Energetics of Human Running: A Mechanistic Perspective

by

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Abstract

There are conflicting explanations for the metabolic cost of energy in human motion. Mechanical work can be measured at each joint, but both muscles and tendons act across joints, and several decades of studies show tendon can perform substantial work elastically, thereby confounding estimates of muscle work. This has motivated the prevailing "mass-spring" model of running, which incorporates a point mass bouncing atop a compliant spring, with no explicit need for muscles. Dispensing with mechanical work as measurement and explanation, the mass-spring model has led to the alternative "cost of generating force" hypothesis, where body weight and ground contact time appear to determine metabolic cost for a variety of animals and running speeds. Although the correlations are quite good, such a cost does not readily admit a mechanistic explanation. I propose that the mass-spring model has fundamental limitations in explaining energetics, and that mechanical work merits re-consideration as a basic mechanism. I introduce refinements to the experimental evaluation of work, new models for the action of muscle and elastic tendon, and experimental procedures that help to explain how mechanical work contributes substantially to the overall metabolic cost of running.

This dissertation first re-examines the experimental measures of mechanical work. Whereas past literature has estimated the work performed by body joints on rigid body segments, our measures include the work of soft-tissue deformations, not previously appreciated as a substantial contribution. I evaluated the aggregate work of soft-tissues in running, and found that they behaved in a manner similar to a damped spring-mass system. I show that damped vibrations, and the active work necessary to compensate for them, may account for 29% of the net metabolic cost for running at 5 m/s. Another issue is that the most directly measurable quantity, joint work, does not account for how

multi-articular muscles transfer energy between joints, and the degree to which tendons perform passive elastic work. Despite the lack of objective information, these phenomena may nevertheless be incorporated into a parametric estimation of the likely contribution of active mechanical work to running. I show that, applying basic parameter values derived from the literature, mechanical work may account for 74% of the net metabolic cost of running.

I then use experiment-based models to re-examine two other aspects of running mechanics. One is the regulation of running speed, which is not considered in most steady-state analyses. Applying mechanical perturbations in the forward and backward directions, I show that runners immediately apply corrections that dissipate or restore kinetic energy in the first step following perturbation. A simple actuated model reproduces the experimental work-loop, whereas the mass-spring model cannot account for such corrections. I also re-examine the role of the foot, which is ignored in mass-spring models, and thought to be dissipative in rigid body models. I use a simple model to show that the apparent dissipation could instead be explained by multi-articular energy transfer across the foot arch and metatarsophalangeal joint via plantar fascia and other tissues. The model shows how energy could be saved, and how features such as foot's length could contribute to economical running.

Chapter 1 : Introduction

The measurement of mechanical work at joints during human locomotion is used to evaluate locomotion, including the energetic benefits of prostheses, orthoses, and exoskeletons (Devita et al., 1992; Gordon et al., 2006; Morgenroth et al., 2011; Zoss et al., 2006). However, measurements of mechanical work in these methodologies have given rise to a few surprising and potentially erroneous conclusions regarding the role of work and elastic tissues in the energetics of running.

Firstly, most measurements of mechanical work in running measure only the contribution of joints acting on rigid body segments. This methodology makes the implicit assumption that the effects of soft tissue contributions are negligible, even though soft tissues are known to have significant contributions in human walking and *ex vivo* tests (Ker et al., 1987; Zelik and Kuo, 2010). Secondly, due to inconsistencies in work-based estimates of metabolic cost, others have popularized the hypothesis that the cost of generating muscle force is the dominant cost, with the cost of mechanical work being negligible (Kram and Taylor, 1990). Thirdly, observing that net-work is zero during steady state level-ground locomotion, the spring-mass model has been widely used to analyze the mechanics of running, including suggesting foot placement and modulating leg stiffness as the dominant mechanisms for control (Geyer et al., 2005). Finally, mechanical work measured in the foot at the metatarsophalangeal (MTP) joint shows almost entirely negative work during walking running, which has been interpreted as mechanical dissipation (Stefanyshyn and Nigg, 1997).

In this dissertation, I address each of these ideas with novel experiments and simple computational models to provide evidence against these four ideas. That is, I show that soft tissues do in fact do significant work during running, accounting for up to 29 % of metabolic cost running at 5 m/s. Next, I use these new soft tissue measurements in conjunction with typical joint-level measurements of work to show that work is the major

determinant of metabolic cost, likely accounting for around 74% of metabolic cost. Then I investigate fore-aft perturbed running to show that the spring-mass model is a poor predictor of how humans respond to perturbations, and develop an energetic model to extend the spring-mass model. Finally, I develop a computational and physical model to show that much of the net-negative work measured at the MTP joint may in fact be energy elastically transferred across the foot and ankle via the plantar fascia.

Soft Tissue Dissipation

The mechanics of passive soft tissues such as the heel pad, intervertebral discs are not typically measured during locomotion. While it is known that such structures are passive and therefore must on average dissipate energy, it is unknown how much they dissipate in aggregate and in comparison to muscles. By estimating this dissipation, it is then possible to estimate the amount of positive muscle work must be used to offset this dissipation. While typically only the energetics of the ankle, knee, and hip are measured in biomechanics studies, it may be important to include the effects of soft tissues as well.

Others have measured individual soft tissues in running and shown that they do significant mechanical work. The heel pad, plantar fascia, the shank, and thigh both cushion the body and provide elastic energy return (Ker et al., 1988; Liu and Nigg, 2000; Nigg and Liu, 1999; Pain and Challis, 2006; Schmitt and Günther, 2011; Wakeling and Nigg, 2001). However, these measurements can be challenging to make, and there appear to be no full-body estimates of the effects of soft tissues in running in the literature.

We therefore measured the net effects of soft tissues in a manner described previously in walking (Zelik and Kuo, 2010) and found that the net negative work is done by soft tissues in running, and resembled a damped oscillator. The soft tissues perform work of a similar magnitude to the knee but with a faster frequency. Assuming an efficiency of 25% (Margaria et al., 1963), the work to offset soft tissues would account for about 319 W at 5 $m \cdot s^{-1}$, or about 29% of the net metabolic power at those speeds. This suggests that it is not appropriate to ignore soft tissues in analysis of energetics, and the ease

with which the measure can be calculated in comparison with direct site-specific measurements lends itself to easy adoption to those studying locomotion.

Mechanical Work as the Dominant Metabolic Cost of Running

Estimating metabolic cost from mechanical work has a long history with diverse and sometimes conflicting results. Some of the earliest work measuring the mechanics of running measure mechanical work and conclude that positive mechanical work is the major determinant of metabolic cost, with tendons doing about half of the work, and muscles operating at 25% efficiency (Cavagna et al., 1964; Margaria, 1968). However in consequent studies, depending on the method of estimation, mechanical work has been shown to predict a muscle efficiency between 31-197 % (Williams Kr, 1985).

To understand why different experiments had such drastic differences in estimating work-based costs, Williams et. al formulated and examined the assumptions underlying the estimates to show how such a range is possible (Williams and Cavanagh, 1983). They showed that assumptions of energy transfer between body segments, the function of tendons, and muscle efficiency performing negative and positive work all directly influence estimates of metabolic cost due to muscle work, resulting in wildly different estimates.

This alarming range prompted questions as to the validity of mechanical work as a determinant of cost, with studies supposing instead that the cost of generating force (COGF) is the major source of metabolic cost (Kram and Taylor, 1990). The idea behind this cost is that muscles may contract mostly isometrically, while tendons stretch to perform the observed work. The increase in metabolic cost due to an increased speed is then interpreted as the cost of muscles having to generate the same average force (body weight) over a smaller amount of time on the ground. Since there is no easy way to measure this cost, the authors used the inverse of contact time as an estimate, showing a strong correlation well with the metabolic cost of running across several animals.

I show here that mechanical work may be the major determinant of metabolic cost. Like the work of Williams et. al (Williams and Cavanagh, 1983), I include the effects of energy transfer, tendon work, and efficiency assumptions; however, I consult the literature to find upper and lower bounds for each assumption in order to make the relationship between each assumption and its effect on cost clear. Importantly, I also include the effects of soft tissues, which to my knowledge have not been incorporated into any existing models of metabolic cost. Since in level ground running net work is zero, the energy dissipated by soft tissues must be directly offset by positive active muscle work. By including soft tissues, the lower and upper bounds of metabolic cost explained by work is between 51-97 %, with 74% being the best estimate based on reasonable assumptions.

While these estimates of metabolic cost due to work are still quite imprecise, the methodology behind the estimates is mechanistic and determinate. Due to the law of conservation of energy, the work measured mechanically is fundamentally related to the metabolic cost of the body to make those movements. While many measurements can correlate well with metabolic cost in running, this model has the advantages that it can be principally combined with other costs, as well as being independent of the type of movements the human or other animal performs.

Spring-Mass Model Insufficient to Explain Fore-Aft Perturbed Running

Blickhan et. al proposed a simple spring-mass model for understanding the mechanics of running (Blickhan, 1989). The Spring Loaded Inverted Pendulum (SLIP) model consists of a single mass at the pelvis and a massless leg which rotates about the pelvis and can compress with a certain stiffness while on the ground. The simplicity of this model as well as its ability to roughly reproduce gait characteristics such as the ground reaction force profile immediately popularized it as a simple yet effective way to understanding the dynamics of running. The model has been used as the basis for many models since, and used to understand potential human control strategies (Geyer et al., 2005; Seyfarth et al., 2003), as well as developing control strategies for locomoting robots (Hurst et al., 2004). Since the model is so simple, the only way for it

to control itself is to alter the stiffness of the leg and to change foot placement, which were shown to be capable of stabilizing simulated running.

I show here that the SLIP model is insufficient to explain how humans stabilize in response to mechanical perturbations. Since the SLIP model has no mechanism to actuate or dissipate energy, it is unable to capture the work loop characteristics that are fundamental to human locomotion. While both humans during level ground steady state running, and springs in general perform zero net work, humans experience perturbations and changes in speed that require non-zero net work to be done. By examining the force-displacement curves of the leg even during steady state running, it is clear that a single stiffness (the slope of a line on this plot) is insufficient to explain the stance phase dynamics of running.

By applying mechanically pulling on subjects running on a treadmill, I found that they compensated by either performing additional actuation or dissipation for aft and fore perturbations respectively. My results suggest that humans control and stabilize in part by altering the amount of net work done, through some combination of increasing positive work via concentric muscle contractions and increasing negative work through eccentric muscle contractions. In contrast, while estimates of leg stiffness and striking angle changed significantly, they changed by a smaller percentage than changes to net work. This suggests that control strategies that rely on striking angle and modulation of stiffness do not explain a majority of human compensation to mechanical perturbations (Seyfarth et al., 2003).

I developed a simple extension to the SLIP model to better interpret the strategy humans use to recover from perturbations. The Damped Actuated Spring-Mass model is the same as the SLIP model, except there is also a damper and a simple actuator in parallel. After being perturbed during simulated running, the model was able to return to its nominal speed and limit cycle by changing the damping constant and actuation gain at the beginning of the first perturbed step. The model showed the same trends in net work as humans in the step after the perturbation, in both fore and aft conditions. We also performed an optimized fit of the human data leg length, compression speed, and force to show significant changes in the model parameters of actuation and damping in

response to perturbations. By including estimates of dissipation and actuation, we have shown that the model better explains the observed human compensation strategy to fore and aft perturbations.

Multi-Articular Elastic Energy Transfer of Foot Appears as Energy Dissipation at the Metatarsophalangeal joint

While the mechanical function of the ankle, knee, and hip are well studied, the role of the foot, especially regarding mechanical energetics, is less understood. Measurements of the metatarsophalangeal (MTP) joint show that the joint does significant amounts of negative work during walking, running, and sprinting during the push-off phase (Stefanyshyn and Nigg, 1997). Since very little positive work is observed at this joint following the negative work, this data was interpreted as the foot behaving mostly as a dissipative element. Because one might expect humans move in ways to minimize metabolic cost, this is a curious result. As stated earlier, any mechanical energy dissipated must thereby be compensated for by active muscle work, thereby increasing the metabolic cost.

I propose that the apparent dissipation at the MTP joint may instead be mostly elastic energy transfer to the rearfoot and ankle via the plantar fascia. Whereas the inverse dynamics model used to conclude that the MTP dissipates energy assumes that each joint is independent, in humans this assumption is clearly not true. The plantar fascia spans not only the MTP, but also the rear and mid foot, inserting near the back of the foot on the calcaneus. The Achilles tendon and the plantar fascia may act in series about the foot and ankle, in which case energy absorbed at the MTP may be elastically transferred into positive work at the ankle. There is recent work showing that the plantar fascia does in fact behave mostly elastically, while negative work is observed at the MTP (McDonald et al., 2016).

The main question then is whether two elastic elements (Achilles and plantar fascia) acting on a single body (Calcaneus) can transfer energy from one joint (MTP) to another (ankle). The idea of energy transfer across human joints during running has been studied in other joints and muscle groups. Other have proposed there is significant

energy across the ankle, knee, and hip by the gastrocnemius and rectus femoris muscles (Prilutsky et al., 1996). To my knowledge, it has not been proposed or studied whether the plantar fascia may have a similar effect in the foot.

I developed a simple computational model to test whether multi-articular tendon structures could result in apparent dissipation at a single joint. During simulated running, I found that the spring modelling the plantar fascia deformed, resulting in net positive and negative work at the ankle and MTP respectively, with time profiles roughly similar to humans. Since the model is energy conservative, there is no dissipation of energy, and all energy absorbed at the MTP was fully transferred to the ankle. This suggests that measurements of net negative work do not necessarily correspond to dissipation. A physical mechanism of the foot was also built and measured, showing as well that while the springs behaved mostly elastically as expected, the mechanical work measured at the MTP and ankle were net negative and net positive respectively.

This model provides a more descriptive interpretation of mechanical work at the performed in the ankle and foot than standard inverse dynamics models. It also suggests caution when interpreting joint mechanics in the absence of explicit models of muscle-tendon units. This model provides evidence that the foot does not dissipate large amounts of energy during push off. Instead, the foot may improve the economy of running by acting as a lever arm which can efficiently transfer energy across the ankle.

Summary

In this dissertation, I investigate interpretations of running dynamics and energetics that are based on misunderstandings of mechanical work. Firstly, I show that the assumption that soft-tissues perform negligible work compared to leg joints is incorrect, and that soft tissue dissipation could account for up to 30% of metabolic cost while running at 5 m/s. Using these new soft tissue measurements, I then show that mechanical work explains a majority of running cost even with conservative estimates of efficiency, muscle work, and joint-energy independence. This provides strong evidence against the popular idea that the major cost of running is the Cost of Generating Force (COGF) which was based on a study in the first place that simply correlated cost with an

indirect measure of COGF. Thirdly, I show that the popular Spring Loaded Inverted Pendulum (SLIP) model leads to an incomplete analysis of human running dynamics, failing to predict human compensation to fore-aft mechanical perturbations. I then construct the Damped Actuated Spring-Mass model to better interpret human data, providing estimates for leg stiffness, damping, and actuation. Finally, I provide evidence against the claim that the foot dissipates significant energy during push-off by using a computation and physical model to show that the plantar fascia is likely to elastically transfer energy from the Metatarsophalangeal joint (MTP) to the ankle.

Chapter 2 : Soft Tissues Store and Return Mechanical Energy in Human Running

Introduction

During steady-state running, the body performs active and passive work summing to zero over each stride. As characterized previously (Farris and Sawicki, 2011; Novacheck, 1998; Schache et al., 2011; Winter, 1983), the leg joints perform positive and negative work within each stride, with active muscles accounting for nearly all of the metabolic energy expenditure (Margaria et al., 1963). Passive "soft tissues" such as the heel pad (Chi and Schmitt, 2005), cartilage, and intervertebral discs (among others, see Fig. 1-1) help cushion the body. That cushioning functions in part to dissipate mechanical energy. Although their mechanical properties are well understood, it is unknown how much energy soft tissues dissipate in aggregate and in comparison to muscles. An estimate of soft tissue work might provide insight on the active work of muscles and the attendant metabolic cost of running.

Figure 2-1. Soft tissues whose deformations may store and return mechanical energy during running. The passive deformation of heel pads, plantar fascia, cartilage at joints, intervertebral discs, muscles (deformations separate from muscle contraction), skin, and even shoes may contribute.

The leg joints account for most of the mechanical power produced during running. Although the joint power trajectories are rather complex, their effect on the whole body is fairly simple: Following a brief small burst of positive work (about 0 – 2.5 % of a stride starting at ground contact), most of the stance phase resembles a mass-spring system (McMahon and Cheng, 1990), with one main large burst of negative work

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(2.5 – 15% stride, termed Collision here), and then one large burst of positive work (15 – 34% stride, termed Rebound) prior to the Aerial (34 – 50%) and Swing (50 – 100%) phases. Much of the work observed at the joints might actually be performed by elastic tendon. The amount is measured to be more than half in turkeys (Roberts et al., 1997), and indirectly projected to be similar in humans (Cavagna and Kaneko, 1977). If there were no other dissipation in the body, then the work fluctuations would be due only to elastic tendon and to equal magnitudes of active negative and positive work by muscle, all summing to zero over a stride.

There is, however additional dissipation by soft tissues. The heel pad, plantar fascia, and other elements of the foot both cushion the body and provide elastic energy return (Ker et al., 1988). Soft tissues in the lower leg explain how impact forces are transmitted and damped during running and jumping (Pain and Challis, 2006) and how they can modulate peak joint forces (Liu and Nigg, 2000; Nigg and Liu, 1999; Wakeling and Nigg, 2001). From measurements of skin motion, the thigh and shank also absorb considerable mechanical energy during each stance phase (Schmitt and Günther, 2011). But soft tissue deformations can be challenging to measure, for example through embedded force recordings in cadaveric specimens (Ker et al., 1987; Pai and Ledoux, 2010), or extensive motion capture of the skin (Günther et al., 2003) and potentially for the entire body. As a result, there are no estimates for the overall work performed by soft tissue deformations during *in situ* running, nor of the active work needed to offset the dissipation.
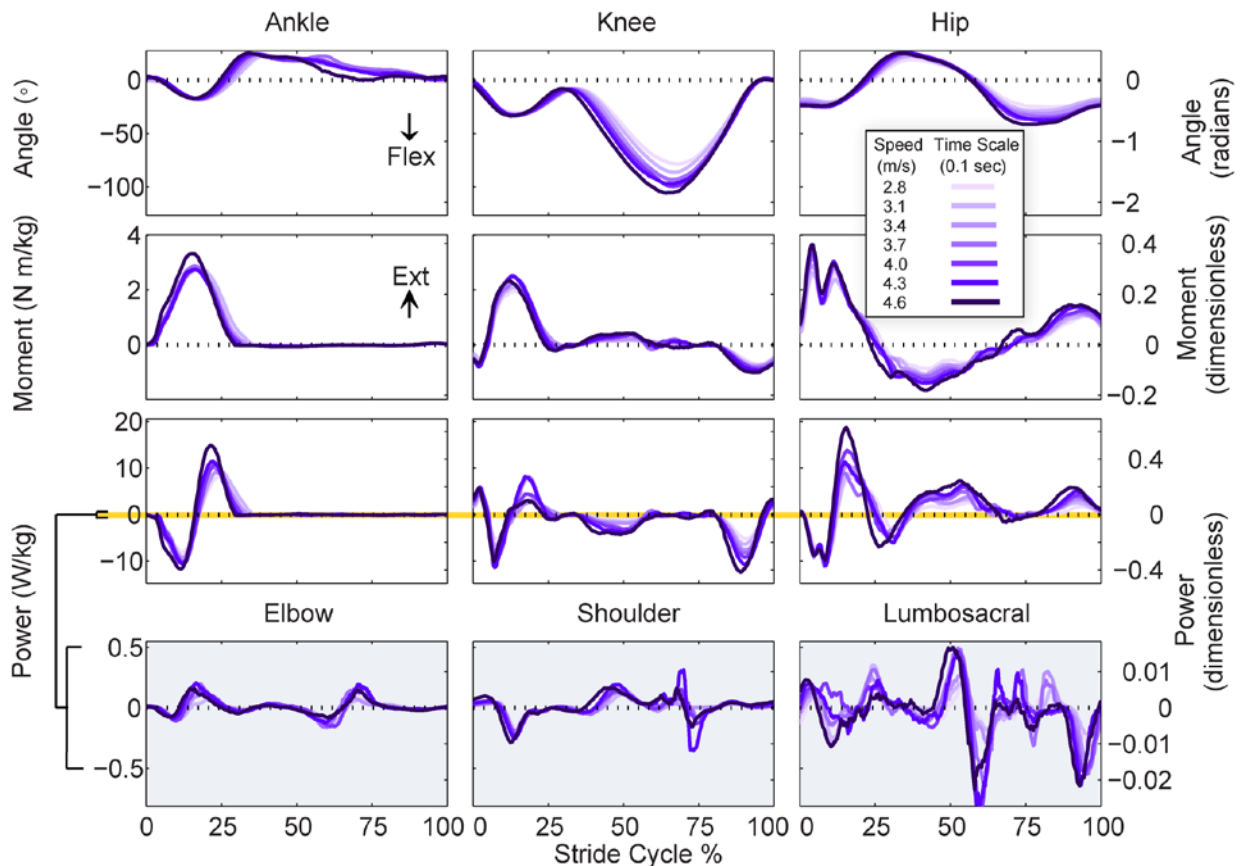
Figure 2-2. Mean joint angle, moment, and power trajectories over a stride at seven running speeds. Angles and moments shown are sagittal plane values, and powers shown include three-dimensional rotation and translation, averaged across subjects (N = 8) at each point in the stride cycle (beginning and ending with same-side ground contact). Elbow, shoulder, and lumbosacral joints are shown on an expanded scale due to smaller power contributions. Angles (°) and moments (N·m·kg-1) are defined as positive in extension. Dimensionless units (right-hand axes) are defined using body mass, leg length, and gravitational acceleration as base units.

The aggregate work of soft tissues can be estimated, albeit indirectly. This relies on the discrepancy of total mechanical work performed according to two different measures: (1) joint powers as estimated by rigid-body inverse dynamics, and (2) rate of work performed on the non-rigid body center of mass (COM) as measured by ground reaction forces, and on the periphery as measured by rigid-body inverse dynamics (Zelik and Kuo, 2012). Their difference indicates work performed by soft tissues, showing substantial dissipation during human walking (Zelik and Kuo, 2010) and particularly in the obese (Fu et al., 2014). The dissipation is also highly dependent on impacts, as demonstrated in jumping (Zelik and Kuo, 2012), suggesting possible contributions to running as well. Because the muscles must actively offset any net dissipation in the body, soft tissue deformations may affect the metabolic cost of both walking and running. The purpose of the present study was to estimate these contributions during
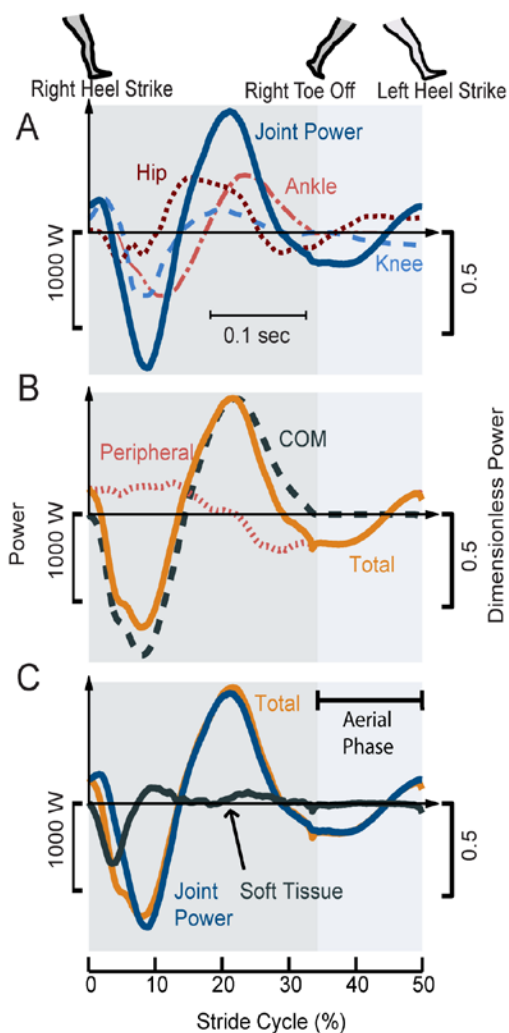
Figure 2-3. Power trajectories over a step (half a stride) for a representative subject running at 3.4 m·s-1. **A)** Joint Power, referring to the summed power of all measured joints, shown here along with stance leg's ankle, knee, and hip. **B)** Center of mass (COM) work rate plus Peripheral power equals Total power for the body. **C)** Soft Tissue power is the estimated as the difference between Total power and Joint Power. Power is shown in W (left-hand axes) and in dimensionless units (right-hand axes). Representative subject has body mass 71.2 kg, leg length 0.94 m.

human running. We expect that (1) soft tissues perform both negative and positive work within each stance phase, (2) yielding substantial net negative work, and (3) in increasing amount at faster running speeds, due to the greater impacts.

Materials And Methods

We estimated the work of soft-tissue deformations for 8 young healthy adults (7 males, 1 female; aged 20 –34 yrs.; body mass M 74.9 ± 13.0 kg, and leg length L 0.94 ± 0.044 m, mean ± s.d.) running at a range of speeds. The subjects ran on an instrumented treadmill at a comfortable range of speeds determined by their level of fitness (a total range of 2.2 to 5 m·s^{-1}) in 7 randomized experimental trials lasting 1 minute each. Of the 8 subjects, 6 landed on their rear-foot, while two tended to land on their mid-foot or fore-foot, as determined by observing the subjects' gait. All subjects gave informed consent according to approved Institutional Review Board procedures.

We recorded ground reaction forces and motion capture. Forces were recorded on a split-belt instrumented treadmill (Bertec, Columbus, OH, USA) at 960 Hz. Kinematic data were collected at 480 Hz with an eight-camera motion capture system (PhaseSpace Inc., San Leandro, CA, USA), with markers placed bilaterally on the ankle (lateral mallelous), knee (lateral epicondyle), hip (greater trochanter), shoulder (acromion of scapula), elbow (lateral epicondyle of humerus), and wrist (trapezium). Additional tracking markers were placed on the shanks, thighs, trunk, upper and lower arm, pelvis (sacrum, left/right anterior
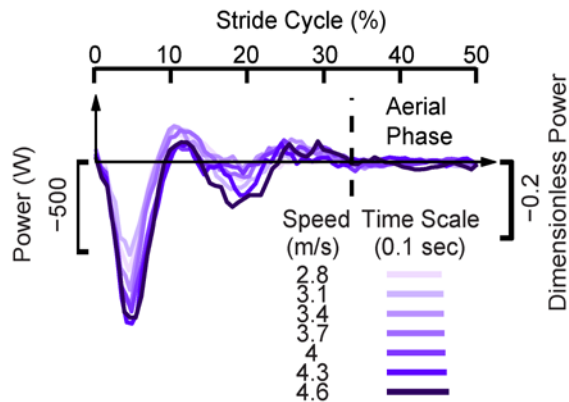
Figure 2-4. Soft-tissue power over a step (half a stride) for a representative subject. Soft tissue performs net negative work during a step, a majority of which occurs as the foot impacts the ground during the stance phase. The profile resembles a spring-mass-damper system, with a damped elastic rebound (about 10 – 15% of stride).

superior iliac spine) and each foot (calcaneus, fifth metatarsal). Inverse dynamics calculations (Fig. 2-2) were performed using standard commercial software (Visual3D, C-Motion, Germantown, MD, USA) and its associated anthropometric model with 6-DOF joints. Analog force data were filtered at 25 Hz and marker motion was filtered at 10 Hz (low-pass Butterworth) before computing inverse dynamics.

These data were used to estimate soft tissue work using a previously developed method (e.g., (Fu et al., 2014; Zelik and Kuo, 2012)). At each point in time during a stride, the joint powers derived from rigid body inverse dynamics, and the unknown soft tissue power, must sum to equal the whole body fluctuations in mechanical power ("total mechanical power"). For the former, we use the term *Joint Power* for the aggregate power from all measured joints using inverse dynamics, summed at each sample in time (Fig. 2-3A). The individual joint powers were computed from relative three-dimensional rotation and translation of each connected pair of body segments (also called "6-DOF powers), which helps account for inaccurate joint center locations (Buczek et al., 1994; Fu et al., 2014).

For total mechanical power, we computed the sum of work rates on the COM (Donelan et al., 2002) and for moving body segments relative to the COM (termed *COM work rate* and *peripheral work rate* or power, respectively). The COM work rate was calculated (Fig. 2-3B) from the three-dimensional dot product of ground reaction force and the COM velocity, the latter estimated by integrating forces assuming periodic strides. Peripheral power (Fig. 2-3B) to move segments relative to the COM was calculated as the time derivative of translational and rotational energy of segments relative to the COM (Cavagna and Kaneko, 1977; Zelik and Kuo, 2012). While COM work includes

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soft tissue motions, peripheral power relies on rigid body kinematics, and therefore neglects soft tissue deformations.

Measure	Normal (SI)	Normal (d'less)	Slope ± c.i.	Offset ± s.d.	R^2	S	*P*
Speed	3.07 ± 0.59 m · s^{-1}	1.01 ± 0.59	NA	NA	NA	NA	NA
Step Frequency, f	2.81 ± 0.17 s^{-1}	0.87 ± 0.053	0.15 ± 0.02	0.72 ± 0.045	0.85	*	8.90E-19
Step Length	1.09 ± 0.174 m	1.1 ± 0.18	0.92 ± 0.036	0.22 ± 0.056	0.98	*	6.20E-39
Stance Time	0.284 ± 0.04 s	0.91 ± 0.13	-0.42 ± 0.042	1.3 ± 0.07	0.91	*	1.00E-22
Aerial Time	0.0727 ± 0.0319 s	0.23 ± 0.1	0.22 ± 0.043	0.00087 ± 0.08	0.73	*	2.60E-13
Pos Total Power	234 ± 47.2 W	0.1 ± 0.021	0.071 ± 0.011	0.033 ± 0.0096	0.8	*	7.80E-16
Pos Joint Power	235 ± 55.4 W	0.11 ± 0.025	0.087 ± 0.014	0.018 ± 0.013	0.79	*	2.50E-15
Pos COM Power	271 ± 49.4 W	0.12 ± 0.022	0.099 ± 0.0052	0.022 ± 0.0074	0.97	*	1.20E-33
Pos Soft Power	40.3 ± 23.5 W	0.018 ± 0.011	0.0011 ± 0.011	0.017 ± 0.0097	0		0.85
Pos Ankle Power	150 ± 34.5 W	0.067 ± 0.015	0.052 ± 0.017	0.015 ± 0.014	0.47	*	3.70E-07
Pos Knee Power	83.6 ± 36.5 W	0.037 ± 0.016	0.015 ± 0.012	0.022 ± 0.015	0.13	*	0.019
Pos Hip Power	197 ± 95.4 W	0.088 ± 0.043	0.15 ± 0.017	-0.066 ± 0.021	0.89	*	5.60E-21
Neg Total Power	-236 ± 53 W	-0.11 ± 0.024	-0.082 ± 0.011	-0.023 ± 0.014	0.84	*	3.90E-18
Neg Joint Power	-219 ± 49.2 W	-0.098 ± 0.022	-0.055 ± 0.012	-0.041 ± 0.015	0.66	*	2.80E-11
Neg COM Power	-271 ± 49.4 W	-0.12 ± 0.022	-0.099 ± 0.0054	-0.021 ± 0.0072	0.97	*	3.80E-33
Neg Soft Power	-59.2 ± 27 W	-0.027 ± 0.012	-0.043 ± 0.012	0.016 ± 0.011	0.57	*	6.10E-09
Neg Ankle Power	-104 ± 29.3 W	-0.047 ± 0.013	-0.039 ± 0.0077	-0.0072 ± 0.011	0.72	*	7.90E-13
Neg Knee Power	-218 ± 64.3 W	-0.098 ± 0.029	-0.12 ± 0.012	0.025 ± 0.019	0.92	*	6.00E-24
Neg Hip Power	-81.1 ± 46.7 W	-0.036 ± 0.021	-0.022 ± 0.0082	-0.013 ± 0.019	0.41	*	3.20E-06
Net COM Power	-0.461 ± 1.65 W	-0.00021 ± 0.00074	-0.00046 ± 0.0014	0.00019 ± 0.00048	0.01		5.10E-01
Net Joint Power	16.9 ± 43.4 W	0.0076 ± 0.019	0.032 ± 0.018	-0.024 ± 0.018	0.23	*	0.00099

Net Soft Power	-18.9 ± 45.5 W	-0.0085 ± 0.02	-0.042 ± 0.02	0.033 ± 0.02	0.31	*	0.00011

Table 2-1. Quantitative results for stride parameters and powers, from linear regressions against running speed. Slope and offset refer to regression coefficients (±95% confidence interval, c.i.), reported with R^2, significance (S) denoted by asterisk with criterion $P < 0.05$. Dimensionless (d'less) quantities are computed using body mass, leg length, and gravitational acceleration as base units.
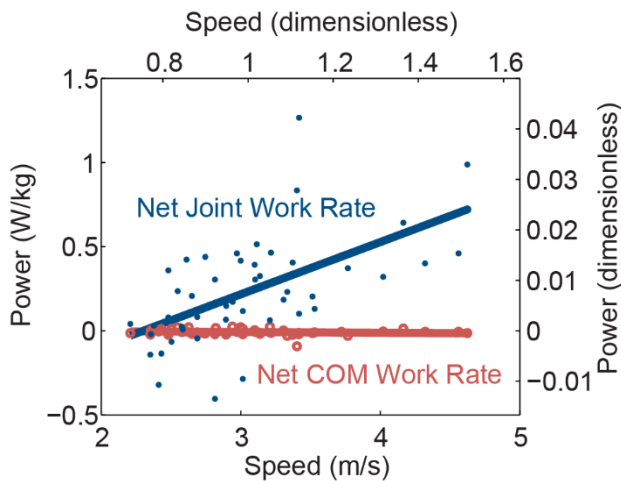
Figure 2-5. Average net work rates for center of mass (COM) work and Joint Work across running speeds. Average work rate, defined as net work per stride multiplied by stride frequency. Net COM work rate is close to zero at all running speeds, as expected during steady gait, while Joint Work rate is net positive at most speeds. Data shown were linearly fit with running speed (N=8).

We used the difference between Total mechanical power and Joint Power as an indicator of soft-tissue work (Figs. 2-3C & 2-4). We expected considerable soft tissue negative work during Collision, with some fraction returned elastically as positive work, but with net negative work over a stride. This also implies that Joint Power might yield net positive work over a stride, as is the case for walking (Kuo et al., 2005; Zelik and Kuo, 2012). To summarize the work over a stride, we computed the positive, negative, and net work for each power quantity, for example by integrating only the positive intervals within a stride to yield positive work per stride. Corresponding average work rates or powers were computed by multiplying work per stride by stride frequency. Because soft tissue deformation is expected to be triggered by impact with ground, we also computed work during the stance phase following ground contact.

Analyses were normalized as follows. Joint moments, angular velocities, and powers were averaged across multiple strides as a function of stride time (0 – 100%) for each subject and condition. To account for differences in subject size, we used body mass M, leg length L, and gravitational acceleration g as base units for non-dimensionalization. Mean power and work normalization constants were $Mg^{3/2}L^{1/2} = 2184$ W and $MgL = 678$ J, respectively; mean running speed normalization constant was $g^{1/2}L^{1/2} = 3.04$ m · s^{-1}.

To summarize how work varied with running speed, we used linear regression fits (Cavagna et al., 1964, 1977). Regressions were performed using a subject-specific random effects model with constant slope, so that each subject was given a best-fit offset and a slope between the two regression variables that was constant across all subjects. Analysis of covariance (ANCOVA) was used to test for differences between regression coefficients across different measures of mechanical power, with specific comparisons made with post-hoc t-tests. Significance of all statistical tests was tested based on α = 0.05. To facilitate comparisons, work measures were also reported from regressions at a nominal speed of 3 m·s^{-1}.

Results

The ankle, knee, and hip were generally observed to produce more power with increasing speed (Fig. 2-2). Each of these joints had distinct phasing, but with a sum (Joint Power) that resembled a simple sinusoid during stance phase (Fig. 2-3A). Peripheral work rate was generally found to be out of phase with the work performed on the COM (Fig. 2-3B). Joint Power qualitatively displayed similar trends of negative and positive work compared to Total work rate during stance phase, with the largest discrepancy occurring at the beginning of collision (Fig. 2-3C).

Soft tissue power exhibited a trajectory over time resembling the damped oscillation of mass-spring-damper system. It began with a large peak of negative

Figure 2-6. Trends in average positive and negative power vs. running speed (N=8). **A)** Average positive and negative work rates for ankle, knee, hip, and soft-tissue, the latter performing work comparable to the leg joints. **B)** Positive and negative work rates for four measures: center of mass (COM) work, Joint Power, Total work (sum of COM and Peripheral work), and Soft Tissue Work (Total minus Joint Power).

power (about -500 W at 3 m· s^{-1}), comparable to the peak for the knee (about –470 W; Fig. 2-3), followed shortly thereafter by a smaller positive peak of power (Fig. 2-4). The first peak increased with running speed, whereas the rest of the oscillation amplitude was less clearly dependent on running speed. Both peaks occurred within the Collision phase for the COM, so that the soft tissue oscillation was about twice the frequency of the COM's oscillation.

There was an increasing discrepancy between positive and negative joint work with speed. The net summed Joint Work rate was positive and approximately linear with running speed (Fig. 2-5). In contrast, net Total work rate was close to zero at all running speeds, as expected.

Much of the joint work discrepancy was explained by soft tissue work, which was net negative. Net soft tissue power was quite small at low speeds, but became more negative in proportion to speed, accounting for over 20% of the total negative work of the body at 5 m·s^{-1} (Fig. 2-6; see Table 2-1 for details). The net power was composed of negative power by soft tissues (about -58 W at 3 m·s^{-1}; see Table 2-1), also changing approximately linearly with speed (-28.5 W per 1 m·s^{-1}), as well as a smaller amount of positive work (at about 40 W rate) not significantly changing with speed (Table 2-1). The negative power from soft tissues was on the same order of magnitude as the negative work of the joints (Fig. 2-6A; Table 2-1), particularly the hip (about –78 W at 3 m·s^{-1} speed).

The magnitudes of negative Total work rate and negative Joint Power increased roughly linearly with running speed (Fig. 2-6B). There was a significant difference between the measures in both the slope (ANCOVA P=1E-5) and the offset (ANCOVA P=4E-12), with total negative work rate (-231 W at 3 m·s^{-1}) larger in magnitude than Summed Joint negative work (-214 W at 3 m·s^{-1}) (paired t-tests, P<0.001). There was a significant difference (ANCOVA P=2E-5) between the slopes for positive Total work rate and positive Joint power, but an insignificant difference in offsets (ANCOVA P=0.65). Total positive work rate (229 W at 3 m·s^{-1}) was not significantly different from Joint Power (229 W at 3 m·s^{-1}) (paired t-tests, p=0.58).

Soft tissue work was most prominent during the stance phase. At nominal 3 m·s⁻¹, soft tissues performed -18.8 J of negative work and 12.6 J of positive work during stance, and practically no work during the aerial phase. Negative soft-tissue work during stance phase accounted for about 27% of negative Total Work during stance phase (about -69.0 J), and 24 % of negative Total Work during the entire step (about -77.6 J).

Discussion

We tested if soft tissues contribute significant mechanical work during locomotion and how its magnitude changes with running speeds. Our results show that soft tissues performed significant negative work and positive work during stance phase, with more negative work at faster running speeds. We interpret these findings to suggest that soft tissues may behave in aggregate in a damped elastic manner. While the negative work may be helpful for cushioning, the net work has implications for the energetics of running. Moreover, the substantial amount of soft tissue work means that traditional inverse dynamics methods may underestimate the work performed by the body during running, particularly at higher speeds.

One of the simplest indicators of soft tissue work is the discrepancy in overall joint work as measured by inverse dynamics. Net Joint Work Rate was positive at about 7% of the negative Total Work Rate magnitude at 3 m·s⁻¹, and nearly 18% at 5 m·s⁻¹. This discrepancy suggests that joint work fails to capture a portion of the body's negative work that increases with running speed. An additional indicator is the soft tissue estimate, with a net rate of about -18 W at 3 m·s⁻¹ speed. Similar types of discrepancies have previously revealed differences, with rigid-body inverse dynamics explaining failing to explain some of the work required to run downhill rather than uphill (DeVita et al., 2008), to land from a jump compared to taking off (Zelik and Kuo, 2012), or to walk at higher speeds (Zelik and Kuo, 2010) or with obesity (Fu et al., 2014). Our present finding for level running is consistent with the expectation that greater impacts excite more movement and thus more energy dissipation within soft tissues.

The main effect of soft tissues during running was to perform negative work shortly after ground contact, at about 5% of a stride (Fig. 2-3). Its negative power peak was

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somewhat in advance of the negative work of the joints and COM. This suggests distal contributions, because upper body deformations would be expected to be in phase with the slower oscillation of the COM. In particular, the plantar fascia, heel pads, and tendons in the leg may dominate the negative power peak. The foot and leg appear well-suited to absorb ground impact peaks (Ker et al., 1988), whereas proximal tissues experience smaller impacts (Pain and Challis, 2006; Riemer et al., 2008). For running at 4.8 m·s^{-1}, Schmitt and Günther (2011), estimated 30-60 J dissipated in the thigh and shank, somewhat exceeding our estimates, perhaps because individual soft tissues can potentially oscillate out of phase with each other, we examine only aggregate effects. Both localized and aggregate measures may help explain soft tissue work and its effect on locomotion.

Soft tissue deformations likely also occur elsewhere in the body. We previously speculated that the intervertebral discs, articular cartilage, and viscera contribute substantially to soft tissue work in walking (Zelik and Kuo, 2010). Here, the earlier timing of soft tissue work relative to COM, suggests that viscera and proximal tissues might perform less mechanical work than an equivalent amount of soft tissue in the leg. In fact, soft tissue appeared to rebound and perform positive work at about the same time that the COM (and therefore viscera and intervertebral discs) was approaching peak negative work. This is consistent with a damped elastic rebound with faster natural oscillation frequency than the overall body.

Our findings may have implications for the energetics of running. Humans expend about 900 W of net metabolic power to run at 3 m·s^{-1}, and about 1100 W at 5 m·s^{-1} (Margaria et al., 1963). Because steady running requires an average of zero net work, the net negative work of soft tissues must be offset by an equal amount of active positive work by muscle. Assuming an efficiency of 25% (Margaria et al., 1963), the work to offset soft tissues would account for about 72 W of metabolic power at 3 m·s^{-1} and 319 W at 5 m·s^{-1}, or about 8% and 29%, respectively, of the net metabolic power at those speeds. Thus, soft tissue dissipation may come at a substantial metabolic cost. While this cost of soft-tissue dissipation is significant, it may in fact be beneficial for running efficiency since the theoretical cost of muscles and tendons performing the work the soft-tissues

do could be higher. This could occur because there would be a cost of negative and positive work (instead of just net work as in the case of soft-tissues), and because it may be costly for the muscles to perform work at the higher frequency of soft-tissues while still performing their nominal lower-frequency work.

One limitation of our soft tissue measure is that it actually captures work not performed at the rigid bodies normally measured during locomotion. Some of our "soft tissues" could therefore actually be considered joints in other methodologies. For example, the longitudinal arch of the foot performs negative and positive work, mediated in part by active muscle (Kelly et al., 2015). The metatarsophalangeal (MTP) joint also performs significant work late in stance during running around -20 J(Stefanyshyn and Nigg, 1997). We did not record from such joints, whose work would either appear as soft tissue work or be attributed to other measured joints. Many structures in the body, some of them joints, could perform significant work not measured by typical methods of inverse dynamics, but perhaps capturable by other means. We expect that the deformation of bone is negligible in our measurement of soft-tissues because the mechanical stiffness of bone (Reilly and Burstein, 1975) is much greater than the corresponding frequency of response we observe.

Our study was confined to slow to medium running speeds. In that range, soft tissues dissipated an amount of energy proportional to the running speed and returned a constant amount of energy. These linear relationships do not necessarily hold for higher running speeds and sprinting, for which the soft tissue contributions remain unknown. Another limitation was that our estimates use rigid-body models for the work performed peripheral to the COM, therefore not capturing some deformations. Peripheral soft tissue work could potentially add to our own central estimates.   While the motion of peripheral soft-tissues may confound our estimates of rigid-body joint work and soft-tissue work, we have no direct estimate of the work by soft-tissues peripherally to the COM. Finally, by assuming that the net work of steady state running is equal to zero on level ground, we have implicitly assumed that the work of overcoming friction in the air and ground is negligible, an assumption argued for by others (Margaria, 1968; Willems et al., 1995).

When soft tissues are of interest and expected to play a significant role, standard inverse dynamics may not accurately reflect the energetics of the body. During running, ignoring the energetics of soft tissue is nearly tantamount to ignoring the knee, which had comparable power trajectories (Fig. 2-3). An understanding of such limitation may be crucial when relying on experimental data to give insight into how humans move or to guide design of locomotive technology.

Soft tissues contribute significantly to the dynamics of running in terms of energy dissipation, storage, and return. Their deformations can help cushion the body, performing some of the negative work required of each stance phase and potentially offloading active dissipation by muscle. It can also return some positive work, but most of the negative work must be offset by active positive work by muscle. Besides being important for understanding normal human gait, analysis of soft tissue dynamics may be important for the production of prostheses and robots, which are often built using mostly rigid components. Most biological tissues, and many non-biological materials, deform under heavy loads, with potential consequences for the dynamics of running.

Chapter 3 : Mechanical Work Fundamentally Explains the Majority of Energetic Cost in Human Running

Introduction

Humans expend considerable metabolic energy to run, almost all of it to move body segments rather than against external resistance. Aside from overcoming air resistance at high speeds, there is practically no energy transfer with the environment. This differs distinctly from pedaling a bicycle or rowing an ergometer, where energy is largely expended in proportion to external resistance (Gaesser and Brooks, 1975). For running, energy is instead expended for muscular effort within each stride, even though ultimately no work is performed over a complete stride. And unlike an external resistance, the work and forces of muscles within a stride are not generally known, making it much harder to explain the metabolic cost. There is nevertheless nearly a century of evidence about important factors such as elastic energy return by tendon, multi-joint energy transfer by muscle, and the energetic cost of work performed by muscle. There are also considerable data showing correlations between energetic cost and measures that are observable. These factors could potentially be combined to compute reasonable bounds on the contribution of muscular work to the overall energetic cost of running, even if there lack sufficient data for an exact explanation.

The metabolic cost of running may be explained in part by the mechanical work of the body. Muscles expend positive metabolic energy for positive and negative work against an external load, with efficiencies of about 25% and -120%, respectively (e.g., (Fenn, 1923), (Abbott et al., 1952)). These same efficiencies apply to running up or down steep slopes (Margaria, 1968), where work is performed against gravity. For steady, level running, work is observable at the body joints, as reported using the "inverse dynamics" technique (e.g., (Belli et al., 2002)). However, this cannot account for multi-articular

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energy transfer, where for example a single muscle can appear to perform positive work at one joint and negative work at another, yet actually perform no work itself (Kuo, 1994; Williams Kr, 1985; Kuo, 2000) Lacking direct measurements, any estimation of multi-articular energy transfer is dependent on assumptions e.g. (Williams Kr, 1985) that may not be regarded as objectively correct. Nonetheless, these estimates may yet have utility, if only to yield rough bounds on the work possibly performed by muscle.

Among the complicating factors regarding muscle work is elastic energy return. Muscles act in series with elastic tendons, which along with other tissues such as the plantar fascia, have great potential to store and return energy passively (Cheng et al., 2008; Ker et al., 1987; McDonald et al., 2016). This is evidenced indirectly by positive work efficiencies that appear much higher than 25% (e.g., 40% reported by (Asmussen and Bonde-Petersen, 1974; Cavagna et al., 1964), because some of the work is attributable to passive tendon. Direct measurements in select muscles (e.g., Roberts et al, 1997), suggest that tendon could account for perhaps half of the observed joint work. That elasticity also suggests that muscle could act nearly isometrically, expending energy mostly to produce force, and in amount less well understood than for work.

Elastic energy return has spurred studies seeking alternative measures, not related to work, that correlate with energy cost. Perhaps the strongest such correlate the "cost of generating force" (CoGF, (Kram and Taylor, 1990), defined as body weight divided by ground contact time. This cost is fully independent of mechanical work, as if elastic tendon were to allow muscle to act isometrically. The CoGF has been found to correlate well for a variety of animals at different scales (Kram and Taylor, 1990), albeit with differing proportionalities for each case. However, the same work-independence is also a weakness of CoGF, because even though the amount of muscle work is uncertain, it is also unlikely to have zero contribution to energetic cost. This makes it difficult to ascertain a causative mechanism from CoGF.

Even though the contribution of mechanical work is uncertain, it may nonetheless be significant. For example, direct measurements of Achilles tendon action reveal that the calf muscles do not act isometrically, and appear to perform positive work during human running (Hof et al., 2002; Lichtwark et al., 2013). Another finding is that soft tissue

deformations may dissipate substantial mechanical energy during running. In steady state, the dissipation must be restored through an equal amount of active muscle work each stride. That active work must exact an attendant energetic cost.

The present study therefore re-evaluates the contribution of muscle work to running. We measure the work of running, including assumptions regarding multi-articular energy transfer, elastic energy return, and muscle efficiency. Recognizing that the assumptions are inexact, our goal is to determine reasonable bounds, rather than an exact estimate, for the cost of work. We then test whether mechanical work can plausibly explain a substantial fraction of the overall energetic cost of running.

Methods

We estimated the mechanical work of the joints and of soft tissue dissipation during running, and their relation to metabolic cost. Mechanical work was assessed using standard inverse dynamics techniques, as well as a separate means to evaluate work performed by soft tissue deformations. These data were then used to estimate contributions to energetic cost. The force and motion data used is the same as that described in chapter 1 of this document. Briefly, 8 subjects ran at a range of speeds on a treadmill, with measurements of ground force as well as motion of the lower and upper body.

These data were used to compute two kinds of mechanical work. First, inverse dynamics was used to compute standard rigid-body joint powers, as the work per time needed to rotate and translate (via joint torque and intersegmental reaction forces, respectively) two connected segments relative to each other. The so-called 6-D joint power is considered robust to errors due to the incorrect determination of joint centers (Buczek et al., 1994; Zelik et al., 2015).

The second quantity was the dissipative work performed by soft tissue deformations. Briefly, this is the difference between rigid-body joint power and the total mechanical work, defined as the rate of work performed on the COM, evaluated using ground

reaction forces with no rigid-body assumptions, plus the rate of work performed to move rigid-body segments relative to the COM (Riddick and Kuo, 2016; Zelik et al., 2015). In running, this quantity is similar in magnitude to the difference between the positive and negative joint work over a stride (Riddick and Kuo, 2016), which itself implies that rigid body work does not capture all of the work of running.

Metabolic cost was estimated through respirometry (Oxycon; CareFusion Inc., San Diego, CA). Both O_2 consumption and CO_2 production were recorded on a breath by breath basis and averaged over the final three minutes of each six-minute trial, and converted to gross metabolic rate (in W). Net metabolic rate was found by subtracting each subject's cost for standing quietly, collected before running. The subjects' respiratory exchange ratio (RER) was measured to be 0.85 ± 0.09 across subjects, with each individual trial having an average RER of less than 1, indicating exercise that is mostly aerobic.
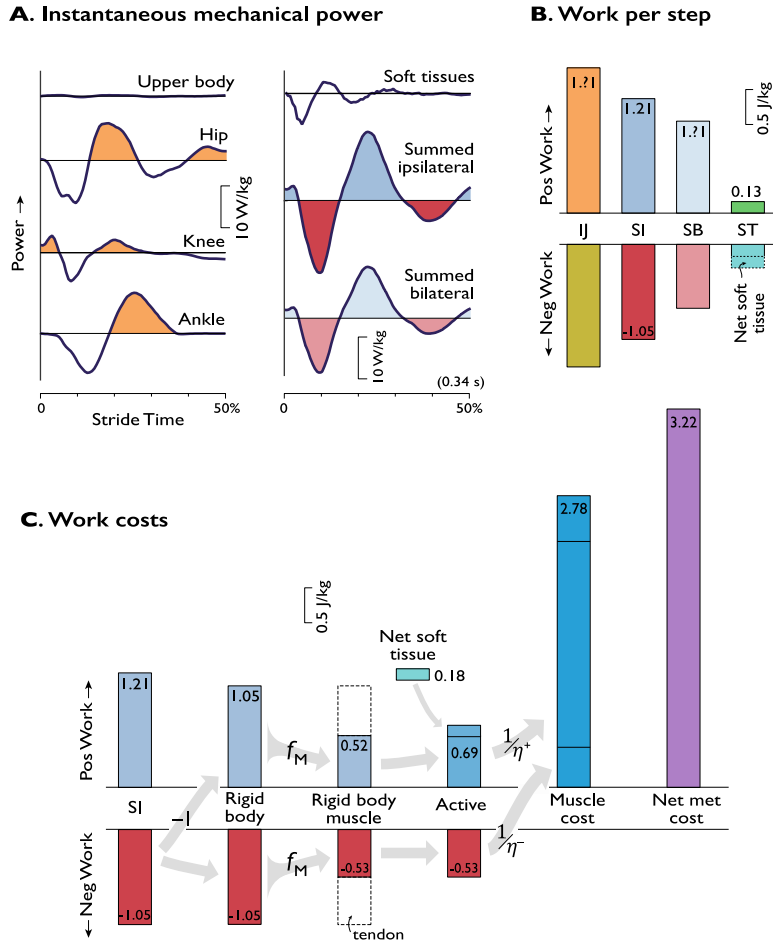
Figure 3-1. Estimation of mechanical work contribution to metabolic energy expenditure, for a representative subject (3.10 m/s). **A)** Instantaneous mechanical power of the joints (ankle, knee, hip and upper body), and from soft tissue deformations, over one running stride (beginning with heelstrike). Also shown are Summed Ipsilateral power (adding all joint and soft tissue powers from one side of the body, at each point in time), and Summed Bilateral power (all joint and soft tissue powers from both sides of body). **B)** Four measures of work per stride (step?): Individual Joints work, Summed Ipsilateral work, Summed Bilateral work, and Soft Tissue work. Positive (negative) work refers to integrated intervals of positive (negative) power. Soft tissues perform net negative (dissipative) work. (C.) Work costs to illustrate how these quantities lead to metabolic cost contributions. The magnitude of Summed Ipsilateral negative work is treated as an estimate of the joint positive and negative work performed on rigid body segments. This is multiplied by muscle work fraction f_M (provisionally 0.5) to yield work due to muscle. Active muscle work also includes positive work to offset net soft tissue dissipation. These are multiplied by positive and negative muscle efficiencies to estimate the energetic cost due to active muscle, in this example about 74% of the net metabolic cost of running.

The work performed by joints and soft tissue deformation was used to estimate that done by the series combination of muscle and tendon. To take into account the dependence on energy transfer assumptions, we initially consider two opposing sets of assumptions before introducing a third measure. The first, termed Individual Joint (IJ) work, assumes no energy transfer between joints, as if all muscles acted uniarticularly. Positive work may thus be evaluated by integrating the positive intervals of each joint's power over a stride, and then summing across all joints in the body. Multiplying by stride frequency then yields the average rate of positive individual-joint work, $\dot{W}_{IJ}^{+}$. This quantity disregards multi-articular energy transfer by multi-articular muscle, such as positive work at one joint to negative at another, and is therefore considered an overestimate of actual muscle-tendon work.

The opposing assumption is that simultaneous positive and negative work always cancel each other. This entails summing the powers from all the joints at each instance in time, yielding summed joint power (Zelik et al., 2015), and then integrating the positive summed joint power over a stride. Multiplying by stride frequency yields the average rate of positive summed joint work, $\dot{W}_{SB}^{+}$, likely an underestimate of actual muscle-tendon work. The two quantities, $\dot{W}_{IJ}^{+}$ and $\dot{W}_{SB}^{+}$, are analogous to the terms "no between-segment transfer" and "total transfer between all segments" of Williams and Cavanagh (Williams and Cavanagh, 1983), except applied here to transfer between joints rather than body segments.

We introduce an intermediate estimate, termed Summed Ipsilateral work. It assumes full energy transfer across the joints on one side of the body, but not between the two sides. The average rate of work $\dot{W}_{SI}^{+}$ entails summing the joint powers on one side of the body at each point in time, integrating the positive intervals of this power, and then multiplying by step frequency. Of course, further examination of musculoskeletal geometry, neural activation patterns, and loading conditions could yield more intricate estimates of muscle-tendon work. But without full knowledge of individual muscle forces and displacements, no estimate can be considered correct. We therefore use the SI estimate as a simple and not unreasonable set of assumptions, within the two IJ and SB extremes.

METABOLIC COST OF MUSCLE WORK

We define two quantitative parameters to link mechanical work to energy expenditure. The first is the proportion of work performed actively by muscle vs. passively by tendon, and second is the efficiency at which the active work is performed. The proportion is defined as f_m, the fraction (ranging 0-1) of muscle-tendon work W_{MT}^+ (e.g. based on SB, SI, or IJ assumptions) performed by muscle fascicles:

Eqn. 3-1 $$W_M^+ = f_M W_{MT}^+$$

where W_M^+ is the positive work of muscle. In vivo measurements suggest a variety of possible values for f_m, for example 0.40 for turkey gastrocnemius (Roberts et al., 1997), and 0.26-0.56 for two muscles of running dogs (Gregersen et al., 1998). For humans, cadaver data suggest 0.52 for the Achilles tendon and foot arch (Ker et al., 1987). Other indirect data suggest a range of 0.4 – 0.625 (Cavagna et al., 1964; Cavagna & Kaneko, 1977), depending on energy transfer assumptions. The correct value is unknown, and almost certainly varies with muscle group, loading conditions, and speed. We use a single parameter f_m to summarize an overall effect for all muscles, and adopt a provisional value of 0.5, while allowing for other possible values.

We characterize muscle efficiencies with separate parameters for positive and negative work. Positive work efficiency η^+ is defined as the active positive work divided by the metabolic energy expended, and similarly for negative work efficiency η^-. We adopt provisional values of 25% and -120%, respectively (e.g., (Margaria et al., 1963)).

The overall energetic cost of work is characterized as follows. Metabolic rate is

Eqn. 3-2 $$\dot{E} = \left(\frac{1}{\eta^+} + \frac{-1}{\eta^-}\right) f_M \left|\dot{W}_{MT}^-\right| + \frac{1}{\eta^+} \left|\dot{W}_{ST}\right|$$

where the muscle-tendon work may be based on IJ, ST, SI assumptions. The right-hand side consists of two costs for active work, one to move rigid body segments, and the second to compensate for soft tissue deformations. Soft tissues dissipate net energy (yielding negative $\dot{W}_{ST}$), and muscles must actively perform net positive work to compensate for those losses. Negative work is also performed on rigid bodies ($\dot{W}_{ST}$) at

the joints, some of it elastic and the remainder (f_M) by muscle. The muscle work exacts a positive energetic cost for both the negative work and the same magnitude of positive work. A graphical depiction of how the model converts mechanical work into metabolic cost is depicted in Figure 3-1.
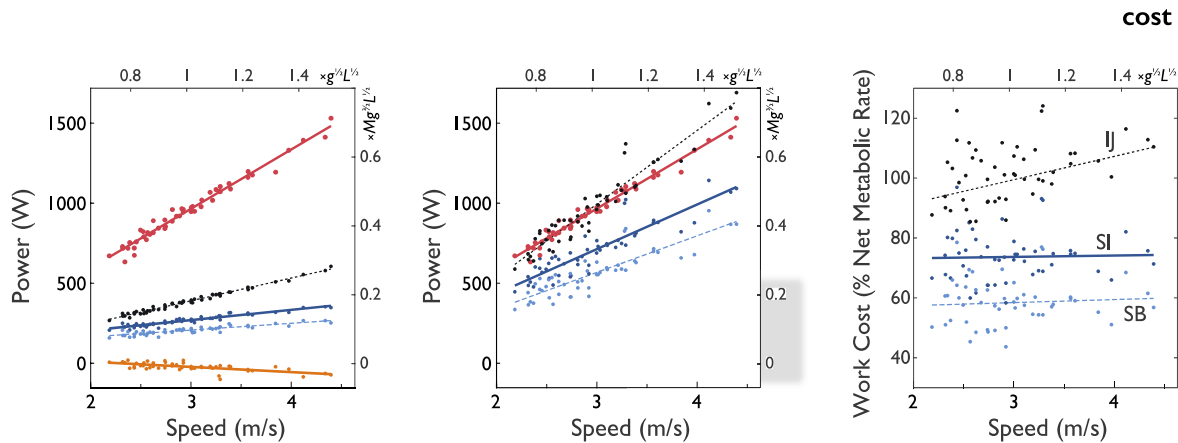
Figure 3-2. Mechanical work and estimates of absolute and relative metabolic cost vs. speed. **A)** Average positive work rates: Individual Joints (IJ), Summed Ipsilateral (SI), and Summed Bilateral (SB), along with net Metabolic rate and net Soft tissue work rate. **B)** Estimated metabolic cost of mechanical work, based on each work rate plus soft tissue deformations. **C)** Relative metabolic cost of mechanical work, showing each cost as a fraction of net metabolic rate. Axes shown include dimensional units, as well as dimensionless units (top and right-hand axes) using body mass, leg length, and gravitational acceleration as base units.

To account for differences in subject size, data were non-dimensionalized using body mass M leg length L, and gravitational acceleration g as base variables. Mean power and work normalization constants were $Mg^{3/2}L^{1/2} = 2184$ W and $MgL = 678$ J, respectively. The mean running speed normalization constant was $g^{1/2}L^{1/2} = 3.04$ m/s. All averaging and statistical tests were performed with dimensionless quantities. In figures, data were plotted with dimensional scales in SI units, using the mean normalization constants.

We performed statistical regression on a number of variables. For the relationship between running speed and mechanical (e.g., IJ, ST, etc.) or metabolic rates, we used a linear fit, minimizing mean-square error. A linear fit was used since both the cost of mechanical work and metabolic cost are both in units of energy. The fits for work

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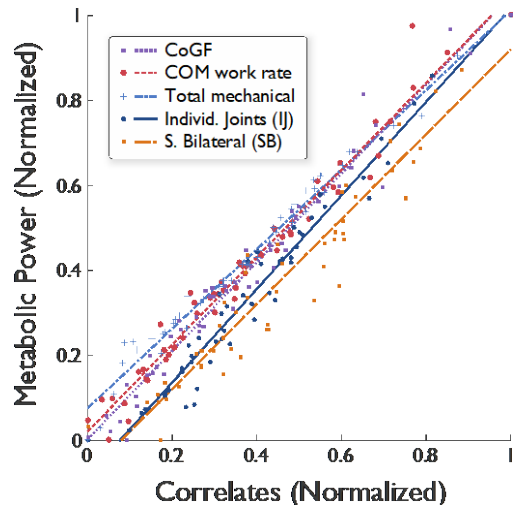
Figure 3-3. Sample correlates of metabolic cost. Correlates: positive COM work rate, Total mechanical work, Individual Joints work, Summed Bilateral work, and Cost of Generating Force (CoGF; Kram & Taylor). Here, none of these costs is considered a good indicator of net Metabolic rate, but all are reasonably good correlates.

measures were then scaled according to Eqn. 3-2 to predict the metabolic cost attributable to work. We also used linear regression to demonstrate how different regressors—the various work measures and the cost of generating force—can each explain metabolic rate. All regressions were performed allowing each subject an individual constant offset, while constraining them all to a single coefficient.

Statistics were performed using analysis of variance (ANOVA) to determine the significance of work trends across running speeds. To examine power across running speeds, we performed a one-way ANOVA with the running speed as the predictor variable and mechanical work as the response. Student's t-tests were used as a second statistical means to compare Total work rate, COM work rate, and Summed Joint Powers at each walking speed. The level of significance was set at $\alpha = 0.05$.

Results

We found that mechanical work rates and metabolic rate all exhibited typical and fairly linear increases with running speed (Fig. 3-2A). As expected, the work rates were highest for Individual Joints estimate and lowest for Summed Joints (overestimate and

underestimate, respectively), with the Summed Ipsilateral joints estimate between the two. Also as expected, soft tissue work rates were negative and increased in magnitude with speed.

Applying the prediction (Eqn. 5) to mechanical work rates resulted in varying amounts of metabolic cost explained (Fig. 3-2B). Notably, the Individual Joints estimate actually exceeded the observed net metabolic rate at higher speeds. Expressed as a relative proportion of metabolic rate (Fig. 3-2C), Individual Joints exceeded 100%. The other two estimates yielded fairly constant proportions, about 71% for Summed Ipsilateral joints and 59% for Summed Bilateral joints.

All of the mechanical work measures correlated well with metabolic cost (Fig. 3-3), with r^2 exceeding 0.89 (Table 3-2). Also included is an additional measure, the total mechanical work ("external" plus "internal") presented by Cavagna (Cavagna and

	Cost Coefficient $c = \dfrac{j}{\eta}$	Ratio of Muscle Work To Tendon Work j	Net Work Efficiency $\eta = \dfrac{-\eta_+\eta_-}{\eta_+ - \eta_-}$	Positive Work Efficiency η_+	Negative Work Efficiency η_-
Upper Bound	3.2	0.65[2]	0.21	0.25[3,4]	-1.2[3,4]
Lower Bound	1.8	0.38[1]	0.21	0.25[3,4]	-Infinity

Table 3-1. The cost coefficient represents how much metabolic energy a unit of mechanical work costs. The cost coefficient is calculated by taking into account the amount of work performed by tendon relative to muscle, and the efficiency of positive and negative muscle work. A range of cost coefficients between 1.8 and 3.2 were found by consulting experimental data from the literature.

1. (Cavagna et al., 1964) 2. (Asmussen and Bonde-Petersen, 1974) 3. (Margaria, 1968) 4. (Abbott et al., 1952)

Kaneko, 1977). In addition, the cost of generating force, Mg/t_c (Kram and Taylor, 1990), also correlated well with metabolic cost.

To facilitate evaluation of assumptions, the fraction of metabolic cost explained by work is illustrated as a function of parameters (Fig. 3-4). Here we use an overall muscle efficiency for combined positive and negative work, $\eta = (\eta^+ + \eta^-)/(\eta^+ \eta^-)$, with nominal value 21%. This efficiency appears with the muscle work fraction f_m, nominally 50%. With these values, the proportion of metabolic cost explained by work was 51% for SB, 63% for Ipsilateral Joints, and 105% for Individual Joints, respectively, across the observed running speeds. Here we examine two extremes for varied assumptions. One is to assume a considerably lower fraction of muscle work, $f_m = 0.38$, which would yield a lower fraction of metabolic cost explained, of 43%. On the other hand, assuming that muscle performs more work, $f_m = 0.65$, yields an unrealistic explained fraction of 1.53.

Discussion

	Slope	Offset	r^2
CoGF	3.58E-4	-0.48	0.97
COM work rate	4.75	-0.13	0.97
Total mechanical	2.71	-1.3E-2	0.97
Indiv Joints (IJ)	2.10	4.67E-2	0.96
S. Ipsilateral (SI)	3.55	-2.85E-2	0.92
S. Bilateral (SB)	4.45	-2.42E-2	0.90

Table 3-2. Regression coefficients for predicting metabolic cost of several measurements of running mechanics. All data presented are in dimensionless units. CoGF is the Cost of Generating Force as defined by Kram et al. 1990, whereas each other measure is a different way of estimating mechanical work done by the body.

We had sought to re-evaluate the degree to which mechanical work performed by muscle can explained the net metabolic cost of running. We considered three sets of assumptions to translate joint work estimates into metabolic cost: How energy is transferred between joints by muscle, how much work is performed passively by tendon, and how much metabolic energy is expended to perform muscle work. Using nominal assumptions derived from the literature (muscle efficiency $\eta = 0.21$, muscle work $f_m = 0.50$, SI energy transfer), we found that about 74% of the metabolic cost of running is

attributable to muscle work We next discuss how our estimates may be interpreted, and how they could be affected by alternate assumptions.

Our estimates are fundamentally based on the technique of inverse dynamics. It treats the body segments as rigid, and yields the torques and powers at the joints. This method is considered superior to examining energy fluctuations of the body segments, which does not take into account inertial interactions between neighboring body segments. One source of error in inverse dynamics is in body anthropometry (e.g., segmental center of mass locations and moments of inertia). However, the total mechanical work of running is quite dominated by work performed on the body COM (Riddick & Kuo, 2016), independent of anthropometry, making the present joint work estimates relatively insensitive to associated errors.

A larger source of potential error is the rigid body assumption. That assumption leads to an imbalance between positive and negative joint work (Riddick and Kuo, 2016; Zelik and Kuo, 2010), which is inconsistent with the fact that zero work is performed during steady-state running. We therefore applied an estimate of mechanical energy dissipated by soft tissue deformation, which largely explains the joint work imbalance, which in turn appears to largely compensate for the dissipation. This cost has not previously been appreciated, and appears to be substantial, account for about 29% of the net metabolic rate for running at 5 m/s (Riddick, 2016).

We also relied on two quantitative parameters. One is the amount of muscle-tendon work performed by muscle, f_m. We selected a nominal value of 50%, based on indirect evidence in the literature. It is conceivable that far different values might be appropriate. For example, the plantaris and gastrocnemius of hopping wallabies range only 3-8%. However, we doubt that humans run with muscle work fractions far below 50%, because many muscles participate in running, not all under conditions ideal for tendon elastic work. Nevertheless a parameter study (Fig. 3-4) allows other candidate assumptions to be evaluated quite readily.

The other main assumption was with regard to muscle efficiency. We assumed a positive energetic cost to negative work. It is also conceivable that lower cost could be achieved, but even if zero, it would only affect our results by a small amount (nominal
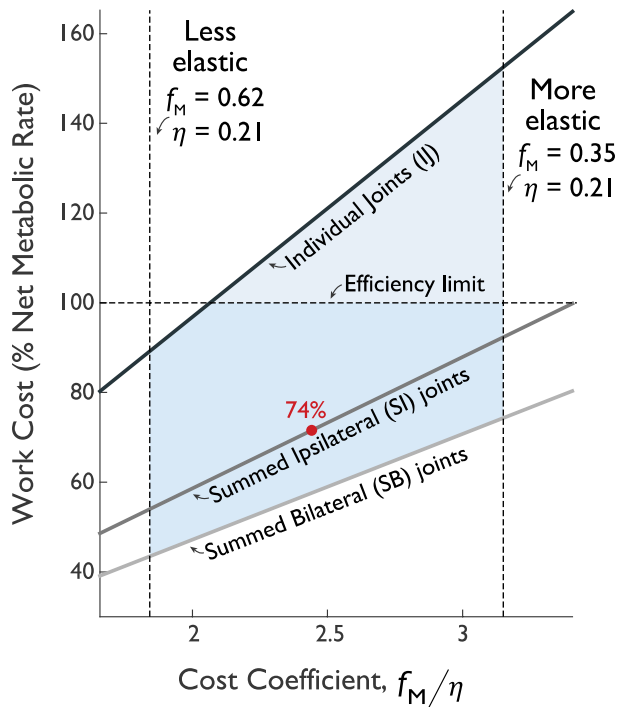
Figure 3-4. Range of possible contributions of mechanical work to metabolic cost. Relative work cost, defined as estimated metabolic cost of mechanical work divided by net metabolic cost, as a function of cost parameter. Cost parameter is defined as fraction of muscle-tendon attributable to muscle, divided by overall efficiency eta of muscle work. Boundaries illustrate range of reasonable contributions. Upper and lower bounds are defined by Individual Joints and Summed Bilateral joint work rates, assuming no transfer of energy between joints and maximal transfer, respectively. Left and right boundaries are for extremes in muscle work fraction, 62% and 35%, respectively, with constant overall muscle efficiency eta = 35%. The proposed Summed Ipsilateral joints measure, along with a muscle fraction of 50%, yields an estimate that 74% of the metabolic cost of running is attributable to active work by muscle.

$\eta = 0.21$ vs. 0.25 if negative work were free). Much more important is the higher cost of positive work, primarily attributable to crossbridge interactions (Woledge et al., 1985). Biochemical constraints dictate that this efficiency cannot greatly exceed 25%, due to biochemical constraints. Lower apparent efficiencies are possible, for example due to muscle co-contraction, isometric force production, or calcium pumping (Bergstrom and Hultman, 1988). Such effects might be lumped into the fraction of energy cost not explained by work, i.e. muscle shortening or lengthening under load.

There are certainly other costs for running, not directly attributable to mechanical work. Among the non-work costs is the proposed "cost of generating force" (Kram and Taylor, 1990), which correlates well with energy cost but has unknown mechanism. A drawback of the correlative approach is that the regression coefficient is drawn from data, and not subject to constraints. The present study suggests that the COGF should indeed be constrained by the high cost of work. But even so, and despite its high correlative value, the present study suggests that the COGF, among other non-work costs, could account for at most 26% of the cost of running.

Unlike mechanical work, COGF, peak ankle moment, and heart rate do not measure any source of metabolic work. The COGF may correlate strongly with the cost of

performing isometric contractions or cocontractions, but it is not a direct measurement, nor is it necessarily independent of the cost of performing mechanical work. Therefore, it cannot be principally combined with other measurements or models to achieve a better estimate of metabolic cost, since the relationship between it and metabolic cost is unknown.

One shortcoming of estimating metabolic cost using mechanical work is determining the amount of associated muscle work done to perform such work. Determining the amount of muscle work required to perform a certain amount of mechanical work at the joints requires additional measurements, or assumptions about how joints can transfer energy between each other. Figure 3-5 shows the efficiency of mechanical work to metabolic cost using joint assumptions SB, SI, and IJ as lines whose slopes are identical to their corresponding cost coefficient. The shaded region encompasses the range of cost coefficients (1.8 to 3.2) predicted by literature data for j, η_+, and η_-. Since the shaded region lies between SI and IJ, this is evidence that the correct model for energy transfer between joints lies between these two measures. In other words, it is unlikely that there is contralateral energy transfer between legs. This result seems plausible since there are no obvious mechanical connections between the legs which would allow substantial energy transfer.

Making further conclusions about energy transfer between joints during running is difficult without direct measurement of the work performed by individual muscles. This is not generally possible in humans, but direct measurement of muscle forces in cat locomotion shows that significant energy is transferred from the ankle to the knee during collision, and from the knee to the ankle during push-off (Prilutsky et al., 1996). These results imply that IJ overestimates mechanical work and therefore mechanical efficiency. As seen in Fig. 3-4, IJ estimates a mechanical efficiency of 102% for running at 3 m/s with nominal values for j and eta, a result which is impossible.

We found that many biomechanical measurements correlate very well with metabolic cost (Fig. 3-3). For the purpose of estimating metabolic cost during level ground running on a treadmill, any of these regressions could be used to obtain a reasonable estimate. However, using the same regression coefficients as in running for other activities such

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as walking and skipping may be inaccurate and require additional measurements of metabolic cost. For discrete activities for which a steady state metabolic measurement cannot be taken, there is no easy way of verifying the accuracy of the prediction.

We have shown that energy transfer assumptions drastically affect estimates of mechanical work and efficiency. However, recent studies that examine mechanical efficiency use IJ to estimate mechanical work without examining how this effects their result (Farris and Sawicki, 2011; Umberger and Martin, 2007). For example, using IJ Farris et al. found that mechanical efficiency increases as running speed increases. If they had instead used SI or SB, our results suggest that efficiency would actually be close to constant, as well as being lower in magnitude at all running speeds. In running, it is possible that there would be more energy transfer between segments and therefore IJ would be more likely to overestimate mechanical work. For these reasons, it is not clear that using IJ as opposed to SI or other energy transfer assumptions in between would give a more accurate representation of total mechanical work.

The estimate of metabolic cost due to mechanical work (eqn. 3-2) is very similar to that presented by Williams (Williams and Cavanagh, 1983). The main difference is that our model also takes into account the positive muscle work needed to offset the measured soft tissue dissipation. As mentioned earlier, another difference is that the energetic analysis in this model is on segments as opposed to joints. Another difference is that their model assumes that work performed by tendon incurs a cost equal to an equivalent amount of unmeasured negative muscle work. We see no reason why the equivalent negative work may not already have been measured as negative work at the joints and therefore include no added cost for unmeasured negative work. The difference in assumptions between their models and the model presented here results in a lower estimate of mechanical work, since we assume that tendons perform the same percentage of negative work as they do positive work, and that the work done by tendons does not incur a metabolic cost associated with unmeasured muscle work.

While we have shown a strong linear relationship between mechanical power and metabolic cost, our results are specific to humans running at a limited range of speeds. Heglund et al. studied the relationship between mechanical power and metabolic cost in

many animals including humans and concluded that mechanical work does not explain the changes in metabolic energy consumption with changes in speed and body mass (Heglund et al., 1982). Because different species may have varying amounts of passive resistance in their joints, it is not clear to us that their data precludes mechanical work from being a major determinant of metabolic cost in the small animals they studied. Regardless, in humans their data show a strong linear relationship between mechanical work and metabolic cost in agreement with our results.

Appendix 1

Evaluation of the Cost of Generating Force (CoGF) correlation reveals a paradoxical prediction. The CoGF is proportional to body weight Mg divided by ground contact time t_c:

$$\dot{E} = Mg/t_c$$

An additional constraint is imposed by human running, for body weight. The overall vertical impulse must equal body weight:

$$Mgt_{\text{stride}} = \bar{F}_c t_c$$

where t_{stride} is stride time and $\bar{F}_c$ is the average vertical force during contact. Combining the two equations and definine E_{stride} as the energetic cost of a stride yields

$$\frac{E_{\text{stride}}}{t_{\text{stride}}} = \frac{Mg}{t_c}$$

$$E_{\text{stride}} = \frac{Mgt_{\text{stride}}}{t_c} = \bar{F}_c$$

In other words, the cost per stride only depends on average contact force. This suggests that the cost of running could be reduced simply by extending contact time to half a stride, at which point $\bar{F}_c$ would equal body weight. This is at odds with the observation that ground contact time decreases with speed, and that substantial time is spent in the aerial phase. Although CoGF is a good correlate of metabolic cost, it also makes paradoxical predictions.

Chapter 4 : Mechanical Work Compensations to Fore-Aft Perturbed Human Running

Introduction

Running requires complex coordination of muscles and body dynamics. This coordination has been studied extensively in steady state treadmill running (Novacheck, 1998), and more recently in more real-world settings by mobile sensors (Chelius et al., 2011; Strohrmann et al., 2012). While the former allows accurate measurement of motion and forces acting on the body, the very controlled environment is not necessarily indicative of how people run outside of the lab. And while using mobile sensors allows study of more spontaneous running, the measurements may be less reliable, and more importantly, there exists a difficult correspondence problem of matching gait events to descriptions such as "slipping on ice" or "tripped on dog". Our goal here is to impose a source of randomness and difficulty into laboratory-constrained running, but where we can still measure what it is that exactly happened to the subject. By literally pushing the subjects, their behavior during recovery gives extra information about the control strategy humans employ as compared to analyzing steady state treadmill running.

There are an increasing number of studies that seek to push the boundaries of the laboratory gait experiment, studying induced stumbling, slipping, lateral perturbations during walking, unexpected landing surfaces, and uneven terrain (Hof et al., 2010; Marigold et al., 2003; Schillings et al., 1996; Voloshina and Ferris, 2015). However, these studies mostly focus on analyses of force, motion, and EMG analysis as opposed to mechanical work. Furthermore, there has been little modelling done in support of such experiments, and no attempt that we can find of relating traditional spring-like models of running to models that explain their experimental results.
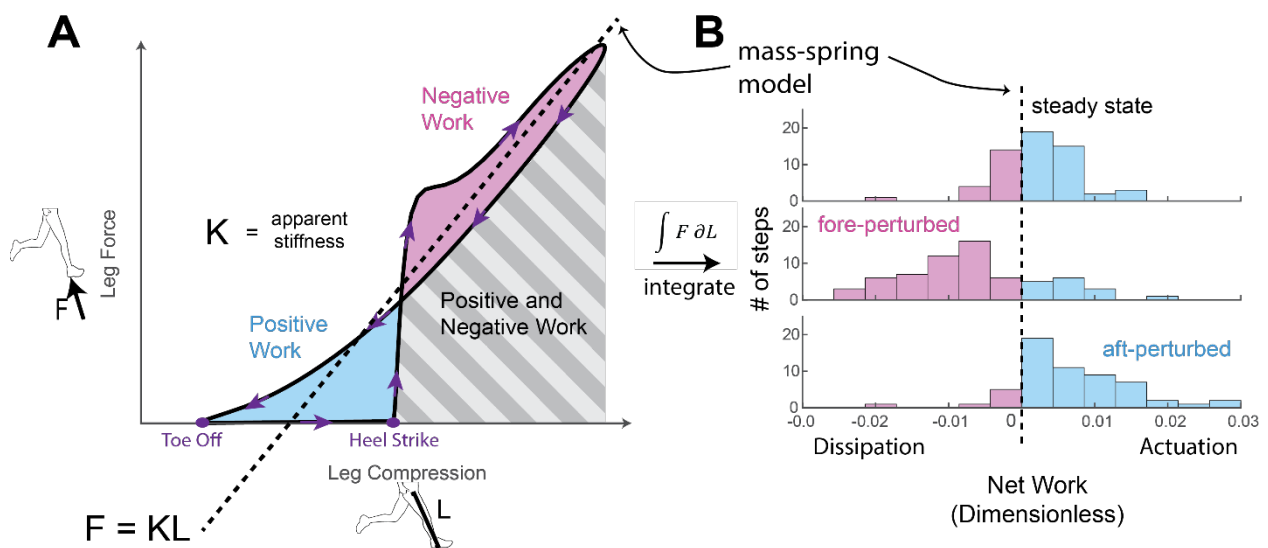
Figure 4-1. Limitations of the mass-spring model in describing the mechanics of human running. **A)** An estimated work loop of the leg during a single step of steady state human running (solid line) is shown along with a spring-mass model estimate of apparent leg stiffness (dotted line). The spring-mass model does not capture characteristics of the human work loop such as asymmetry between negative and positive work and the change in leg length between heel strike and toe off. **B)** A histogram of per-step net work per-step is shown in steady state, fore-perturbed, and aft-perturbed running. In steady state, the average net work is about zero, coinciding with the spring-mass model. In the fore and aft perturbed cases, the net work is negative and positive respectively, of which the mass-spring model makes no prediction,

The Spring Loaded Inverted Pendulum (SLIP) model is a canonical running model consisting of a point mass pelvis, and a massless leg with compliance used for over 20 years (Blickhan, 1989; McMahon and Cheng, 1990), and roughly reproduce human gait characteristics such as Ground Reaction Forces (GRF). In terms of control, conservative spring-like models of running suppose that people adjust speed and stabilize by adjusting their leg angle at heel strike and stiffness of the leg during stance (Geyer et al., 2005; Seyfarth et al., 2003).

Whereas the SLIP model is conservative, robots must of course experience energy dissipation and use motors to compensate. Even in 1984, Raibert had great success modulating actuation amounts to control hopping robots (Raibert et al., 1984; Raibert and Brown, 1984). More recently, work has been done to add explicit damping and actuation components to the SLIP for a control law dubbed "active energy removal" for the purposes of stabilizing robots running over uneven terrain (Andrews et al., 2011; Schmitt and Clark, 2009).

Even though actuation and damping are clearly critical in controlling real world robots, the conservative SLIP model is still widely used to interpret human running dynamics. It
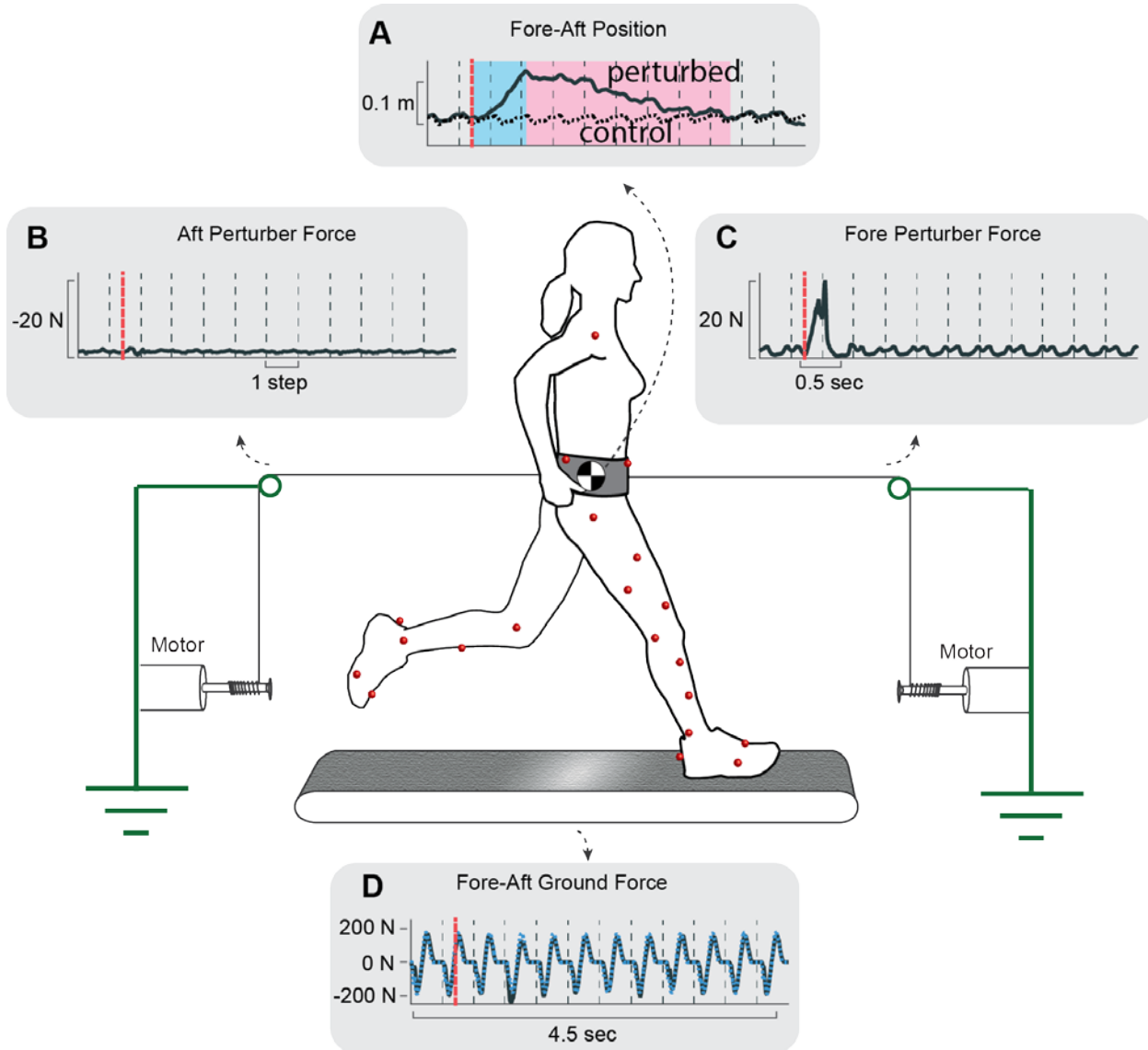
Figure 4-2. Subjects running at 3 m/s on a treadmill were mechanically perturbed in fore and aft directions, with a representative trial of a fore-perturbation depicted above. **A)** Fore-aft Center of Mass position of subject in fore-perturbed step (solid line) compared to the control (dotted line), with onset of the perturbation (vertical red line) and instances of heel strikes (dotted vertical lines). Subjects made a quick compensation in the first 2 to 3 steps after the perturbation (blue shaded region), followed by a slower compensation to return to a nominal position at the center of the treadmill (red shaded region). **B)** The motors maintain a light tension in the rope to eliminate slack. **C)** The perturbations on average took 0.12 seconds and peaked at a force of 20 N. **D)** Ground reaction forces were measured to estimate changes in mechanical work performed by the subject in response to perturbations.

has been used to estimate leg stiffness and interpret how humans respond to various experimental conditions such as running at different speeds (Arampatzis et al., 1999), running on uneven terrain (Ferris et al., 1998), running with a load (Silder et al., 2015), and minimalist-shoe running (Lussiana et al., 2015). These studies make a linear fit from measured force-displacement data to estimate stiffness without any consideration of damping and actuation.

There are a couple of major discrepancies when comparing the SLIP model to humans. Firstly, although the model exhibits GRF to the humans, the SLIP model does not accurately model the hysteresis and actuation shown in the human leg (Fig. 4-1A). Secondly, while net work is zero in human running on average in steady state, it is net negative when accelerating and decelerating in response to fore and aft perturbations respectively (Fig. 4-1B). The SLIP model is incapable of predicting human compensation to mechanical perturbations, since it is unable to modulate kinetic energy by changing per-step stiffness and leg striking angle.

We hypothesize a simple energy-based framework for controlling running: people increase speed (recover from aft perturbations) by increasing muscle work, and decrease speed (recover from fore perturbations) by dissipating more energy during collision. We show here that subjects compensate to fore-aft perturbations by adjusting their kinetic energy, while making only small changes to estimated stiffness and leg striking angle.

To bridge the gap between human locomotion studies and real world energy-based robotic control strategies, we developed a simple extension to the SLIP model named the Damped Actuated Spring-Mass model. It is similar to the "active energy removal" model (Andrews et al., 2011) in that it actively modulates energy dissipation and actuation to stabilize. When exposed to mechanical perturbations, the model successfully reproduces human changes in net work, mostly by modulating actuation and damping. We show that it better fits the human work loop than the SLIP model, and also provides explicit estimates for leg stiffness, damping, and actuation. These estimates may be an important first step for separating contributions in human dynamics among tendons, muscles, soft tissues, and shoes. At the very least, it is clear that lumping stance phase dynamics into a single stiffness value is clearly inaccurate and potentially misleading.

Materials & Methods

IMPLEMENTATION AND MEASUREMENT OF FORE-AFT PERTURBATIONS IN TREADMILL RUNNING
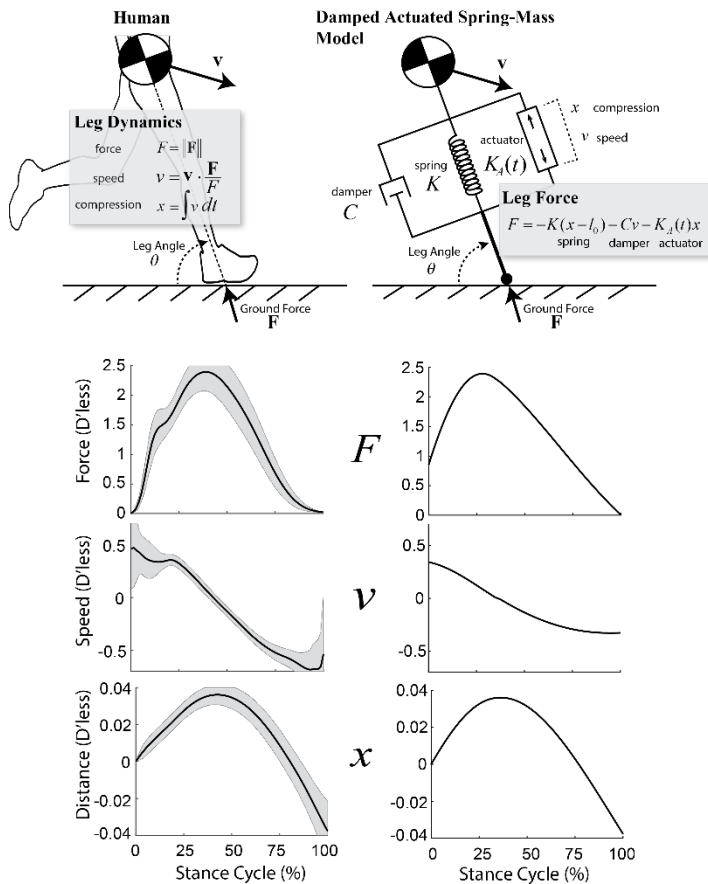
Figure 4-3. The force, compression, and speed of leg compression are measured in humans (N=7) compared to the Damped Actuated Spring-Mass model. In the human, the speed of leg compression (v) is defined by projecting the COM velocity onto the direction of ground force. In the model, force is generated in the leg via a spring, damper, and actuator in parallel. The model modulates kinetic energy to compensate to perturbations, in contrast to the classical SLIP model in which the leg consists only of a spring.

We applied fore and aft perturbations randomly during the gait cycle to subjects running on a treadmill and measured how they responded (Fig. 4-2). We measured 7 subjects running at 3 m/s on an instrumented treadmill. All subjects (4 male, 3 female) were healthy and had no known gait impairments or abnormalities. This study was approved by the University of Michigan Institutional Review Board and all subjects gave informed consent prior to participation in the experiment. Ground reaction forces were recorded on a split-belt instrumented treadmill at the Human Biomechanics Laboratory at the

University of Michigan. Force plates (Bertec, Columbus, OH, USA) underneath each belt independently measures reaction forces at 980 Hz.

Subjects wore a tight leather belt to which ropes were attached, one in the front and one in the back. These ropes were threaded through pulleys mounted on a metal structure housing the motors. Within the pulleys were force sensors that measured the force of tension in the ropes. The forces were measured at 120 Hz from force sensors and using LabView myRIO. The motors applied perturbations a ramp perturbation force that lasted 0.122 ± 0.011 seconds and had a peak of 18.9 ± 3.81 N randomly during the gait cycle as determined from identifying heel strikes in the ground reaction forces.

Throughout this study, the step before a perturbation was used as a control to investigate the effects of the perturbation, to eliminate confounding variables such as the effect of having the harness equipped and positional drift along the treadmill.

To estimate how long it took subjects to recover from perturbations, we calculated how many steps it took to return to the nominal Center of Mass (COM) position and velocity during the control step. In the steps following the perturbation, an average position and velocity were calculated, and the number of steps it took for this per-step position and velocity to first return to the nominal values were used as the number of steps that it took to recover.

To analyze the energetics in a way comparable to the model, the dynamics of the leg were estimated for the leg as a whole. The leg force was defined as the magnitude of the Ground Reaction Force (GRF). The speed of leg compression was therefore defined as the speed of the COM projected onto the direction of the GRF. The leg compression was the integral of leg compression speed with respect to time. To estimate subjects' usage of their swing leg as a mechanism of positioning their feet, the striking angle of the leg was measured as the angle between ground and the direction of the GRF at the moment of heel-strike (Fig 4-3).

All data presented are non-dimensionlized by using the subjects' leg lengths, body masses, as well as the gravitational constant. The mean work normalization constant

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was $MgL = 648$ J; mean leg length was L = 0.936 m; the mean time constant was $g^{-1/2}L^{-1/2} = 0.309$ sec.

MODELLING AND SIMULATION OF AN ACTUATED AND THE DAMPED-ACTUATED SPRING-MASS MODEL RECOVERING FROM FORE-AFT PERTURBATIONS

We compared the Damped Actuated Spring-Mass model, a computational model with a mass, spring, damper and actuator, to human running. The body was modelled as a point mass at the pelvis, with a leg spring sufficient to roughly produce human-like ground reaction forces and body center-of-mass motion (Fig. 4-3). The actuator does no work during compression, and then during extension, continuously extends the rest length of the leg spring, doing positive work. This model supposes that the motor simply maintains the passive force of the spring and damper during compression, and then does positive work during extension.

The model was constrained to run on a limit cycle with the same speed and leg striking angle as the average human data (Fig. 4-3). An optimization was performed to fit the model parameters to minimize the error between the simulated step and the human steps. The cost function used was a weighted sum of the error between human and model of maximum leg force, maximum leg compression, maximum leg extension, and net work.

Results

HUMAN COMPENSATION TO FORE AND AFT PERTURBATIONS
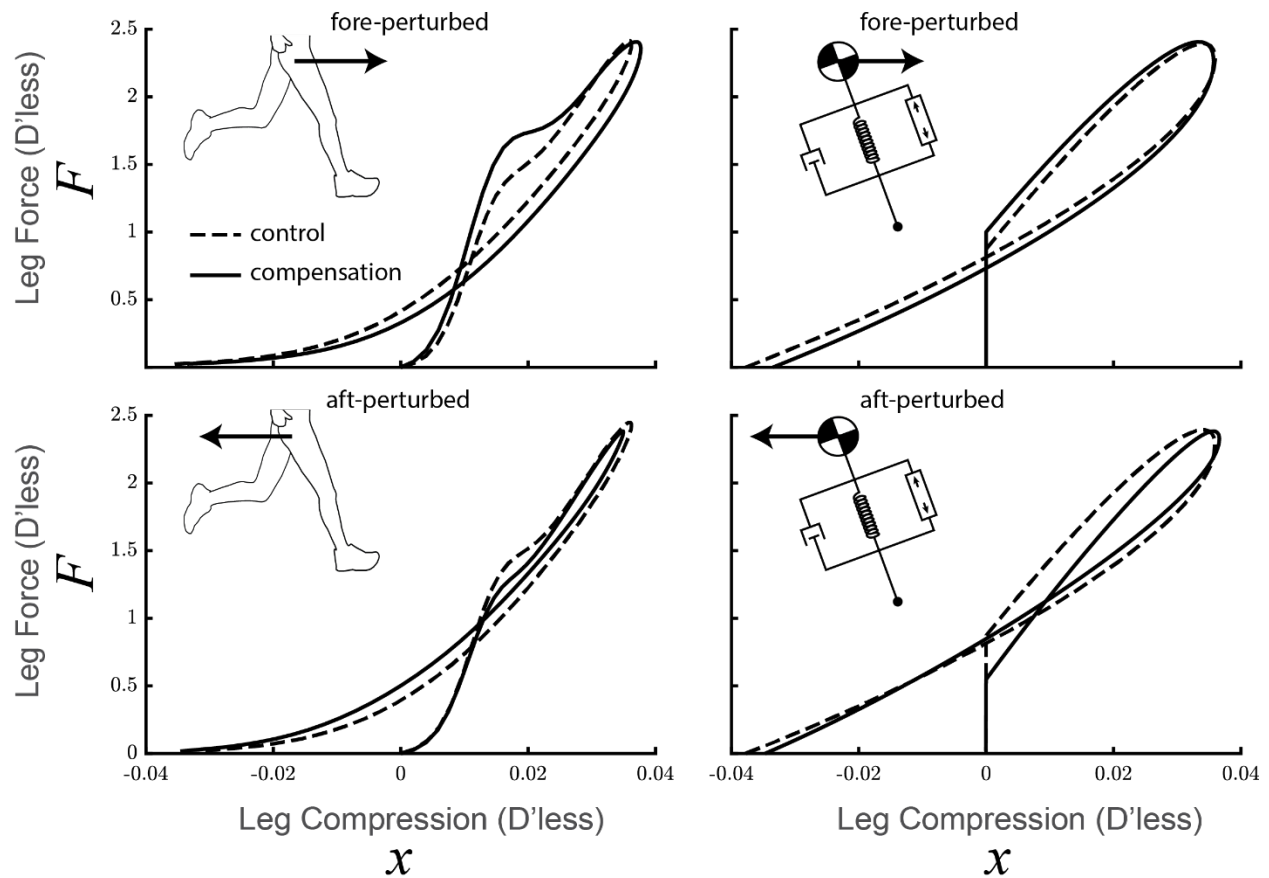
Figure 4-4. On the left, the work loop of the human leg during the second step after the perturbation (solid line) is compared to the work loop of the step prior to the perturbation (dotted line), in both fore (top plot) and aft perturbations (bottom plot). A widening/narrowing of the hysteresis loop is interpreted as increased/decreased negative leg work during compression during human running. There is a notable widening and narrowing of the hysteresis loop (the top loop in the plots) in response to fore and aft perturbations respectively. On the right, we see the optimized Damped Actuated Spring-Mass model fit to the human data and similarly observe similar trends in regards to the widening and narrowing of the work loop. Conversely, the traditional SLIP model (not shown) is energy conservative and is unable to make predictions about changes to the work loop and net mechanical work performed across a step.

Subjects were perturbed by being pulled forward at random points during their stride. The results presented here are for perturbations starting in the first 33% of a step, measured from heel strike of one leg to the heel strike of the other leg.

In fore-perturbations we found that subjects compensated to the peak imposed increase in speed of 0.206 ± 0.0926 m/s by slowing down to their nominal speed in 2.23 ± 0.602 steps. While subjects' speed returned to nominal relatively quickly, there was a small overshoot in speed to slower than nominal, enabling recovery from a peak positional disturbance of 0.177 ± 0.0528 meters in 8.43 ± 4.31 steps (Fig. 4-2).
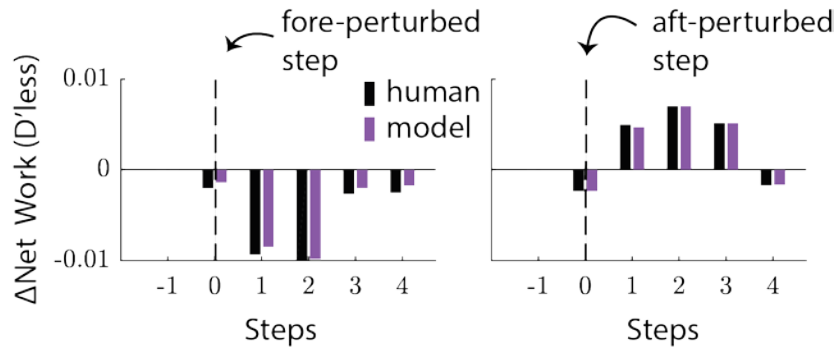
Figure 4-5. Changes in net work relative to the control step (step -1) are compared between model (purple bars) and human (black bars) in the perturbed step and the 4 steps after the perturbed steps. After fore-perturbations occurred (left plot) both model and human increase the magnitude of net negative work performed to dissipate excess energy. Conversely, following aft-perturbations (right plot) both model and human increase the magnitude of net positive work to offset a decrease in speed imposed by the perturbation.

Fore Perturbed

	Net Work	Pos Work	Neg Work	Strike Angle	Step Times	Air Times
Control	0.00177	0.0468	-0.0451	1.42	1.19	0.23
Step 1	-0.00746	0.0400	-0.0475	1.29	1.20	0.27
Step 2	-0.00878	0.0428	-0.0515	1.38	1.20	0.24
Step 3	-0.00135	0.0446	-0.0460	1.44	1.20	0.23

Aft Perturbed

	Net Work	Pos Work	Neg Work	Strike Angle	Step Times	Air Times
Control	0.00097	0.0463	-0.0453	1.38	1.19	0.24
Step 1	0.00670	0.0488	-0.0421	1.53	1.17	0.21
Step 2	0.00907	0.0499	-0.0408	1.39	1.18	0.22
Step 3	0.00614	0.0504	-0.0442	1.36	1.20	0.25

Table 4-1. Human data reported on a per-step basis for the steps before the perturbations (Control) and the first, second, and third step after. All measures are reported dimensionlessly, see Methods for the dimensionalization constants.

In aft-perturbations we found that subjects compensated to the peak imposed decrease in speed of 0.233 ± 0.078 m/s by slowing down to their nominal speed in 2.56 ± 0.60 steps (again with overshoot), and returning from a peak positional disturbance of 0.161 ± 0.084 meters in 10.2 ± 4.7 steps (Fig. 4-3).

We measured the force-length relationship of the leg during the stance phase in the steps after the fore perturbation, and observed that the hysteresis in the loop was larger (Fig. 4-4). By integrating the work loop, we found that net work significantly decreased in the first 3 steps after the perturbation when compared the step before the perturbation (Fig. 4-5). The net negative work in the first, second, and third steps after the perturbation were was -0.00923 ± 0.00890, -0.0105 ± 0.0086, and -0.00312 ±

0.00951 respectively (P < 0.01 for each) (Fig. 4-5, Table 4-1). We found that the striking angle of the leg was shallower by -0.124 ± 0.203 radians (P = 5E-7) (Table 4-1).

In aft perturbations, we observed that the hysteresis loop narrowed, in contrast to the fore-perturbed work loop (Fig. 4-4). We found that net work significantly increased in the first 3 steps after the perturbation when compared the step before the perturbation (Fig. 4-5). The net positive work in the first, second, and third steps after the perturbation was 0.00572 ± 0.00977, 0.00810 ± 0.00972, and 0.00517 ± 0.00978 respectively (P < 0.01 for each) (Fig. 4-5, Table 4-1). We found that the striking angle of the leg was steeper by 0.145 ± 0.182 radians (P = 7E-9) (Table 4-1).
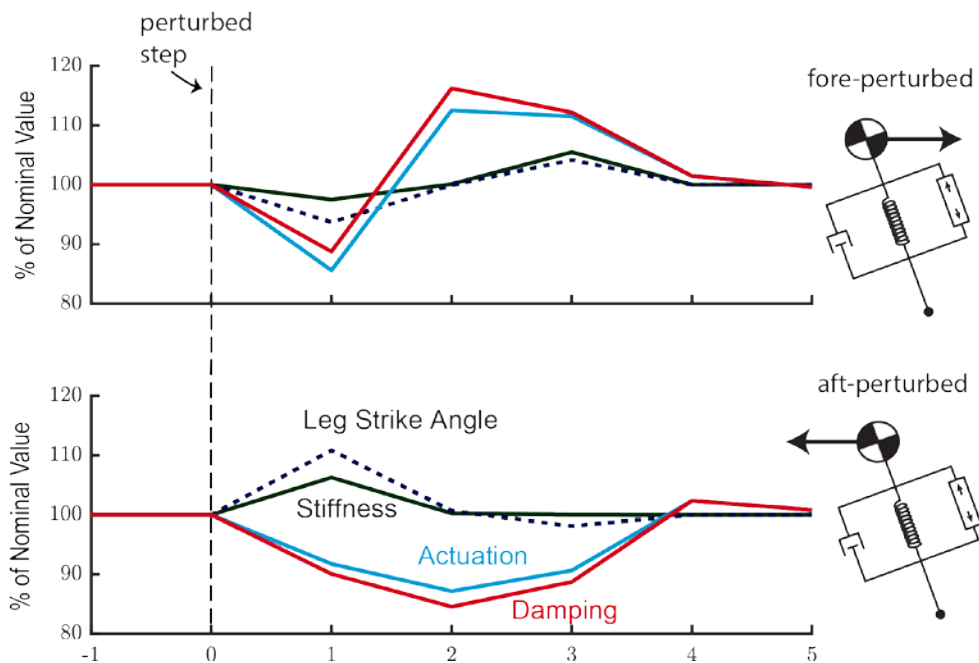
Table 4-2. The Damped Actuated Spring-Mass model was fit to human force-displacement data of fore and aft perturbation data. The percentage change in the model parameters at each step relative is shown relative to perturbation onset (step 0). In both aft and fore perturbations, the model is observed up to 15% changes in damping and actuation. The difference between actuation and damping equals the percentage change in net work. The two main control parameters of the classical SLIP model, leg stiffness and leg strike angle are observed to change to a smaller extent (0 to 10%).

FITTING THE DAMPED ACTUATED SPRING-MASS MODEL TO HUMAN DATA OF RECOVERY TO FORE-AFT PERTURBATIONS

We performed an optimization to match the Damped Actuated Spring-Mass model to the human force-displacement data from the step before to 5 steps after the perturbation. We found that the model reproduced the widening and narrowing of the hysteresis loop in human fore and aft perturbation data respectively (Fig. 4-4). The model also matched well with the net mechanical performed by the human each step after the perturbation, with increased net negative work and increased net positive work in response to fore and aft perturbations respectively (Fig. 4-5).

In fore-perturbations, we found that the model compensated by doing more net negative work by modulating actuation and damping (Fig. 4-6). On the first step after perturbation onset, both damping and actuation decreased, where the actuation work decreased more than the damping work resulting in net negative work. In the second step, damping and actuation increased above the nominal value, with increases in damping resulting in more dissipation than the increased actuation work. Leg striking angle and stiffness changed by a smaller amount, with an initially more compliant and shallower leg the first step after the perturbation in comparison to nominal values (Fig. 4-6).

In aft-perturbations, we found that the model compensated primarily by large decreases in both damping and actuation, resulting in net positive work (Fig. 4-6). Leg striking angle and stiffness changed by a smaller relative amount, with a steeper and stiffer leg on the first step after the perturbation (Fig. 4-6).

Discussion

We imposed fore-aft perturbation on running subjects and showed that subjects compensated for a majority of changes in kinetic energy within 2 to 3 steps after the perturbation. By comparing the step after a perturbation to the step before the perturbation, we show that subjects performed additional net negative and net positive work for fore and aft perturbations respectively in order to stabilize from mechanical perturbations.

Previous studies have examined the force-displacement profile of the leg in running and reduced the differences found between across conditions to a single estimate of

stiffness (Arampatzis et al., 1999; Lussiana et al., 2015; Silder et al., 2015); however, we have shown that only estimating stiffness leads to a poor fit of the force-displacement data (Fig. 4-1A). Furthermore, by only using a linear fit, there is no way to estimate differences between positive and negative work done by the subject, which have been shown here to be significant in perturbation recovery. By fitting the force-displacement-speed data to a model with elasticity, damping, and actuation, the output of the Damped Actuated Spring-Mass model better fits the human data and provides explicit estimates for changes in energy (Fig. 4-5).

Using the Damped Actuated Spring-Mass model, we showed that it is possible to recover from fore-aft perturbations completely, mostly by adjusting damping and actuation (Fig. 4-6). The modulation of damping and actuation resulted in changes in net mechanical work that closely resembled the human data (Fig. 4-5). The majority of the compensation occurred in the first two to three steps after the perturbation, suggesting it may be advantageous to react quickly to recover from perturbations. From the perspective of an inverted pendulum model, any uncompensated for changes in speed will accumulate in a larger and larger lean, which would then require a greater effort to compensate for. One constraint of the experiment that may confound this conclusion is that the length of the treadmill constrained subjects to recover more quickly than if they were running over ground.

While there is no direct measurement of leg stiffness in human data, the model showed a less than 5% difference in leg stiffness between control and recovery steps (Fig. 4-6). Additionally, the human data showed that the leg striking angle was about 7 degrees shallower and 9 degrees steeper in the first step after fore and aft perturbations respectively, with the model producing similar results. While the SLIP model predicts changes in stiffness and leg angle in response to perturbations (Seyfarth et al., 2002), it makes no prediction of the proportionally larger changes to actuation and damping which we observed. Fitting a linear relationship between force and displacement in human data may provide little information, or even mistakenly attribute changes in dynamics to variations in stiffness.

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A limitation to fitting human data to Damped Actuated Spring-Mass model is that we have assumed that actuation is linearly proportional to leg length during extension. While it has been shown that certain muscles such as vastus lateralis and gastrocnemius lateralis activate more strongly as push-off progresses (Cappellini et al., 2006), there is no strong evidence to suggest that humans actually use such a control law proportional to displacement to activate their muscles during push off. Furthermore, in humans the elastic and dissipative elements are not all in parallel with muscles, meaning that the parameters of the Damped Actuated Spring-Mass model presented here may not physiologically correspond to discrete elements in human anatomy, but instead represent an arbitrary average of such elements.

Chapter 5 : Modelling Apparent Energy Dissipation at the Metatarsophalangeal Joint as Multi-Articular Energy Transfer of the Plantar Fascia

Introduction

The biomechanical action of the human foot during locomotion is often examined in terms of joint work between rigid bodies. Such inverse dynamics-based analysis shows significant negative work at the metatarsophalangeal (MTP) joint, which may therefore be a major source of energy dissipation (Stefanyshyn and Nigg, 1997), and contribute to metabolic cost. However, inverse dynamics analysis depends on the assumed interactions across joints, and could yield significantly different results with other assumptions. The muscles, tendons, and ligaments on the plantar aspect of the foot cross multiple joints could potentially transfer energy across joints, without being apparent from joint analysis. Indeed, the arch of the foot and plantar fascia have been shown to behave elastically (Gefen, 2003; Ker et al., 1987), and recent evidence suggests that the MTP transfers energy to the plantar fascia (McDonald et al., 2016).

In Chapter 3, we showed how energy transfer has a significant effect on the estimation of metabolic cost, and there are studies that attempt to directly estimate the amount of energy transfer in locomotion. In running and jumping, the rectus femoris and gastrocnemius muscles were found to exhibit significant energy transfer across the ankle, knee, and hip, with a possible maximum of 97% of the hip work being transferred to more distal joints, by fitting a muscle model to human data (Prilutsky and Zatsiorsky, 1994). In cat locomotion with direct measurements of tendon force, ankle to knee and knee to ankle energy transfer was estimated to transfer up to 22% and 14% respectively (Prilutsky et al., 1996). Our hypothesis is that the plantar fascia may behave in a similar manner, contributing to both work done by the arch of the foot which is typically unmeasured, as well as to work done by the ankle extensors, which also attaches to the calcaneus via the Achilles tendon.

We developed a simple model to examine whether elastically conservative multi-joint energy transfer could explain the apparent single-joint energy dissipation observed during running at the MTP joint. We found that a simple model of foot arch and plantar fascia deformation (Fig. 5-1) resulted in net-negative, non-dissipative work at the MTP, the measure of which in humans has previously been interpreted as dissipation. All energy lost at the MTP joint was recovered at the ankle, which performed an equal and opposite amount of net positive work.

We tested this model by designing and testing a light-weight mechanical leg and having a subject manipulate it to run on a treadmill. By measuring the dynamics of the subject and mechanism, we found that the subject manipulated the leg to run roughly with human-like gait ground reaction forces. We then calculated both the powers of the tendons and the joints and showed that, like in humans, the MTP did mostly negative work, but that the power going through the tendons were mostly elastic, with some dissipation offset by the positive work supplied by the subject.

Additionally, we used the simple foot model to explore potential benefits of the structure of the foot in regards to muscle energetics. The speed of muscle contractions in running is faster than the measured optimal contraction speed for muscle contraction (Hill, 1922). The model shows that the time duration of the extension phase of running directly depends on the length of the foot. A longer foot results in a less symmetric ground reaction force in which the impact and peak occur sooner, thereby extending the extension phase during which positive work is done to jump into the next step. One possible benefit of a longer foot is that it could decrease the muscle contraction speed during push-off thereby increasing the efficiency of performing positive work, acting as a lever arm which allowing the muscles to contract over a greater period of time.

While the measurements of single joints is convenient and useful, drawing conclusions about muscles and energetics of the body as a whole from these measurements must be made carefully, since the architecture of tendons, muscles, and energy transfer across joints all influence estimates of metabolic cost from mechanical work. The arch of the foot is often treated as a rigid body, perhaps because displacements are so small relative to motions of the larger leg segments, but this work suggests that the arch,
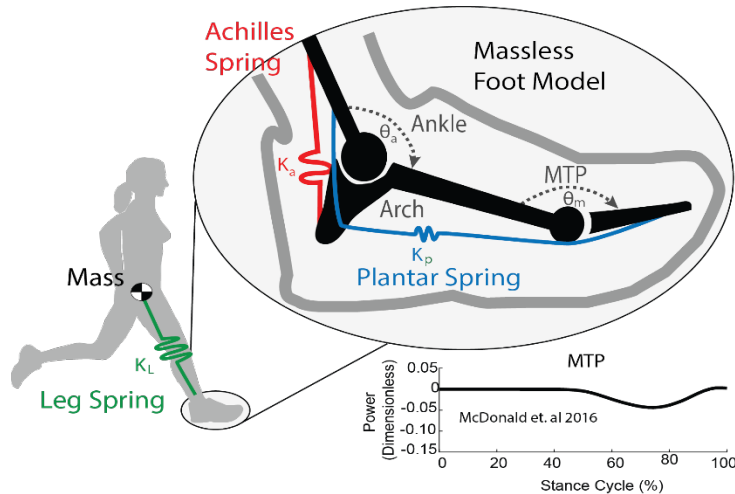
Figure 5-1. Typical Inverse Dynamics on the foot estimates joint torques at the Metatarsophalangeal (MTP) and Ankle joints. We construct a simple foot model which rotate about the ankle and MTP, and includes springs modelling the effects of the plantar fascia and Achilles tendon. As shown in the plot of MTP joint power during stance, the MTP appears to mostly absorb energy during human running during the push-off phase. However, the plantar fascia may transfer that energy to the ankle, and this model shows how multi-articular forces can produce net work at joints independent of dissipation.

MTP, plantar fascia, and ankle are highly dependent on each other, and that measurements of foot deformation may be important for understanding the energetics of human running.

Materials & Methods

MULTI-ARTICULAR FOOT DEFORMATION MODEL

We compared a computational model of running with a two-segment foot to human running. The body was modelled as a point mass at the pelvis, with a leg spring sufficient to roughly produce human-like ground reaction forces and body center-of-mass motion. The foot is modelled with two segments: a rear-foot and fore-foot (Fig. 5-1). One spring acts between the rear-foot and leg, analogous to the Achilles tendon, while another spring acts bi-articularly between the fore-foot and leg, analogous to the action of the foot arch and plantar fascia. The model has four kinematic degrees of freedom: leg angle, leg displacement, ankle angle, and MTP angle.

In the computational model, the arch does not undergo displacement, even though there in both humans and in the physical model presented in the next section there is significant displacement. While it would be more accurate to allow the arch to compress, it adds unnecessary complexity to the model for the purpose of demonstrating multi-articular energy transfer to the ankle. Namely, it adds a degree of freedom and

introduces the need for non-static contact mechanics (and assumptions for those mechanics).

The physics of the model were constructed using Kane's method and were simulated in 4 distinct phases governed by which parts of the foot are in contact with the ground. During the first phase, the heel, ball of the foot, and toe are all flat on the ground. The second phase begins once the heel comes off of the ground (as measured by the vertical contact force), leaving the ball and toes in contact. The next two phases start when the ball and toes leave contact with the ground respectively, with the latter being the aerial phase in which no part of the model is in contact with the ground. An instantaneous collision was imposed on the model using the Impulse Momentum equation (from Newton's 2nd Law) at the beginning of stance to enforce the ground contact constraint.

The model was constructed such that the total amount of mechanical energy remains constant across all 4 phases of gait. Firstly, there are no sources of damping, actuation, or changes in terrain that would increase or decrease energy in the model. Secondly, the foot has no mass, such that collisions with the ground after aerial phase result in no loss of energy.

Because the foot has zero mass, the equations of motion during the second and third phase of stance are singular, resulting in a system of Differential Algebraic Equations (DAEs). Since the DAEs are linear with a non-identically zero matrix pencil, there is a unique solution to the problem (Petzold, 1982). Briefly, the DAEs were analytically reduced to standard non-singular ODEs by performing Gaussian elimination to decouple the differential and algebraic equations. Differentiation with respect to time was performed twice on the algebraic equations to obtain new differential equations linear with respect to accelerations. Because the foot has zero mass, the system has non-realistic behaviors such as conservative collisions and instantaneous changes to the speed of the foot without any change in total model energy.

Multi-Articular Deformable Foot Mechanism
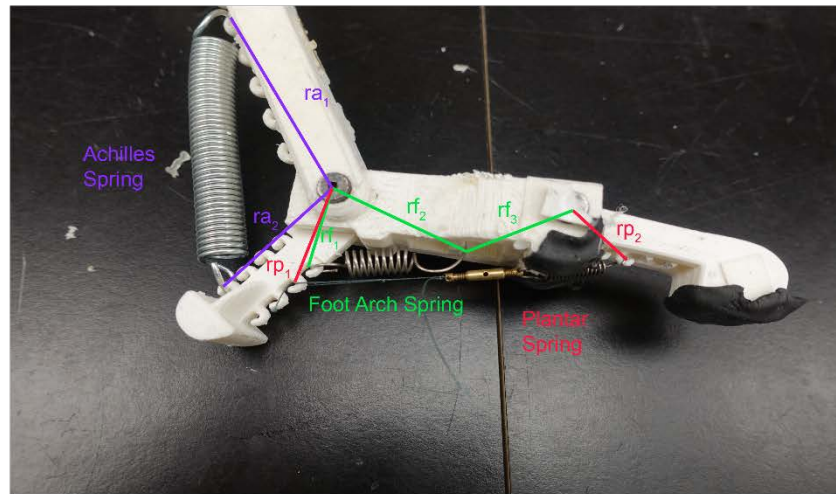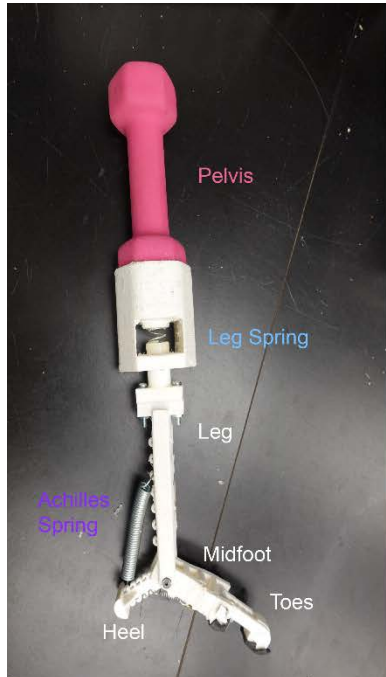
Figure 5-2. The experimental mechanism designed to test the energetics of the foot during running. The mechanism consists of 5 segments: pelvis, leg, midfoot, heel, and toes, and 4 springs Leg, Achilles, foot arch, and plantar fascia. The mechanism is designed to model human foot and leg dynamics in the sagittal plane, particularly how energy lost at the MTP joint can be redirected to the ankle.

All models were constrained to run with similar dimensionless speed and stance time as the human running data (McDonald et al., 2016), using the Levenberg-Marquardt algorithm. Joint torques of the ankle and MTP joints were calculated as the next moment created by each spring about the joint. Joint angular velocities were calculated as the difference in angular velocity of the two segments connected by the joint. Joint power is the dot product of joint torque and joint angular velocity.

DESIGN OF A SIMPLE MODULAR RUNNING LEG

A physical mechanism was designed to simply illustrate the dynamics of the foot. It serves as a bridge relating the complex human anatomy to the abstract results of our simplified model. The mechanism consists of 5 rigid bodies: a pelvis, leg, heel, midfoot, and toes. Figure 5-2 shows a sagittal plane view of the mechanism designed. The body of each segment was 3D printed in ABS plastic. The leg spring is a compression spring, whereas the Achilles, Foot Arch, and Plantar Fascia springs are all extension springs. A

	Achilles	Foot Arch	Plantar Fascia	Leg
Stiffness (N/m)	211	201	118	379
R1 (mm)	71.7	20.28	24.34	N/A
R2 (mm)	39.2	34.02	16.9	N/A
R3 (mm)	N/A	24.31	N/A	N/A

Table 5-1. Measurement of stiffness for each spring distance between joints and tendon attachment points also calculated (see figure 5-2 for definitions of springs and moment arms).

3 lb hand weight was used as both the grip for subjects to manipulate the mechanism, as well as to serve as the mechanism's pelvis. We measured the weight of each segment, as well as the stiffness & attachment points of each spring (Table 3).

The main difference between the computation and physical model is that the arch is locked in the computational model, whereas in the physical model a stiff foot arch spring spans the arch allowing small displacements. This design was chosen such that it more closely resembles human anatomy and thereby be a more relatable learning tool, even though it is not strictly necessary for showing multi-articular energy transfer.

EXPERIMENT: HUMAN-IN-THE-LOOP CONTROL OF A SIMPLE MECHANICAL LEG

We characterized the mechanical properties of the components, and then performed an experiment in which subjects (N=1) grabbed the mechanism by a handle and manipulated it to run on a treadmill for 1 minute at 0.8 m/s. We measured the kinematics of both the foot and human arm and torso, as well as the ground reaction forces exerted by the foot using the same equipment described in Chapter 1. We measured the stiffness of each

vertical ground reaction force
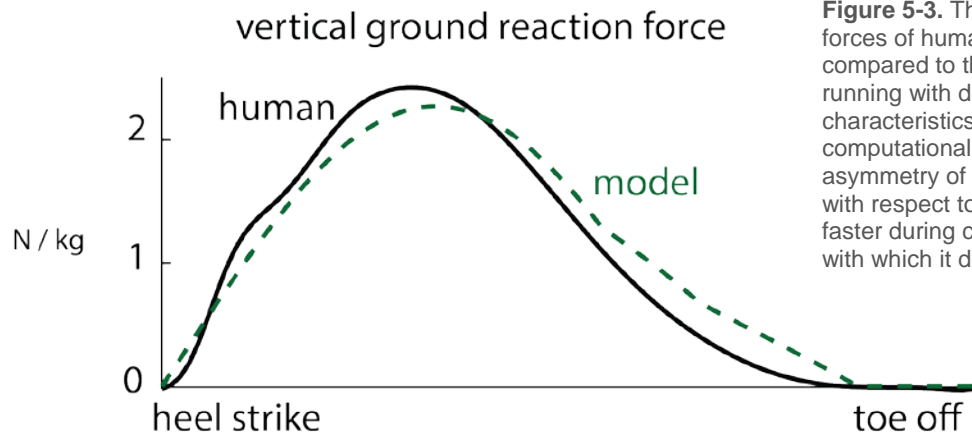
Figure 5-3. The vertical ground reaction forces of humans running at 3 m/s is compared to the multi-articular foot model running with data-matched gait characteristics across stance phase. The computational model captures the asymmetry of the ground reaction force with respect to time, the force increasing faster during compression than the speed with which it decreases during extension.

tendon as well as their attachment points to each segment (Table 5-1).

Using the kinematics of the foot and the stiffness & moment arm of each tendon, we estimated the force produced by each tendon. Tendon power was calculated as the dot product of this force with the relative speed between the tendon attachments. To calculate joint power, the tendon force about each joint was projected into equivalent torques about that joint. Joint power was then calculated as the dot product of joint torque and joint angular velocity.

To calculate the amount of energy the subject supplied to the foot, we assumed that the mass of the foot and leg was negligible compared to the mass of the mechanism's pelvis (compare 1607 g to 247 g). By making this assumption, the force acting on the mechanism from the ground is exactly equal to the force exerted by the ground on the mechanism's pelvis. From the motion data we calculated the acceleration, and we had measured its weight previously, thus allowing us to solve for the force and torque applied by the user onto the mechanism's pelvis. We estimated the position on which the hand applied this force and torque from markers on the hand in order to calculate the user mechanical power.
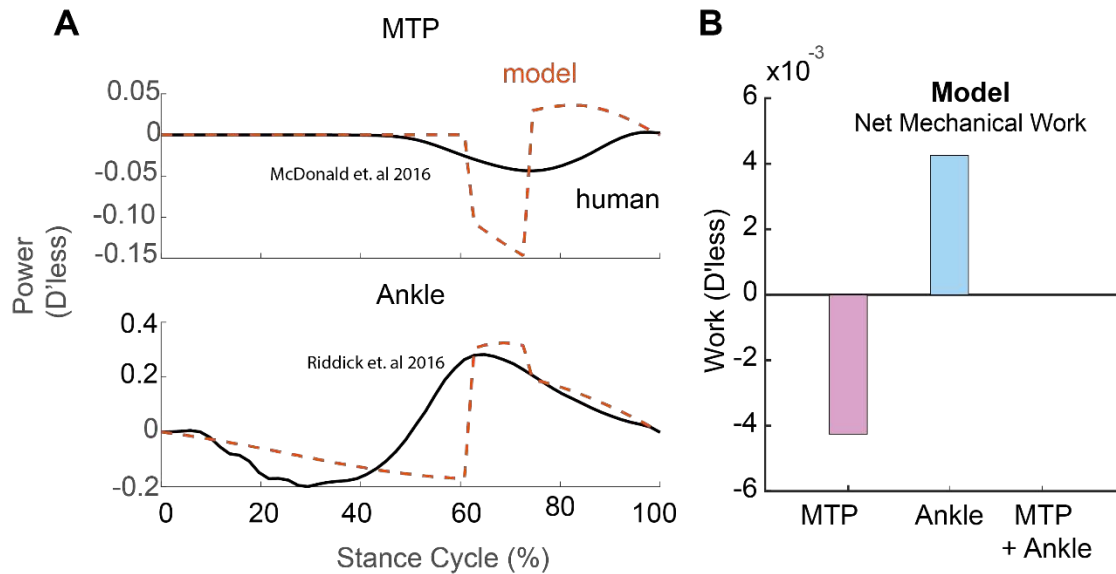
Figure 5-4. A) The MTP and Ankle joint powers are compared between the computational model (red dotted line) and human data (black solid line) during stance phase. In humans, the MTP joint is observed to perform mostly negative work during, with a very small amount of work at the end of stance. The MTP joint of the model behaves similarly, except there is more positive work. In both human and model, the ankle does negative work followed by positive work. **B)** Integrating the power curves of the model over stance phase, the net negative work observed at the MTP is exactly offset by net positive work produced at the ankle, with 0 energy dissipation.

Results

COMPARING THE MODEL TO THE HUMAN

We compared the model's kinetics to humans (Man et al., 2016), and found that the ground reaction forces were qualitatively similar (Fig. 5-3). Humans produce a relatively faster increase in ground reaction force compared to the slower decrease later in stance, an effect not captured by the mass-spring model with point foot. The two-segment model reproduces this time-asymmetry of human data. Defining push-off as between the peak of the ground reaction force and toe off, a consequence of having a two-segment foot versus a point-foot is to increase the time over which push-off occurs (Fig. 5-7).

The model showed net negative work at the MTP and net positive work at the ankle, both roughly like observations of humans (Fig. 5-4A). However, because the foot model was elastic, it performed zero net work, and the negative work at the MTP joint was exactly offset by the positive work at the ankle joint (Fig. 5-4B).

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Foot Mechanism Vertical GRF
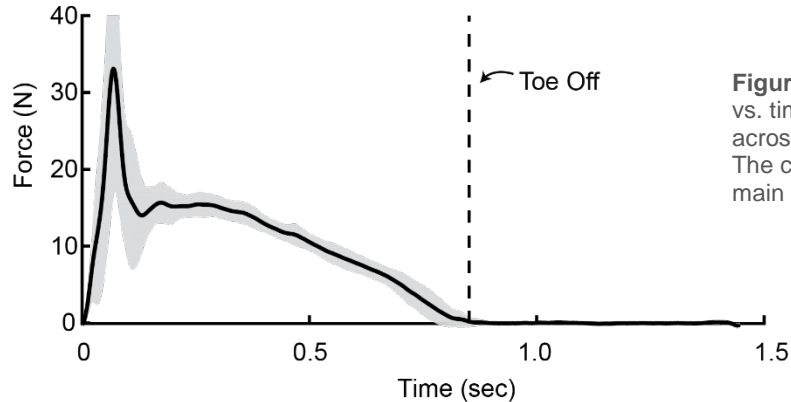
Figure 5-5. The vertical ground reaction force vs. time acting on the mechanism averaged across each step from heel strike to heel strike. The collision peak is larger in comparison to the main peak than in human running.

COMPARING THE MECHANISM TO THE HUMAN

In the physical foot mechanism, we found that the ground reaction forces of the foot were qualitatively similar to human running in that there was a single lower frequency peak, and higher collision peak. In the experiment, the collision peak was higher than is observed in human running (Fig. 5-5). The subject on average supplied 0.119 ± 0.144 J (P=1E-4) of net positive work offsetting the dissipative and friction losses due to the mechanism (Fig. 5-6C). We found that the Achilles, Plantar Fascia, and Foot Arch did net work not significantly different than 0 (P>0.05), and the leg spring did net negative work of -0.0116 ± 0.0221 J (P=0.03). (Fig. 5-6D). Calculating joint powers, we found that the ankle and MTP joints did net 0.0186 ± 0.0187 (P=0.0012) J and -0.0108 ± 0.0120 J (P = 0.032) respectively over a step (Fig. 5-6A,B).
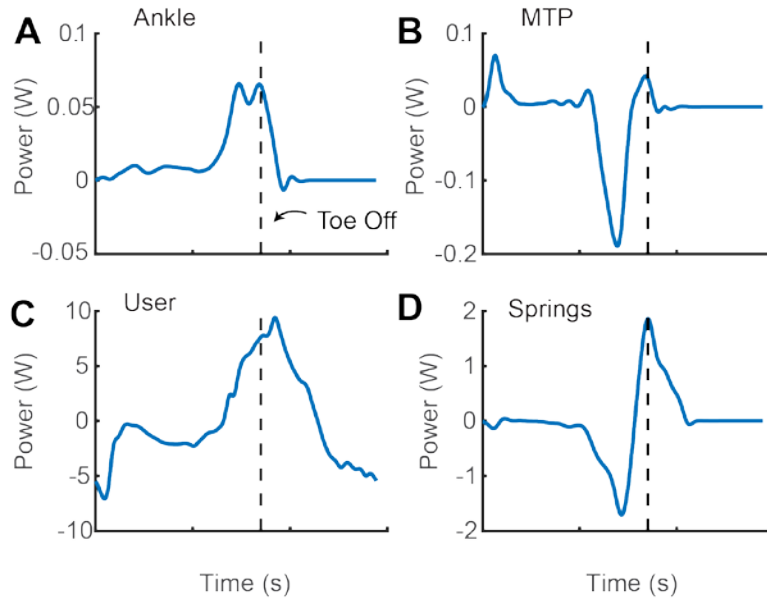
Figure 5-6. Average mechanical power measurements of the multi-articular foot mechanism being manipulated on a treadmill to locomote at 0.8 m/s, shown from heel strike to heel strike. **A, B)** The joint power analysis shows that the Ankle and MTP do net positive and net negative wok respectively during push off, mirroring net work trends in humans and in the computational model. **C)** The power trajectory of the user acting on the leg shows that the subject tended to accelerate the leg towards the end of stance, and decelerate it near the end of swing and early stance. **D)** The combined power trajectories of the Leg, Achilles, Plantar, and Foot Arch springs show that they perform a small amount of work during collision, and then do about an equal amount of negative and positive work during push-off, as expected from elastic springs.

Discussion

The simple foot model and mechanism shows how net negative work performed at the MTP may mostly be energy transferred via multi-articular elements. These models are surely insufficient to explain the actual mechanics of human running, but serve to illustrate how assumptions regarding multi-joint tendons can affect interpretation of inverse dynamics measurements. Apparent MTP dissipation could be transferred to other parts of the foot such as the arch or plantar fascia, although not with the perfect elasticity of model.

In the model, we showed how apparent dissipation at the MTP is exactly offset by apparent power generation at the ankle (Fig. 5-4B). Furthermore, we observed similar behavior at the ankle and MTP in the experiment with the foot mechanism (Fig. 5-6b), where the Ankle mostly generated positive work while the MTP generated mostly negative work even though the springs generated roughly 0 net work (Fig. 5-6A,B,C).

vertical ground reaction force
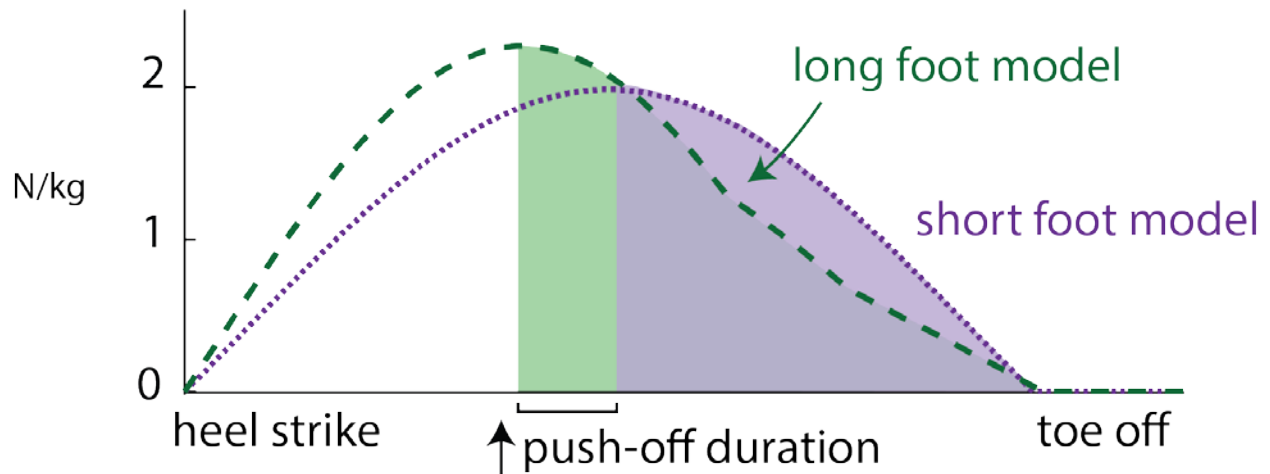
Figure 5-7. Ground reaction forces are compared between a computation model with a short foot and a long foot. A longer foot produces more asymmetry in the ground reaction force than a shorter foot. The asymmetry produced from a longer foot lengthens the period of time over which push-off occurs, potentially allowing muscles acting during push off to contract a speed that is more efficient.

Given the elastic nature of the plantar fascia and foot arch, it is possible that such a mechanism of energy transfer also exists in humans.

Our findings may have important implications for the direction of research in regards to the foot, shoe design, and prosthesis design. Based on the conclusion that the MTP dissipates energy, several studies have designed shoes and experimental conditions to improve energy return at the MTP joint (Nigg, B.M., 2000; Stefanyshyn, D. J., 2006; Toon et al., 2011; Willwacher et al., 2013). While these studies had some success in recovering energy at the MTP joint by using stiff plates in shoes, our results suggest that such efforts may hamper power production at the ankle. Our model shows that any energy lost at the MTP is recovered at the ankle; any decreases in net negative work at the MTP that shoes impose may be offset by decreases in net positive work at the ankle. Whether such shoes would be beneficial for running economy would then depend on timing and whether additional positive work at the ankle or MTP is more effective. Given that humans can control their intrinsic foot muscles to modulate the stiffness of the foot arch (Kelly et al., 2014), we hypothesize that humans activate these muscles in coordination with ankle extensors to maximize efficiency. As such, constraining the foot and ankle to do mechanical work in ways that modulate instead of enhance the normal dynamics of the foot and ankle may serve to decrease the efficiency of running.

Additionally from the model, we observed that a longer foot tends to create more asymmetry in the ground reaction force than a shorter foot (Fig. 5-5). This asymmetry may have consequences for the efficiency of muscle contractions. The force-velocity relationship shows that muscle is most efficient when it contracts over a period of about 0.8 seconds (Hill, 1922). Since in running the push-off phase is generally much faster than 0.8 seconds, increasing the duration of the push-off phase by having a longer foot may improve the efficiency of pushing off. However, this increase in efficiency in push-off work may be offset by an increased cost in swinging the leg due to having a longer and heavier leg. We propose that the length of the human foot may have evolved to balance these two costs across the distribution of speeds and frequency with which humans stand, walk, and run.

Chapter 6 : Conclusion

This work provides new future research directions in soft tissues, running energetics, modelling human dynamics and control, and foot dynamics. I have presented four novel interpretations of running dynamics and energetics with human subject experiments and simple models. These experiments, models, and conclusions provide strong evidence against several popular interpretations of running that rely on a misunderstanding of mechanical work, which I will now review.

Firstly, biomechanics research often focuses on measuring the function of the ankle, knee, and hip to interpret experimental results. While these joints certainly play a vital role in running, soft tissues make up a majority of the body, and we have shown that soft-tissues play a large role in running dynamics. We measured the previously unknown net mechanical power of soft tissues in running and found that they oscillated like a damped spring-mass system. These oscillations dissipated significant amounts of energy; since net work is zero on level ground running, this dissipation must be offset by active muscle work that would account for almost 30% of the metabolic cost of running at 5 m/s.

Secondly, using these new soft tissue measurements, we reviewed the current state of knowledge in estimating metabolic cost from mechanical measurements. Previous estimates of the metabolic cost of work were erratic and lacked a thorough understanding or sensitivity analysis to the assumptions and parameters involved in such an estimation. Due to these poor predictions of cost, the idea that the Cost of Generating Force (COGF) is the major cost of running became popular, especially with a series of experiments across several animals showing high correlation between cost and an indirect estimate of COGF. By including soft tissues into the model of cost due to mechanical work, and exploring the effects of each assumption that goes into the model, we showed that mechanical work explains a majority of cost even with conservative assumptions. With the reasonable assumptions of 21 % net muscle efficiency, 50% of work done by muscle as opposed to tendons, and no contralateral energy transfer, mechanical work explains about 74% of metabolic cost for slow to medium running speeds. This provides strong evidence against the COGF being the dominant cost, and calls into question the correlating approach for the COGF, which has no mechanistic explanation.

Thirdly, we explored the limitations of the Spring Loaded Inverted Pendulum (SLIP) model in explaining human running mechanics. A hallmark of steady-state level ground running is that there is zero net mechanical work over an average period of time. The SLIP model became a popular model of running in part due to its conservative

energetics matching well with this assumption. However, net mechanical work in humans is only zero on average on level ground, and it is not generally true when there are changes in elevation or perturbations that cause increases or decreases in energy. While the SLIP model roughly explains steady-state running dynamics, it cannot predict how humans will respond to perturbations, which require a change in net mechanical work to compensate. We measured subjects running on a treadmill exposed to mechanical fore-aft perturbations and showed that a primary compensation mechanism was to modulate net work performed in the first two to three steps after the perturbation. We then extended the SLIP model to the Damped Actuated Spring-Mass model, which includes actuation and damping, to provide explicit estimates for how humans are adjust their leg properties to recover from perturbations. This model provides an updated understanding of human running dynamics, and suggests that the common practice of estimating a single net leg stiffness from a linear fit may be inaccurate and lead to erroneous conclusions.

Finally, the metatarsophalangeal (MTP) joint does mostly negative work in walking and running, leading to the conclusion that it is dissipating large amounts of energy. We constructed a simple computational model to show that this negative work may in fact be energy transferred from the MTP to the ankle via the plantar fascia. We also constructed a simple physical mechanism and measured it to find similar relationships in MTP and ankle work in comparison to the human and model. The computational model suggests that efforts to design shoes to maximize energy return at the MTP may be misguided, since that energy is in fact not being lost, but in some way already being used to propel the body forward by transferring to the ankle. In fact, the model shows that the foot may increase the efficiency of running by extending the time over which push-off occurs, thereby potentially increasing the efficiency of muscle contractions by allowing them to happen more slowly.

These four pieces of work are tied together under the framework of mechanical work being a fundamental part of human locomotion. This dissertation uses mechanical work to give insight into the cost of running, soft tissue dynamics, recovery to perturbations, and the role of the foot. These insights provide a new and more comprehensive for

evaluating the cost of locomotion from mechanical measurements. This work aids in the design of prostheses, robots, shoes, and orthoses by explaining some of the dynamic complexities of the foot including multi-articular energetics and soft-tissue vibrations, providing a model and framework for evaluating the designs using mechanical work and metabolic cost, and how to expect people to use their devices when responding to mechanical perturbations.

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