Achilles tendon strain energy in distance running: consider the muscle energy cost

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Fletcher JR, MacIntosh BR. Achilles tendon strain energy in distance running: consider the muscle energy cost. J Appl Physiol 118: 193–199, 2015. First published November 13, 2014; doi:10.1152/japplphysiol.00732.2014.—The return of tendon strain energy is thought to contribute to reducing the energy cost of running (E_{run}). However, this may not be consistent with the notion that increased Achilles tendon (AT) stiffness is associated with a lower E_{run}. Therefore, the purpose of this study was to quantify the potential for AT strain energy return relative to E_{run} for male and female runners of different abilities. A total of 46 long distance runners [18 elite male (EM), 12 trained male (TM), and 16 trained female (TF)] participated in this study. E_{run} was determined by indirect calorimetry at 75, 85, and 95% of the speed at lactate threshold (sLT), and energy cost per stride at each speed was estimated from previously reported stride length (SL)-speed relationships. AT force during running was estimated from reported vertical ground reaction force (Fz)-speed relationships, assuming an AT:ground reaction force moment arm ratio of 1.5. AT elongation was quantified during a maximal voluntary isometric contraction using ultrasound. Muscle energy cost was conservatively estimated on the basis of AT force and estimated crossbridge mechanics and energetics. Significant group differences existed in sLT (EM > TM > TF; P < 0.001), the latter ranging from 10 to 70 J/stride. At all speeds and in all groups, estimated muscle energy cost exceeded energy return (P < 0.001). These results show that during distance running the muscle energy cost is substantially higher than the strain energy release from the AT.

Achilles; energy cost; tendon; running

IT HAS BEEN GENERALLY ACCEPTED that a primary role of the muscle-tendon unit in the lower limbs during running is the storage and release of tendon strain energy (3, 4). This storage and release of tendon strain energy are thought to be important factors in keeping the energy cost of running (E_{run}) at a low value. During running, the Achilles tendon (AT) is stretched, storing strain energy. A portion of this strain energy is returned during the subsequent shortening phase thereby reducing the work required by the muscle (8, 41). There have been several suggestions that the elastic recoil provided by the AT contributes a significant portion of the energy for propulsion (5, 22, 31); however, no study to date has considered the energy cost of muscle contraction for the muscle in series with the tendon releasing energy. This energy cost would be necessary for the tendon strain energy storage to occur.

Estimates of strain energy storage of the AT are typically performed by either directly or indirectly measuring AT elongation as a function of AT force (39). The area under the force-elongation curve is considered AT energy storage. Considering estimates of tendon hysteresis or measuring the tendon translation as a function of force during force decline provides a measure of AT energy release. AT energy storage can be estimated in vivo by combining simultaneous measurements of AT elongation and torque using ultrasonography and dynamometry, respectively.

The amount of AT strain energy storage/release varies as a function of AT stiffness. For a given AT force, energy storage would be proportional to elongation; a stiffer tendon will store less energy. Considering that it has been demonstrated that AT stiffness is higher in trained compared with untrained runners (2, 21) and changes in AT stiffness are associated with changes in E_{run} (5, 15), more highly trained runners should have a lower capacity for AT energy storage/release and yet this deficiency is associated with a lower E_{run}. These recent results seem difficult to rationalize with the notion that the AT serves to store and release energy. Thus it appears as though the energy-saving contribution of the stiffer AT cannot solely be a result of stored strain energy return.

Ker et al. (28) have estimated that the strain energy stored in the AT during running at 4.5 m/s was 35 J/step, and this was considered to contribute a substantial proportion of energy to the total E_{run}. However, the estimated AT forces required (4,700 N) to store this amount of energy are near published estimates of maximum isometric force of 5,000–6,000 N (1, 15). A similar amount of energy storage has been reported in human hopping (38 J), contributing ∼16% of the total mechanical work of the hop (32). Using a buckle-type transducer to measure AT force directly, Fukashiro et al. (17) found a smaller amount of tendon strain energy was stored (6–7 J/jump) in squat and countermovement jumps, and this represented 17–23% of total calf muscle work; a result of a lower measured AT force (<2,300 N) during the jumps. It would be expected that AT energy storage during running would be smaller than that found in hopping, as a result of lower vertical ground reaction forces (10) and therefore lower AT force. AT force can be estimated during running from ground reaction forces, and the ratio of the resultant ground reaction forces and AT moment arms (28).

Considering E_{run} of trained and elite male and female distance runners measured in our laboratory (13, 15) and others (40) is within the range of 4.2–4.6 J·kg^{-1}·m^{-1}, the energy storage/release of the AT would appear to be a small proportion of the total E_{run}. To date, however, no study has evaluated estimates of the AT energy storage and release during running from measurements of AT elongation and moment arm using ultrasound. Furthermore, no study has considered that to store energy in a tendon, the muscle in series with that tendon must contract, using additional energy. This muscle energy cost would be a portion of the E_{run}, effectively reducing the value of...
storing energy in the tendon and may be the reason that improved economy is associated with a stiffer AT.

A recently proposed alternative view of the role of tendons is in reducing the energy cost of muscle contraction by minimizing the amount and/or velocity of muscle shortening (14). The tendon, if optimally stiff, may allow the muscle fascicles to remain nearly isometric during running, while muscle-tendon unit lengthening and shortening can be accommodated primarily by the tendon (24, 30). In keeping the muscle fascicle shortening velocity low, the muscle can operate near its optimal sarcomere length (6), and the required level of muscle activation is minimized (14). Considering that during running the triceps surae muscle fibers do not undergo substantial shortening (24, 30), an optimally-tuned AT would result in less fiber shortening to achieve active joint rotation. As a result, the joint range of motion can be accommodated primarily by the tendon, keeping the energy cost of the contraction low (35). However, to do so, AT stiffness must be appropriately tuned to minimize the amount of fascicle shortening. With less than optimal stiffness, the amount and/or velocity of muscle fiber shortening is increased and this shortening will increase muscle energy cost (14), elevating Erun.

Therefore, the purpose of this study was threefold:  
1) To estimate the proportion of strain energy storage/release of the AT relative to total Erun.  
2) To estimate the energy cost of muscle contraction required by the muscle in series with the AT.  
3) To determine whether the contribution of strain energy storage/release differed between runners of different abilities and/or of different sexes, because it is known that the mechanical properties of the AT would differ.

METHODS

A total of 46 distance runners participated in this study. Some of these runners had previously participated in studies performed in our laboratory (13, 15). Those data were combined with new data to address the specific research questions posed here. The runners gave their informed written consent to participate in the experimental procedures, which were approved by the University of Calgary Conjoint Health Research Ethics Board.

Runners were divided into either “elite” or ‘trained’ based on the highest level of competition achieved. Subjects were considered to be elite male runners (n = 18) if they had competed at a National Championship (1,500 m or longer, including marathon and cross country race distances) within 6 mo of the study and running a minimum of six times per week, with a minimum average training volume of 70 km/wk of running for at least 6 wk before participating in the study. Trained runners (n = 28, 16 males and 12 females) were those runners not meeting the inclusion criteria for the elite group but participating in run training a minimum of five times per week, with a minimum average training volume of 40 km/wk during the 6 wk before the beginning of the study. All runners were following a similar periodized training plan for either the 10 km or half-marathon race distance and were free of any neuromuscular or musculoskeletal injuries at the time of the study. Subject characteristics are shown in Table 1.

Experimental protocol. The subjects visited the laboratory on two separate occasions. On the first visit, an incremental exercise test to exhaustion was performed on a treadmill (Woodway Pro, Waukesha, WA) to determine the subject’s maximal oxygen uptake (V\textsubscript{O\textsubscript{2}}\text{max}) and speed associated with the lactate threshold (sLT). V\textsubscript{O\text{2}\text{max}} and sLT were determined based on methods used previously in our laboratory (15, 16). sLT was defined as the speed at the stage preceding that which elicited a [BLa\textsubscript{-}1] increase >1 mM. All tests were terminated due to volitional exhaustion V\textsubscript{O\text{2}\text{max}} was defined as the highest 30-s average V\textsubscript{O\text{2}} during the test. All subjects attained V\textsubscript{O\text{2}\text{max}} based on primary or secondary criteria previously reported from our laboratory (13).

Between 48 and 72 h following the V\textsubscript{O\text{2}\text{max}} testing session, the subjects returned to the laboratory for determination of AT stiffness and E\textsubscript{run}. AT stiffness of the right AT was determined on a dynamometer (Biodex System 3, Shirley, NY) as described previously (14, 15). The subjects performed three isometric ramp maximal voluntary contractions (MVC) of the right plantarflexors. Moment elicited during the MVC was sampled at 100 Hz. The trial eliciting the highest moment was used for analysis. During each MVC, a 12.5-MHz linear array ultrasound probe (50 mm, Philips Envisor; Philips Healthcare, Eindhoven, The Netherlands) was used to visualize the medial gastrocnemius muscle (MG) fascicles at 49 Hz, close to the AT. The ultrasound probe was placed on the MG muscle belly, near the myotendinous junction, and secured using a custom-built apparatus. AT tendon elongation was estimated by the displacement of an insertion of a fascicle into the deep aponeurosis, measured using ImageJ (National Institutes of Health, Baltimore, MD) during the MVC. Measured moments and AT elongations were corrected for joint rotation (14, 15), and AT moment arm length at the 90° ankle angle was estimated using the tendon travel method (26). AT force was calculated by dividing the ankle joint moment by the estimated AT moment arm. AT force (F\textsubscript{AT})-elongation (d\textsubscript{L}) data were fitted to a quadratic regression equation using:

\[ F = Ad\textsubscript{L}^2 + Bd\textsubscript{L} \]  

where A and B are constants. AT stiffness was defined as the slope of the fitted F-d\textsubscript{L} equation from 50–100% of maximum isometric plantarflexion force.

AT force during running was estimated from the assumed vertical ground reaction forces (F\textsubscript{z}) during running, estimated as a function of running speed and body mass (27), assuming the F\textsubscript{z} moment arm at peak F\textsubscript{z} was 1.5× greater than the AT moment arm (19). The F\textsubscript{z} represents the major component (>90%) of the resultant ground reaction forces during steady-state running (29); however, we acknowledge that by not considering the horizontal forces, we have underestimated the required AT force during running. AT energy storage during running was estimated from the area under the measured AT force-d\textsubscript{L} curve (Fig. 1). AT energy release was estimated assuming an AT hysteresis of 10% (12).

Immediately following the measurement of AT force and elongation, E\textsubscript{run} was measured. After a 10-min warm up at 8 km/h for the females and 9.6 km/h for the males, the subjects ran at 75, 85, and 90% of the resultant ground reaction forces (F\textsubscript{z}) during running, estimated as a function of running speed and body mass (27), assuming the F\textsubscript{z} moment arm at peak F\textsubscript{z} was 1.5× greater than the AT moment arm (19). The F\textsubscript{z} represents the major component (>90%) of the resultant ground reaction forces during steady-state running (29); however, we acknowledge that by not considering the horizontal forces, we have underestimated the required AT force during running. AT energy storage during running was estimated from the area under the measured AT force-d\textsubscript{L} curve (Fig. 1). AT energy release was estimated assuming an AT hysteresis of 10% (12).

Table 1. Subject characteristics

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Age, yr</th>
<th>Height, m</th>
<th>Mass, kg</th>
<th>V\textsubscript{O\text{2}\text{max}}, ml·kg\textsuperscript{-1}·min\textsuperscript{-1}</th>
<th>sLT, m/min</th>
</tr>
</thead>
<tbody>
<tr>
<td>TF</td>
<td>16</td>
<td>31.4 ± 8.9</td>
<td>1.66 ± 0.08‡</td>
<td>58.1 ± 7.0*</td>
<td>50.3 ± 6.3</td>
<td>206 ± 22*</td>
</tr>
<tr>
<td>TM</td>
<td>12</td>
<td>35.8 ± 8.5</td>
<td>1.76 ± 0.06</td>
<td>76.0 ± 9.0</td>
<td>54.8 ± 8.5</td>
<td>230 ± 32</td>
</tr>
<tr>
<td>EM</td>
<td>18</td>
<td>24.6 ± 5.1†</td>
<td>1.78 ± 0.07</td>
<td>67.8 ± 7.2</td>
<td>66.3 ± 5.8†</td>
<td>260 ± 31</td>
</tr>
</tbody>
</table>

Values are means ± SD. sLT, speed associated with the lactate threshold. *Significantly different (P < 0.05) between groups. †Significantly different (P < 0.05) elite male (EM) vs. trained female (TF) and trained male (TM). ‡Significantly different (P < 0.05) TF vs. EM and TM.
95% sLT for 5 min each, with a 5-min standing rest period between speeds. The steady-state \( \dot{V}O_2 \), defined as the average \( \dot{V}O_2 \) over the final 2 min of each stage, was used to calculate \( E_{\text{run,avg}} \). \( E_{\text{run,avg}} \) (J/stride) was calculated similar to Fletcher et al. (15):

\[
E_{\text{run}} = \dot{V}O_2 \times (5.1583 \times \text{RER} + 15.972) \times S^{-1} \times SL
\]

where \( \dot{V}O_2 \) is measured in ml/min, speed (S) is measured in m/min, stride length (SL) is measured in m, and RER is the respiratory exchange ratio. SL, defined as the distance between successive contacts of the same foot, was estimated for each subject at each speed based on the previously reported SL-speed relationship for both males and females (9). Consequently, the estimate of AT energy storage and release is double that measured for one tendon because it includes two footstrikes per stride.

**Muscle energy cost.** In order for the AT to store and release strain energy during ground contact, active muscle contraction must occur because the triceps surae muscles are in series with the AT. The energy cost of this muscle contraction was calculated by first estimating the number of active in-parallel cross bridges (per half-sarcomere) required to produce the AT force, and this was multiplied by the number of cross-bridge cycles expected for the estimated shortening during each stance phase and the number of half-sarcomeres in series.

To estimate the number of cross-bridges required in parallel, AT force was divided by the estimated force per cross bridge of 3 pN (11, 37). The number of half-sarcomeres in series was estimated as the ratio of medial gastrocnemius fascicle length during ground contact to half-sarcomere length. The MG fascicle length during ground contact was calculated for each subject based on the fascicle length-force relationship for each subject measured during the MVC, as described previously by Fletcher et al. (14). Sarcomere lengths at rest and during running were calculated based on force-fascicle length values from Maganaris (33) and assuming an optimal sarcomere length during maximal activation of 2.6 \( \mu \)m at the short side of the plateau region of the force-sarcomere length relationship (20). The number of cross-bridge cycles was estimated from the amount of shortening within each half-sarcomere. This was estimated from the magnitude of MG fascicle shortening from rest to stance and accounting for shortening due to anticipated joint rotation. To estimate the number of cross-bridge cycles required to accommodate this magnitude of shortening, we assumed the filaments move 12 nm with each cross-bridge cycle (7). The amount of joint rotation during stance was considered 10° (30). The estimated fascicle shortening due to joint rotation was calculated for each subject as the product of AT moment arm length (mm) and joint rotation (rad), based on the tendon travel method, as described by Fletcher et al. (15). The shortening due to joint rotation was added to the shortening due to force-dependent stretch of the tendon to calculate total shortening during the stance phase of running. We further assumed an ATP cost to cross-bridge cycle ratio of 1:1 and an energy release of 48 kJ/mol ATP (23).

**Statistics.** Values are presented as means ± SD, unless otherwise indicated. A two-way ANOVA (group × speed) with repeated measures (speed) was used to test for differences in \( E_{\text{run}} \), energy storage/return, sLT, and muscle energy cost. When there was no significant interaction and a significant main effect was found, Tukey’s post hoc test was used to detect significant differences between the three speeds. Pearson product-moment correlation analysis was used to examine the relationship between AT stiffness and strain energy contribution to \( E_{\text{run}} \). All analyses were performed using GraphPad Prism version 6.01 for Windows (GraphPad Software, La Jolla, CA; www.graphpad.com). The a priori level of statistical significance was set at alpha <0.05.

**RESULTS**

As shown in Table 1, sLT was significantly different between groups (\( P < 0.001 \)). Consequently, since we estimated SL from running speed, a significant group × speed interaction existed in SL (\( P < 0.001 \)). Mean SL ranged between 2.34 ± 0.23 m at 75% sLT and 2.86 ± 0.30 m at 95% sLT in elite males (EM). SL in trained males (TM) and trained females (TF) across speeds was 2.11 ± 0.10 m to 2.57 ± 0.31 m and 1.93 ± 0.16 to 2.34 ± 0.21 m, respectively. \( E_{\text{run}} \) for all groups at all measured speeds is shown in Fig. 2. There was no significant group × speed interaction; however, there was a significant main effect of speed on \( E_{\text{run}} \) (\( P < 0.001 \); \( E_{\text{run}} \) increased with relative speed.

Maximum isometric force was 5,180 ± 1,998 N in EM, 3,528 ± 1,196 N in TM, and 2,151 ± 759 N in TF, respectively. One-way ANOVA revealed a significant effect of group for maximum isometric force (\( P < 0.001 \)). Furthermore, AT stiffness was significantly different between groups (\( P < 0.001 \)); AT stiffness was 408 ± 128 N/mm in EM, 188 ± 62 N/mm in TM, and 135 ± 57 N/mm in TF.

**Fig. 2. Energy cost of running (\( E_{\text{run}} \)) at the 3 measured relatives speeds for all groups. No group × speed interaction existed; however, there was a significant main effect of speed on \( E_{\text{run}} \) (\( P < 0.001 \)). TM, trained male; TF, trained female; sLT, speed at lactate threshold.
responded to an average resting sarcomere length of 3.35 mm in TM, and 57.2% shorter in EM. Estimated sarcomere lengths at rest were significantly lower in EM (25%). In none of the subjects in EM was estimated AT force greater than maximum isometric force. Estimated sarcomere lengths during running were not different between groups at any of the measured speeds (P = 0.48) but decreased as a function of relative speed (P < 0.001); a result of higher estimated AT forces, and thus fascicle shortening as a function of relative running speed. Average running sarcomere lengths across groups was 2.74 ± 0.53 μm, 2.62 ± 0.52 μm, and 2.50 ± 0.52 μm at 75, 85, and 95% sLT, respectively.

Combining the results for Erun and SL, the estimated energy cost per stride revealed a significant group × speed interaction (P < 0.001). These results are shown in Fig. 4 and suggest that across all speeds the energy cost per stride was lowest in TF and highest in EM.

Given the estimated AT forces during running, we estimated the AT energy release (J/stride) from the area under the F-dL curve. The amount of energy released is shown in Fig. 5. AT energy release increased as a function of relative running speed (P < 0.001) and was significantly higher in TM compared with either EM or TF (P < 0.02). AT energy release was not related to sLT (Fig. 6).

A portion of the energy cost per stride consists of the energy cost of triceps surae muscle contraction, which is necessary to allow energy storage in the AT to occur. Estimating this energy cost from AT forces and sarcomere shortening during the stance phase of running revealed a significant group × speed interaction (<0.001). Values for muscle energy cost are presented in Fig. 5.

**DISCUSSION**

Based on our above-mentioned aims and assumptions, we show here that:

Fascicle length at MVC was 37.4 ± 10.1 mm in EM. This was significantly longer (P < 0.05) than the measured fascicle lengths at MVC of either TM (32.4 ± 10.7 mm) or TF (31.2 ± 7.7 mm), respectively. Estimated fascicle shortening during running increased as a function of speed but was significantly less (P < 0.001) in EM (14.0 ± 2.8 to 15.9 ± 3.3 mm across speeds) compared with either TM (23.3 ± 6.6 to 27.3 ± 8.0 mm) or TF (23.9 ± 6.1 to 28.0 ± 7.5 mm).

Table 2. \( F_z \) (N) as a function of %sLT

<table>
<thead>
<tr>
<th></th>
<th>75%</th>
<th>85%</th>
<th>95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>TF</td>
<td>1,013 ± 121</td>
<td>1,131 ± 136</td>
<td>1,251 ± 151</td>
</tr>
<tr>
<td>TM</td>
<td>1,467 ± 206</td>
<td>1,641 ± 232</td>
<td>1,816 ± 259</td>
</tr>
<tr>
<td>EM</td>
<td>1,468 ± 233</td>
<td>1,646 ± 262</td>
<td>1,823 ± 262</td>
</tr>
</tbody>
</table>

Values are means ± SD. \( F_z \), vertical ground reaction forces. Two-way ANOVA revealed no group × speed interaction. A significant main effect of speed existed (P < 0.001).

Fig. 4. Comparison of the energy cost per stride for all groups and across relative speeds. A significant group × speed interaction existed in the energy cost per stride (P < 0.001).

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1) The amount of strain energy release from the AT was 10–70 J/stride across male and female runners of different performance capabilities.

2) The range of energy cost of muscle contraction in order for this AT energy storage/release to occur across all subjects and running speeds is estimated to be 90 to 525 J/stride.

3) AT energy release was significantly higher in TM compared with either EM or TF; however, the estimated muscle energy cost required for this energy release to occur was lowest in EM.

Energy return alone contributing significantly to reducing the metabolic cost of running.

As an extreme, assuming (unrealistically) that maximum isometric force is generated during each stride and a conservative estimate of AT hysteresis of 10% (12), the average maximum possible amount of energy released from the AT is

As a result, we have very likely overestimated the AT force during running, particularly in TF, where 5 of 16 subjects’ AT force was greater than maximum isometric force. Overestimating AT force would result in both an overestimate of the AT energy release per stride as well as the muscle energy cost for this AT release to occur.

It has previously been shown that the AT releases 1.3 J/step during walking (34) and up to 38 J per jump during continuous, one-legged hopping (32). In the latter case, estimated AT forces during hopping approached 5,000 N, which explains the larger AT energy storage compared with the estimates made here, where AT forces at the highest measured speeds were <2,800 N. In spite of these high forces during hopping, tendon strain energy return represented a small portion of the total mechanical work (<16%), and energy would have been required for muscle contraction to achieve this energy return.

Although many studies have presented estimates of energy storage and release from the AT, none have considered the need for simultaneous muscle contraction to allow the tendon stretch and energy release to occur. Here, we provide an estimate for that muscle energy cost. This muscle energy cost represents a portion of the total metabolic cost of running and is necessary for tendon strain energy storage and release to occur. The energy cost of this muscle contraction is directly proportional to muscle shortening, so a compliant tendon increases this energy cost.

Estimates of muscle energy cost to allow for tendon strain energy storage. In accounting for the energy cost of muscle contraction to allow for AT energy storage/release, these results demonstrate that the return of elastic strain energy is less than the muscle energy cost required for storage/release to occur. This brings into question the relevance of tendon strain energy return alone contributing significantly to reducing the metabolic cost of running.

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Fig. 5. AT energy release relative to estimated muscle energy cost required to allow AT energy storage to occur (EMc, TMc, and TFc, respectively) for all groups and all measured running speeds. AT energy release and muscle energy cost increased across speeds in all groups (P < 0.001).

![Graph showing AT energy release vs. estimated muscle energy cost](image)

Fig. 6. Relationship between AT energy release and 95% speed at lactate threshold (sLT). Filled, grey, and open squares represent EM, TM, and TF subjects, respectively. When assessed across all groups the relationship was not significant (dashed line, $r^2 = 0.01$). The relationship was similar when assessed across the other 2 measured speeds (75 and 85% sLT).
34 J/stride in TF to 71 J/stride in EM; clearly a small portion of the total metabolic cost (500–900 J/stride). Any shortening during $F_z$ would contribute to elevate muscle energy cost above our estimate, as a result of the muscle’s force-length-velocity relationships and subsequent increases in the required level of muscle activation (14) and due to shortening-induced increase in cross-bridge turnover (7). Presumably, this shortening-induced energy cost would be higher in the lesser-trained subjects (38), given their relatively compliant tendons, and greater relative force required to generate $F_z$. Here we have calculated this shortening-induced energy cost to be on average more than eightfold higher than the energy released from the stretched AT. Therefore, a considerable muscle energy cost can be saved if muscle-tendon unit shortening can be accommodated by the AT alone and MG fascicle shortening is minimized as would be the case with a stiff AT.

It seems unlikely that sarcomere length is longer than what we have estimated, particularly for those who activate near maximum. If the true sarcomere length is shorter, then more sarcomeres will be needed in series and this will increase the estimate of the energy required. To further highlight our conservative estimate of the shortening-induced muscle energy cost, our estimated force per cross bridge (3 pN) is the force associated with the isometric cross-bridge force. The force per cross bridge would be considerably lower during shortening [Barclay et al. (7)]. For example, if the force per cross bridge was actually 2 pN, 30% more cross bridges would need to be engaged and the energy cost would be 30% higher. A similarly conservative estimate of the muscle energy cost is the estimated cross-bridge step size (12 nm), which is the stepsize at which efficiency is maximal. Stepsize decreases at slow shortening velocities (7); thus any error associated with the reduction in stepsize from 12 nm would result in a proportional increase in the estimated muscle energy cost.

We also recognize some variability in our estimated AT forces during running as a result of estimating these forces from the $F_z$-speed relationship (27). The variability associated with estimating $F_z$ from running speed is in the order of 10–20%. Using mean values for our subjects, overestimating $F_z$ by 10% would result in both an overestimated muscle energy cost and AT strain energy release of 15%. A similar underestimate in $F_z$ would result in a 17% lower muscle energy cost and tendon strain energy release. Thus any error associated with the reduction in stepsize from 12 nm would result in a proportional increase in the estimated muscle energy cost.

Therefore, we acknowledge a very conservative estimate of the muscle energy cost to allow tendon strain energy storage to occur.

It is well established that much of the required length change of the muscle-tendon unit during running can be taken up by stretch of a relatively compliant in-series tendon, thus allowing the active muscle fascicles to shorten to a lesser extent and at a slower velocity (18, 24). This minimizes the required level of muscle activation to achieve the target force as a result of the muscle’s force-velocity relationship. In so doing, the muscle energy cost is reduced considerably (14). Relative to the total metabolic cost per stride, the amount of tendon strain energy that is stored and released per stride is small. Our estimates shown here demonstrate that this energy release is on average <42 J/stride. Therefore, we argue that the energy savings in reducing the muscle energy cost more than makes up for decreased energy storage and release when the tendon’s mechanical properties are optimal.

If mechanical properties are optimal, the role of a tendon connected in-series with the muscle is to minimize muscle fascicle shortening by taking up much of the length change required by the whole muscle-tendon unit (36). This effect serves to minimize muscle metabolic cost to a much greater extent than the storage and release of tendon strain energy; by keeping fiber shortening to a minimum, the muscle’s force-length-velocity properties and muscle activation can be optimized (14). The range of sarcomere lengths used during locomotion corresponds to the plateau region of the relevant force-length curves (24). This maximizes the amount of force for a given level of activation, or conversely as would be the case in steady-state submaximal running, minimizing the required level of activation for a given force. The fact that we saw no difference in estimated sarcomere lengths between groups suggests similar sarcomere lengths are achieved to run at a common relative speed.

**Conclusion.** From our estimates of tendon strain energy storage and release and muscle energy cost for this storage/release to occur, we conclude that the amount of tendon strain energy released represents a very small portion of the total metabolic cost to run a given speed. Furthermore, this energy return comes at a considerable muscle energy cost. Therefore, reducing muscle energy cost through reductions in muscle fascicle shortening during running, even if this means less energy return from the tendon, contributes to an improved economy of running.

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**DISCLOSURES**

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**AUTHOR CONTRIBUTIONS**


**REFERENCES**


