

Running biomechanics: shorter heels, better economy

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SUMMARY

Better running economy (i.e. a lower rate of energy consumption at a given speed) is correlated with superior distance running performance. There is substantial variation in running economy, even among elite runners. This variation might be due to variation in the storage and reutilization of elastic energy in tendons. Using a simple musculoskeletal model, it was predicted that the amount of energy stored in a tendon during a given movement depends more critically on moment arm than on mechanical properties of the tendon, with the amount of stored energy increasing as the moment arm gets smaller. Assuming a link between elastic energy reutilization and overall metabolic cost of running, a smaller moment arm should therefore be associated with superior running economy. This prediction was confirmed experimentally in a group of 15 highly trained runners. The moment arm of the Achilles tendon was determined from standardized photographs of the ankle, using the position of anatomical landmarks. Running economy was measured as the rate of metabolic energy consumption during level treadmill running at a speed of 16 km h⁻¹. A strong correlation was found between the moment arm of the Achilles tendon and running economy. Smaller muscle moment arms correlated with lower rates of metabolic energy consumption ($r^2=0.75$, $P<0.001$).

Key words: moment arm, tendon, elastic, energy, strain, stretch, long distance, runner, oxygen uptake.

INTRODUCTION

Running economy is defined as the amount of metabolic energy needed to displace a unit of body mass over a certain distance or, equivalently, the metabolic power per unit of body mass required to run at a certain speed. At any given speed, better running economy refers to a smaller rate of energy consumption. There are substantial inter-individual differences in running economy. Typically, variations in the order of 20–30% are reported, even among international-caliber long-distance runners (di Prampero et al., 1986; Heise and Martin, 2001; Saunders et al., 2004; Williams and Cavanagh, 1987). Previous studies on running economy have revealed that running economy is an important determinant of running performance (Anderson, 1996; di Prampero et al., 1986; Joyner, 1991; Saunders et al., 2004). Training has little or no effect on running economy; the best results were achieved after high-intensity interval training and resistance training and were in the order of 5–7% improvement (Bailey and Pate, 1991; Billat et al., 2002; Franch et al., 1998; Lake and Cavanagh, 1996; Midgley et al., 2007). This suggests that running economy is determined by intrinsic morphological and physiological properties.

Several hypotheses have been put forward to explain the variation in running economy among participants. First, it has been hypothesized that some runners are more economical because they require less energy to swing their legs (Holden, 2004; Larsen, 2003). However, it is very unlikely that variations in leg-swing cost can account for 20–30% variation in running economy because the total metabolic cost of swinging the legs is only about 20% of the metabolic cost of running (Marsh et al., 2004; Modica and Kram, 2005). Second, it has been proposed that the rate and magnitude of muscular force generation explain the rate of metabolic energy consumption during running; this hypothesis is known as the ‘cost

of generating force’ hypothesis (Kram and Taylor, 1990). Although it accounts for much of the variation in the metabolic cost of running between different animal species, it is not able to explain inter-individual differences in running economy for reasons explained elsewhere (Heise and Martin, 2001). Third, it is generally accepted that storage and reutilization of elastic energy in tendons substantially reduces energy demands in running (Cavagna et al., 1964). However, it is not known if and how economical runners could store and recover more tendon elastic energy compared with uneconomical runners. Hence, at this point, there is no conclusive mechanical explanation for the inter-individual differences in running economy (di Prampero et al., 1986; Kyrolainen et al., 2001; Saunders et al., 2004; Williams and Cavanagh, 1987).

The amount of energy stored in a tendon depends on the mechanical properties of the tendon (compliance and rest length) and on the force that stretches the tendon. For a given kinematic pattern, and hence kinetic pattern, tendon force is inversely related to the moment arm of the tendon. The importance of moment arm scaling and locomotion energetics/elastic storage and return has been pointed out by others (Biewener, 2005; Carrier et al., 1994). However, moment arm length has not been investigated in the context of inter-individual variations in running economy.

The purpose of the current study was to test if and how tendon mechanical properties and musculoskeletal geometry can account for inter-individual differences in running economy. Since tendon mechanics cannot be changed experimentally without disrupting the integrity of the participant and/or the movement, we first adopted a musculoskeletal modeling approach and addressed the following question: what is the most effective way to enhance storage and release of tendon energy during a given stretch–shortening cycle? A simple musculoskeletal model undergoing stretch–shortening

cycles was developed to explore how the storage of energy in the tendon depends on the mechanical properties of the tendon and the length of the muscle moment arm. It will be shown in this paper that for a given joint moment history the moment arm of the muscle–tendon complex is the most important determinant for energy storage in the tendon. Subsequently, we tested experimentally whether a relationship exists between the moment arm of the Achilles tendon and running economy.

MATERIALS AND METHODS

Model

We developed a simple model to examine if energy storage in a tendon is more sensitive to changes in muscle moment arm or changes in mechanical properties of the tendon. To study tendon energetics during stretch–shortening cycles, we used a single-joint-model with the following characteristics: (1) the movement is restricted to cyclical flexion and extension of one joint (e.g. ankle bouncing); (2) the joint is actuated by one muscle–tendon unit (MTU), comprised of a contractile element (CE) in series with an elastic element (SE) and there is no redundancy of agonists and no co-contraction of antagonists; (3) kinematics and joint moments are given; and (4) net joint work over one full cycle is zero.

Under these assumptions, it is evident that joint moment equals MTU moment, and joint work equals MTU work. Changes in MTU length are a function of both joint angular displacement and moment arm of the MTU at the joint. During the stretch phase, work is done on the MTU (by gravity) and the MTU, as a whole, is lengthening; in this phase, energy can be stored in the tendon. During the subsequent shortening phase, the MTU does work while shortening; in this phase stored energy can be released from the tendon.

The mechanical behavior of a tendon has been described as a quadratic spring (Rosager et al., 2002; van Ingen Schenau, 1984) or a linear spring with a quadratic toe region (Hof, 1998). To accommodate quadratic and/or linear spring characteristics, we adopted a generalized model for a spring of n th order:

$$F = ku^n, \quad (1)$$

where F is the magnitude of the tendon force, u is the elongation of the tendon (the difference between actual tendon length and tendon slack length) and k is the spring constant. The latter is determined by the mechanical properties of the spring.

If either F or u is known for a given tendon, tendon energy (E) can be calculated as follows:

$$E = \left(\frac{1}{n+1} \right) ku^{(n+1)}. \quad (2)$$

or

$$E = \left(\frac{1}{n+1} \right) F \left(\frac{F}{k} \right)^{\left(\frac{1}{n} \right)}. \quad (3a)$$

and

$$E = \left(\frac{1}{n+1} \right) F \left(\frac{n+1}{n} \right) k^{-\left(\frac{1}{n} \right)}. \quad (3b)$$

In the current simplified situation, F can be calculated from joint moment as:

$$F = \frac{M_j}{r}, \quad (4)$$

where M_j is joint moment, and r is the moment arm of the MTU with respect to the joint axis of rotation.

Inserting Eqn4 into Eqn3b yields:

$$E = \left(\frac{1}{n+1} \right) M_j^{\left(\frac{n+1}{n} \right)} r^{-\left(\frac{n+1}{n} \right)} k^{-\left(\frac{1}{n} \right)}. \quad (5)$$

In biomechanics, k is commonly parametrized in terms of the amount of stretch at maximal CE force (i.e. van Soest and Bobbert, 1993):

$$k = \frac{F_{\max}}{(l_{se0}u_{\max})^n}, \quad (6)$$

where F_{\max} is the magnitude of the maximal isometric muscle force, l_{se0} is the rest length of the series elastic element and u_{\max} is the elongation of the tendon at F_{\max} as a fraction of l_{se0} .

Inserting Eqn6 into Eqn5 yields the final equation:

$$E = \left(\frac{1}{n+1} \right) M_j^{\left(\frac{n+1}{n} \right)} r^{-\left(\frac{n+1}{n} \right)} F_{\max}^{-\left(\frac{1}{n} \right)} l_{se0}u_{\max}. \quad (7)$$

For a given M_j , Eqn7 indicates the following: (1) the smaller the moment arm, the more energy is stored elastically; and (2) for any n , the energy stored in a tendon is more sensitive to moment arm than to mechanical properties of the tendon (l_{se0} and u_{\max}), as can be seen by the magnitude of the exponents. The lower the order of spring (n), the more pronounced this difference in sensitivity.

In summary, in a given musculoskeletal system, the amount of tendon energy storage during a given movement increases as l_{se0} and u_{\max} increase and as F_{\max} and r decrease. Reducing r , which results in a higher tendon force F (Eqn4), is the most effective way to increase energy storage in the tendon.

Since joint work is assumed constant in the model, increased reutilization of tendon energy reduces the amount of mechanical work that the CE has to produce as well as the metabolic energy required to generate CE work. This is expected to reduce overall metabolic energy cost of the movement because, in terms of metabolic cost, generating CE work (concentric contraction) is the most expensive mode of muscle functioning (i.e. Ryschon et al., 1997).

In humans, the most prominent tendon in the leg is the Achilles tendon. Based on Eqn7, it was predicted that runners with smaller moment arms of the Achilles tendon can run more economically. To test this prediction, the relationship between running economy and the moment arm of the Achilles tendon was determined in an experiment conducted with a group of experienced runners.

Experiment

Participants

Fifteen highly trained, healthy, male runners gave written informed consent to participate in this study. All participants had been training for, and participating in, regional, national and/or international running competitions for several years. Thirteen participants reported their personal record (PR) for 10 km, which was 33 min 52 s \pm 3 min 22 s (mean \pm s.d.). Two participants reported a PR of less than 30 min. Participant characteristics are listed in Table 1.

This study was performed in accordance with the guidelines of the Declaration of Helsinki and was approved by the ethics committee of the Faculty of Human Movement Sciences, VU University Amsterdam, The Netherlands.

Running economy and $\dot{V}_{O_{2,\max}}$

For each participant, running economy was determined as the rate of oxygen consumption (\dot{V}_{O_2}) per kg body mass when running at

Table 1. Participant characteristics

Participant	Age (years)	Height (cm)	Mass (kg)	$\dot{V}_{O_{2,max}}$ (ml kg ⁻¹ min ⁻¹)
1	23	184	76	61.1
2	28	184	71	53.47
3	21	171	60	66.56
4	19	165	50	48.73
5	28	185	69	69.3
6	21	178	67	62.04
7	20	169	51	NA
8	26	164	52	60.73
9	34	173	62	67.85
10	36	171	60	51.83
11	24	167	63	53.92
12	19	187	82	60.33
13	44	175	66	45.05
14	22	173	58	58.22
15	20	181	70	63.76
Mean \pm s.d.	26 \pm 7.3	175 \pm 7.6	64 \pm 9.2	54.86 \pm 16.73

NA; not available (participant terminated test prematurely because of physical discomfort when running uphill).

16 km h⁻¹. After several minutes of habituation to the treadmill (STM-55; Schiller, Baar, Switzerland) and warming-up, participants ran at 16 km h⁻¹ on the level for 5 min. For these participants, this was a submaximal task (see 10 km race times, Table 1). Steady-state oxygen consumption was recorded during the last minute of running using a gas analyzer (Cardiovit CS-200 Ergo-Spiro; Schiller, Baar, Switzerland). After determining anthropometrics (see below), the same setup was used to measure maximum rate of oxygen consumption ($\dot{V}_{O_{2,max}}$) using an incremental protocol with increasing running speed and treadmill slope.

Moment arm of the Achilles tendon

By definition, the moment arm of the Achilles tendon is the shortest distance from the line of action of the Achilles tendon to the center of rotation of the ankle. The center of rotation of the ankle has been shown to be located close to the midpoint of the line between the tips of the medial and lateral malleoli (Lundberg et al., 1989). To estimate the moment arm of the Achilles tendon in our participants, we marked the malleoli and took standardized photographs of the medial and lateral side of the foot: each participant was seated on a chair with their left foot placed on a reference block (see Fig. 1). The lateral edge of the foot was aligned with the reference block; this way, the lateral malleolus was in the same sagittal plane as the edge of the reference block, which served as a scale object. The leg was positioned so that the anterior border of the tibia was vertical. We established the vertical position

using a spirit level. The most prominent aspect of the tip of the lateral malleolus was marked with a small dot of paint. Foot and leg were photographed from the lateral side (SONY Cybershot W7; Minato, Tokyo, Japan). This procedure was repeated for the medial side of the same leg; the medial edge of the foot was aligned with the reference block, the anterior border of the tibia was positioned vertically, the most prominent aspect of the tip of the medial malleolus was marked and a photograph was taken. The horizontal distance from the marked spot to the posterior aspect of the Achilles tendon was determined on the picture, both on the lateral and on the medial side (Didge Image Digitizing Software for Windows, courtesy of A. J. Cullum, Omaha, NE, USA). The moment arm was taken to be the mean of these two distances.

We also measured body mass and height, calculated body mass index (BMI) and determined the following anthropometric variables on the left foot and leg of each participant: foot length (measured from the back of the heel to the tip of the longest toe); lower leg length (measured from the tip of the lateral malleolus to caput fibulae); lower leg circumference (determined using a tape measure) at various positions along the leg, including maximal lower leg circumference; and total leg length (measured from the ground to spina iliaca anterior superior).

A truncated cone model of the lower leg was constructed based on the length of the lower leg and the circumferences of the lower leg at four points along its length (Crompton et al., 1996). Assuming a density of 1.1×10^3 kg m⁻³, we derived lower-leg volume and

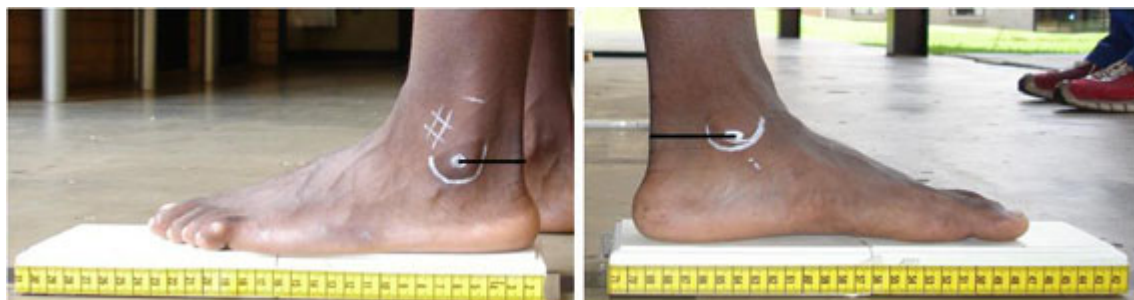


Fig. 1. Standardized picture of the lateral (A) and medial (B) side of the left foot, placed on, and aligned with, a reference block. The horizontal distance from the lateral and medial malleolus to the Achilles tendon was determined (black lines). Moment arm was calculated as the mean of these two distances.

Table 2. Running economy and anthropometrics

Participant	\dot{V}_{O_2} (ml kg ⁻¹ min ⁻¹) at 16 km h ⁻¹	Moment arm (cm)	Foot length (cm)	Lower-leg length (cm)	Lower-leg volume (l)	Lower-leg moment of inertia (kg m ⁻²)
1	51.3	5.3	25.5	38	2.7	0.0287
2	48.9	5.1	25.8	38	3.17	0.0327
3	51.1	4.7	26.5	38	2.48	0.0248
4	34.5	4.2	23.7	35	1.71	0.0168
5	42.0	4.9	26.5	38.5	2.51	0.0267
6	47.3	4.8	26	36	2.55	0.0232
7	45.4	4.4	24.3	39.5	2.11	0.0255
8	43.0	4.2	23	37	2.01	0.0206
9	55.9	5.3	27.5	42	2.32	0.0326
10	51.4	5.1	24.3	38	2.31	0.024
11	50.5	4.9	25	36	2.49	0.0245
12	48.7	5.2	27.6	39	3.12	0.0334
13	47.7	4.7	23.7	37.5	2.26	0.0231
14	51.8	5.0	27	37	2.1	0.0211
15	57.5	5.0	26.8	37	3.07	0.0322
Mean \pm s.d.	48.45 \pm 5.69	4.85 \pm 0.36	25.55 \pm 1.48	37.77 \pm 1.67	2.46 \pm 0.42	0.0260 \pm 0.00501

lower-leg moment of inertia for rotation about the center of mass in the sagittal plane from this reconstruction.

Statistics

To analyze the relationship between running economy and the anthropometric characteristics of the foot and lower leg, we calculated the Pearson correlation coefficients between \dot{V}_{O_2} at 16 km h⁻¹ and all anthropometric variables. Partial correlation (Draper and Smith, 1981) was used to test and correct for possibly confounding anthropometric variables that covaried with moment arm.

The relationship between moment arm and \dot{V}_{O_2} at 16 km h⁻¹ was fitted with a non-linear model of the form $y=ax^{-2}+b$, which was derived from the theoretical relationship between tendon energy and moment arm, assuming $n=1$ (Eqn 7).

Inter- and intra-observer reliability for the determination of Achilles tendon moment arm from pictures of the ankle was assessed by comparing two measurements made by the same person several months apart as well as two measurements made by different people, using Pearson correlation.

RESULTS

Running economy, Achilles tendon moment arm and other anthropometrics are listed in Table 2 for each subject. The intra- and inter-observer reliability for the moment arm measurement was high ($r^2>0.95$, $P<0.001$). A strong correlation ($P<0.001$) was found between running economy and moment arm, with moment arm explaining 56% of the variance in running economy. The relationship between running economy and the moment arm of the Achilles tendon is shown in Fig. 2. The non-linear model fitted the data slightly better than the linear one (Pearson correlation) and accounted for 58% of the variance in running economy. r^2 values and slopes for the correlations between running economy and all other anthropometric variables are listed in Table 3. Besides the high correlation with moment arm, there were also significant correlations ($P<0.05$) between running economy and BMI, foot length, lower-leg volume and lower-leg moment of inertia. However, partial correlation revealed that these correlations were no longer significant when corrected for covariance with moment arm (Table 4). The correlation between running economy and moment arm remained significant even when corrected for covariance with other variables (Table 5).

DISCUSSION

In the current study, we modeled a tendon, integrated in a musculoskeletal system undergoing stretch–shortening cycles, and studied its effect on energetics. It was concluded that for a given movement, the energy that is stored in a tendon is most sensitive to the moment arm of the tendon. The smaller the moment arm, the more energy is stored in the tendon at given kinematics and kinetics. Mechanical properties of the tendon also affect energy storage in the tendon, but to a lesser degree, as can be seen in the exponents in Eqn 7.

Qualitatively, this conclusion does not depend on the order of the spring, which has been reported to be purely quadratic or a combination of linear and quadratic. However, the effect is quantitatively stronger in a linear spring ($n=1$) than in a quadratic spring ($n=2$).

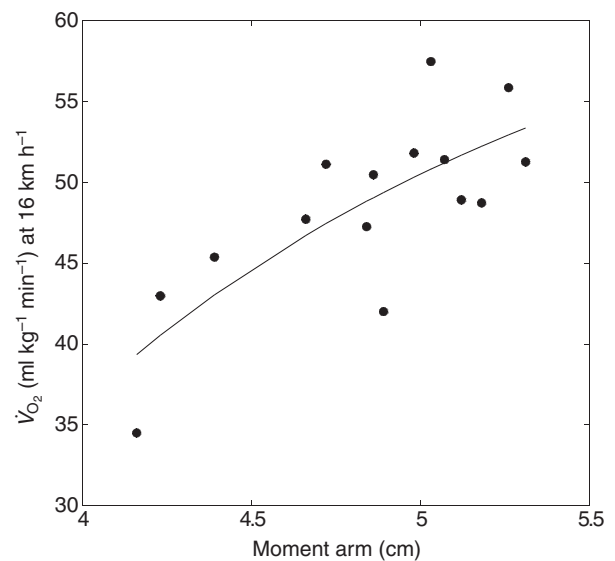


Fig. 2. Relationship between moment arm and oxygen consumption rate (\dot{V}_{O_2}) in ml kg⁻¹ min⁻¹ at 16 km h⁻¹. Dots are individual participants, the line is the best fit for the theoretical model $y=ax^{-2}+b$, where x is moment arm in cm and y is \dot{V}_{O_2} in ml kg⁻¹ min⁻¹ at 16 km h⁻¹ ($a=-628.1$, $b=75.65$, $r=0.77$). This model was derived from Eqn 7, assuming a linear spring ($n=1$). A very similar fit with $r=0.76$ can be obtained for the model $y=cx^{-1.5}+d$, which is based on the assumption that $n=2$.

Table 3. Correlations between anthropometric variables and \dot{V}_{O_2} at 16 km h⁻¹ (N=15)

Anthropometric variable	r^2	Slope	P-value
Mass	0.17	0.25	0.12
Height	0.09	0.22	0.29
Body mass index (BMI)	0.26	1.77	0.05*
Foot length	0.33	2.20	0.03*
Lower-leg length	0.18	1.43	0.12
Total leg length	0.14	0.47	0.17
Lower-leg volume	0.28	7.19	0.04*
Lower-leg moment of inertia	0.39	709	0.01*
Moment arm	0.56	11.91	0.00*
Lower-leg circumference	0.24	0.85	0.07

r^2 , explained variance (* $P \leq 0.05$). N, number of subjects.

Table 4. Partial correlations between selected anthropometric variables and \dot{V}_{O_2} at 16 km h⁻¹, corrected for covariation with moment arm (in parentheses) (N=15)

Anthropometric variable	r^2	P-value
BMI (moment arm)	0.00	0.85
Foot length (moment arm)	0.00	0.82
Lower-leg volume (moment arm)	0.00	0.98
Lower-leg moment of inertia (moment arm)	0.02	0.64

BMI, body mass index. r^2 , explained variance. N, number of subjects.

Table 5. Partial correlations between moment arm and \dot{V}_{O_2} at 16 km h⁻¹, corrected for covariance with selected anthropometric variables (in parentheses) (N=15)

Anthropometric variable	r^2	P-value
Moment arm (BMI)	0.41	0.01*
Moment arm (foot length)	0.35	0.03*
Moment arm (lower-leg volume)	0.38	0.02*
Moment arm (lower-leg moment of inertia)	0.29	0.05*

BMI, body mass index. r^2 , explained variance (* $P \leq 0.05$). N, number of subjects.

An experiment was conducted to test whether there was indeed a relationship between Achilles tendon moment arm and running economy. Despite the fact that a low-tech method was used to estimate the moment arm of the Achilles tendon *in vivo*, the values we found for the moment arm of the Achilles tendon are of similar magnitude to those found by Rugg et al. using magnetic resonance imaging (MRI) data (Rugg et al., 1990).

A strong relationship was found between running economy and the moment arm of the Achilles tendon. This relationship was expected: a small moment arm is associated with high tendon energy storage. Any energy stored in the tendon does not have to be generated by the CE. Reducing CE energy generation is expected to lead to lower metabolic cost, because energy generation by CE is metabolically the most expensive process in muscle contraction. The total metabolic energy consumption of a muscle, however, also depends on the amount of force that is generated (Minetti and Alexander, 1997), and muscle force is higher if the moment arm is smaller. Nevertheless, we found that participants with small moment arms required less energy per kg body mass to run at the speed of 16 m s⁻¹. This indicates that inter-individual variations in running economy were dominated by variations in the metabolic cost associated with generating CE work not force.

Variations in moment arm explained 56% of the variation in running economy. As in previous studies, a relationship was found

between running economy and foot length (Anderson, 1996) and between running economy and BMI or lower-leg volume/moment of inertia (Anderson, 1996; Larsen et al., 2004). However, we showed that these relationships were no longer significant after correcting each variable (i.e. foot length, BMI, lower-leg volume, lower-leg moment of inertia) for covariation with moment arm. This means that runners with smaller moment arms tend to have lighter and more slender limbs (Table 4) but a light and slender build does not relate to better running economy if moment arm is held constant (Table 5). Hence, the reason for better running economy is mainly attributed to greater energy storage in the tendon and not smaller leg-swing cost.

Unlike the model, which has a constant size and was shown to store more elastic energy with a relatively short moment arm (relative to all other linear dimensions), the participants in this study were not all of the same size. This must have caused variations in peak ankle moment, which together with muscle-tendon properties determines maximal tendon energy storage. Hence, elastic energy storage did not depend on moment arm length of the Achilles tendon alone. We expect that most of the variation in peak ankle moment can be attributed to the large differences in body mass between participants. To correct for differences in body mass and to bring out the empirical relationship between running economy and moment arm of the Achilles tendon even better, we can normalize moment arm by some linear dimension that correlates well with body mass. Height is an obvious choice: the correlation between height and body mass is very strong ($r=0.91$, $P<0.001$). Indeed, the relationship between running economy and moment arm, normalized by height, is stronger than the relationship between running economy and absolute moment arm ($r=0.81$, $P<0.001$ vs $r=0.75$, $P<0.001$).

Although we lack sufficient information to quantify tendon energy storage in individual runners, we would like to get an idea regarding the magnitude of the effect that a difference in moment arm has on metabolic energy consumption using existing literature. To do so, we assumed that all the extra energy stored in the tendon is useful and saves CE work and that the extra cost of activating the triceps surae to generate tension can be ignored. Ker et al. calculated that 35 J is stored in the Achilles tendon of a 70 kg man when loaded with 4700 N, describing the tendon as a linear spring (Ker et al., 1987). The stiffness (k) of this tendon can be obtained from Eqn 3a,b. If the moment arm was 10% smaller, force on the tendon would increase from 4700 N to 5170 N and, hence, energy storage would increase from 35 J to 42.4 J (Eqn 3), an increase of 7.4 J or 21%. Storing an additional 7.4 J in the Achilles tendon during every landing while running at 16 km h⁻¹, with 3 landings s⁻¹ (Scardina et al., 1985), reduces CE mechanical power requirement by approximately 22 W. Assuming a CE mechanical efficiency of 25% (Cavagna and Kaneko, 1977), metabolic power would be reduced by about 88 W. Given a body mass of 70 kg and an energetic equivalent of 21 kJ l⁻¹ O₂, this yields a difference of 4.2 ml kg⁻¹ min⁻¹ in \dot{V}_{O_2} . Hence, this approximation shows that a 10% difference in moment arm of the Achilles tendon alone can account for a 4.2 ml kg⁻¹ min⁻¹ difference in \dot{V}_{O_2} . This is more than 8% for a person with a \dot{V}_{O_2} of 50 ml kg⁻¹ min⁻¹ at 16 km h⁻¹. For a 10% difference in moment arm, the predicted difference in \dot{V}_{O_2} compares reasonably well to the differences observed in this study. Note that the moment arm length in the group of runners who participated in the current study varied by more than 10%, as did \dot{V}_{O_2} (Table 2).

We expect that some of the residual variation in running economy can be accounted for by inter-individual variations in peak joint moment, which was not measured in the current study.

Runners with similar Achilles tendon moment arms might generate different peak ankle joint moments, as reflected by the magnitude of ground reaction forces and the point of application of the ground reaction force with respect to the ankle. Different peak ankle joint moments yield different amounts of tendon energy storage and, hence, differences in running economy. For future studies on running economy, we propose to measure not only the moment arm of the Achilles tendon but also the peak ankle moment so that the maximal amount of energy stored in the tendon can be calculated and related directly to running economy. Unfortunately, the necessary equipment to measure ankle moment during running was not available in the current study.

Peak ankle moment and running economy were measured in a recent study on midsole stiffness (Roy and Stefanyshyn, 2006). In this study it was shown that running with a shoe with a stiffer midsole was associated with increased peak ankle moment and improved running economy. An underlying mechanism for this improvement in running economy was not proposed by the authors. Based on the results of the current study, we hypothesize that the stiff midsole, which was associated with a significantly higher peak ankle moment, resulted in an improvement in running economy because of increased energy storage in the Achilles tendon. Note that Roy and Stefanyshyn used two types of alternative midsoles: 'stiff' and 'stiffest' (Roy and Stefanyshyn, 2006). Only the stiff midsole resulted in an improvement of running economy compared with using a normal midsole, the stiffest midsole did not. It is beyond the scope of this study to speculate on possible causes for this.

Aside from the positive effect on running economy, a small moment arm of the Achilles tendon may have less desirable consequences. It has been shown that a high peak joint moment in combination with a small moment arm of the tendon [a low effective mechanical advantage (EMA)], compromises the safety factor of the tendon (Biewener, 2005). The high tendon forces that occur due to a small moment arm may increase the risk of tendon overuse or rupture or trigger adaptations of the tendon that will enable it endure higher peak loads but may cause it to be stiffer and, therefore, to store less energy for the same submaximal force. This leads to two questions: (1) do runners with small moment arms have different tendon properties from runners with large moment arms and (2) do interactions between moment arm and tendon properties affect the proposed theoretical relationship between moment arm and running economy?

The comparative literature suggests that there is little variation in the tissue properties of tendons in different species so it is unclear what kind of interactions, if any exist between joint moment, moment arm length and the properties of the tendon (Bennett et al., 1986; Pollock and Shadwick, 1994). However, even if there is an inverse linear relationship between k and r , which implies that the tendon is stiffer in subjects with smaller moment arms, it is advantageous to have a small moment arm. This is seen by multiplying k by r^{-1} in Eqn 6 and inserting into Eqn 5, yielding E proportional to r^{-1} .

In summary, this study has established a causal relationship between the variation in running economy and the moment arm of the Achilles tendon. Smaller moment arms are associated with better running economy. This relationship was predicted based on a simple musculoskeletal model of tendon energy storage and was confirmed experimentally.

REFERENCES

- Anderson, T. (1996). Biomechanics and running economy. *Sports Med.* **22**, 76-89.
- Bailey, S. P. and Pate, R. R. (1991). Feasibility of Improving Running Economy. *Sports Med.* **12**, 228-236.
- Bennett, M. B., Ker, R. F., Dimery, N. J. and Alexander, R. M. (1986). Mechanical Properties of Various Mammalian Tendons. *J. Zool.* **209**, 537-548.
- Biewener, A. A. (2005). Biomechanical consequences of scaling. *J. Exp. Biol.* **208**, 1665-1676.
- Billat, V., Demarle, A., Paiva, M. and Koralsztejn, J. P. (2002). Effect of training on the physiological factors of performance in elite marathon runners (males and females). *Int. J. Sports Med.* **23**, 336-341.
- Carrier, D. R., Heglund, N. C. and Earls, K. D. (1994). Variable gearing during locomotion in the human musculoskeletal system. *Science* **265**, 651-653.
- Cavagna, G. A. and Kaneko, M. (1977). Mechanical work and efficiency in level walking and running. *J. Physiol.* **268**, 467-481.
- Cavagna, G. A., Saibene, F. P. and Margaria, R. (1964). Mechanical work in running. *J. Appl. Physiol.* **19**, 249-256.
- Crompton, R. H., Li, Y., Alexander, R. M., Wang, W. and Gunther, M. M. (1996). Segment inertial properties of primates: new techniques for laboratory and field studies of locomotion. *Am. J. Phys. Anthropol.* **99**, 547-570.
- di Prampero, P. E., Atchou, G., Brueckner, J.-C. and Moia, C. (1986). The energetics of endurance running. *Eur. J. Appl. Physiol.* **55**, 259-266.
- Draper, N. R. and Smith, H. (1981). *Applied Regression Analysis*. New York: Wiley.
- Franch, J., Madsen, K., Djurhuus, M. S. and Pedersen, P. K. (1998). Improved running economy following intensified training correlates with reduced ventilatory demands. *Med. Sci. Sports Exerc.* **30**, 1250-1256.
- Heise, G. D. and Martin, P. E. (2001). Are variations in running economy in humans associated with ground reaction force characteristics? *Eur. J. Appl. Physiol.* **84**, 438-442.
- Hof, A. L. (1998). *In vivo* measurement of the series elasticity release curve of human triceps surae muscle. *J. Biomech.* **31**, 793-800.
- Holden, C. (2004). Peering under the hood of Africa's runners. *Science* **305**, 637-639.
- Joyner, M. J. (1991). Modeling-optimal marathon performance on the basis of physiological factors. *J. Appl. Physiol.* **70**, 683-687.
- Ker, R. F., Bennett, M. B., Bibby, S. R., Kester, R. C. and Alexander, R. M. (1987). The spring in the arch of the human foot. *Nature* **325**, 147-149.
- Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.
- Kyrolainen, H., Belli, A. and Komi, P. V. (2001). Biomechanical factors affecting running economy. *Med. Sci. Sports Exerc.* **33**, 1330-1337.
- Lake, M. J. and Cavanagh, P. R. (1996). Six weeks of training does not change running mechanics or improve running economy. *Med. Sci. Sports Exerc.* **28**, 860-869.
- Larsen, H. B. (2003). Kenyan dominance in distance running. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **136**, 161-170.
- Larsen, H. B., Christensen, D. L., Nolan, T. and Sondergaard, H. (2004). Body dimensions, exercise capacity and physical activity level of adolescent Nandi boys in western Kenya. *Ann. Hum. Biol.* **31**, 159-173.
- Lundberg, A., Svensson, O. K., Nemeth, G. and Selvig, G. (1989). The axis of rotation of the ankle joint. *J. Bone Joint Surg. Br.* **71**, 94-99.
- Marsh, R. L., Ellerby, D. J., Carr, J. A., Henry, H. T. and Buchanan, C. I. (2004). Partitioning the energetics of walking and running: swinging the limbs is expensive. *Science* **303**, 80-83.
- Midgley, A. W., McNaughton, L. R. and Jones, A. M. (2007). Training to enhance the physiological determinants of long-distance running performance? Can valid recommendations be given to runners and coaches based on current scientific knowledge? *Sports Med.* **37**, 857-880.
- Minetti, A. E. and Alexander, R. M. (1997). A theory of metabolic costs for bipedal gaits. *J. Theor. Biol.* **186**, 467-476.
- Modica, J. R. and Kram, R. (2005). Metabolic energy and muscular activity required for leg swing in running. *J. Appl. Physiol.* **98**, 2126-2131.
- Pollock, C. M. and Shadwick, R. E. (1994). Allometry of muscle, tendon, and elastic energy storage capacity in mammals. *Am. J. Physiol.* **266**, R1022-R1031.
- Rosager, S., Aagaard, P., Dyhre-Poulsen, P., Neergaard, K., Kjaer, M. and Magnusson, S. P. (2002). Load-displacement properties of the human triceps surae aponeurosis and tendon in runners and non-runners. *Scand. J. Med. Sci. Sports* **12**, 90-98.
- Roy, J. P. R. and Stefanyshyn, D. J. (2006). Shoe midsole longitudinal bending stiffness and running economy, joint energy, and EMG. *Med. Sci. Sports Exerc.* **38**, 562-569.
- Rugg, S. G., Gregor, R. J., Mandelbaum, B. R. and Chiu, L. (1990). *In vivo* moment arm calculations at the ankle using magnetic resonance imaging (MRI). *J. Biomech.* **23**, 495-501.
- Ryschon, T. W., Fowler, M. D., Wysong, R. E., Anthony, A. and Balaban, R. S. (1997). Efficiency of human skeletal muscle *in vivo*: comparison of isometric, concentric, and eccentric muscle action. *J. Appl. Physiol.* **83**, 867-874.
- Saunders, P. U., Pyne, D. B., Telford, R. D. and Hawley, J. A. (2004). Factors affecting running economy in trained distance runners. *Sports Med.* **34**, 465-485.
- Scardina, N., Daniels, J., Vanhandel, P., Bradley, P. and Troup, J. (1985). Running cadence, stride length, ve and respiratory frequency during treadmill and track running at sea-level and altitude. *Med. Sci. Sports Exerc.* **17**, 249-249.
- van Ingen Schenau, G. J. (1984). An alternative view of the concept of utilisation of elastic energy in human movement. *Hum. Mov. Sci.* **3**, 301-336.
- van Soest, A. J. and Bobbert, M. F. (1993). The contribution of muscle properties in the control of explosive movements. *Biol. Cybern.* **69**, 195-204.
- Williams, K. R. and Cavanagh, P. R. (1987). Relationship between distance running mechanics, running economy, and performance. *J. Appl. Physiol.* **63**, 1236-1245.