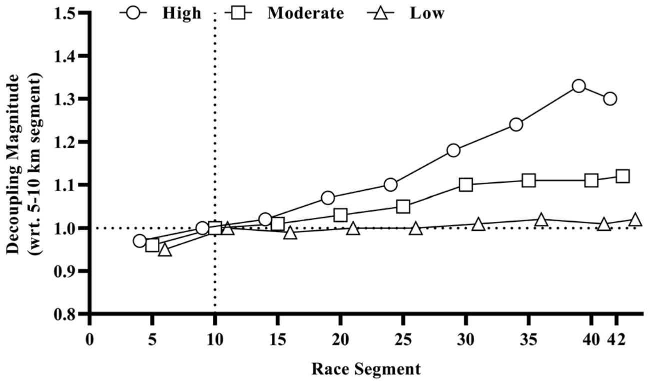

Figure 4. Substantial variability in the magnitude and time course of ‘decoupling’ of heart rate and running speed (as proxy indices of internal and external work, respectively) during a 42.2 km marathon in 82,303 recreational runners
The ratio of heart rate and running speed was given a notional value of 1.0 at 10 km. Changes in either or both variables at 5 km intervals thereafter enabled calculation of decoupling of one variable from the other (i.e. increasing heart rate for the same speed, deceasing speed for the same heart rate, or concurrent increasing heart rate and decreasing speed). Low, medium and high decoupling groups were identified. Individuals who evidenced less decoupling completed the marathon in less time and inclusion of a decoupling metric in a prediction model improved its accuracy. Redrawn from Smyth et al. (2022).

individuals and not correlated with measurements of ventilatory threshold, $\dot{V}_{O_2max}$ or peak power output measured during an incremental exercise test. These results reinforce the notion that resilience represents an independent, non-traditional, physiological determinant of performance. In contrast, Spragg et al. (2023a) reported that cyclists in whom CP fell less following a fatiguing exercise protocol had better gross efficiency and a lower rate of CHO oxidation during submaximal exercise, as well as higher values for the traditional indices of aerobic fitness (i.e. relative $\dot{V}_{O_2max}$, and respiratory gas and ventilatory thresholds). Additional studies are required to resolve whether resilience can be predicted from standard laboratory- or field-based measurements of physiological status.

Considerations for understanding elite endurance performance

As reviewed herein, there is a growing evidence base that physiological resilience is important to endurance exercise performance, with appreciable differences in resilience between individual athletes. It is possible that, in elite athletes, resilience might differentiate the 'crème-da-la-crème' from the remainder. For example, Eliud Kipchoge's superior marathon performances compared to other world-class athletes points to a contribution from an additional physiological factor that is not typically measured during laboratory tests (Jones et al., 2021). Moreover, it might be speculated that the dominance of East African athletes in long distance running competitions is related to better resilience given that comparisons of East African with Caucasian athletes has not revealed clear differences in $\dot{V}_{O_2max}$ and running economy (Bosch et al., 1990; Coetzer et al., 1993). This would be consistent with evidence that East African athletes demonstrate greater skeletal muscle fatigue resistance (Coetzer et al., 1993; Harley et al., 2016). On this point, when Eliud Kipchoge received an honorary doctorate for services to sport from the University of Exeter in 2019, he was asked by the university's Vice-Chancellor just how hard it was to break 2 h for the marathon, and replied, 'Actually, it was quite easy!'

One other factor that might be relevant is differences in lower limb architecture. Relative to other nationalities, elite Kenyan runners have been reported to have longer shank, Achilles tendon and Achilles tendon moment arms, thinner calf muscles and lower foot lever ratios (Kunimasa et al., 2014, 2022). It has been suggested that these characteristics reduce muscle-tendon stretch-shortening loading and muscle activation, and therefore enhance elastic energy storage and return during running (Sano et al., 2013, 2015). It is feasible that these characteristics result in a blunted deterioration of running economy during long distance races, enabling CS to be better preserved and enhancing performance.

The existence of the stretch-shortening cycle in running, which involves a combination of concentric and 'more efficient' eccentric muscle actions, represents a point of difference with cycling which exclusively involves concentric contractions (Bijker et al., 2002). This raises the question of whether resilience might differ between these two modes of exercise, and also across other modes of exercise which are yet to be investigated. On the one hand, it might be hypothesised that the stretch-shortening cycle in running would enhance fatigue resistance and result in superior delta efficiency compared to cycling not only in a non-fatigued situation but also in the later stages of an endurance running bout. On the other hand, repetitive foot strikes during a long-distance running race might evoke muscle damage (Takayama et al., 2018) and accelerate any loss of efficiency via, for example, effects on fibre recruitment. It should be noted here that recent innovations in running shoe technology have likely impacted on several of these factors (i.e. muscle damage, economy and resilience) and have therefore contributed to significant improvements in world record times (Black et al., 2022; Cigoja et al., 2021; Senefeld et al., 2021).

Another important factor when considering possible differences in resilience between running and cycling may be the relationships between fatigue development, changes in O_2 cost and changes in biomechanics or technique, with

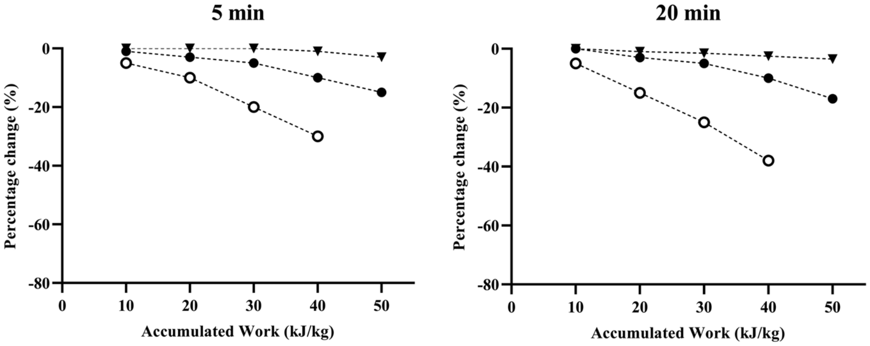

Figure 5. Influence of accumulated work (in kJ/kg body mass) on performance during 5 and 20 min efforts in professional cyclists (filled triangles), and elite under-23 (filled circles) and junior (open circles) cyclists
Note the marked difference in the ability to reproduce maximal performance in the professionals even following the completion of significant work. Redrawn from Gallo et al. (2022b).

the latter being much more obvious in fatigued runners compared to fatigued cyclists due to the greater 'degrees of freedom' during running. Changes in the extent of fatigue, O_2 cost and kinematics may occur simultaneously during long distance running such that it is difficult to discern cause and consequence. For example, fatigue may influence O_2 cost and running form, but a higher O_2 cost may, in turn, expedite fatigue development, and changes in running technique with fatigue may increase O_2 cost. However, adaptations to running form, including possible changes in stride length and rate, in the face of developing fatigue might serve to change both the pattern of muscle and motor unit recruitment, minimising the increase in O_2 cost and mitigating fatigue development. Interdisciplinary studies will be necessary to generate a comprehensive understanding of these phenomena.

At present, while it is known that O_2 cost increases during both long duration running (Brueckner et al., 1991; Kyrolainen et al., 2000) and cycling (Clark et al., 2018; Passfield & Doust, 2000), little is known about possible differences in resilience between these exercise modalities. However, it appears that while the magnitude of force loss is similar following duration and intensity-matched bouts of running and cycling, the nature of fatigue differs with greater loss of neural function in running and greater loss of contractile function in cycling (Brownstein et al., 2022a). There are suggestions that these differences in the nature of fatigue development between exercise modalities might result in a greater change in energy cost for cycling compared to running when matched for intensity and duration (Sabater-Pastor et al., 2023), and that changes in energy cost during running are complex and depend on factors such as distance covered (Sabater-Pastor et al., 2021). A complication here is that energy cost (which takes into consideration changes in substrate utilisation) and O_2 cost do not always show the same patterns of change (Beck et al., 2018), and it is controversial as to which one better tracks performance. Nevertheless, these results are consistent with reports that, for shorter bouts of heavy and severe intensity exercise, the $\dot{V}_{O_2}$ slow component is substantially greater in cycling than running, a phenomenon that has been speculated to be related to higher intramuscular tension development in cycling and consequent effects on fibre recruitment (Carter et al., 2000). Possible differences in resilience between running and cycling, and the mechanistic bases thereof, might be resolved through studies of elite triathletes.

Interventions and applications

While there is a clear need for more mechanistic studies to explain the physiological underpinnings of resilience, potential interventions to enhance resilience are also of great interest to athletes, coaches and sports scientists. Two such interventions were alluded to earlier. In running, it is possible that the influence of neoteric footwear on race performances (Hébert-Losier & Pamment, 2023) might be mediated, at least in part, by effects on athlete resilience. While it is known that shoes incorporating a carbon plate and lightweight, energy-returning foam can improve running economy by ~4% when athletes are tested while running for short durations in a fresh state (Black et al., 2022; Hoogkamer, Kipp et al., 2018), it is feasible, though yet to be confirmed, that the effect might be at least as great towards the end of a race when athletes are fatigued. Moreover, when training in 'supershoes', elite distance runners report faster recovery which may help them absorb a higher volume and/or greater intensity of training. Improved race performances in neoteric footwear may therefore be a function of both acute in-race effects and enhanced athlete conditioning.

The importance of a high rate of CHO oxidation, achieved via a combination of high pre-race muscle glycogen concentration and a high rate of in-race CHO ingestion (with up to 120 g/h now believed to be achievable; Viribay et al., 2020) to prevent or offset a substrate-mediated rise in O_2 cost during exercise is clear (Clark et al., 2019a; Krogh & Lindhard, 1920). However, excellent gross efficiency or running economy measured in a fresh condition, and the ability to preserve muscle glycogen concentration during endurance exercise through a greater reliance on intramuscular fat metabolism and/or blood-borne CHO utilisation may also be important in resilience (Spragg et al., 2023a). Although yet to be addressed experimentally, it is reasonable to expect that environmental factors such as hypoxia, and high ambient temperature or humidity, which would challenge muscle O_2 supply and expedite fatigue development, may influence resilience. In such situations, appropriate mitigations might include altitude acclimatisation and an effective hydration strategy, respectively (Bergeron et al., 2012). With regard to in-race hydration and fuelling strategies, it should be borne in mind that, at least for weight-bearing sports such as running, some loss of body mass has the potential to enhance performance by reducing the O_2 cost of locomotion and by increasing $\dot{V}_{O_2\text{max}}$. It has been reported that loss of body mass in a world championship marathon can average 1.3% in women and 2.6% in men (Racinais et al., 2021). The effect of such losses on submaximal $\dot{V}_{O_2}$ may be similar to, or greater than, the effects associated with an increased rate of fat oxidation. A small loss of body mass might therefore help to offset an increased O_2 cost and support resilience during endurance exercise. Therefore, careful management of fuel and fluid intake during endurance competition may help maintain CHO availability and optimise the change in body mass to take advantage of a lower O_2 cost, while avoiding the detrimental effects of frank dehydration and associated challenges to thermoregulation. In terms of other putative nutritional ergogenic aids, the potential for caffeine to influence neuromuscular fatigue development makes it an obvious candidate for enhancing resilience. It has also been reported that ingestion of inorganic nitrate, in the form of beetroot juice, before and during 2 h of endurance exercise attenuates the rise in $\dot{V}_{O_2}$ and spares muscle glycogen degradation, although it did not enhance subsequent time trial performance (Tan et al., 2018). Further studies are required to investigate optimal nutritional strategies to enhance resilience.

The physical training sessions or training programmes that might specifically develop resilience are not known. Inter-individual differences in efficiency or economy measured in an unfatigued situation do not appear to predict differences in resilience (Clark et al., unpublished observations). Nevertheless, while genetic predisposition cannot be ruled out, reports that experienced, senior cyclists with many years of accumulated training display excellent resilience (Gallo et al., 2022b) suggests that age and/or consistent, long-term, perhaps high volume, training may play an important role (Almquist et al., 2023; Gallo et al., 2022a; Spragg et al., 2023b). With the assumption that East African distance runners are more resilient than their counterparts in other world regions, it might also be speculated that a high volume training programme with a pyramidal intensity distribution (Burnley et al., 2022), which includes regular training in a fasted and/or glycogen-depleted state (through, for example, twice-daily training or overnight CHO restriction), might stimulate metabolic adaptations (Hansen et al., 2005; Impey et al., 2018; Lane et al., 2015) that contribute to resilience. Also, assuming that the specificity of the stimulus is important in developing physiological resilience, then regular exposure to a situation wherein resilience is challenged, namely long endurance training sessions where the speed is held constant at close to race effort or progressively increases with time (as practiced by, for example, Eliud Kipchoge), may be effective. Whether certain types of strength or plyometric training, which focus on maintaining form when fatigued or enhancing elastic recoil during the stretch-shortening cycle (Blagrove et al., 2018), might be beneficial to physiological resilience remains to be determined. Intriguingly, countermovement jump height is increased as speed decreases during a 30 km run, suggesting that post-activation potentiation might play a role in mitigating fatigue development during endurance exercise (Del Rosso et al., 2016). Finally, although the influence of ‘mental fatigue’ on exercise performance is controversial, psychological factors and/or changes in brain neurotransmission or oxygenation (Santos-Concejero et al., 2015) might feasibly also impact on resilience, perhaps via effects on perceived exertion (Meeusen et al., 2021). If so, then interventions including specific physical and/or psychological skills training (McCormick et al., 2015; Meijen et al., 2023) might enhance resilience during fatiguing endurance exercise.

The acceptance of physiological resilience as a bona fide fourth determinant of endurance performance also has implications for sports physiologists who evaluate and advise endurance athletes. Presently, physiological assessment of endurance athletes typically involves incremental-type ergometer tests designed to appraise the three main factors in the Joyner model, namely $\dot{V}_{O_2\mathrm{max}}$, economy or efficiency, and fractional utilisation of $\dot{V}_{O_2\mathrm{max}}$ (LT, CP, etc.), (Jones et al., 2021). Such tests can be used to appraise the efficacy of training longitudinally across a season or multiple seasons. However, assessing resilience is challenging since it is not practical to ask athletes to complete ∼90–180 min of exercise to measure changes in O_2 or energy cost or CP/CS. The growing sophistication of training monitoring applications may permit resilience, and its changes over time, to be ascertained using algorithms linked to decoupling of internal and external workload measures (Smyth et al., 2022) during training or via field tests. A practical laboratory-based expedient might be to measure O_2 and energy cost at a fixed submaximal speed or power output before and after the completion of a traditional exhausting incremental multi-stage exercise test, although it is recognised that the ‘type’ of fatigue elicited might differ from that experienced in long races. It is ironic that while testing athletes in a fresh or rested condition is often recommended and considered best practice (Davison et al., 2009), measurements made in this condition will be incomplete given that the athletes will be in some state of fatigue for a high proportion of their endurance sports event. The potential value of assessing power–time or speed–time profiles in a fatigued as well as a fresh state was recently underlined by a study which showed, in highly trained cyclists, that while fresh power–time profiles barely changed over the course of a competitive season, fatigued profiles deteriorated (Spragg et al., 2023a). Such results suggest that markers of resilience may be more sensitive to changes in fitness status resulting from changes in training volume and/or intensity, and might also correlate better with performance potential, than the traditional physiological variables that are routinely monitored by sport scientists. Finally, it should be noted that while the focus herein has been on long endurance events such as the marathon, resilience (that is, the fatigue- and time-dependent deterioration of physiological variables considered to be predictive of performance) is likely to be a relevant concept in both shorter, more intense, and longer, less intense, sports events as well as in high intensity, intermittent activities and team sports (Black et al., 2023).

Conclusions

The ‘Joyner model’ describing the physiological determinants of endurance exercise performance has proven to be highly influential (Joyner, 1991; Joyner & Coyle, 2008; Jones, 1998; van der Zwaard et al., 2021). While Joyner (1991) noted that the O_2 cost of running might increase over time during long-distance races, this aspect has been neglected in subsequent experimental studies and in applied practice. Recent studies, however, have raised awareness that the three traditional physiological pillars of endurance exercise performance are not static but are rather dynamic and may change substantially *during* fatiguing endurance exercise with remarkable inter-individual variability in the magnitude of deterioration (Clark et al, 2018; Clark et al., 2019a; Clark et al., 2019b; Stevenson et al., 2022). It is clear, therefore, that endurance exercise performance is not a function solely of an athlete’s physiological status on the start line but is also related to the athlete’s fatigue resistance or resilience to changes in indices of aerobic function during the race itself. The lack of a consistent correlation between changes in CP during endurance exercise and baseline physiological variables indicates that resilience should be considered an independent physiological determinant of endurance exercise performance. For this reason, it is suggested that the classic Joyner model be modified to incorporate this additional variable (Fig. 6). It might be speculated that superlative endurance performances, such as achievement of the first sub-2 h marathon, owe

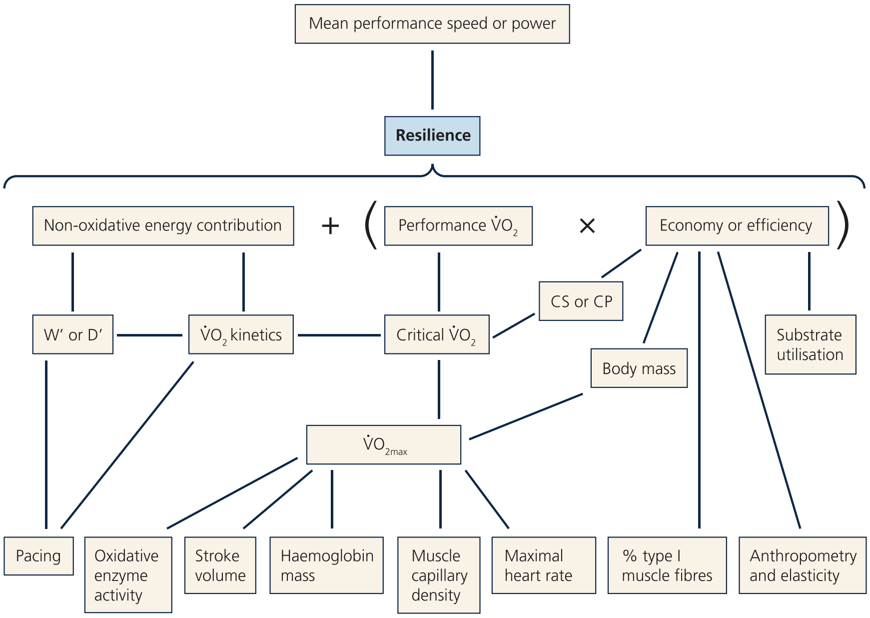

Figure 6. Contemporary representation of the physiological determinants of endurance exercise performance

Modifications to the Joyner model include the addition of critical $\dot{V}_{O_2}$, critical power or critical speed (CP or CS), W' or D', and $\dot{V}_{O_2}$ kinetics along with the inclusion of a ‘resilience’ term to recognise that the key variables in the model are not static but are subject to deterioration during endurance exercise. Note that endurance performance is complex and the model is conceptual and not comprehensive. Relationships between variables are illustrated with connecting lines. As represented on the left-hand side of the figure, there is an obligatory contribution to energy metabolism from substrate-level phosphorylation for all exercise bouts irrespective of intensity but this will be relatively small in comparison to mitochondrial respiration, especially for the longer endurance events. On the right-hand side of the figure are the factors determining the $\dot{V}_{O_2}$ that can theoretically be sustained for the distance and the efficiency or economy characteristics of the individual that are important in translating this $\dot{V}_{O_2}$ into power output or running speed. As discussed in the text, the non-oxidative energy contribution, performance $\dot{V}_{O_2}$, and efficiency or economy are all subject to change during endurance exercise as fatigue develops, glycogen stores are depleted, respiratory quotient falls, movement patterns are perturbed, and plasma volume and body mass decline. Therefore, the mean performance speed or power that may be sustained during endurance exercise is moderated by a ‘resilience’ term. Resilience appears to vary substantially between individuals but extraordinary resilience appears to characterise superlative endurance athletes. It is proposed that resilience be considered an additional, apparently independent factor that helps to explain human endurance exercise performance.

something to outstanding physiological resilience as well as to better-known factors such as a high initial CS (Jones et al., 2021). Focused research is required to enable a better understanding of the physiological mechanisms underpinning resilience, the factors that determine inter-athlete variability in resilience, and the interventions that might improve resilience. There are also important implications for the physiological testing of athletes (i.e. in a fatigued as well as a rested state), performance prediction (i.e. with athlete resilience characteristics factored in to existing or new models) and training prescription. It is therefore proposed that physiological resilience be considered the 'fourth parameter' of endurance exercise physiology.

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