

Evolutionary Robotic Approaches in Primate Gait Analysis

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Abstract Understanding how primates move is particularly challenging because many of the experimentation techniques that would normally be available are unsuitable for ethical and conservation reasons. We therefore need to develop techniques that can maximize the data available from minimally intrusive experimentation. One approach for achieving this is to use evolutionary robotic techniques to build a musculoskeletal simulation and generate movement patterns that optimize some global parameter such as economy or performance, or to match existing kinematic data. If the simulation has a sufficiently high biofidelity and can match experimentally measured performance criteria then we can use it to predict aspects of locomotor mechanics that would otherwise be impossible to measure. This approach is particularly valuable when studying fossil primates because it can be based entirely on morphology and can generate movements spontaneously. A major question in human evolution is the origin of bipedal running and the role of elastic energy storage. By using an evolutionary robotics model of humanoid running we can show that elastic storage is required for efficient, high-performance running. Elasticity allows both energy recovery to minimize total energy cost and also power amplification to allow high performance. The most important elastic energy store on the human hind limb is the Achilles tendon: a feature that is at best weakly expressed among the African great apes. By running simulations both with and without this structure we can demonstrate its importance, and we suggest that identification of the presence or otherwise of this tendon—perhaps by calcaneal morphology or Sharpey’s fibers—is essential for identifying when and where in the fossil record human style running originated.

Keywords Achilles tendon · bipedalism · computer simulation · elasticity · locomotion · virtual ablation

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Introduction

In a classic paper, Carrier (1984) drew attention to the “energetic paradox of human running”: humans are poor sprinters but excellent endurance runners. He suggested that these abilities evolved as an adaptation to running down prey over long distances, in the manner of the living Kalahari San (Lee and DeVore 1968). His idea has recently been elaborated in more detail by Bramble and Lieberman (2004), who, however, restrict this adaptation to *Homo*. They list a substantial number of anatomical features of *Homo* that they regard as specifically adaptive for endurance running (ER). It is certainly the case that although our sprint performance is relatively poor, human ER abilities are outstanding: humans have recently outrun horses over 25- and 50-mile distances (although it is worth noting that the latter race imposed rest stops). However, these abilities compromise others, e.g., as Bramble and Lieberman (2004) indicate, humans have poor capacity for sudden changes in direction in comparison with, e.g., antelopes. One adaptive feature in particular, the presence in humans of a long Achilles tendon (Triceps surae tendon), is curious in its distribution (Frey 1913): short or absent in other great apes, but long not only in humans but also in the almost totally arboreal gibbon (certainly no endurance runner). Such a structure is ideally suited for elastic energy storage, and indeed the Achilles tendon has been shown to be an important energy store in hopping (Lichtwark 2005), walking, and running (Lichtwark and Wilson 2006), with its measured stiffness being most helpful in running (Lichtwark and Wilson 2007).

Elastic mechanisms allow energy saving, power amplification, and force regulation during locomotion (Alexander 2002). The effortlessly smooth appearance of animal locomotion, which is often lacking in man-made legged machines, can also be attributed to elastic mechanisms. Movements of the internal, rigid, jointed skeleton of vertebrates are driven by forces generated by muscles and acting via a series of levers to affect locomotion. Early physiological experiments (Hill 1938) quantified the contractile and force-generating properties of the musculo-tendinous unit, separating out the roles of the force-generating contractile element and the series and parallel passive elastic elements. Anatomical observations indicate that the amount of elastic tissue varies considerably between muscles. In particular, muscles in the proximal segments of limbs tended to have less elastic tissue than those in the more distal elements (Alexander 1974). In extreme cases, such as horses and camels, some distal muscles were little more than sheets of elastic tissue with minimal contractile component (Alexander *et al.* 1982; Dimery *et al.* 1986). Theoretical work on running, galloping, and hopping demonstrates that these gaits can be modeled as a mass-on-a-spring, allowing a theoretical zero cost for locomotion if the spring could store all the kinetic and gravitational energy lost on impact and return it on takeoff (Cavagna *et al.* 1977). Empirical data on the metabolic costs of locomotion in kangaroos support this notion, wherein the cost of traveling unit distances actually falls at high speed (Taylor *et al.* 1982). The use of leg tendons in energy storage was later confirmed by experiments on wallabies that measured the stretch of the triceps surae tendon in vivo (Biewener *et al.* 1998). In the case of nonhoppers the situation is less obvious. Human runners, e.g., also have lower costs of transport as running speed increases, and indirect experimental data have suggested that considerable elastic storage could occur (Ker *et al.* 1987). More direct information from running

turkeys has shown that most of the work of the gastrocnemius muscle comes from elastic recoil of the tendon (Roberts *et al.* 1997), illustrating their importance for energy storage. However, in work on the desert rat, a much smaller bodied hopper, Biewener and Blickhan (1988) were unable to find any energy storage. This may be a general finding related to body size and scaling rules, or may be specific to the ecological role of hopping in this species, perhaps relating to the role of leaping in predator avoidance, which might be expected to be more extreme in smaller animals (Crompton and Sellers 2007).

Elastic tissues also function in power amplification. The force a muscle is able to generate rapidly falls to zero as contraction speed increases, whereas elastic recoil in a tendon can occur more rapidly. Similarly the maximum stress that a tendon can withstand is much higher than the stress that a muscle can generate. These properties allow a tendon to act as an effective power amplifier, allowing a force that is generated slowly by a muscle to be released more quickly. This function is used for generating large leap distances in small mammals, wherein high forces are required for relatively short periods of time due to scaling considerations of leg length (Aerts 1998; Sellers 1996). Tendons have the added benefit of improving energetic efficiency, as they allow muscles to operate at lower contraction speeds where their efficiency is greater. Elastic recoil also plays an important role in meeting the large power requirements during high-speed limb retraction in galloping horses (Wilson and Watson 2003). The presence of elastic tissue also has implications in terms of locomotor control. A feature of having an elastic element in series with a force-generating contractile element is that the system becomes easier to control in terms of force but harder to control in terms of total length. This is exacerbated as the stiffness of the tendon is reduced. This feature is clearly important in the highly compliant so-called low stress tendons that occur in the human forearm (Alexander 2002), which allow precise, low forces to be applied for manipulation of delicate objects. More easily controllable elastic elements may also be significant during locomotion because the force applied to the substrate may be more important for stable locomotion than the absolute position of the foot.

Experimental approaches to investigating the role of elastic tissue, although extremely valuable, can tell us only a limited amount about the role of elasticity within a highly evolved elastic system and cannot compare performance with a similarly evolved nonelastic system. Similarly, the presence of elastic tissue may in fact be a phylogenetic constraint of the vertebrate musculoskeletal system wherein long tendons are needed to allow the proximal location of muscle mass and that performance may actually suffer because of this. The collagen fibres in tendon have a Young's modulus of $1.5 \times 10^9 \text{ N m}^{-2}$ (Bennett *et al.* 1986), which although high for flexible biological tissues, is much lower than the $200 \times 10^9 \text{ N m}^{-2}$ found in steel cable (Vogel 1998). Elastic storage may be unavoidable instead of desirable, which is an important consideration when building robots. Modeling approaches are advantageous in that they allow the complete removal of such constraints and allow the production of models that have no elastic component but are otherwise reasonably lifelike. Bipedal locomotor modeling is a popular activity, with models varying from the highly theoretical (Alexander 1992; McGeer 1992; Minetti and Alexander 1997; Srinivasan and Ruina 2006) to more realistic simulations (Nagano *et al.* 2005; Sellers *et al.* 2003; Yamazaki *et al.* 1996). Modeling approaches have

been used both to understand the fundamental mechanics of bipedal gait and also to predict gait parameters: either internal values that are difficult to measure directly or for fossil vertebrates where experimentation is impossible. Two approaches have been taken when considering the locomotion of fossil species. First, one can make assumptions about the kinematics of the fossil, and this is used to drive an inverse dynamic model. The kinematics can be from motion capture of modern species such as chimpanzees and humans (Crompton *et al.* 1998), or based on human data alone (Kramer 1999). Second, no assumptions about kinematics are made and the model control system is generated entirely by global optimization criteria and a forward dynamic simulation, which is the approach we have followed in the past. Alternatives mix in degrees of global optimization with a reduced reliance on kinematic constraints. Thus, e.g., models can use global optimization to minimize energy cost within a single step but with the start and end posture defined (Nagano *et al.* 2005), or, alternatively, they can kinematically constrain only part of the motion such as the foot and use global optimisation to control the rest of the body (Nicolas *et al.* 2007). These approaches all have their uses: if kinematics are known then inverse dynamics gives precise values for mechanical work. If kinematics are not known then a forward dynamic solution requires the minimum assumptions; however, these approaches can be extremely computationally expensive and may not be able to distinguish between alternative hypotheses (Sockol *et al.* 2007). Hybrid approaches can overcome both these difficulties and are certainly the only current way of investigating locomotion in full 3D but at the cost of making additional assumptions about expected kinematics that need to be justified.

Simple locomotor models have the great advantage of being straightforward to understand and unequivocal in their predictions. More complex models depend on a much greater number of modeling parameters and are therefore more difficult to interpret. However, because they are based more closely on real organisms they can be directly tested through comparison of their predictions to those obtained experimentally, and some aspects of locomotion such as the interplay of different energy storage mechanisms are fundamentally complex and cannot be adequately expressed with simple models. Complex models are computationally expensive to calculate. Whereas the simplest models can be solved analytically (Alexander 2003), numerical methods are required to calculate the model outcomes for complex models and even then it is impractical to explore exhaustively the solution space, and a selective search is needed to find solutions. Popular techniques are to use finite steps within the search space (Srinivasan and Ruina 2006); to constrain parts of the model using functional linkage and predesigned neural networks (Yamazaki *et al.* 1996); and to use genetic algorithms to explore selectively profitable areas of the search space (Sellers *et al.* 2003). These approaches are frequently combined with genetic algorithms, and this combined approach is particularly popular in robotics, leading to the term evolutionary robotics (Nolfi and Floreano 2000). The internal, rigid, jointed skeleton of vertebrates is moved by forces generated by muscles and acts as a series of levers to affect locomotion. In anatomically realistic models this is represented as a series of rigid segments that are constrained at joints, with forces generated by gravity, external contact, and internally by simulated muscles. The equations of motion for such a system can be generated by hand (Winter 1990) or more commonly today can be generated automatically by suitable physics simulation

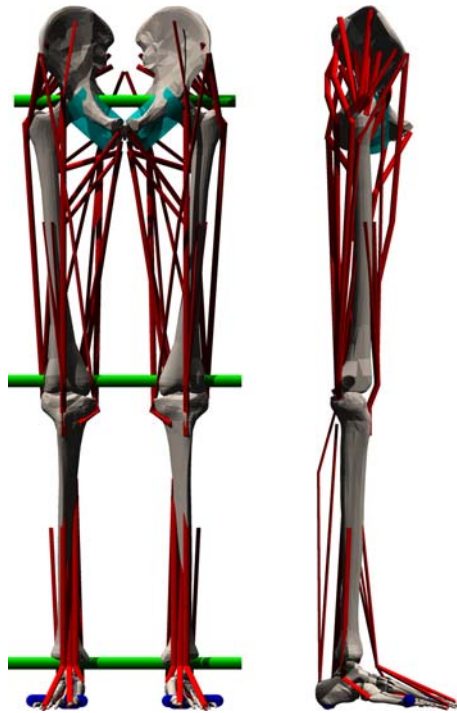
software that allows both the specification and numerical solution of such linked segment models. We have previously used both Dynamechs (Sellers *et al.* 2003) and Open Dynamics Engine (ODE; Sellers & Manning 2007) and there are now plenty of alternatives, both commercial [e.g., MSC.ADAMS (www.mscsoftware.com), SDFast (www.sdfast.com), MADYMO (www.tass-safe.com)] and open source [e.g., PhysSym (physsim.sourceforge.net), Tokamac (www.tokamakphysics.com)], along with front ends that allow simplified construction of biomechanical models [e.g., SIMM (www.musculographics.com), OpenSIMM (www.simmtk.org), Marilou Robotics Studio (www.anycode.com), LifeMod (www.lifemodeler.com)].

Methods

The first requirement for this project was a high-quality bipedal musculoskeletal model. The AnyBody Research Project (www.anybody.aau.dk) has produced a number of human models and we chose the Leg3D Model from Model Repository 6.1. This model has 7 segments (Head+Arms+Torso [HAT] plus left and right thigh, shank and foot), 70 muscles, and 6 joints (Fig. 1). For this project we needed to make a number of alterations to the original model. First, this model ignores the mass of the body above the pelvis, so we replaced the inertial parameters of the pelvis segment with the combined head, arms, and torso values from the FullBodyModel, bringing the total mass of the model up to 75.351 kg. Second, the model does not contain joint ranges of motion, so we obtained suitable values from the literature (Silder *et al.* 2007). We took muscle fiber lengths and physiological parameters, attachments, and lines of action from the original model and we calculated tendon lengths so that all muscles were slack in a slightly flexed posture (22.5° at the hip and 45° at the knee). We set tendon elasticity such that there was 6% strain at the maximum isometric contraction force, and we set the passive elasticity of the muscles such that there was 60% strain at the maximum isometric contraction force because we have used these values previously (Sellers *et al.* 2005; Sellers and Manning 2007) and they are very similar to the values in the AnyBody model (5.3% serial, 50% parallel). These value gives an approximate Achilles tendon stiffness of 183 k Nm⁻¹, which matches very well to the value of 180 k Nm⁻¹ used elsewhere (Lichtwark and Wilson 2007). We calculated the force generated by the contractile units and elastic elements analytically at each time step via a custom implementation of a Hill-style contractile model combined with a metabolic energy cost prediction function (Minetti and Alexander 1997). This model uses a nonlinear fit to empirical values of metabolic energy costs for muscular contraction (Ma and Zahalak 1991). An analytically solved combination for the contractile, serial elastic, and parallel elastic elements avoids the numerical difficulties of having relatively stiff elastic elements in the simulation. Details of this are given in the Appendix. We modeled contacts with the ground as capped cylinder geometries that interacted with a ground plane with a friction coefficient of 1 and spring constant of 1×10^5 N m⁻¹. The damping constant of the interactions is set automatically using a contact specific Error Reduction Parameter of 0.1, as recommended for numerical stability by the OpenDE manual (opende.sourceforge.net).

We used the OpenDE version GaitSym simulator (Sellers and Manning 2007) and followed our standard gait morphing protocol (Sellers *et al.* 2004). This is a genetic

Fig. 1 Diagram showing the individual muscles used in the reconstruction from an anterior and lateral view. Full path definitions for these muscles are in the human-readable XML file available at www.animalsimulation.org.



algorithm based global optimization system where the mid-simulation conditions of a previous run are used as the starting conditions for a subsequent run. The approach allows the use of very basic initial starting conditions—limbs in anatomical position, torso moving forward—with an initial random genome and generates high quality gait using simple cyclic muscle drivers with 5 phases per step. Initial testing showed that whereas the full model could easily be simulated, the search space for the 70 muscle controllers was too large. To overcome this, we ganged together muscles with similar actions such that, e.g., all muscles that were simple hip flexors were controlled together. This reduced the number of controllers to 18. Even then a fully 3D model, although able to walk and run, produced poor-quality gait because there was a large degree of vertical torsion from step to step. We therefore constrained the model to move in the parasagittal plane by converting all joints to hinge joints and by attaching a sliding hinge to the HAT segment. The advantage of this approach over flattening the model to 2D is that the lengths of the muscles and tendons do not need to be altered. For running, the simulation was first required to move as far forward as possible in a fixed time to provide an estimate of the maximum running speed that the simulator could achieve. Subsequently the model was required to move as far forward as possible for a fixed amount of metabolic energy while keeping the minimum instantaneous speed above 3.6 ms^{-1} , which produces an average speed of about 4 ms^{-1} while maximizing efficiency. This combination ensures the simulator produces efficient, high-speed running. To explore the function and utility of elastic tissue, we varied the stiffness of the tendons within the model. We made individual or groups of tendons highly stiff to remove almost all elastic

storage capability and we measured the effect on the simulation's performance. An example simulated gait is shown in Fig. 2 and the full specification for the model is in the human-readable XML file available from the authors. The simulator used, with versions for both Windows and MacOSX, and all files can be downloaded from www.animalsimulation.org.

We tested four conditions: 1) a model with normal tendons; 2) a model with tendons at 100 times normal stiffness; 3) a model with normal tendons except for the Achilles tendons, which were made 100 times normal stiffness; and 4) a model with normal Achilles tendons but with all the other tendons set at 100 times normal stiffness.

Results

The summary parameters of the generated gaits are shown in Table I. Figure 3a shows the effects of the 4 test conditions on the maximum running speed predicted by the model. The normal model predicts a top running speed of 5.6 m s^{-1} but the model with stiff tendons is unable to maintain a steady state and slows down from 4.7 to 3.6 m s^{-1} over 10 repeated gait morphs when the experiment was terminated. The intermediate models both achieve steady state and show that normal Achilles tendon with all the other tendons stiff is slightly faster (4.9 m s^{-1}) than the model with stiff Achilles tendon and all other tendons normal (4.6 m s^{-1}). This shows the importance of elastic elements in maximizing speed. It can be achieved by a combination of increased mean and peak power outputs, as shown in Fig. 4. The effect is particularly large for the Achilles tendon and the soleus and gastrocnemius muscles. Figure 3b shows the effect on energetics using the models where speed is constrained above a minimum value and the simulation optimized to minimize metabolic energy consumption. When comparing the cost of locomotion, the normal-tendon condition was the most efficient with a score of $1.1 \text{ J kg}^{-1} \text{ m}^{-1}$ and the all-stiff condition was the least efficient, with a value of $3.8 \text{ J kg}^{-1} \text{ m}^{-1}$. The Achilles-normal condition was again the better of the 2 mixed conditions, with an efficiency of $2.4 \text{ J kg}^{-1} \text{ m}^{-1}$ vs. $3.2 \text{ J kg}^{-1} \text{ m}^{-1}$ for the Achilles-stiff condition. The energetic costs can be further investigated by looking at the energy partition for a single step (Fig. 5). Here we can see how energy is transferred between the various internal forms: linear and rotational kinetic energy, gravitational potential energy,

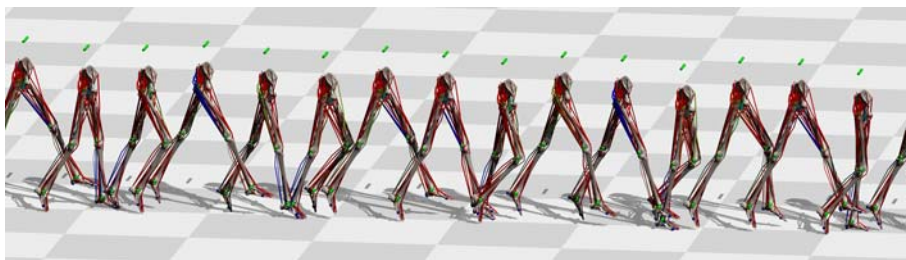


Fig. 2 Composite picture of the simulation output sampled at 0.1-s intervals. The checkerboard spacing is $1 \text{ m} \times 1 \text{ m}$.

Table I Summary parameters of the generated gaits

Optimization criteria	Tendon Stiffness	Velocity (m s ⁻¹)	Net cost of locomotion (J kg ⁻¹ m ⁻¹)	Gait cycle duration (s)	Stride length (m)	Froude number	Relative stride length
Speed	Normal tendons	5.55	4.16	0.707	3.93	3.18	3.97
	Stiff tendons	3.62	4.51	0.555	2.01	1.35	2.03
	Normal tendons + stiff AT	4.56	4.42	0.481	2.20	2.14	2.22
	Stiff tendons + normal AT	4.93	3.74	0.601	2.97	2.51	3.00
Speed + efficiency	Normal tendons	4.03	1.06	0.631	2.54	1.67	2.57
	Stiff tendons	3.76	3.85	0.554	2.08	1.45	2.10
	Normal tendons + stiff AT	4.18	3.15	0.492	2.06	1.80	2.08
	Stiff tendons + normal AT	4.24	2.25	0.602	2.55	1.85	2.58

serial elastic strain energy, and parallel elastic strain energy. The option of allowing storage in the serial elastic elements greatly reduces the variation in total mechanical energy per stride, and hence the external energy input required per stride. In Fig. 6 we compare the mechanical and metabolic work done by the contractile and elastic

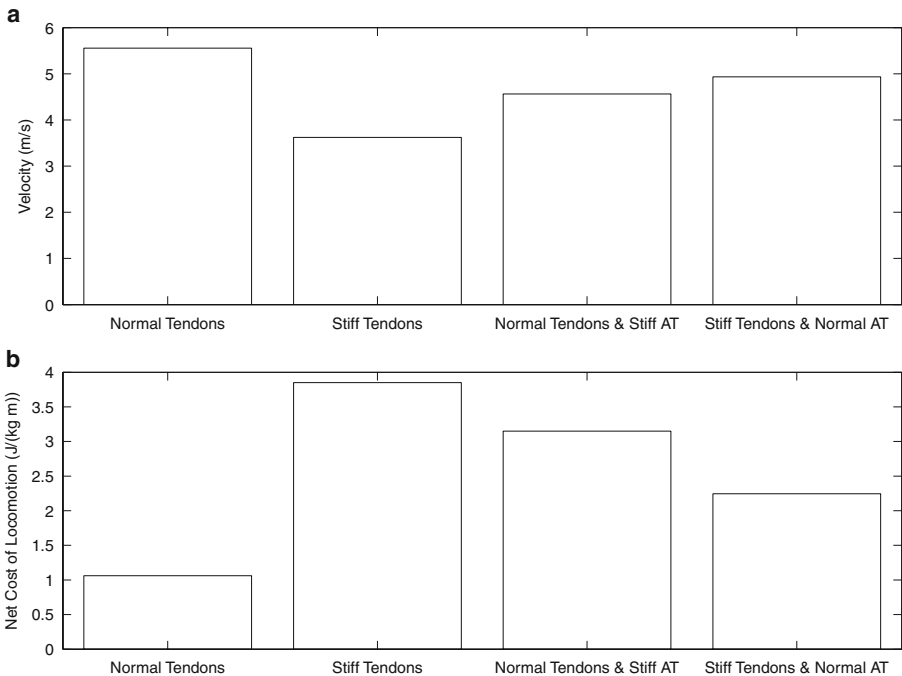


Fig. 3 (a) Graph showing the maximum average velocity achieved by the models in a 3-s simulation period. (b) Graph showing the net cost of locomotion predicted by the model. The bars represent the different tendon stiffness patterns used in the simulation.

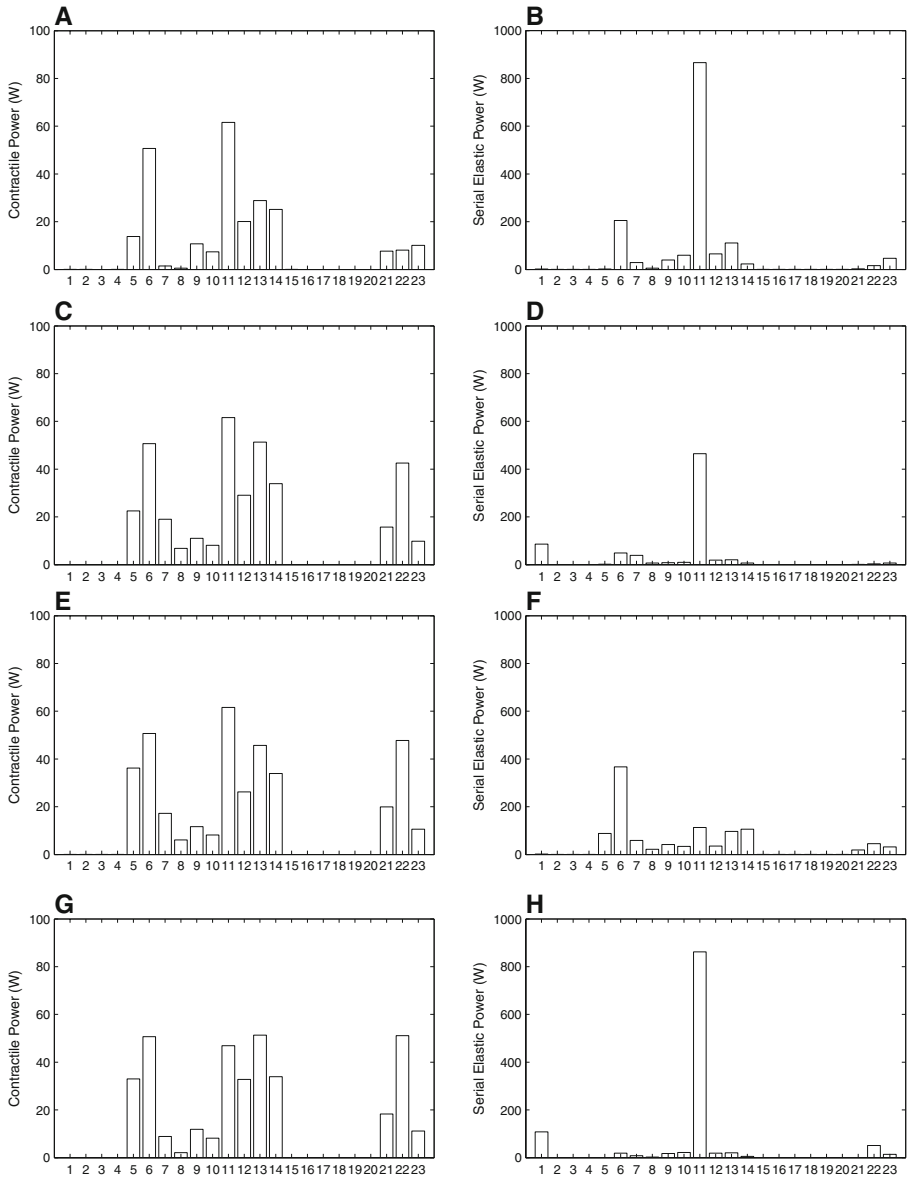


Fig. 4 Graphs showing the peak contractile and serial elastic powers produced by the individual muscles within the model. **(a, b)** Normal tendons; **(c, d)** stiff tendons; **(e, f)** normal tendons with stiff Achilles tendon; **(g, h)** stiff tendons with normal Achilles tendon. Separate values are shown for contractile elements and elastic elements. The muscles are coded as follows: 1, adductor longus; 2, adductor magnus; 1, 3, adductor magnus; 2, 4, adductor magnus; 3, 5, biceps femoris caput breve; 6, biceps femoris caput longum; 7, extensor digitorum longus; 8, extensor hallucis longus; 9, flexor digitorum longus; 10, flexor hallucis longus; 11, gastrocnemius; 12, gluteus maximus; 1, 13, gluteus maximus; 2, 14, gluteus maximus; 3, 15, gluteus medius; 1, 16, gluteus medius; 2, 17, gluteus medius; 3, 18, gluteus minimus; 1, 19, gluteus minimus; 2, 20, gluteus minimus; 3, 21, gracilis; 22, iliopsoas; 23, peroneus brevis.

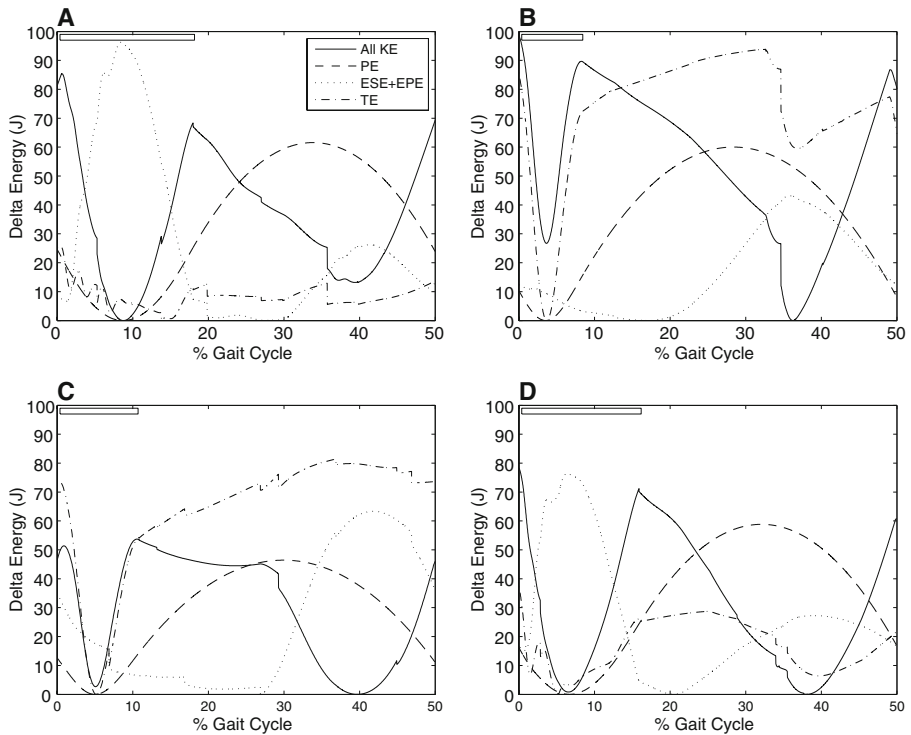


Fig. 5 Graphs showing the energy partition in a single step (half a full gait cycle) in terms of the change in total linear and rotational kinetic energy (All KE), gravitational potential energy (PE), elastic strain energy (ESE+EPE), and the sum of all these separate components (TE). The rectangle in the top left shows when the foot is in contact with the floor. The variation in total energy is a measure of the minimum external energy input required per stride. (a) Normal tendons; (b) stiff tendons; (c) normal tendons with stiff Achilles tendon; (d) stiff tendons with normal Achilles tendon.

elements and again we can see how the presence of serial elastic elements reduces the metabolic work and particularly how large the contribution of the Achilles tendon is.

Discussion

It is clear from these simulations that the effect on running performance of elastic storage in general and the Achilles tendon in particular is profound. The presence of compliant tendons increases the top running speed by >80% compared to the noncompliant tendon condition. The effect on energy costs is even larger, with the cost of locomotion in the compliant condition <25% of the cost of locomotion in the noncompliant condition. Simulations wherein compliance was mixed showed the best performance when compliant Achilles tendons were added to otherwise noncompliant models. This indicates that although all elastic tissue has significant beneficial effects, most of this can be attributed to the presence of the Achilles tendon. This sort of performance improvement is strongly supportive of the idea that the Achilles tendon is necessary

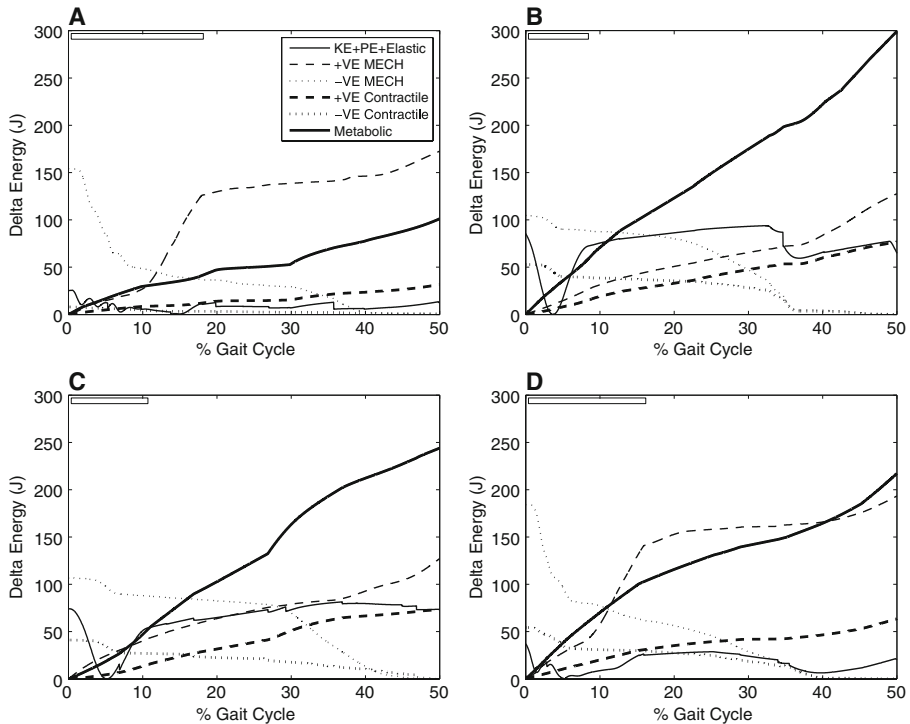


Fig. 6 Graphs showing the actual work done by the individual components of the model: the sum of the energy stored as kinetic energy (both linear and rotational), gravitational potential energy and elastic strain energy (KE+PE+Elastic); the positive and negative mechanical work of the complete musculotendinous unit (\pm VE MECH); the positive and negative mechanical work of contractile elements (\pm VE Contractile); and the metabolic work of the contractile elements (Metabolic). The rectangle in the top left shows when the foot is in contact with the floor. (a) Normal tendons; (b) stiff tendons; (c) normal tendons with stiff Achilles tendon; (d) stiff tendons with normal Achilles tendon.

for efficient bipedal running. Thorpe *et al.* (2004) showed that chimpanzees are limited in their ability to run bipedally by the ability of their hind limb muscles to exert large moments, but all else being equal, absence of a well-developed Achilles tendon in the nonhuman African apes would preclude them from effective running, both at high speeds and over extended distances.

On the other hand, the presence of a marked Achilles tendon in hylobatids, although it may have evolved as a means of enhancing jumping performance, is certainly related to their ability, likely to be expressed only on the ground, to sustain bipedal running for distances of several hundred yards (K. Isler, *pers. comm.* to R. H. Crompton). The Achilles tendon may also play a role in walking. In our recent pixel-level statistical comparison of plantar pressures at varying walking speeds (Pataky *et al.* 2008), we found a negative correlation between peak pressure and walking speed over the midfoot and proximal forefoot. If the arch were only passively supported, primarily by tension in the plantar aponeurosis (PA), we would expect the arch to collapse to a greater degree under the larger ground reaction forces, which Keller *et al.* (1996) have shown are associated with faster walking. Muscle activity before or early in stance must therefore be implicated, and indeed ankle EMG increases with

walking speed (Hof *et al.* 2002; Neptune and Sasaki 2005; Warren *et al.* 2004). Toe dorsiflexors (Carlson *et al.* 2000; Hicks 1954), via the windlass mechanism, or ankle plantarflexors (Carlson *et al.* 2000; Erdemir and Piazza 2004), by applying tension to the calcaneus, could act to increase tension in the PA, and hence stiffen the foot. Arch stiffness might have propulsive benefits via elastic energy return, although this is expected primarily when running (Ker *et al.* 1987). Data showing compromised propulsion after plantar fasciotomy (Daly *et al.* 1992) suggest that tension in the PA may improve propulsive force transmission (Erdemir *et al.* 2004), perhaps by providing semirigid leverage for propulsion (Bojsen-Møller 1979), or might increase the rearwards pull during late stance and hence directly assist propulsion. It is not so much bipedalism *per se* that distinguishes hominin walking, as even erect bipedalism is found in untrained orang-utans and some abnormally raised chimpanzees, but the ability to walk rapidly in bipedal posture (Crompton *et al.* 2003, 2008). This capacity is certainly related in part to the higher forces, for lower stresses, which can be generated by human hind limb muscles, including triceps surae (Thorpe *et al.* 2004) but equally by a human capacity to accelerate the body with the forefoot, a capacity that can be enhanced in chimpanzees by training (Kimura 1996; Yamazaki 1985), but by no means equalled. It would appear that triceps surae, and hence the Achilles tendon, may be implicated in both.

Thus, evidence for a well-developed Achilles tendon would be a good indicator of locomotor performance of early hominins, both for effective fast walking and running. We suggest that efforts to identify the presence of this tendon should be pursued because there should be measurable bony changes with the presence of a well-marked tendon in life, particularly in the calcaneus. These might be associated with a general need for a stronger bone to support the extra power requirements engendered by high-speed running, or more specific tendon indicators that might be found in the micro- or nanostructure of the bone such as detailed trabecular patterning (Ryan and Van Rietbergen 2004) or Sharpey's fibers (Benjamin *et al.* 2002).

The strength of such conclusions relies heavily on the validity of the model. The AnyBody musculoskeletal models are widely used in both biomechanics research and industry. That means that the anatomical information (segmental mass properties, joint locations, muscle attachments) is reasonably accurate. However, our physiological understanding of muscle is still not perfect, and there are parameters such as the elastic properties of tendons and in particular the slack lengths and passive muscle properties that are not well known even for modern humans. A full sensitivity analysis would be desirable to identify the effects of uncertainty but currently this is computationally impractical. Recent work looking at the sensitivity of running models to input parameters suggests that muscle mass and contraction speed are the major areas of uncertainty, but this study did not specifically look at the effects of elastic tissue (Bates *et al.* in press). Similarly, the optimisation system is not an exhaustive search of all possibilities and because of the computationally intensive nature of the process it is not possible to perform a large number of independent repeats. The simulation itself is a first-order process, and this will lead to numerical errors but these are likely to be small compared to any biological uncertainty. Future work clearly needs to concentrate on higher biorealism in the foot, and its interactions with the ground, which for computational reasons was modeled as 3 simple contact elements on a rigid foot. A multisegment model,

with not only the ability to flex at the metatarsophalangeal joints, but that could also simulate the changes in stiffness, and hence in the position of the center of pressure, and the effective lever arm/gearing of the ankle plantarflexors, would be ideal, although such improvements would almost certainly necessitate a fully 3-dimensional model. Similarly, it would be extremely useful to improve the validation of the model, particularly when applied across species. The major difficulty here is that this requires extensive experimental data on a range of hominoids. This is currently extremely scarce with limited kinematic and metabolic information (Sockol *et al.* 2007; Taylor and Rowntree 1973; Taylor *et al.* 1972) and even more limited EMG data (Larson and Stern 1986; Larson *et al.* 1991; Susman and Stern 1980) available from laboratory studies on chimpanzees. However, modern, noninvasive techniques such as surface ultrasonometry (Lichtwark and Wilson 2006), may allow more extensive data to be collected in the future.

The restriction to 2D is also a current necessity. Realistic 3D movement would almost certainly require subdividing the trunk and allowing spinal and pelvic movements to prevent the observed vertical torsion effects (Witte *et al.* 2004). This would greatly increase model complexity, both in terms of joints and muscles. However, the predictions made by the current model with normal tendon properties are in line with those expected from experimental studies. The calculated values for external work on the center of mass and the metabolic cost of locomotion are broadly in line with those expected for the body mass used suggesting the model is producing reasonably good gait (Full and Tu 1991). The Froude numbers are entirely appropriate for running [varying from 1.5 to 3.2, calculated as v^2/gl (Alexander 2003)] but the relative stride lengths in both cases running are slightly longer than would be predicted for animals in general (Alexander and Jayes 1983), but are more consistent with the values for primates (Alexander and Maloiy 1984) and well within the range of variation in modern humans, although above the mean (Sellers *et al.* 2005). The energy expenditure per stride for running (2.70 J kg^{-1}) is lower than that predicted for a wide size-range of mammals running at trotting/gallop transition speed (5.34 J kg^{-1} ; Heglund and Taylor 1988), but nevertheless is a reasonable approximation for a simulation.

Conclusions

This article demonstrates the use of virtual ablation to test the overall value of elasticity and particularly of the Achilles tendon in human running. The results suggest that the latter structure is the single most important elastic energy store and that efficient high-speed running is unlikely in hominoids that do not possess it. We therefore suggest that identifying which early hominin species possess such a tendon will enable us to decide whether a particular species was capable of such locomotion and the behavioral adaptations that this implies.

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Appendix

This section describes the muscle model used. All equations are given in Mathematica format so that they can simply be copied into a notebook and solved as required. The muscle model consists of the standard Minetti and Alexander contraction model (Minetti and Alexander 1997) that represents concentric and eccentric contractions by the following equations (rearranged from the originals so that they incorporate linear rather than rotational quantities and altering the sign of the contraction direction so that a negative velocity represents shortening):

Eccentric ($v_{ce} > 0$)

$$eq1 := fce == \alpha f_0 (1.8 + (0.8 k (v_{ce} - 1. v_{max})) / 7.56 v_{ce} + k v_{max})$$

Concentric ($v_{ce} \leq 0$)

$$eq2 := fce == (\alpha f_0 k (v_{ce} + v_{max})) / (-v_{ce} + k v_{max})$$

where

fce	contractile element force (N)
α	activation (0–1)
k	shape constant (generally 0.17)
v_{ce}	contractile element velocity (m/s)
v_{max}	maximum shortening velocity (m/s)
f_0	isometric force (N)

Serial and parallel springs are then added in the Hill style and are implemented using the following equations:

$$eq3 := fce + fpe == fse$$

$$eq4 := fse == ese(lse - sse)$$

$$eq5 := fpe == epe(lpe - spe)$$

where

fce	contractile force (N)
lpe	contractile and parallel length (m)
spe	slack length parallel element (m)
epe	elastic constant parallel element (N/m)
fpe	parallel element force (N)
lse	serial length (m)
sse	slack length serial element (m)
ese	elastic constant serial element (N/m)
fse	serial element force (N)

Two other equations can be derived based on the total length of the muscle-tendon unit and the previous model state:

$$eq6 := len == lpe + lse$$

$$eq7 := vce == (lpe - lastlpe)/timeIncrement$$

where

len total length of system (m)
lastlpe length of the parallel element at the last time step (m)
timeIncrement integration time step of the simulator (s)

For the concentric case the C code can now be generated using the Mathematica command:

```
CForm[FullSimplify[Solve[{eq2, eq3, eq4, eq5, eq6, eq7}, {lpe, lse, fpe, fse, fce, vce}]]]
```

Similarly for the eccentric case:

```
CForm[FullSimplify[Solve[{eq1, eq3, eq4, eq5, eq6, eq7}, {lpe, lse, fpe, fse, fce, vce}]]]
```

These results need to be checked for validity because the solutions are not unique. However, there is a unique solution when range criteria are checked. There are also special cases when springs are slack. If both parallel and serial springs are slack then the model reverts back to the non-spring version. If just the parallel spring is slack then Eq. 5 changes and there are different solutions:

$$eq5b := fpe == 0$$

The concentric case C code is now generated by:

```
CForm[FullSimplify[Solve[{eq2, eq3, eq4, eq5b, eq6, eq7}, {lpe, lse, fpe, fse, fce, vce}]]]
```

The eccentric case C code is now generated by:

```
CForm[FullSimplify[Solve[{eq1, eq3, eq4, eq5b, eq6, eq7}, {lpe, lse, fpe, fse, fce, vce}]]]
```

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