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More than energy cost: multiple benefits of the long Achilles tendon in human walking and running

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ABSTRACT

Elastic strain energy that is stored and released from long, distal tendons such as the Achilles during locomotion allows for muscle power amplification as well as for reduction of the locomotor energy cost: as distal tendons perform mechanical work during recoil, plantar flexor muscle fibres can work over smaller length ranges, at slower shortening speeds, and at lower activation levels. Scant evidence exists that long distal tendons evolved in humans (or were retained from our more distant Hominoidea ancestors) primarily to allow high muscle–tendon power outputs, and indeed we remain relatively powerless compared to many other species. Instead, the majority of evidence suggests that such tendons evolved to reduce total locomotor energy cost. However, numerous additional, often unrecognised, advantages of long tendons may speculatively be of greater evolutionary advantage, including the reduced limb inertia afforded by shorter and lighter muscles (reducing proximal muscle force requirement), reduced energy dissipation during the foot–ground collisions, capacity to store and reuse the muscle work done to dampen the vibrations triggered by foot–ground collisions, reduced muscle heat production (and thus core temperature), and attenuation of work-induced muscle damage. Cumulatively, these effects should reduce both neuromotor fatigue and sense of locomotor effort, allowing humans to choose to move at faster speeds for longer. As these benefits are greater at faster locomotor speeds, they are consistent with the hypothesis that running gaits used by our ancestors may have exerted substantial evolutionary pressure on Achilles tendon length. The long Achilles tendon may therefore be a singular adaptation that provided numerous physiological, biomechanical, and psychological benefits and thus influenced behaviour across multiple tasks, both including and additional to locomotion. While energy cost may be a variable of interest in locomotor studies, future research should consider the broader range of factors influencing our movement capacity, including our decision to move over given distances at specific speeds, in order to understand more fully the effects of Achilles tendon function as well as changes in this function in response to physical activity, inactivity, disuse and disease, on movement performance.

Key words: gait, locomotion, elastic energy, economy, human evolution, muscle function, muscle–tendon unit.

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I. INTRODUCTION

Muscle–tendon units (MTUs), in which relatively long, compliant tendons are arranged in series with a work-producing muscle, are common in the distal regions of limbs of terrestrial, especially cursorial, animals (Alexander, 2002). In humans, the long Achilles tendon is located distal to the plantar flexor muscles that cross the ankle and plays a critical role in activities such as walking, running, and jumping. These tendons differ from more proximally located tendons, not only in their length but also their strain energy storage capacity (higher), failure/injury rating (higher force and strain yield points), and hysteresis (lower) or elastic modulus (higher) (Thorpe *et al.*, 2015). The Achilles tendon in particular also differs markedly from the shorter, stiffer foot extensor tendon found in other primates (Vereecke *et al.*, 2005), suggesting that it plays an important locomotor role that is distinct from that of our closest relatives and hinting at its evolutionary importance.

For high-speed movement tasks such as sprint running, jumping, and throwing, long in-series tendons help to overcome the shortening velocity-related limitations of muscular force production (Arnold *et al.*, 2013; Farris & Sawicki, 2012; Lai *et al.*, 2014; Caldwell, 1995). Such tendons can store strain energy that is produced relatively slowly by working muscles, or by gravity or inertia when external forces induce joint rotation whilst the muscles operate at relatively slow velocities (e.g. during ground contact in constant-speed running) and then release that energy at higher speeds as the tendon recoils later in the movement (Bobbert, Huijing & van Ingen Schenau, 1986; Farris & Sawicki, 2012). This ‘catapult’ effect allows the required force levels to be achieved at higher muscle–tendon shortening speeds than could be provided by muscles alone, or greater muscle forces to be produced at a given MTU shortening speed [for review, see Alexander (2002); Roberts, 2016]. Muscle power amplification through the storage and release of elastic strain energy is thought to be substantial [~1.3–2.0-fold in non-latched systems under inertial and gravitational loads (Galantis & Woledge, 2003; Paluska & Herr, 2006; Sawicki, Sheppard & Roberts, 2015)] and to contribute decisively to performance of high-speed movements. This would have been critical to our acquisition of the ability to move at high speeds on the rare occasions it was needed, such as when chasing prey, avoiding capture or, unique to humans, swinging an object or releasing a projectile with both speed and accuracy using the upper limbs (Young, 2003; Isaac, 1987). That such tendons would provide advantage in these (often) life-threatening scenarios would submit them to evolutionary pressure, and a longer tendon may thus have been inevitable. Following this, humans also subsequently would have developed efficient movement strategies that best utilise a compliant MTU during slower-speed locomotion (walking and running) in order to retain the ability to function well in rare moments of high-speed locomotion.

Humans, however, are relatively poor sprinters relative to other animals (Carrier, 1984) and perform few high-speed movements in activities of daily living. We also have a lower percentage of fast-twitch fibres in lower-limb propulsive muscles, which provide the highest muscle power outputs, compared to other animals, and even compared to our closest relatives, the chimpanzees (*Pan* spp.) (de Diego *et al.*, 2020; O’Neill *et al.*, 2017). Therefore, it may be considered unlikely that the Achilles tendon evolved (or was retained) for the main purpose of power amplification. Instead, the plantar flexor MTU (and its analogue in many other cursorial species) is more commonly recruited during lower-speed activities such as walking and jogging. Economical walking and running are thought to have provided an important biological advantage to humans over other animals as well as our primate relatives (Carrier, 1984; Liebenberg, 2006; Steudel-Numbers & Wall-Scheffler, 2009; Hora *et al.*, 2022), especially as food sources became sparse and travel distances greater from around 8–5 million years ago (Mya) (Cerling, Ehleringer & Harris, 1998; Cerling *et al.*, 1997). Therefore, a long-standing hypothesis is that hominin transition towards competent bipedalism, and the anatomical and morphological adaptations that allowed it, served to reduce locomotor metabolic cost as compared to non-bipedal lineages including those of modern chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) (Rodman & Mchenry, 1980). As human walking is at least as efficient as other animal species (Rubenson *et al.*, 2007), this evolution appears to have been relatively successful.

Important to this ‘locomotor cost’ hypothesis is that the long, elastic Achilles tendon plays an important energy-storing role that reduces the cost of muscle contraction. Achilles tendon elongation and subsequent recoil during the stance phase of walking and running increases the MTU excursion range relative to muscle length change, reducing the need for muscles to perform mechanical work over large muscle excursions or at fast muscle shortening speeds, and thereby reducing the metabolic cost of force production (Bohm *et al.*, 2019; Fletcher, Pfister & Macintosh, 2013; Lichtwark & Wilson, 2007; Pontzer, Raichlen & Sockol, 2009). During such quasi-isometric contractions, the force–velocity relationship of muscle largely dictates the *maximal* force at any given shortening velocity. However, during walking and running, in which force is generated *submaximally*, shortening velocity dictates the level of activation required to generate a given submaximal force (Fletcher *et al.*, 2013; Stainsby & Lambert, 1979). Reducing the required activation level subsequently reduces the active muscle volume and the considerable metabolic cost of activation (Bergstrom & Hultman, 1988; Chasiotis, Bergstrom & Hultman, 1987; Stainsby & Lambert, 1979). Together, these factors present a model in which the stretch–recoil action of the Achilles tendon optimises the force–velocity profile of the triceps surae muscles to reduce energetic cost for a given locomotor velocity (see Fig. 1). Additionally, the isometric force produced by a muscle depends on its sarcomere length, so an optimal muscle length exists (Gordon, Huxley & Julian, 1966) and muscle contraction at longer or shorter lengths than optimum results in a lower isometric muscle force (Gordon *et al.*, 1966; Ramsey & Street, 1940). During walking or running, the activation level necessary to produce a given muscle force can be minimised if the muscle operates near optimal length (Fig. 2). This optimum may (Holt & Azizi, 2016; Ichinose *et al.*, 1997; Rack & Westbury, 1969; Rassier, MacIntosh & Herzog, 1999), or may not (MacDougall *et al.*, 2020), shift to longer lengths with reduced levels of activation and/or force. In keeping the level of activation low, muscle metabolic cost is also low. A higher metabolic cost is seen at shorter than optimal muscle lengths (Hilber, Sun & Irving, 2001) since active force production for a

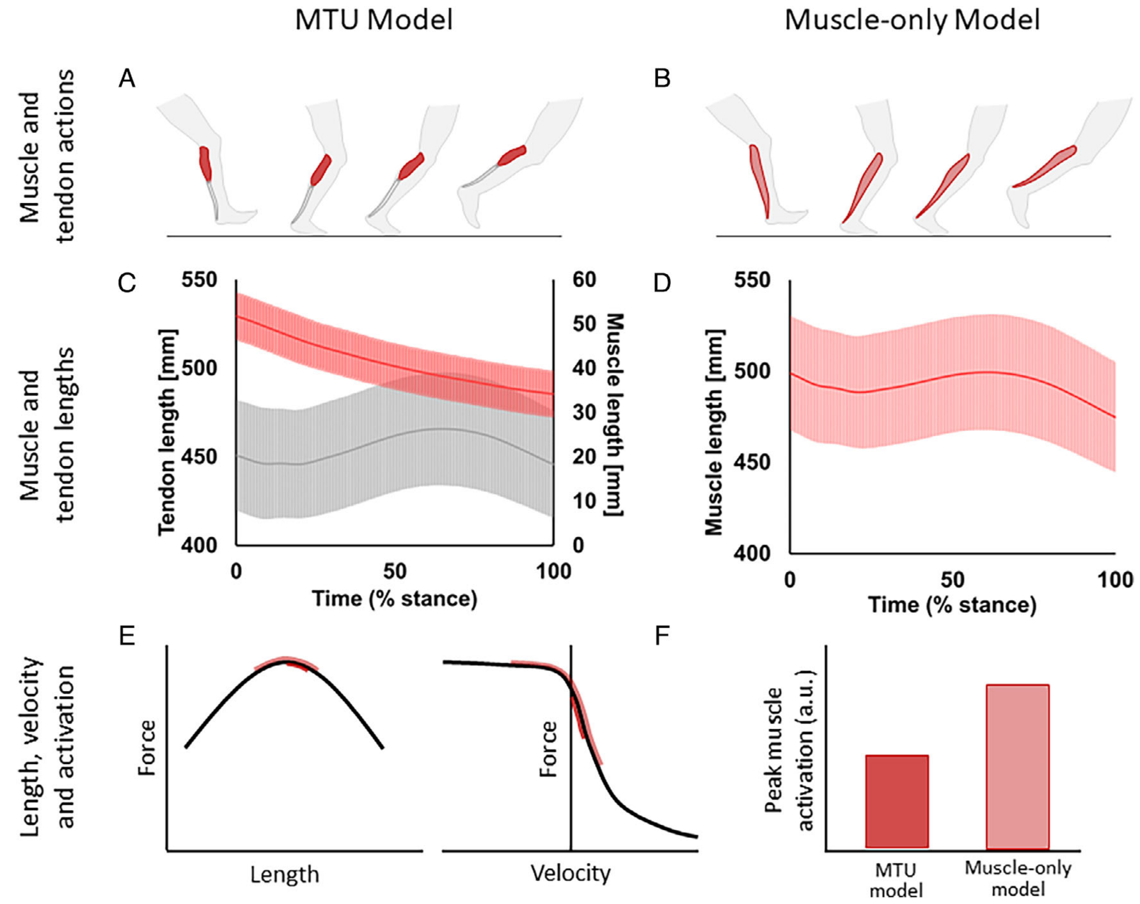

Fig. 1. (A–D) Effect of a muscle–tendon unit (MTU; left column) and muscle-only (right) model of muscle and tendon function. (A, B) Pictorial representations of MTU and muscle-only models. (C, D) Muscle- and tendon-specific length changes for MTU (C; red = muscle, grey = tendon) and muscle-only (D; pink = muscle) models during stance. In the muscle-only model, MTU length change must be accommodated entirely by the muscle, so the magnitude and velocity of shortening is higher. (E) Operating lengths (left; force–length relationship) and velocities (right; force–velocity relationship) of a muscle working according to MTU (red) and muscle-only (pink) models. (F) The impact of additional shortening and shortening velocity on the required level of activation [greater muscle activation in the muscle-only (pink) than MTU (red) model]. a.u., arbitrary units.

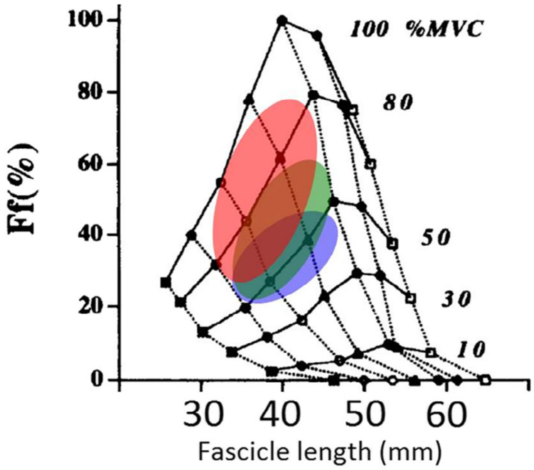

Fig. 2. Force (Ff)–fascicle length relation as a function of level of muscle force, expressed as percent of maximal voluntary contraction (%MVC). Modified from Ichinose *et al.* (1997). Blue, green, and red circles indicate operating ranges for highly trained males, trained females, and trained males, respectively, while running at 75–95% of the speed associated with the lactate threshold whose metabolic cost of running differed concomitantly. Optimal fascicle length is the length at which maximal force is achieved. In running, metabolic cost can be minimised if the muscle operates near this optimal length. Data from Fletcher & MacIntosh (2015).

given level of activation is reduced (Hill, 1953; Gordon *et al.*, 1966).

The tendon operates in the toe region of its recoil force–length relation when muscle forces are relatively low, i.e. it is relatively 'slack' at short MTU lengths (Huijing, van Lookeren Campagne & Koper, 1989), so muscle shortening is required to stretch the tendon before appreciable force is transmitted and requisite joint moments are produced (Fukutani *et al.*, 2014; Herbert *et al.*, 2015). For a given MTU length, higher forces evoke greater tendon stretch and a corresponding additional muscle shortening. This additional shortening could result in sarcomere length being shorter than optimum or cause shortening-induced force depression, the phenomenon in which active muscle force is depressed during shortening to a given length compared to the isometric force otherwise generated at that same length (Abbott & Aubert, 1952; Edman, Caputo & Lou, 1993; Herzog & Leonard, 2000; Rassier & Herzog, 2004). Both factors would necessarily increase the muscle activation level required to reach a given force (Ichinose *et al.*, 1997), thus increasing metabolic cost, and also increase the rate of activation (i.e. rate of force development) to allow the greater length change in a given time, incurring an additional metabolic cost (Doke & Kuo, 2007; van der Zee & Kuo, 2021).

The capacity to generate the necessary forces in propulsive muscles like the triceps surae is a major factor limiting upright bipedal walking in other primates (Thorpe, Crompton & Wang, 2004). However, the ability to store and release elastic energy in the lower limb is also substantially less in other primates than in humans and would strongly increase the necessary forces during bipedal locomotion if the relevant force capacity even existed (Sellers *et al.*, 2010). This results directly (but not exclusively) from most primates having short Achilles tendons (Hanna & Schmitt, 2011; Kuo *et al.*, 2013). For example, the Achilles tendon spans ~65% of the length of the plantar flexor–Achilles MTU in humans (Prejzner-Morawska & Urbanowicz, 1981; Frey, 1913) but only ~7.5% in chimpanzees (Rauwerdink, 1991) and <10% in bonobos (Vereecke *et al.*, 2005). While this MTU design, with longer muscle fibres, may assist arboreal locomotion by permitting a greater ankle joint range of motion and for an animal to remain closer to the vertical substrate (DeSilva, 2009), it is clearly detrimental for bipedal locomotion. Instead, current evidence is taken to suggest that long Achilles tendons may have evolved in the ancestors of modern humans after divergence from the other great apes, with recent anatomical evidence that the *Australopithecus afarensis* (3.9–2.9 Mya) Achilles tendon possibly spanned ~63% of MTU length (mean of two specimens) (McNutt & DeSilva, 2020). *Ipso facto*, the triceps surae muscles, and their constituent fibres, would have been necessarily shorter, reducing the number of active in-series sarcomeres during contraction and thus reducing metabolic cost. This evidence is consistent with the theory that the long, in-series, distal lower-limb tendon is an important and mostly unique adaptation in humans over other great apes, providing an important functional benefit during activities such as walking. An alternative view is that long Achilles tendons may be ancestral for Hominoidea, being still present in old world monkeys (e.g. baboons, gibbons) despite contributing little to positive mechanical work during ground-based locomotion. They may therefore have been 'retained' in *Homo*, although further evolution of the tendon also seems to have occurred (Aerts *et al.*, 2018). Regardless of its evolutionary path, the long Achilles tendon is unique amongst primates, contributes strongly to the work performed during locomotion, and is considered an important evolutionary asset to economical upright locomotion.

Nonetheless, contributions from elastic energy storage–return in walking appear to be modest when compared to those at higher locomotor speeds (Lichtwark & Wilson, 2007; Sawicki, Lewis & Ferris, 2009). Substantial mechanical energy savings are observed during running (Bramble & Lieberman, 2004; Lichtwark & Wilson, 2007; Sellers *et al.*, 2010), with mechanical energy savings of ~35% estimated to arise from energy storage–return in the Achilles tendon alone (Ker *et al.*, 1987). Humans are unique amongst primates in our capacity for endurance running. The ability to run over long distances with low locomotor cost, e.g. during persistence scavenging and hunting, is speculated to have been of great evolutionary benefit (Bramble & Lieberman, 2004; Hora *et al.*, 2022). The benefit of economical running would have driven further the progression towards bipedalism and triggered the anatomical and morphological adaptations required for efficient locomotion. This theory is consistent with the observation of distinct anatomical differences between modern humans and Neanderthals such as a shorter calcaneal tuberosity in humans (Raichlen, Armstrong & Lieberman, 2011), indicating a shorter plantar flexor moment arm (Miller & Gross, 1998) that would have increased tendon forces to allow greater elastic energy storage in the Achilles tendon, at least during running (Raichlen *et al.*, 2011; Scholz *et al.*, 2008). Short Achilles moment arms also minimise muscle shortening for a given joint rotation (Nagano & Komura, 2003), reducing the metabolic cost of shortening. Hypothetically, a low locomotor cost may be a key factor influencing the progression towards bipedalism (and particularly running) in humans as well as the simultaneous evolution of distinct anatomical features such as the long Achilles tendon.

II. LIMITATIONS OF, AND ALTERNATIVES TO, THE LOCOMOTOR COST HYPOTHESIS

(1) Is locomotor cost the key?

Some limitations exist within this 'locomotor cost' hypothesis. For example:

(1) Some other great apes have relatively long Achilles tendons and yet are almost completely arboreal and have never been known to demonstrate terrestrial endurance capacity. For example, the Achilles tendon of gibbons (*Hylobates lar*) spans 35–45% of muscle–tendon length and is therefore much longer than in the chimpanzee and bonobo (Rauwerdink, 1991), consistent with the notion that long, distal Achilles tendons in humans have been evolutionarily maintained, rather than (re-)acquired over time (Aerts *et al.*, 2018).
(2) Although faster runners may present with better running economy (Fletcher, Esau & Macintosh, 2009) and the best marathon runners (e.g. those approaching sub-2 h for the 42.1 km marathon) present with exceptional running economy (Jones *et al.*, 2021; Lucia *et al.*, 2006), running performances and economy are not always strongly associated in elite runners (Mooses *et al.*, 2015). Furthermore, performance times in many endurance running events tend to be only rather moderately correlated with low locomotor cost; for example, between 25 and 65% in among-athlete 10-km race time variation in well-trained distance runners (Conley & Krahenbuhl, 1980; Morgan, Martin & Krahenbuhl, 1989; Powers *et al.*, 1983) and <10% of 5-km time variation (Nummela *et al.*, 2006) can be explained by differences in running economy alone. In shorter races (i.e. those above the anaerobic threshold; Svedahl & MacIntosh, 2003), locomotor cost likely plays a much smaller role in dictating performance compared to maximal oxygen consumption ($\dot{V}O_{2\max}$) capacity or fractional utilisation of $\dot{V}O_{2\max}$. Running economy is also sometimes poorly correlated with performance over the longer marathon and ultramarathon distances (Davies & Thompson, 1979; Millet *et al.*, 2011*a*; Sjodin & Svedenhag, 1985), and marathon performance is better predicted when $\dot{V}O_{2\max}$, running economy, and fractional utilisation are considered together (Jones *et al.*, 2021).
(3) In at least some locomotor tasks, we tend to choose a cadence that is suboptimum from an energetics perspective [e.g. we may transition from walking to running and *vice versa* despite incurring an increased energetic cost (Hreljac, 1993; Tseh *et al.*, 2002)], which in some cases may allow the major propulsive muscles to work at shortening speeds commensurate with peak power production (e.g. in bicycling; Brennan *et al.*, 2019), or we might choose to optimise gait stability at the expense of energetic cost (e.g. when walking downhill; Hunter, Hendrix & Dean, 2010), or choose to locomote under conditions of lower total muscle activation, and presumably sense of effort (crouched walking), rather than conditions requiring higher energetic cost (e.g. walking uphill) (McDonald *et al.*, 2023). That is, we may choose to move under conditions that are energetically more expensive if some other outcome (e.g. power, stability, sense of effort) is optimised, even in prolonged, submaximal exercise.

Of course, a low locomotor cost enables a similar performance to be achieved with a lower $\dot{V}O_{2\max}$ (Jones *et al.*, 2021), and low cost should mitigate the rise in both muscle and whole-body temperature, which are key factors influencing the ability to traverse long distances and allowed our ancestors to become diurnal, high-temperature predators (Smil, 2016). However, the focus on locomotor economy ignores the numerous other outcomes that are consequent to the evolution of a long Achilles tendon, including minimisation of both muscular fatigue and sense of effort during locomotion (Carrier, 1984) and the prevention, or minimisation, of muscle damage, such as seen in ultra-marathoning (Millet, Hoffman & Morin, 2012). These factors will ultimately determine the capacity to continue at a given speed, or the voluntary decision to change locomotor speed (i.e. change the pacing strategy to reduce speed) during locomotion (Marcora, Staiano & Manning, 2009; Martin *et al.*, 2018). Additionally, minimisation of limb inertia and transmission reduction of potentially damaging vibrations to bones, muscles and other tissues would be direct and beneficial outcomes of a long Achilles tendon that may theoretically have played an important role in the evolution of bipedalism. Consideration of the importance of these additional factors is needed in order to develop a complete theory as to the role of long distal tendons across cursorial animals, and specifically the evolution (or retention from Hominoidea) of the long Achilles tendon in humans.

(2) Work and metabolic cost in muscle-only *versus* MTU work-production systems

If a muscle must lengthen and then shorten in a cyclic manner during locomotion, then that muscle (or those muscles) must perform repeated eccentric-concentric work cycles. In a system in which the muscle's tendon is very short or stiff, i.e. it is essentially a 'muscle-only' system, the cost of producing eccentric force (and thus work) during lengthening is less than the cost of isometric force, but the cost of doing concentric work is greater. The total cost is the sum of eccentric and concentric costs. This hypothetical muscle-only model approximately reflects that of the chimpanzee (Crompton, Sellers & Thorpe, 2010) and bonobo (Vereecke *et al.*, 2005) and provides a useful comparative model. The alternative is to place a long, compliant and elastic tendon in series with the muscle, as in modern humans, which will be referred to here as the MTU model. In this model the muscle undergoes less length change during locomotion, although it produces force sufficient to drive an oscillating system, and is exemplified by significant tendon lengthening and shortening (Alexander, 1997) (see Fig. 1). The muscle must produce brief concentric contractions at discrete points in the cycle to add energy to the system to replace energy that is inevitably lost, but these contractions would occur with minimal length change and at a relatively slow velocity (Bohm *et al.*, 2019; Fletcher *et al.*, 2013; Lichtwark & Wilson, 2007). In the MTU model, the tendon would dissipate some additional energy, as it displays hysteresis (∼10%) (Bennett *et al.*, 1986). The total mechanical work done within the system in the MTU model must be higher (and certainly not less) than the muscle-only model because additional mechanical work needs to be done by the muscle, or gravity or other antagonist muscles, to compensate for hysteresis loss by the tendon. The muscle belly itself within the model will perform less mechanical work and therefore consume less metabolic energy.

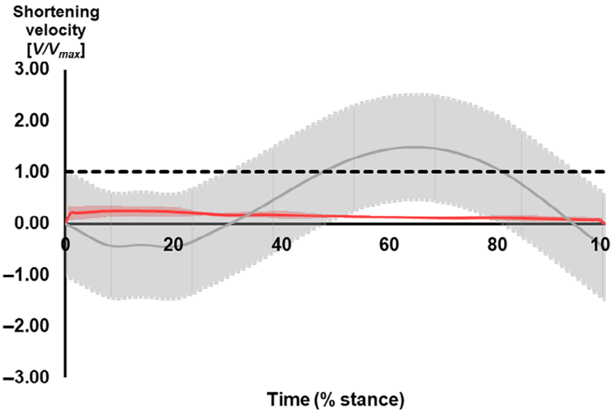

Fig. 3. Shortening velocity (V) relative to maximal shortening velocity ($V_{\max}$) during the stance phase for muscle fascicles in the muscle–tendon unit (MTU) model (pink) and the muscle-only model (grey). Because the tendon can accommodate much of the (rapid) lengthening and shortening of the entire MTU in the MTU model, the muscle fascicle shortening velocity is low. In the muscle-only model, any MTU length change must be accommodated solely by the muscle fascicles themselves. The dashed black line indicates maximal shortening velocity of the medial gastrocnemius fascicles (10.8 fascicle lengths per second). Note that in the latter portion of the stance phase, muscle fascicles would not be able to shorten rapidly enough to accommodate the required length change. Data from Bennett *et al.* (2023).

(3) Effect of muscle-only *versus* MTU designs on energetic cost and muscle fatigue

The total mechanical work done by a muscle when it acts in concert with a long tendon to drive locomotion (i.e. the MTU model) is always greater than that of a muscle directly powering motion (muscle-only model) because energy is inevitably lost from the tendon during its stretch and recoil in each cycle (energy will be lost from the muscles themselves in both systems, so will be disregarded here for simplicity). However, muscle length change is minimised in the MTU model as tendon length change can account for a large proportion of the whole MTU length change (Lichtwark, Bougoulias & Wilson, 2007) (e.g. Fig. 1). The muscle fibres therefore shorten less and at a slower velocity for a given MTU length change and velocity (Sawicki *et al.*, 2009) (Fig. 3). Since both the greater length change and velocity tend to increase the muscular metabolic cost (assuming a constant muscle force) (Chow & Darling, 1999; Woledge *et al.*, 1988; Alexander, 1997), and increases in the rate of force production further add to energetic cost (Doke & Kuo, 2007; van der Zee & Kuo, 2021), the insertion of a long in-series tendon can reduce the metabolic cost of producing the required MTU work, as discussed in Section I.

The reduced energetic cost results from the fact that the cost of force generation is not only dependent upon the total muscle work (Fenn, 1923, 1924) but by independent, and partly cumulative, effects of muscle shortening, shortening velocity and, consequently, motor unit recruitment (Fletcher *et al.*, 2013; Roberts *et al.*, 1997). With respect to muscle shortening, concentric muscle work is more costly than isometric force production at a given force level (Woledge *et al.*, 1988; Hill, 1938) yet the force generated at a given level of motor unit recruitment is also smaller, in accordance with the force–velocity relationship (Hill, 1922; Katz, 1939). Therefore, greater muscle activation, and consequently greater motor unit activation, is needed to produce the required force and this is itself associated with an energetic cost (Stainsby & Lambert, 1979). It has been long known that the oxygen requirement of a muscle, which is commensurate with its metabolic cost, is more strongly associated with the number of neural pulses provided to the muscle than its shortening or work performed (Fales, Heisey & Zierler, 1960). In humans, increases in either the force or velocity of shortening in submaximal contractions are predominately influenced by the number of active motor units (Bigland & Lippold, 1954), so the greater the activity of the muscle, the greater the metabolic cost. This is reflected in the strong relationship between oxygen consumption and the integrated electromyogram (EMG) amplitude in human muscles (Bigland-Ritchie & Woods, 1974, 1976). Thus, mechanisms reducing the level of muscle activation will subsequently reduce energetic cost. Since higher muscle forces can be produced during isometric than concentric contractions, a lower muscle activation level is required to meet the force requirements. The smaller proportion of activated muscle mass requires less metabolic energy investment to meet force (and work) demands during locomotion. This effect will be greater at faster movement speeds where a muscle operating without an in-series tendon (muscle-only model) would need to produce larger forces at faster shortening speeds to drive motion – at some reasonable running speed, the muscles would not be capable of producing sufficient power to increase velocity further (e.g. see Fig. 4). It also follows that an optimum tendon stiffness in the MTU model would allow muscle length change to be minimised and for metabolic cost to be optimised – a very compliant tendon will stretch further under high forces and increase the shortening required by the muscles whilst a very stiff tendon will not stretch appreciably and thus increase the requirement for active muscle length lengthening and then shortening. Muscle metabolic cost would also be maximised if the tendon was infinitely stiff (consistent with the muscle-only model) because it would not appreciably change length, so the term 'stiffer' in relation to the tendon is used to represent some optimum stiffness that lies within the biological range of tendon stiffness values.

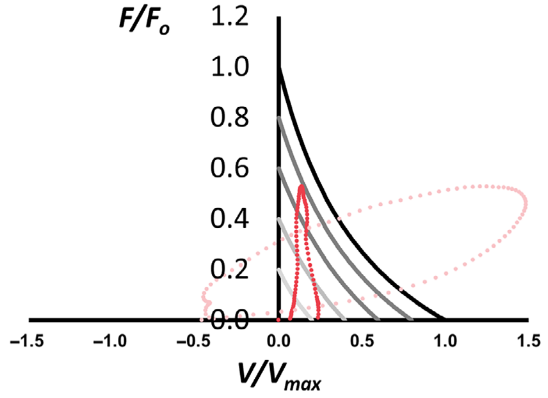

Fig. 4. Force–velocity relations plotted to demonstrate the operating ranges for muscle fascicle force and shortening velocity in the muscle–tendon unit (MTU) model (red) and the muscle-only model (pink). Force–velocity relations are scaled to activation from 20% activation (light grey) to 100% activation (black). In the MTU model, muscle fascicles can shorten at a velocity that would be predicted from the force–velocity relationship, and maximal estimated activation during stance is 80%. These data align well with the measured and estimated levels of medial gastrocnemius activation during running (75–85% maximum activation). In the muscle-only model, the absence of a compliant tendon requires that muscle fascicles shorten rapidly while developing force to support body weight during the stance phase. This shortening is much faster than what would be predicted from the maximal force–velocity relation for skeletal muscle. Therefore, to accommodate this rapid shortening, muscle forces must be drastically reduced and running speed would suffer. Data are mean data from 14 male runners running at 90% of the speed associated with the lactate threshold (Cigoja *et al*., 2021). F/F_o, muscle force relative to maximum; $V/V_{\max}$, rate of muscle length change (velocity) relative to maximum.

However, maintaining a quasi-isometric muscle state may also reduce metabolic cost according to the force–length relation. Assuming that the muscles work near their optimum length then the metabolic cost will be low compared to contractions performed at longer or shorter lengths in which a greater neural drive is required for the equivalent force. The activation cost is relatively lower (i.e. it represents a lower proportion of the total metabolic cost) at optimal length. Evidence for this complex interplay between muscle shortening, shortening velocity, and activation state has been provided for the human plantar flexors (Bohm *et al*., 2019; Fletcher *et al*., 2013; Lichtwark & Barclay, 2010). Based on these arguments, the energy cost of mechanical work during walking can be reduced by the incorporation of a long tendon (of some 'optimum' stiffness; Lichtwark & Wilson, 2007) into an MTU largely due to its effects on the force–length and force–velocity requirements, and thus activation level, of the muscle. A proportion of the mechanical work during walking can be performed by the tendon, adding to the total mechanical work of the system in which muscle work is minimised. As evidence for this, muscle efficiency during hopping and running tasks is ~40% (Cavagna, Saibene & Margaria, 1964; Thys, Cavagna & Margaria, 1975) (calculated as mechanical work output per unit metabolic rate), which is much higher than the ~25% efficiency of muscle's conversion of metabolic to mechanical energy during concentric work (Margaria *et al*., 1963; Barclay, 2019; Margaria, 1968). That is, movement efficiency is improved, and therefore muscle (metabolic) 'fatigue' will be reduced, when tendons are able to return previously stored elastic strain energy during movement. Thus, it makes sense that a key benefit of the MTU system is that it reduces the energetic cost of tasks such as locomotion; hence, energetic cost is a primary outcome variable measured in most locomotion studies.

III. BROADER EFFECTS OF MUSCLE-ONLY AND MTU SYSTEMS ON ENERGETIC COST

Whilst the economic (metabolic cost) benefits of a long distal tendon are clear and well documented, an important question remains as to whether this is the only, or at least the main, benefit of long, distal tendons.

(1) Effects on limb inertia

In addition to the above, locomotor cost is strongly influenced by limb moments of inertia as they swing about their local and remote axes (Gottschall & Kram, 2005; Umberger, 2010; Willems, Cavagna & Heglund, 1995) because this affects the internal work required for limb movement. In human walking, the cost of moving the legs alone may contribute ~30% to the total metabolic cost of walking (Doke, Donelan & Kuo, 2005; Umberger, 2010) – by contrast, the cost of arm swing is probably very small (Collins, Adamczyk & Kuo, 2009) and may even provide a small overall economic advantage (~3%) (Arellano & Kram, 2014) by reducing shoulder and pelvis rotation. The longer muscles required in the muscle-only model will increase distal limb mass and thus limb moment of inertia, and consequently increase energetic cost (Myers & Steudel, 1985). However, insertion of a long tendon reduces distal mass and allows a more proximal mass location. The decreased inertia reduces the cost of moving the limb, which is additional to the economic advantage of elastic mechanisms. The energetic saving from this effect is difficult to determine experimentally, although ~50% greater work is required to swing the lower limb in chimpanzees (with greater distal limb mass) than in humans (O'Neill *et al.*, 2022). As detailed in the online Supporting Information, Appendix S1, by way of example, for an 80-kg male with 1-m leg length and running at 5 m s^{-1} (18 km h^{-1}), and thus with a hip retraction angular velocity of ~5 rad s^{-1} (287° s^{-1}), the relocation of shank muscle mass 5 cm proximally toward the knee could reduce leg kinetic energy, and thus the mechanical work required for limb movement, from 34.1 to 31.6 J, representing a 7.3% reduction; a more conservative 3-cm shift would reduce metabolic cost by 4.4%. Assuming that muscle operates concentrically at ~25% efficiency (Barclay, 2019; Margaria, 1968), total muscle work would be reduced by 29.2% and 17.6% for 5 and 3-cm mass relocations, respectively. Commensurate with a meaningful inertia-reduction benefit is the smaller size (e.g. cross-sectional area and fibre length) of the plantar flexor muscles in highly trained east African runners who have exceptional running economy (Lucia *et al.*, 2006; Sano *et al.*, 2015).

The effect of limb inertia is amplified as locomotor speed increases, for example increasing internal work (i.e. kinetic energy) in several species of birds and mammals according to the relation $0.478v^{1.53}$ J kg^{-1} m^{-1}, where v is locomotor speed (m s^{-1}) (Fedak, Heglund & Taylor, 1982). Based on this relation, internal work increases with speed, and since distal limb segments show larger changes in velocity than proximal segments, reducing distal mass is critical for internal energy cost minimisation (Alexander, 1997, 2002). The evolution of the Achilles tendon would have significantly reduced lower-limb mass, with additional benefit because this mass reduction is provided in the most distal segment. The greater effect of limb inertia reduction at faster locomotor speeds suggests that the adaptation would benefit human running more than walking, consistent with the hypothesis that human running capacity was a key driver of bipedal locomotion in humans.

(2) Effects on collisional energy loss

The foot, and therefore the body, collides with the ground at each step, causing leg compression and restitution during the ground-contact period and providing propulsive force development to propel the body into the next step. This collision, during which the ground reaction force redirects (accelerates) the body's centre of mass (CoM) upward and forward, is an important source of energy loss (Donelan, Kram & Kuo, 2002; Ruina, Bertram & Srinivasan, 2005; Saunders, Inman & Eberhart, 1953) as CoM acceleration requires force production and therefore costs metabolic energy. A compliant limb system characterised by bent-knee (crouched) gait could be used to reduce the amplitude of discontinuities in the path of the CoM and thus minimise collisional energy loss (Bertram & Hasaneini, 2013; Donelan *et al.*, 2002; Ruina *et al.*, 2005; Saunders *et al.*, 1953). This may be done easily in a system driven only by muscles (e.g. the muscle-only model), which would lengthen and shorten to change limb length through the stride cycle to produce a horizontal CoM path. That is, tendons are not explicitly necessary for collision minimisation. However, greater energetic and mechanical costs of transport are observed when a bent-knee gait pattern is adopted than in traditional walking in which the CoM rises and falls slightly within each step (Massaad, Lejeune & Detrembleur, 2007; McMahon, Valiant & Frederick, 1987; Wang *et al.*, 2003), despite collisional forces being smaller (McMahon *et al.*, 1987). Part of the additional metabolic cost comes from the larger external moment arms of force and consequent increases in required joint moments. The associated increased muscular force production would not only increase metabolic cost but also accelerate muscle fatigue and body temperature rise (Crompton *et al.*, 1998) (see Section III.6), and thus be expected to impact locomotor performance negatively.

Based on the above, neither a straight-leg gait (with large collisional energy loss) nor a crouched gait (with larger active muscle requirement) are optimal locomotor strategies (Massaad *et al.*, 2007). Instead, a hybrid solution in which a relatively straight-leg gait is used but small-amplitude joint flexions are initiated at the point of foot–ground impact to reduce collision magnitude appears optimal. This gait pattern could be performed using either the muscle-only or MTU models, however some of the collision energy that would be lost during the braking phase of the gait cycle could be stored in the active MTUs unique to the MTU model. That is, energy can be stored briefly in the tendon and then used later during propulsion rather than being lost to the environment. Thus, collisional energy can be 'recycled' to aid propulsion, analogous to a vehicular kinetic energy return system (Boretti, 2013); in this way, the tendon makes an effective kinetic energy return system. Indeed, the propulsion provided by ankle plantar flexion, when appropriately timed, can reduce collisional forces by redirecting the body's CoM just prior to foot–ground contact (Zelik *et al.*, 2014) so a circular argument is created: collision energy can be stored in the Achilles tendon for subsequent propulsion, and the plantar flexion-based propulsion can then help to reduce subsequent collision amplitude and energy loss. As locomotor speed increases and both the ground impact force and requirement for concentric muscle work increase, the re-use of stored collisional energy would become even more useful from an energetic perspective.

(3) Effects on muscle damage

An important assumption so far is that the main potential benefit of in-series tendons is their effect on the locomotor cost (through alteration of muscle force production requirements, reduced limb inertia, and storage–release of collisional energy), which then influences fatigue based on the intensity–duration relationship. However, an argument can be made that this cost is the primary determinant of neither our choice of gait, the locomotor parameters associated with 'optimum' gait (e.g. stride length and frequency), nor the evolution of long tendons into the human force-production machinery (MTU model). Instead, broader benefits of a long-tendon MTU model should be considered to better understand our capacity to tolerate a given locomotor speed for a given distance, or the decision to adapt movement speed (i.e. alter the pacing strategy) when required.

Micro-level muscle and connective tissue damage is common during prolonged running (Hoffman *et al.*, 2012; Kim, Lee & Kim, 2007; Millet *et al.*, 2011*b*). Such damage would need to be avoided in humans running over long distances, especially in hot environments, because of the detrimental effect on running capacity and increased risk of terminal muscle cramping (Hoffman & Stuempfle, 2015; Martinez-Navarro *et al.*, 2020). Limiting the magnitude of concentric–eccentric work cycles (i.e. using an MTU model) reduces both myocellular and connective tissue damage and the resulting disruption of calcium release channels that can occur during unaccustomed, repetitive eccentric muscle contractions (Hyldahl & Hubal, 2014). To minimise muscle damage, and thus to both prolong locomotor activity and ensure adequate performance in subsequent locomotor bouts (e.g. in the hours or days after the first, damaging bout), reduction of both muscle force and length change during eccentric contractions is required (Penailillo, Blazevich & Nosaka, 2015). In a muscle-only model, large eccentric muscle excursions would trigger damage because muscle fibre length change (negative strain) critically affects damage magnitude (Butterfield & Herzog, 2006; Penailillo *et al.*, 2015). However, distal limb muscles tend to remain quasi-isometric during locomotion in an MTU model (Alexander, 2002) so eccentric lengthening is minimised or absent; this system design therefore minimises damage (Caldwell, 1995). Using this strategy, highly trained human athletes have been known to complete competitive marathon races (42.1 km) without detectable reductions in muscle function (Petersen *et al.*, 2007) and complete both very long (e.g. 50–100 km) and extremely long (>300 km) races with detectable but not critical levels of damage (Fallon *et al.*, 1999; Millet *et al.*, 2011*b*; Saugy *et al.*, 2013).

One counterargument is that, if the muscle-only model were standard then muscles would perform eccentric contractions on a daily basis, which would confer protection against eccentric exercise-induced muscle damage (i.e. a repeat bout effect would be induced) (Hyldahl, Chen & Nosaka, 2017). However, it would still be problematic in circumstances in which (*i*) activity levels are low for at least several days, after which the resumption of daily activities could trigger significant muscle damage, or (*ii*) an unaccustomed task is performed for which there is no protection. Thus, an important benefit of the long in-series distal tendon is its capacity to protect the muscle from potentially harmful eccentric contractions, minimising fatigue during exercise and ensuring the ability is retained to perform repeated bouts in the hours and days after an initial bout. This would seem to be a critical, yet often overlooked, evolutionary benefit of the long Achilles tendon in humans and its counterpart in other, particularly cursorial, animals.

(4) Tendons as vibration dampers

A collision event is prominent during locomotion even when using a 'minimal joint flexion' technique. The higher-frequency components of the ground reaction force during collision at foot–ground contact initiate tissue vibrations, which would travel rostrally to the head if they remained undamped (Wakeling, Pascual & Nigg, 2002; Coyles, Lake & Lees, 1999). Active muscles are excellent dampers because strongly bound cross-bridges convert vibrational energy into heat energy for dissipation (Wakeling & Nigg, 2001; Wilson *et al.*, 2001). Muscle activity is therefore required during locomotion for this purpose, i.e. even if muscles were not necessary to drive locomotion, they would be necessary to minimise vibrational energy transmission (Nigg & Liu, 1999; Wakeling *et al.*, 2002). The larger muscles inherent to the muscle-only model might be considered advantageous in this case. However, force production is an inevitable consequence of muscle activation, and this incurs a metabolic cost. So, if the muscle must be active to dampen vibration during the braking phase of foot–ground contact then a strategy in which the energy associated with the muscle work is then stored for subsequent reuse during propulsion might prove useful. Thus, in a system that requires active muscle contraction for vibrational damping, energy storage by an in-series tendon may minimise wasteful energy loss – again, the system functions as an effective energy return system. Evidence indicates that plantarflexor/dorsiflexor co-activation successfully induces fascicle shortening prior to perturbed ground contact in order to protect the muscle from damage from a rapid and forceful lengthening during energy dissipation (Dick *et al.*, 2021). A long, in-series tendon would contribute to some of this additional length change. At faster walking/running speeds where vibrational energy is greater there should be a greater absolute benefit of the MTU model design.

More directly, the tendon itself may also assist with vibration attenuation. The plantar fascia and Achilles tendon form an excellent low-pass filter (Pratt & Williamson, 1995), minimising high-frequency vibrational energy transfer from the foot through the proximal upper limb (and head), and subsequently minimising vibration-related damage to muscle (Necking *et al.*, 1992, 1996), tendon (Hansson *et al.*, 1988; Wang, Ker & Alexander, 1995) and bone (Carter, 1984). It would also potentially reduce muscle fatigue since less muscle activity would be required for vibrational damping. Correspondingly, reductions in metabolic cost (through lower muscle activation) would reduce both the rate of muscular fatigue and tissue damage.

(5) Fibre type use and fatigue

To generate high power over considerable excursion range, a muscle working in a muscle-only model will need to make use of high-threshold motor units, i.e. faster-twitch fibres. As slow-twitch fibres are more efficient than fast-twitch fibres, at least when muscle speeds are relatively slow (Barclay, 1994; Barclay, Constable & Gibbs, 1993; He *et al*., 2000), additional recruitment of faster fibres will be required, which will further increase metabolic cost if shortening velocity is not increased (Woledge, 1998). Because shortening velocity associated with optimal efficiency is increased with progressive motor unit recruitment, energy cost will increase because some of the now-active motor units (the newly recruited fast-twitch fibres) will shorten at an energetically inefficient velocity, and fatigue will increase if shortening velocity is not then increased to this optimal velocity. However, the additional mechanical work per unit time would then incur additional metabolic cost. An MTU model circumvents this issue by minimising muscle work and activation, reducing the need for activation of higher-threshold, usually faster-twitch, motor units.

(6) Effects on muscle and body temperature

An increase in muscle, and thus whole-body, temperature is another source of muscle (and whole-organism) fatigue that would be amplified by the greater metabolic cost of the muscle-only model. Increasing temperatures would be problematic because muscular heat accumulation can reduce net mechanical efficiency of muscular force production (Ferguson, Ball & Sargeant, 2002; Krustrup *et al*., 2003) and increase metabolic cost (Brooks *et al*., 1971; Ferguson *et al*., 2002), which would reduce exercise endurance time (Edwards *et al*., 1972; Segal, Faulkner & White, 1986), at least during prolonged bouts. Further, whole-body heat accumulation critically affects exercise capacity, with core (and muscle) temperatures >40°C generally being considered terminal for exercise progression (Gonzalez-Alonso *et al*., 1999*b*). The accumulation of heat within muscles and the body depends on the relative rate of heat production to heat dissipation (Taylor, Kondo & Kenney, 2008). Although speculatively there may be some benefits of an MTU system with regard to heat dissipation (see Appendices S2 and S3), heat production minimisation might be of relatively greater benefit.

Muscles such as those working in the muscle-only model would perform cycles of concentric and eccentric work, both of which generate significant heat through metabolism (concentric; positive work) (Hill, 1949) and the degradation of mechanical energy to heat (eccentric; negative work) (Abbott, Aubert & Hill, 1951; Hill, 1938). On the other hand, the use of long in-series tendons reduces muscular work by approximately half during locomotion (or more at faster running speeds) (Cavagna & Kaneko, 1977; Monte *et al*., 2020) and this would significantly reduce heat production, providing a clear heat-minimisation benefit for prolonged work without critical heat accumulation (Ruxton & Wilkinson, 2011). Thus, for the same external work, greater heat is produced in muscles working according to the muscle-only model than the MTU model.

The balance of heat transfer from the working muscles to neighbouring tissues and the overlying skin *versus* that transferred by blood-based convective heat transfer to the core is affected by numerous factors, however when ambient temperature is high (near to or greater than core temperature) >35% of heat production would be directed to the core (Gonzalez-Alonso, Calbet & Nielsen, 1999*a*). The significant rise in core temperature can rapidly become critical, e.g. in minutes to hours depending on exercise intensity, metabolic cost, ambient temperature and relative humidity. Furthermore, as heat production through aerobic metabolism exceeds that of anaerobic metabolism (Krustrup *et al*., 2003), greater heat is generated as a proportion of external work when longer exercise bouts are performed, such as those required for persistence hunting, scavenging, and foraging. Thus, not only would a mechanism by which muscular heat production is minimised provide a significant advantage when ambient temperatures are high, but it provides benefit when prolonged, lower-intensity exercise must be sustained. Thus, the evolution of muscles operating within an MTU system should provide an advantage for longer-duration exercise, especially in warm environments, by minimising both muscular and core temperature increases. This may have been particularly critical during Pliocene (>3 Mya; 3 °C warmer than today) (Haywood & Valdes, 2004) and other climatic warm periods, as well as for incursions of hominins into warmer latitudes.

It is notable that increases in muscle temperature enhance cross-bridge cycling rates, reducing net mechanical efficiency (Ferguson *et al*., 2002) and subsequently increasing muscular power output during brief or higher-speed/higher-intensity exercise (Bergh & Ekblom, 1979; Ferretti *et al*., 1992; Sargeant, 1987). So larger muscles that work at higher speeds through larger ranges and with smaller surface area-to-volume ratios might provide an advantage to humans (or other animals) in communities in which such activities predominate over endurance-type behaviours. Thus, whilst the evolution of modern humans in relatively warmer, flat-terrain environments might have benefited from the smaller muscle mass of the MTU model, the possibility cannot be discounted that the migration of humans to colder or mountainous regions may have benefited from larger, less-efficient MTU designs.

IV. EFFECTS OF MTU DESIGN ON PERCEPTION OF EFFORT

A fundamental concept so far is that our locomotor capacity is critically linked to physiological and biomechanical phenomena (Rodman & Mchenry, 1980). However, the decision to move is also strongly influenced by our perceptions of both effort and reward; we act (e.g. we move) when the outcome is determined to be subjectively worthwhile (Gendolla & Richter, 2010). When we perceive that a task is more difficult we then have to make decisions as to whether and how to continue, and then exert effort to enact that strategy

(Shenhav *et al.*, 2017). Mental effort is laborious and therefore minimised when possible (Kool & Botvinick, 2014), so one might expect that we choose to locomote, or locomote faster, when minimal effort is required yet the reward is great. Mechanisms reducing effort should therefore promote locomotion, and in the much longer term promote the evolution of better movement strategies.

According to the sensory tolerance limit hypothesis (Gandevia, 2001), we may choose to reduce locomotor speed even if the locomotor cost is relatively low in conditions in which movement becomes difficult, including when muscles tire, breathing becomes arduous, pain is felt in exercising or non-exercising muscles, or either ambient or body temperature is high (e.g. Hureau, Romer & Amann, 2018; St Clair Gibson *et al.*, 2006). That is, global feedback in relation to our physiological state is an important limiter of exercise, including locomotor, performance. Global feedback includes that from the working muscles themselves, which strongly influences perception of effort through both feedback and feedforward pathways. In situations of increasing muscle fatigue, defined as a less than anticipated force production for a given level of stimulation (MacIntosh & Rassier, 2002), any pain or ill-feeling in the muscle may directly influence our decision to move and require greater effort to do so. However, a greater number of motor units also need to be recruited and firing frequency increases in order to maintain power (i.e. greater effort evokes greater muscle activation). With it, it is theorised, more efferent copies of the motor command are sent from motor to sensory areas of the brain in order to provide a perception of effort associated with the motor output (de Morree, Klein & Marcora, 2012; Duncan, Al-Nakeeb & Scurr, 2006). Perception of effort therefore increases during fatiguing tasks as a result of elevated efferent input in a feedforward process. As perception of effort increases, the capacity to reach the endpoint of an exercise task may be judged to decrease (in persistence hunting the endpoint may not be defined so the goal may be set to allow exercise for at least several hours, but in many modern sports the endpoint is well known) and power output, i.e. locomotor speed, may be voluntarily reduced in order to reduce effort. Our decision to reduce effort at the expense of increased energetic cost is exemplified by our choice to transition from a high-power running gait to a low-power walking gait at speeds that would increase energetic cost yet reduce sense of effort (Hreljac, 1993; Tseh *et al.*, 2002). It may also explain findings of modelling studies showing that running during a persistence hunt may be preferrable to walking under many climatic conditions by minimising hunt duration and the relative level of exhaustion despite an increase in metabolic energy expenditure (Hora *et al.*, 2022). Reductions in locomotor speed (or power) or gait transitions may therefore reflect a pacing strategy alteration that ultimately dictates our speed (St Clair Gibson *et al.*, 2006). That is, locomotor speed may be influenced not only by locomotor cost or absolute muscle fatigue, as discussed above, but also by the pacing strategy adopted which is established in relation to the cost: reward precept.

Although perception of reward can impact the pacing strategy (motivation, anxiety, stress, hunger/thirst, etc., will influence this) (Lambert, St Clair Gibson & Noakes, 2005), the incorporation of long in-series distal tendons will strongly affect the perception of cost. During a fatiguing locomotor task, an in-series tendon improves the muscle's ability to maintain work output and to reduce the metabolic cost of contraction because mechanical efficiency is thus improved (Lichtwark & Barclay, 2012). Therefore, both the effort required for muscle contraction and the feedback signals providing information in relation to muscle fatigue (e.g. metabosensitive and pain afferents) will be reduced, so perception of effort is reduced. A human should thus 'feel' more comfortable to locomote at a relatively higher speed for a given distance. According to this hypothesis, a longer Achilles tendon (i.e. the MTU model) increases the likelihood of an individual choosing or continuing to move, subsequently increasing food yield or the capacity to migrate to more habitable regions, hence increasing the chance of reproductive success in those individuals and leading to the evolution of a longer Achilles tendon.

However, the reduced metabolic cost of locomotion associated with an MTU model also minimises heat production, and thus reduces the potential negative perceptions of heat accumulation within the body. This increases the likelihood of a human deciding to run longer distances in warmer climates, thus improving long-distance scavenging and hunting practice (Hora *et al.*, 2022). Furthermore, if the MTU model is better able to dampen vibration within the musculoskeletal system, then both acute and ongoing benefits may be derived. Acute vibration during submaximal muscle actions tends to increase the perceived effort associated with maintaining a given level of muscle force (Cafarelli & Kostka, 1981; Jones & Hunter, 1985) and negatively affect other psychological states such as perception of comfort during tasks in which vibrations are usually minimal (e.g. bicycling) (Ayachi *et al.*, 2018). Also, at least under some conditions, prolonged vibration reduces subsequent muscle activation capacity and thus limits force production (e.g. 20 min vibration) (Barrera-Curiel *et al.*, 2019), subsequently increasing the voluntary effort required to drive the muscles to maintain force production. In both cases, an increase in voluntary drive to the muscles would increase perception of effort and thus reduce muscular output. In this sense, a long (compliant) distal tendon can both reduce muscle fatigue and the total sensory load projected to the brain, reducing perception of effort and allowing for faster or more prolonged locomotor performance. Given the above, a model in which feedback from numerous systems is influenced by the incorporation of a long, in-series distal tendon, and thus ultimately affects our decision (i.e. capacity) to move, is supported.

V. IS THERE A GREATER BENEFIT OF MTU SYSTEMS AT FASTER LOCOMOTOR SPEEDS?

Numerous benefits to locomotor performance have thus far been described for the MTU model, but some of these benefits are potentially amplified as movement speed increases. With an increase in locomotor speed, at least to speeds $\sim 7 \text{ m s}^{-1}$, the greatest additional work is done by the plantar flexors (Dorn, Schache & Pandy, 2012) largely because of the

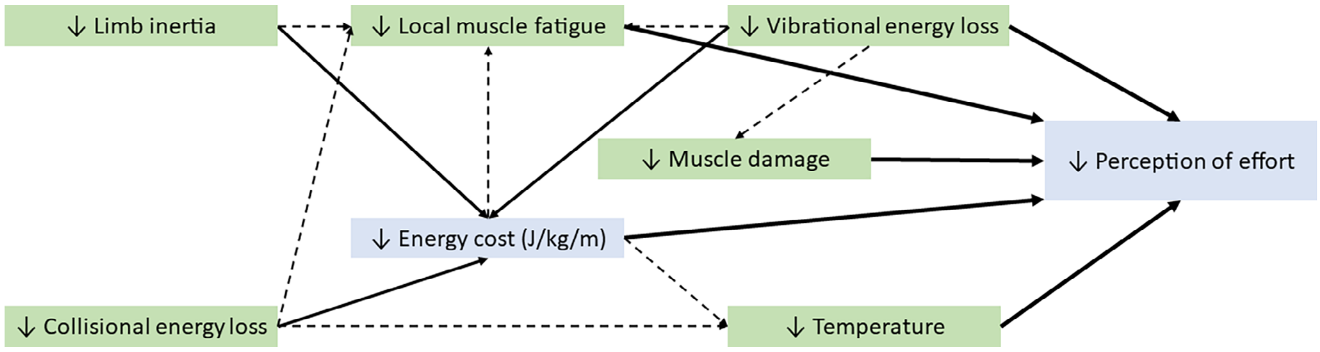

Fig. 5. The incorporation of a long tendon into the distal muscle–tendon unit will both reduce energy cost, and thus fatigue, as well as decreasing the sense of effort during locomotion (blue boxes). Chief protagonists include reductions in limb inertia, reduced energy loss during foot–ground collisions, storage and reuse of the muscle work required for vibration damping, and reduced muscle damage through both the decreases in muscle length change and vibration propagation, which will also minimise body temperature increases (green boxes). These benefits should increase both the speed and ease of movement and have greater effect at faster locomotor speeds (i.e. running > walking).

increase in stride length required [for further speed increases the proximal (hip) muscles become increasingly important]. Thus, it is reasonable to ask whether there is a specific benefit to placing long, energy-returning tendons in series with distal limb muscles when movement speeds increase.

As the rate of muscle length change increases with locomotor speed in the muscle-only model, the cost of eccentric work will remain relatively constant whilst the cost of concentric work will increase. By contrast, in an MTU system higher muscle forces will be required in order to drive the system at faster speeds (Dean & Kuo, 2011), although the total cost of producing repeated (cyclic) isometric contractions will increase less with movement speed because there is limited need for greater mechanical work to be performed (see Figs 1 and 3); additional work is done by tendon recoil. Increases in the rate of force development at faster locomotor speeds will also be accomplished by increasing activation rates, which adds its own cost) (Doke & Kuo, 2007; van der Zee & Kuo, 2021), and recruitment of faster-twitch fibres (larger motor units) at lower force levels, i.e. earlier in the force rise phase (Duchateau & Baudry, 2014; Maffiuletti *et al.*, 2016) in both models. This activation increase may thus increase the cost of force production (Bigland-Ritchie & Woods, 1974, 1976; Dean & Kuo, 2011; Stainsby & Lambert, 1979), but is expected to be less than the increasing cost of concentric work and less in the MTU model. Therefore, theoretically, the muscle-only model will become more energetically expensive than the MTU model at higher movement speeds. Based on this consequence, evolutionary pressure for tendon lengthening exerted by the need to locomote at faster speeds (e.g. jogging) may be greater than for slower (e.g. walking) locomotor speeds.

VI. CONCLUSIONS

(1) Long distal leg tendons such as the Achilles tendon are common in cursorial animals and are known to both amplify muscle power and allow muscle fibres to work over smaller length ranges and at slower shortening speeds, with that energy replaced by stored elastic potential energy.

(2) Long distal tendons in humans are unlikely to have evolved (or been retained from Hominoidea ancestors) solely for the benefit of increasing muscle–tendon power output, as there is little evidence supporting this possibility and we are clearly less powerful than many other species.

(3) Whilst reduced energetic cost of locomotion would be a beneficial adaptive trait, allowing us to walk and run with minimal energy consumption, other potentially greater benefits exist (Fig. 5); long distal tendons would reduce muscle fatigue, which is influenced by metabolic cost but also: (*i*) reduce limb inertia, afforded by the longer tendon and shorter muscles (and corresponding reduced muscle force requirement); (*ii*) reduce energy loss during foot–ground collisions; (*iii*) reduce exercise-induced muscle damage (especially during eccentric contractions or prolonged vibration); (*iv*) allow storage and reuse of the muscle work required to dampen the vibrations induced by foot–ground collisions (and act as a low-pass vibration filter in themselves); and (*v*) attenuate muscle and whole-body temperature increases.

(4) Many of the above benefits are expected to be greater during running than walking, supporting the hypothesis that running might have been a primary driver of distal muscle–tendon unit morphology in humans. Collectively, these benefits would have strongly influenced perception of effort during locomotor (and other) activities, ultimately allowing a choice to move at faster speeds or for longer.

(5) The long distal tendon in modern humans, the Achilles, may therefore be a singular adaptation that provided numerous physiological, biomechanical, and psychological benefits and thus influenced behaviour across multiple tasks, including locomotion.

(6) While energy cost may be a variable of interest in locomotor studies, future research should consider the broader range of factors influencing our movement capacity as well as our decision to move over given distances at specific speeds

in order to understand more fully the effects of Achilles tendon function, or other factors, on movement performance.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Effect of shank mass distribution on kinetic energy of the leg during running.

Appendix S2. Possible effects of muscle model on heat dissipation.

Appendix S3. Effect of muscle model on surface area-to-volume ratio.

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