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REVIEW ARTICLE

Mechanical work as a (key) determinant of energy cost in human locomotion: recent findings and future directions

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Abstract

During locomotion, muscles use metabolic energy to produce mechanical work (in a more or less efficient way), and energetics and mechanics can be considered as two sides of the same coin, the latter being investigated to understand the former. A mechanical approach based on König's theorem (Fenn's approach) has proved to be a useful tool to elucidate the determinants of the energy cost of locomotion (e.g., the pendulum-like model of walking and the bouncing model of running) and has resulted in many advances in this field. During the past 60 years, this approach has been refined and applied to explore the determinants of energy cost and efficiency in a variety of conditions (e.g., low gravity, unsteady speed). This narrative review aims to summarize current knowledge of the role that mechanical work has played in our understanding of energy cost to date, and to underline how recent developments in analytical methods and their applications in specific locomotion modalities (on a gradient, at low gravity and in unsteady conditions) and in pathological gaits (asymmetric gait pathologies, obese subjects and in the elderly) could continue to push this understanding further. The recent *in vivo* quantification of new aspects that should be included in the assessment of mechanical work (e.g., frictional internal work and elastic contribution) deserves future research that would improve our knowledge of the mechanical–bioenergetic interaction during human locomotion, as well as in sport science and space exploration.

KEYWORDS
apparent efficiency, gradient locomotion, low gravity, mechanical energy, pathological gait, unsteady locomotion

1 | INTRODUCTION

During locomotion, muscles use metabolic energy to produce mechanical work; hence, measuring the latter is fundamental to understand the former, and when investigating both, the apparent efficiency of locomotion (AE; the ratio between mechanical work and energy cost) can be determined (e.g., Cavagna & Kaneko, 1977). Energetics and mechanics can thus be considered as two sides of the same coin, and indeed, 'the study of locomotion first requires the determination of the energy cost of this exercise and secondly a detailed analysis of the mechanical work performed' (Margaria, 1938).

The energy cost (or cost of transport; CoT) is the metabolic energy needed to move 1 kg of body mass over 1 m (J kg^{-1} m^{-1}) (Saibene & Minetti, 2003). In walking, net CoT (calculated based on the metabolic energy expended above rest) shows a 'U-shaped' response as a function of speed, with a minimum of about 2 J kg^{-1} m^{-1} at speeds ranging from 1.1 to 1.4 m s^{-1}; when walking at faster or slower speeds CoT is higher (Margaria, 1938). In running, net CoT is about 4 J kg^{-1} m^{-1} and is essentially unaffected by the speed (Margaria et al., 1963). Walking and running CoT is increased in some conditions such as in pathological gait (Zamparo et al., 1995), in the elderly (Mian et al., 2006) or when locomoting in specific conditions (e.g., uphill or extreme downhill (Margaria, 1938), non-steady conditions (Zamparo et al., 2016)), and decreased in simulated low gravity (Pavei et al., 2015), and analysing the work performed in these conditions could help in understanding the reason for these differences.

Two simple paradigms were proposed to physically describe the mechanics of human gait, starting from the motion of the body centre of mass (BCoM) and the analysis of the mechanical energies (kinetic (KE) and gravitational potential (PE)) associated with this motion (see Figure 1). Walking has been presented as a 'rolling egg' or 'inverted pendulum' model where PE and KE are out of phase as in a pendulum-like motion. Running has been presented as a 'bouncing ball' or a 'spring-mass model', where PE and KE are in phase and at minimum in the middle of foot contact, when the BCoM trajectory is inverted from a downward to an upward displacement (for an overview, see Minetti, 1998).

The first attempt to determine the mechanical work of human locomotion was performed by Fenn (1930a,b). Based on 'Fenn's approach', Cavagna and colleagues improved mechanical work estimates using accelerometers and force platforms in the 1960 and '70s (Cavagna, 1975; Cavagna & Kaneko, 1977; Cavagna et al., 1963, 1964), and in the 1990s, Minetti and colleagues set up a method based on three-dimensional motion capture analysis (Minetti et al., 1993, 1994). According to 'Fenn's approach', the total mechanical work (W_{TOT}) performed during locomotion can be divided into two components (see Figure 1): the external mechanical work (W_{EXT}) needed to raise and accelerate the BCoM within the environment (Cavagna et al., 1963), and the internal mechanical work (W_{INT}) needed to accelerate the limbs in respect to the BCoM (Cavagna & Kaneko, 1977); both terms are generally normalized for mass and distance (J kg^{-1} m^{-1}).

W_{EXT} is calculated as the sum of the increments of BCoM total mechanical energy (E_{TOT} = KE + PE) (Cavagna et al., 1963) and W_{INT} is calculated as the sum of the increments of the limbs' KE (e.g., the sum of the rotational and translational KE with respect to BCoM) (Cavagna & Kaneko, 1977; Minetti et al., 1993; Willems et al., 1995). This procedure is based on König's theorem of mechanics, which defines the overall KE of a linked multi-segment system as the sum of the KE of the BCoM of the system (which is incorporated in W_{EXT}) and the KE (translational and rotational) of the segments (which represents W_{INT}) (Cavagna et al., 1963; Fenn, 1930b). The W_{TOT} is then computed from the sum of W_{EXT} plus W_{INT} (see Figure 1).

The AE can also be defined as the efficiency of positive work production by the muscle–tendon units. Indeed, as suggested by Alexander (1991), measuring AE contributes to understanding whether mechanical work is 'recycled' via storage and release of elastic energy: this energy-saving strategy occurs when AE exceeds 'pure' muscular efficiency (about 0.25–0.30, Woledge et al., 1985), providing important information on the energy-saving mechanism of walking and running, on the locomotor capability of a subject and on eventual impairment due to pathological conditions.

'Fenn's approach' has been a useful tool for understanding human (and animal) locomotion, and has resulted in many advances in both mechanical and bioenergetics aspects allowing, for example, (i) elucidation of the fundamental mechanisms of locomotion (e.g., the pendulum-like model of walking and the bouncing model of running; Cavagna et al., 1977); (ii) identification of the determinants of the optimum stride frequency in walking (e.g., Minetti et al., 1995; Minetti & Saibene, 1992) and running (e.g., Cavagna et al., 1997); (iii) understanding of the mechanical determinants of the CoT optimum gradient in human walking (e.g., Minetti et al., 1993) and running (e.g., Minetti et al., 1994); and (iv) determination of the gait of choice in low gravity environments (e.g., Margaria & Cavagna, 1964; Pavei et al., 2015). In addition, understanding the mechanical determinants of locomotion energetics is key in promoting health and well-being across the life span. In many disorders and diseases, robust links have been shown between mechanical work generation, increased metabolic requirements and reduced mobility (e.g., Detrembleur et al., 2003, 2005; Peyré-Tartaruga & Coertjens, 2018).

This narrative review aims to summarize current knowledge about the role that mechanical work and CoT have played in our understanding of human locomotion to date, and to underline how recent developments in analytical methods and their applications in the study of health and pathological gait could continue to push this understanding forward.

Recent studies on the determinants of mechanical work in specific human locomotion modalities will be reviewed first (on a gradient, at low gravity and in unsteady conditions); applications of these studies in pathological gait (asymmetric gait pathologies and walking in obese people) will then be discussed.

New Findings

- **What is the topic of this review?**
  This narrative review explores past and recent findings on the mechanical determinants of energy cost during human locomotion, obtained by using a mechanical approach based on König's theorem (Fenn's approach).
- **What advances does it highlight?**
  Developments in analytical methods and their applications allow a better understanding of the mechanical–bioenergetic interaction. Recent advances include the determination of 'frictional' internal work; the association between tendon work and apparent efficiency; a better understanding of the role of energy recovery and internal work in pathological gait (amputees, stroke and obesity); and a comprehensive analysis of human locomotion in (simulated) low gravity conditions.

2 | MODIFICATION OF THE TWO BASIC MECHANISMS OF HUMAN LOCOMOTION ON SLOPED SURFACES

A.H. Dewolf, P.A. Willems

Various aspects of human locomotion have been extensively studied in the laboratory in 'steady state', that is, while moving on a straight trajectory, at an average constant speed and on a flat and firm terrain. In this particular case, muscles are performing as much positive as negative work. However, in daily life, this steady state situation is rather infrequent. For example, sloped surfaces require special mechanical demands on the musculoskeletal system since the amount of positive and negative work performed are not equal any more. Interestingly, in both walking and running, the CoT is minimal on an 'optimal' slope around −10% (Margaria, 1938; Minetti et al., 1993, 1994).

A crucial factor explaining this optimal slope is that our muscles use much less metabolic energy to do negative than positive work. Since the internal work is not affected by the slope of the terrain (Dewolf et al., 2016, 2017; Minetti et al., 1993, 1994), the imbalance between net positive and negative work performed is directly related to the motion of the BCoM, which in turn affects the two basic mechanisms of locomotion. Therefore, the influence of the slope of the terrain and of the speed of progression on the pendulum-like mechanism of walking and on the bouncing mechanism of running has been examined.

Both in walking and in running on slopes, the amount of energy recovered through the two saving mechanisms is reduced when the inclination of the terrain increases (Dewolf et al., 2016, 2017; Gomeñuka et al., 2016). Indeed, these mechanisms must be adapted to modify the height of the BCoM with each step (Dewolf et al., 2016, 2017). Therefore, the amount of energy saved in walking through the KE–PE exchange and in running through the storage–release of elastic energy is reduced when the slope and the speed increase.

It should be noted that, in some situations, as one saving mechanism disappears the other mechanism comes into play. This phenomenon is due to the fact that, unlike the energy due to the vertical movements of the BCoM (E_v), the energy due to its horizontal movements (E_{kf}) changes little or not at all with slope (Dewolf et al., 2016, 2017). For example, during downhill walking, the pendulum-like mechanism is jeopardized especially at higher speeds and slope. In this case, part of the external energy lost during double contact and early single contact can be stored in biological elastic structures to be reused to reaccelerate the BCoM forward during the next part of single contact. In the same vein, in running, as the bouncing mechanism progressively fades away with speed and slope, the KE–PE exchange starts to appear because the E_v–time and the E_{kf}–time curves are no longer in phase (Dewolf et al., 2016). For example, when running uphill, the minimum of E_v occurs before the minimum of E_{kf}. Between these two minima, the E_{kf} energy lost can be used to increase E_v.

It has been suggested that the trajectory of the BCoM may serve as a target for motor control of locomotion. When moving on a slope, the modification of BCoM trajectory involves some changes in the neuromuscular control strategy of locomotion (Dewolf et al., 2019). Interestingly, similar modifications of the control of locomotion were observed when the imbalance between positive and negative work was generated by a horizontal traction force (Dewolf et al., 2020). These results suggest that, though factors other than work also clearly influence the preferred movement strategy, the choice of gait pattern largely depends on the mechanical work that must be performed. Taken together, investigating the modification of BCoM trajectory and the associated adjustments of the two basic mechanisms in relation to changes in the mechanical energy of BCoM can help in understanding the general rules by which the neuromuscular system produces locomotion.

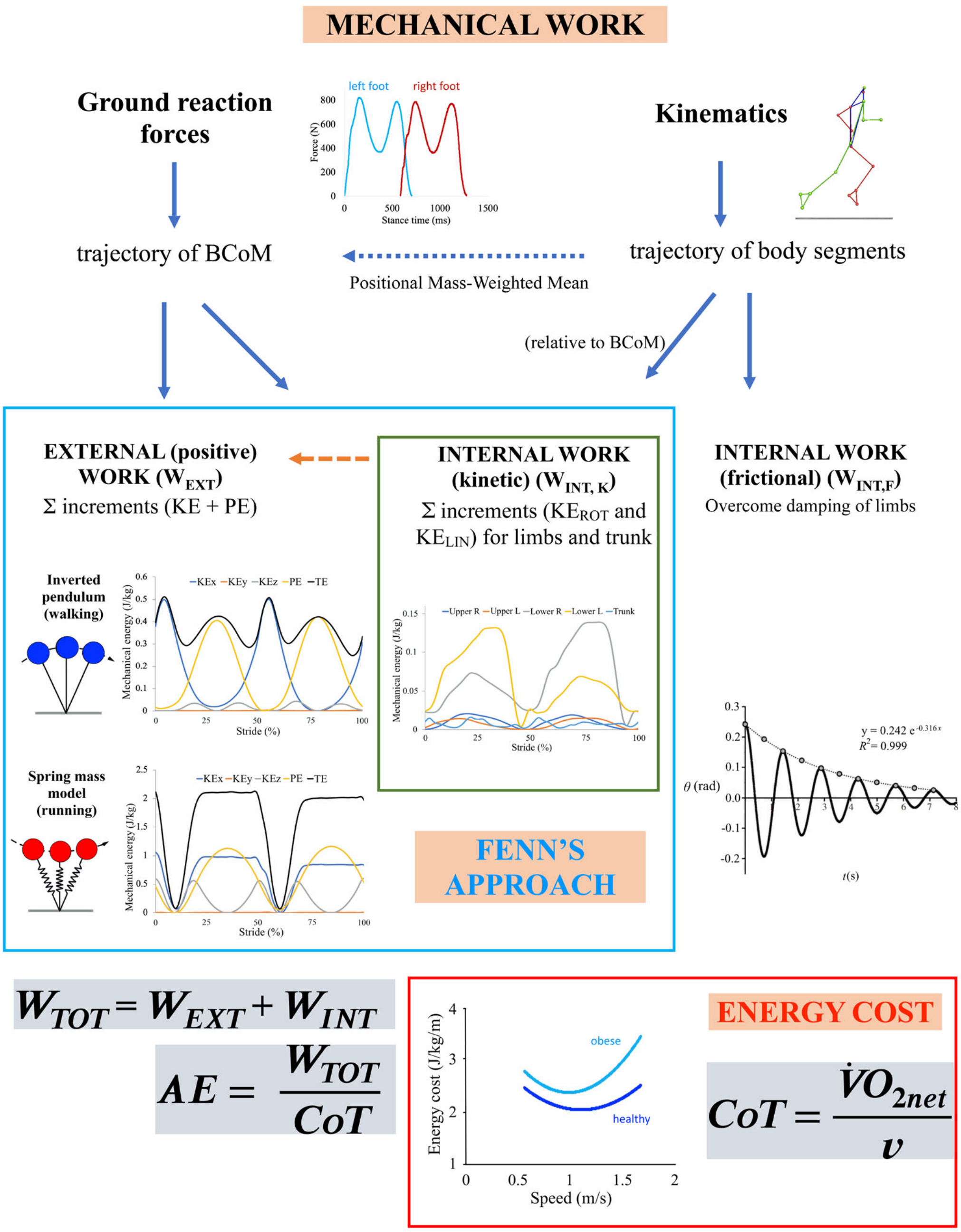

FIGURE 1 Schematic representation of the procedures for measuring total mechanical work (W_{TOT}), energy cost (CoT) and apparent efficiency (AE). The external mechanical work (W_{EXT}) can be measured based on the trajectory of the body centre of mass (BCoM, derived from ground reaction forces, which is the gold standard) or the trajectory of body segments (derived from motion analysis, inverse dynamics). The (blue) dotted arrow indicates the inverse dynamic technique that can be used to calculate the trajectory of BCoM from that of the body segments (by computing the positional mass-weighted mean). The calculation of the internal mechanical work (W_{INT}) necessarily requires kinematic data to record segmental movements (relative to BCoM position in the case of the Fenn's Approach: $W_{INT,K}$). The methods to derive W_{EXT} and W_{INT} by means of Fenn's approach are shown in detail in the blue box: BCoM motion resembles a simple rigid inverted pendulum and a compliant spring-mass model during the stance phase of walking and running, respectively. External work is thus computed based on the summation of the (positive) energy increments in total energy (TE, black tracings) associated to BCoM during a stride; in turn, TE is the sum of gravitational potential energy (PE), forward kinetic energy (KE_x), mediolateral kinetic energy (KE_y) and vertical kinetic energy (KE_z). Note that scale values on vertical axes are different between graphics. The method to derive $W_{INT,K}$ is reported in the green box: it is based on the summation of the increments in linear and rotational kinetic energy of trunk and upper and lower limbs (right (R) and left (L) side) during a stride. The dashed (red) arrow indicates an interplay probability from W_{INT} to W_{EXT} (see Discussion for this point). Recently, a new method to compute an additional internal work (frictional work, $W_{INT,F}$) was proposed, based on the damping oscillation of the limbs (modelled as a straight pendulum with a viscous rotational friction in the pivot) (the figure is taken from Minetti et al., 2020). Finally, CoT is calculated from the ratio of net oxygen consumption (above resting values) and horizontal velocity (red box). An example of the U-shaped CoT versus speed relationship in walking is reported in healthy (blue traces) and obese (light blue) adults as a reference: obese adults expend more metabolic energy in walking than eutrophic controls (lean), increasing the difference at faster speeds

3 | LOCOMOTION AT LOW GRAVITY

A.E. Minetti, G. Pavei

Over time, human evolution has adapted the musculoskeletal apparatus to a posture that, by coping with Earth's gravity, ensures an efficient and economical locomotion in a variety of 'terrestrial' terrains and inclines. It seems unlikely that a long human presence on planets/moons with a different gravity will be enough to produce body changes other than muscle size. It seems quite appropriate, then, to keep on studying how extant body structure will react to different gravity and adapt its locomotor repertoire.

Low gravity studies on human locomotion started a few years before the Apollo missions to the Moon. Rodolfo Margaria and Giovanni Cavagna correctly suggested that walking on the Moon at normal to high speed would be impaired (Margaria & Cavagna, 1964). Also, from ground reaction forces of emulated low gravity jumping they concluded that running could be replaced by a more appropriate hopping gait (Cavagna et al., 1972). About 30 years later, a 'terrestrial' study on the mechanics of skipping (Minetti, 1998), a mixed bouncy–pendular gait, indicated its suitability in low gravity and contributed to explaining why astronauts often preferred this gait on the Moon.

Recently, the increasing interest in space exploration stimulated more sophisticated analyses of gaits at different gravity. In Milan, a new Analog Laboratory allowed the measurement of CoT and W_{TOT} (with its components) of level walking, running, skipping and hopping in a range of different speeds and simulated gravities, from terrestrial to lunar values (Minetti et al., 2012; Pavei et al., 2015; Pavei & Minetti, 2016).

The surprise was that gaits associated to very different metabolic economy on Earth (hopping < skipping < running < walking) were found to have almost the same, much lower, CoT (with hopping showing the lowest value at about 1.3 J kg^{-1} m^{-1}) when performed at the Moon's gravity (Pavei & Minetti, 2016). Also, within each relevant operative range, the different bouncing gaits exhibited an almost speed-independent CoT. It is remarkable that a previous theoretical paper on the minimization of effort and other metabolically related parameters in low gravity locomotion pointed out that skipping should be the gait of choice on the Moon (Ackermann & van den Bogert, 2012), as it was for the Apollo's astronauts.

The W_{TOT} shows a similar trend in all gaits, with a decrease in absolute values, as reported by (and with similar values to) Cavagna et al. (1998, 2000) when walking at Mars' gravity (0.4 g) during parabolic flights – the 'gold standard' low gravity simulator. On the Moon, similar values of mechanical work were shown for running, skipping and hopping, with walking being the least expensive gait (it has to be remembered that W_{EXT} actually incorporates unknown amounts of mechanical energy released at no CoT by previously tensioned elastic structures). Despite this source of uncertainty, graphs of decreasing AE towards 'muscle efficiency' values, particularly in bouncing gaits, seemed to suggest that the coupling inside muscle–tendon units during locomotion at low gravity is not as effective as on Earth (Pavei et al., 2015). A compromised muscle–tendon coupling during reactive drop jumps, which could in a certain way mimic the contact time of a bouncing gait, has been recently shown at a variety of low gravity levels during parabolic flights (Waldvogel et al., 2021).

These findings, although deserving further investigation, reinforce the initial idea of considering our spring-actuator system as the final, after a very long-lasting evolution, optimized solution for energy saving gaits at gravity = 1 *g*. There is room for improvement at lower gravity, but it is more likely that man-made passive (or muscle-activated) tools, rather than evolution, will facilitate faster and economical muscle-powered transportation in that condition.

4 | UNSTEADY LOCOMOTION: SPRINTS AND SHUTTLES

P. Zamparo, A. Monte

The majority of the studies on human or animal locomotion are conducted at constant speed even if, in real life, human and animal gaits very often occur at variable or unsteady speed. Sprint running is a good model to investigate the acceleration capabilities in humans, whereas in shuttle running, different accelerations (and decelerations) could be attained by increasing either the velocity or the distance of the shuttle run.

In shuttle running, CoT increases with shuttle velocity and decreases with shuttle distance; the net CoT of short shuttle runs (5 m) is about 30 J m^{-1} kg^{-1} at maximal speed (Zamparo et al., 2015) and approaches that of constant speed linear running (4 J m^{-1} kg^{-1}) over longer distances (20 m) covered at slow running speeds (Buglione & Di Prampero, 2013). W_{TOT} in shuttle running is also larger the faster the velocity and the shorter the shuttle distance (Zamparo et al., 2016, 2019) and approaches the typical steady-state level running values at slow shuttle speeds over long distances. W_{INT} is a strong determinant of W_{TOT} in shuttle running, being about half of W_{TOT} at maximal shuttle velocity (Zamparo et al., 2016, 2019).

Whereas, in constant speed-linear running, AE steadily increases with running speed (range: 0.50–0.80; Cavagna & Kaneko, 1977), in shuttle running it increases as a function of distance but decreases as a function of speed (range 0.20–0.50; Zamparo et al., 2016, 2019). A greater relative importance of the constant speed phase, associated to a better exploitation of the elastic energy-saving mechanisms, is probably responsible for the higher AE at the longer shuttle distances.

Internal and external power output during the sprint running acceleration phase were recently investigated by Pavei et al. (2019): they account for 41% and 59% of total power output, respectively; internal power is, thus, an important component of total power, as in shuttle running. No data of CoT are reported in the literature for sprint running, essentially because of the difficulty of separating the acceleration phase from a (necessary and following) deceleration phase. A way to estimate the energy demands in sprint running is based on the concept of 'equivalent slope': CoT of level accelerated running can be inferred by considering it an analogue of running uphill at constant speed, a condition for which CoT as a function of the incline is known (Minetti & Pavei, 2018). When the runner accelerates (when

TABLE 1 Mechanical and energetic parameters of running and muscle–tendon function in different experimental conditions

Condition		CoT (J kg^{-1} m^{-1})	W_{EXT} (J kg^{-1} m^{-1})	W_{INT} (J kg^{-1} m^{-1})	AE	Muscle–tendon function: Energy saving	Power amplifier	Power absorption
Constant-speed level running[a]	*v* ↑	=	↓	↑	↑	↑	/	/
Constant-speed running on incline[b]	*i* ↑	↑	↑	=	↓	↓ *	↑	/
Constant-speed running in low gravity[c]	*g* ↓	↓	↓	↓	↓	↓ †	/	/
Shuttle running[d]	*v* ↑	↑	↑	↑	↓	↓	↑	↑
	d ↑	↓	↑	↑	↑	↑ ‡	↑ ‡	↑ ‡
Sprint running[e]	*a* ↑	↑	↑	↑	↓	↓	↑	↓

Arrow direction indicates a parameter's response (e.g., when linear running velocity increases, AE increases as well). Experimentally determined response (increase/decrease) is represented by black arrows while grey arrows indicate the expected/estimated response of a parameter (e.g., AE in sprint running). /: impaired function (e.g., during constant speed level running, the muscle–tendon units are not working as power amplifier or absorber). *During uphill and downhill running, the elastic elements operate as power amplifiers and power absorbers, respectively (e.g., the capability of the muscle–tendon units to operate as energy savers is thus reduced). Note that the expected response of the energy saving function coincides with that of AE. †Despite constant-speed running being characterized by an energy-saving mechanism, in a low gravity environment, apparent efficiency decreases due to an impairment of the elastic elements in the stretch-shortening cycle (lower gravity acceleration decreases the forces acting along the tendon, reducing the amount of strain). ‡Despite the acceleration and the deceleration phase of a shuttle run being characterized by a power amplification and a power absorption mechanism, respectively, apparent efficiency increases as a function of shuttle distance because part of the shuttle could be performed at constant speed allowing the muscle–tendon units to operate as energy savers. Representative references: [a]Cavagna & Kaneko (1977); [b]Minetti et al. (1994); [c]Pavei et al. (2015); [d]Zamparo et al. (2019); [e]Pavei et al. (2019).

Abbreviations: *a*, acceleration; AE, apparent efficiency; CoT, energy cost of transport; *d*, distance; *g*, acceleration of gravity; *i*, incline; *v*, velocity; W_{EXT}, external mechanical work; W_{INT}, internal mechanical work.

the equivalent slope increases), AE decreases reaching a value of about 0.25 at (positive) equivalent slopes >0.35, since only positive work is performed in these conditions. This suggests that, as in shuttle running, the elastic energy-saving mechanism is impaired in the sprint running acceleration phase, as indicated also by other studies (e.g., Lai et al., 2016).

These recent data on sprint and shuttle running allow for a deeper understanding of the interplay between AE and muscle–tendon responses (Table 1). Indeed, during short shuttles, accelerated running or when running on a slope, the lower limb's muscle–tendon units operate as power amplifiers, rather than energy savers, generating net positive mechanical energy (Roberts & Azizi, 2011): since tendons cannot generate net positive work, the muscle's fascicle work must increase, as well as the metabolic demands, and AE is bound to decrease.

The association between AE and muscle–tendon responses was recently investigated by Monte and co-workers (2020) who observed a positive relationship between AE and the mechanical work performed by the series elastic components of the gastrocnemius medialis during steady-state running at different speeds (2.8–4.4 m s^{-1}): the larger the speed, the larger the tendon work and AE. The intercept of this relationship corresponds to a value of AE of 0.33, supporting previous suggestions that AE values close to muscle efficiency values should be expected when no elastic energy can be stored in the elastic elements. Thus, determining AE is a way to get insight into muscle–tendon function, providing important information about the role of elastic structures in determining the energy cost of human locomotion.

5 | ASYMMETRIES IN PATHOLOGICAL GAIT

G. Fábrica, V. Silva-Pereyra

Asymmetries associated with pathologies can significantly alter mechanical work during walking. Therefore, the quantification of mechanical work can provide relevant information for interventions aimed at improving gait. However, studies to date are scarce and limited to a few populations.

Subjects with unilateral lower limb amputation present a high CoT, which tends to decrease with increasing speed (Bona et al., 2019; Detrembleur et al., 2005). Detrembleur et al. (2005) found that pendulum-like recovery increased with gait speed and remained close to typical values in vascular transtibial and post-traumatic transfemoral amputees, while CoT was two times greater at low speeds and 0.5 times greater at intermediate speeds. Further, the AE is reduced due to similar W_{TOT} values for amputees and healthy

TABLE 2 Mechanical and energetic parameters of walking (normal and pathological gait) in different experimental conditions

		CoT ($J\ kg^{-1}\ m^{-1}$)	W_{EXT} ($J\ kg^{-1}\ m^{-1}$)	W_{INT} ($J\ kg^{-1}\ m^{-1}$)	AE	%R
Healthy subjects						
Constant-speed level walking (at $v \geq$ OWS*)[a]	v ↑	↑	↑	↑	↓	↓
Constant-speed walking on incline[b]	i ↑	↑	↑	=	↓	↓
Constant-speed walking in low gravity[c]	g ↓	↓	↓	↓	↓	↓
Comparisons with healthy controls (constant-speed level walking)						
Unilateral amputees[d]	For $v <$ OWS	↑	=	↑	↓	=
Stroke patients[e]	For $v <$ OWS	↑	↑	↑	↓	↓
Obese population[†,f]	For $v <$ OWS	↑ ‡	=	=	↓	↑ ‡
	For $v >$ OWS	↑	↑	=	↓	↑

In the upper part of the table (healthy subjects), arrow direction indicates a parameter's response (e.g., when level walking velocity increases, W_{INT} increases as well); in the lower part of the table (pathological gait), arrow direction indicates if a parameter is increased/decreased in comparison with healthy subjects. Note that in healthy subjects, the response of %R mostly coincides with that of AE. *Because of the U-shaped CoT versus v relationship, it is important to specify whether the changes in v, i and g refer to the descending or ascending limb: in this case, data are reported for the ascending limb ($v \geq$ OWS). Patients with impaired locomotory function generally walk at speeds lower than the OWS of controls, and therefore comparisons are mainly reported for the descending limb. †In obese individuals, W_{EXT} and W_{INT}, when expressed in $J\ m^{-1}$ (absolute values), are always larger than in healthy controls. ‡Significant difference only in class III obesity. Representative references: [a]Cavagna & Kaneko (1977); [b]Minetti et al. (1993); [c]Pavei et al. (2015); [d]Bona et al. (2019); [e]Balbinot et al. (2020); [f]Fernández Menéndez et al. (2020). Abbreviations: %R, energy recovery; AE, apparent efficiency; CoT, energy cost of transport; g, acceleration of gravity; i, incline; OWS, optimal walking speed in healthy subjects; v, velocity; W_{EXT}, external mechanical work; W_{INT}, internal mechanical work.

individuals, although the W_{EXT} is lower at fast speeds in amputees (Table 2). These results suggest that the gait velocity is a useful clinical indicator of rehabilitation staging, and the velocity increment should be emphasized during the rehabilitation period.

Significant changes observed in gait kinematics of stroke patients (Farris et al., 2015) produced vertical oscillations of the BCoM, increasing the W_{EXT}. The W_{TOT} has an increase proportional to the increase in CoT. The W_{INT} is two times higher in stroke patients walking slowly (0.28–0.69 m s^{-1}) and only slightly higher in fast stroke patients (0.69–1.11 m s^{-1}) in comparison to healthy individuals (Detrembleur et al., 2003). Moreover, W_{INT} is mainly performed during the swing phase to move forward the lower limb, showing higher values for the unaffected side than for the affected side.

Two recent studies analysed the energy transfer within the different phases of the gait cycle in stroke patients. In the first article (Fábrica et al., 2019), the pendular mechanism's alteration was associated with a longer duration of the double support phase. In Balbinot et al. (2020), the higher W_{INT} was primarily related to exaggerated movements between BCoM and upper- and lower-body non-paretic segments, the paretic lower limb also contributing to increase vertical internal work. They concluded that energy conservation was likely optimized by the paretic lower limb, acting as a rigid shaft. The non-paretic limb pushed BCoM forward at a slower walking speed. W_{INT} production following a stroke is, thus, characterized by non-paretic upper-limb compensation and an exaggerated lift of the paretic leg.

Future research considering mechanical work may contribute relevant information in patients with different pathologies. Comparisons of the values obtained on treadmill and floor for these variables at different speeds may be of interest for gait rehabilitation. Special care should be given to the values of anthropometric tables used in the study of particular populations. A key point in future work is an in-depth discussion of segmental actions and the transfer between different limb segments.

6 | OBESITY

D. Malatesta, P. E. di Prampero

Walking is the most popular physical activity to prevent obesity. In obese individuals, the bioenergetics and biomechanics of walking show several differences compared to non-obese subjects. Indeed, the CoT is higher (~+10%) in obese children (Oliveira et al., 2020), adolescents (Peyrot et al., 2009) and adults (Browning & Kram, 2007; Fernández Menéndez et al., 2019, 2020; Peyrot et al., 2009), indicating that body mass is a critical factor affecting the poorer economy in this population. Studies on the role of mass distribution have shown that the cost of adding a given mass to the limbs is appreciably greater than adding it to the BCoM and that this response becomes more pronounced as the loads are moved distally (Myers & Steudel, 1985). The effect of mass distribution on CoT was attributed to an increase in W_{INT} in lower and upper limbs (Browning, 2012). In obese children and adults, the 'additional mass distribution' does not affect CoT proportionally due to its most proximal location (Fernández Menéndez et al., 2020; Oliveira et al., 2020). Increased CoT may lead to an increased relative effort during walking (Browning et al., 2006) and fatigue during daily life in obese subjects, and thus contribute to a decreased free-living walking distance (Levine et al., 2008), and an increment in the daily sitting time (+2.5 h day^{-1}) (Levine et al., 2005) globally inducing lower non-exercise activity thermogenesis (NEAT; the energy expenditure associated to the free daily activities) (Levine et al., 2005). However, a decreased CoT is related to an increase in NEAT after a walking training programme (Hunter et al., 2015) suggesting that improving the walking economy can be a useful strategy to prevent and treat obesity.

Browning and Kram (2007) argued that the gait pattern changes (larger lateral movement during swing phase) due to the larger body mass and heavier lower limbs in obese individuals should induce an increase (>80%) in CoT greater than the observed 10%. The same authors suggested that, as observed in African women carrying loads on their heads (Heglund et al., 1995), this relatively small increase in CoT in obese individuals may be due to a more effective pendular transduction recovery (Browning & Kram, 2007). This response has indeed been observed in adults with class III obesity (body mass index >40 kg m^{-2}) characterized by significantly higher recovery than lean counterparts during walking from 0.55 to 1.67 m s^{-1} (+9.5% averaged values across all speeds) (Fernández Menéndez et al., 2020), whereas in individuals with class I and II obesity, energy recovery was higher (+7%) only at fast speeds (Browning et al., 2009; Fernández Menéndez et al., 2019; Malatesta et al., 2009). These findings seem to suggest that the levels of adiposity may be involved in the pendular exchange optimization; however, further studies are needed to confirm this suggestion. The more skilful recovery in obese individuals was achieved by applying a toe-off impulse immediately before heel strike. This response may reduce the amount of dissipative collision loss allowing individuals with obesity to decrease the mass-normalized W_{EXT} needed to redirect the BCoM (Fernández Menéndez et al., 2019, 2020). This change in the gait pattern may also be responsible for a reduced maximum possible elastic energy usage (−16%) during walking in obese individuals due to a decreased maximum possible elastic energy release during the double contact phase (Fernández Menéndez et al., 2019).

Since W_{EXT} and inverted pendulum mechanism seem to be only marginally involved in the increased net CoT, W_{INT}, the second component of W_{TOT}, may be responsible for this extra-cost of walking in obese, as compared with lean, individuals (see Table 2). However, it has been shown that mass-normalized W_{INT} was unaffected by obesity and was not involved in the higher net CoT in obese adults (Fernández Menéndez et al., 2020) and children (Oliveira et al., 2020). Obese adults may adapt their gait pattern in order to reduce lower limbs W_{INT}, thus compensating for the larger W_{INT} performed by other body segments (upper limbs and head-trunk), hence limiting the overall increase of W_{INT}. Regardless of the lower mass-normalized W_{EXT} arising from these gait adaptations, W_{TOT} remained similar to that of lean individuals. Therefore, the locomotor efficiency in obese individuals is reduced because of their higher CoT (see Table 2). This may be related to a more erect gait pattern requiring larger muscle activation and/or requiring the muscles to operate under less favourable lengths and/or velocities and hence producing poorer muscle efficiency in obese than in lean individuals.

7 | DISCUSSION

The pendulum-like model of walking predicts that CoT will be the lowest and AE the highest when energy recovery is maximized (in healthy subjects, this occurs around the optimal walking speed). The bouncing model of running predicts that AE will increase with running speed along with the increase in tendon elastic recoil, limiting the increase in CoT that would otherwise occur. The expected behaviour of the energy saving function indeed coincides with that of AE in running (Table 1) and the expected behaviour of recovery mainly resembles that of AE in walking, at least in healthy subjects (Table 2). This is not necessarily the case in pathological gait where an increased CoT, compared to healthy controls, is not always attributable to a decrease in recovery. As an example, in the obese population, the pendulum-like recovery mechanism is actually improved (Fernández Menéndez et al., 2019, 2020), whereas, in other movement disorders (amputees, Parkinson's disease, stroke and others), the higher CoT can be attributed, at least in part, to an impairment of the pendulum-like recovery mechanism since these patients tend to walk at speeds lower than the optimal walking speed (Bona et al., 2019; Detrembleur et al., 2005; Dipaola et al., 2016; Fábrica et al., 2019).

Furthermore, increased and asymmetric internal work production from lower limbs hamper the mobility of people with neurological disorders, as in stroke, but with substantial compensations between paretic and non-paretic sides (Balbinot et al., 2020), thus reducing the expected increase in (overall) W_{TOT} and CoT in this population.

Locomotion under conditions of acceleration or positive inclination leads to higher CoT values than under deceleration or negative gradient due to the parallel changes in W_{TOT} (higher in the former compared to the latter condition) and the specific efficiencies of positive and negative work. In addition, the pendulum-like mechanism of walking and the elastic recoil in running are impaired in these situations due to an asymmetry in the production of positive and negative power (Dewolf et al., 2016, 2017; Zamparo et al., 2019). W_{INT} is deeply affected by acceleration (Zamparo et al., 2019) but not by gradient, where the role of vertical W_{EXT} is fundamental in determining the response of CoT and AE (Dewolf & Willems, 2019; Minetti et al., 1993, 1994). Similarly, due to an inevitable reduction in PE, W_{EXT} is decreased in low gravity locomotion (Pavei et al., 2015); this mechanical response ultimately reduces the range of walking speeds that can be used in low gravity (Cavagna et al., 1998; Pavei et al., 2015). The W_{EXT} during walking is also predominantly affected by body mass (obesity) similar to that observed in hyper-gravity (Cavagna et al., 2000). In low gravity, a decrease in CoT is observed, especially in bouncing gaits, although a reduction of AE (approaching muscle efficiency values) due to a decrease of elastic contribution is observed (Pavei et al., 2015). Further, the historical finding of Margaria & Cavagna (1964) indicating a 'jumping gait' as the preferred gait on the Moon has been confirmed by recent studies showing that the biomechanical aspects and enhancing grip control on slippery grounds when skipping (Minetti, 1998) are enhanced with a decrease in CoT in low gravity (Pavei et al., 2015; Pavei & Minetti, 2016).

These considerations confirm the role of integrative mechanisms to minimize energy expenditure and support the notion that measuring only the metabolic counterpart (CoT), as well as not considering W_{INT} in the computation of W_{TOT}, prevents an appropriate energy assessment in human locomotion. It is also worth considering that AE is a product of the combined effect of mechanical (W_{INT} and W_{EXT}) and metabolic factors (CoT) and is thus a key contributor to our understanding of metabolic cost in human locomotion.

7.1 | Methodological considerations

'Fenn's approach' is not the only method for calculating mechanical work in locomotion, although it was the first (and is still the most used) approach to relate metabolic energy expenditure and mechanical work.

From Winter's formulation (Winter, 1979) and successive adaptations, joint work calculations are usually focused on the work performed at lower limbs joints; with this method, the estimation of total muscle work depends on the assumed energy transfer among multi-articular muscles and/or segments (Williams & Cavanagh, 1983). The cost of generating force (Kram & Taylor, 1990) was another method that gave promising results on the explanation of 'running cost' on level surfaces but less so on gradients and was subsequently updated to take into account the antero-posterior (Chang & Kram, 1999) and medio-lateral work (Arellano & Kram, 2012, 2014). The collisional model (Kuo et al., 2005; Ruina et al., 2005) is based on the work to redirect BCoM at each foot contact (which is qualitatively close to W_{EXT}), which is usually added to the work performed against the leading leg in walking double support (Donelan et al., 2002; Meurisse et al., 2019) or against soft tissues (Riddick & Kuo, 2016). These methods do not consider the work to accelerate the limbs (W_{INT}), although this has been shown to be relevant from metabolic measurements (Marsh et al., 2004).

'Fenn's approach' is not free from limitations either. The separate calculation (by means of energy increases) and final summation of W_{INT} and W_{EXT} could overestimate W_{TOT} (see Figure 1). This point can be illustrated by a simple physical model, resembling the reciprocal swing of limbs, where we expect zero extra work to keep the limbs moving: two passive frictionless pendula, attached to a cart at the same pivot point, swinging forever half a cycle out-of-phase. Actually, the calculated mechanical work shows a non-zero amount of W_{INT} for the swinging pendula, and as far as the system centre of mass is concerned, the fluctuations in PE (vertical movement) are not compensated by a reciprocal KE time course, which results in a non-zero W_{EXT}.

The effects of such a bias, in real locomotion, will depend on gait type and on the fractional mass of limbs with respect to the whole body, but the exact amount still needs to be substantiated. The new measurements of frictional W_{INT} (Minetti et al., 2020), by completing the work balance of locomotion, should help shed light on the interplay between W_{INT} and W_{EXT} in different gait paradigms (Figure 1). Finally, there is still no gold standard in the literature that deterministically considers all parts of mechanical work (and their 'interdependence'). As shown in this review and many previous papers, when W_{TOT} is converted into the metabolic counterpart (CoT), reasonable and insightful results are obtained, indirectly indicating a small bias and suggesting acceptable reliability of 'Fenn's approach'.

It should be mentioned that all the metabolic estimates derived from different mechanical methods (Fenn's method included) are subject to an additional bias as they cannot include the effects of isometric contractions or co-contractions: these activities do not perform work by definition but require metabolic energy to be carried out.

8 | CONCLUDING REMARKS

The importance of taking into account mechanical work for a better understanding of the determinants of energy expenditure in human locomotion is beyond doubt. 'Fenn's approach' has shed light on many aspects of human locomotion and has proved to be relevant in explaining CoT differences due to speed, gradient, size and gravity, but many aspects remain unresolved. The recent *in vivo* quantification of new aspects that should be included in the computation of W_{TOT} (such as the frictional internal work and the elastic contribution) impacting the computation of AE deserve future research and should improve our knowledge on the mechanical–bioenergetic interaction during walking (normal and pathological gait) and running, as well as in sport science and space exploration applications.

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COMPETING INTERESTS

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

L.A.P.-T. and P.Z. jointly conceived the review paper idea. All authors contributed to writing and editing the manuscript. Section 2: A.H.D. and P.A.W.; section 3: A.E.M. and G.P.; section 4: P.Z. and A.M.; section 5: G.F. and V.S.-P.; section 6: D.M. and P.E.diP. 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.

DATA AVAILABILITY STATEMENT

Data sharing not applicable – no new data generated.

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