Influence of the muscle–tendon unit's mechanical and morphological properties on running economy

Adamantios Arampatzis*, Gianpiero De Monte, Kiros Karamanidis, Gaspar Morey-Klapsing, Savvas Stafilidis and Gert-Peter Brüggemann

Adamantios Arampatzis, German Sport University of Cologne, Institute of Biomechanics and Orthopaedics, Carl-Diem-Weg 6, 50933 Cologne, Germany

*Author for correspondence (e-mail: Arampatzis@dshs-koeln.de)

Summary

The purpose of this study was to test the hypothesis that runners having different running economies show differences in the mechanical and morphological properties of their muscle–tendon units (MTU) in the lower extremities. Twenty eight long-distance runners (body mass: 76.8±6.7 kg, height: 182±6 cm, age: 28.1±4.5 years) participated in the study. The subjects ran on a treadmill at three velocities (3.0, 3.5 and 4.0 m s^{-1}) for 15 min each. The $\dot{V}_{O_2}$ consumption was measured by spirometry. At all three examined velocities the kinematics of the left leg were captured whilst running on the treadmill using a high-speed digital video camera operating at 250 Hz. Furthermore the runners performed isometric maximal voluntary plantarflexion and knee extension contractions at eleven different MTU lengths with their left leg on a dynamometer. The distal aponeuroses of the gastrocnemius medialis (GM) and vastus lateralis (VL) were visualised by ultrasound during plantarflexion and knee extension, respectively. The morphological properties of the GM and VL (fascicle length, angle of pennation, and thickness) were determined at three different lengths for each MTU. A cluster analysis was used to classify the subjects into three groups according to their $\dot{V}_{O_2}$ consumption at all three velocities (high running economy, N=10; moderate running economy, N=12; low running economy, N=6). Neither the kinematic parameters nor the morphological properties of the GM and VL showed significant differences between groups. The most economical runners showed a higher contractile strength and a higher normalised tendon stiffness (relationship between tendon force and tendon strain) in the triceps surae MTU and a higher compliance of the quadriceps tendon and aponeurosis at low level tendon forces. It is suggested that at low level forces the more compliant quadriceps tendon and aponeurosis will increase the force potential of the muscle while running and therefore the volume of active muscle at a given force generation will decrease.

Key words: tendon elasticity, tendon stiffness, running economy, ultrasonography, running kinematics, energy exchange, skeletal muscle.

Introduction

The literature defines running economy as the rate of oxygen consumption per unit body mass when running at a constant pace (Daniels et al., 1978; Cavanagh and Kram, 1985; Williams and Cavanagh, 1987). It has been shown that distance runners demonstrate significant differences in the rate of oxygen consumption while running at the same velocity (Williams and Cavanagh, 1987; Daniels and Daniels, 1992). Furthermore, at a wide range of velocities there is a close relationship between metabolic energy cost and mechanical power (Bijker et al., 2001). As a consequence, many studies on running economy have been motivated by the suggestion that biomechanical factors might explain the differences of running economy between individuals (Cavanagh and Williams, 1982; Williams and Cavanagh, 1987; Kyröläinen et al., 2001). However, in

general the relationship observed between biomechanical factors and running economy is weak and it has been concluded that descriptive kinematic and kinetic parameters alone cannot explain the complexity of running economy (Williams and Cavanagh, 1987; Martin and Morgan, 1992; Kyröläinen et al., 2001).

It has been suggested that variables that describe muscle force production (i.e. force–length–velocity relationship and activation) are probably more suitable for explaining running economy (Martin and Morgan, 1992). From a mechanical point of view there are two main issues that can affect the force–length–velocity relationship and the activation of the muscles while running. The mechanical advantages of the muscles (ratio of an agonist muscle group moment arm to that of the ground reaction force acting about a joint) may affect the

force production in relation to the active muscle volume. For example, it is well accepted in the literature that small mammals show lower effective mechanical advantages during running than larger mammals (Biewener, 1989; Biewener, 1990), which lead to a decrease in the force production per active muscle volume. Recently Biewener et al. reported that differences in the effective mechanical advantages between walking and running explain the higher energy transport during running compared to walking (Biewener et al., 2004). A second issue that can influence the force–length–velocity relationship and activation of the muscles is the non-rigidity of the tendon and aponeurosis (Bobbert, 2001; Hof et al., 2002; Roberts, 2002). A higher compliance will allow the muscle fibres to contract at lower shortening velocities than the whole muscle–tendon unit (MTU) (Ettema et al., 1990a; Ettema et al., 1990b), and as a consequence of the force–velocity relationship their force-generating potential will be higher (Hof et al., 1983; Hof et al., 2002; Bobbert, 2001). Furthermore, due to the non-rigidity of the tendon and aponeurosis, when the MTU is elongated, strain energy can be stored that is independent of metabolic processes (Roberts, 2002). This way the whole mechanical energy produced during the shortening of the MTU can be enhanced (Alexander and Bennet-Clark, 1977; Ker et al., 1987; de Haan et al., 1989; Ettema, 1996; Roberts et al., 1997).

Despite these phenomena being well known, there is currently no study showing the influence of the mechanical properties of the MTU on running economy in humans, nor has the role of muscle architecture in enhancing running economy been studied. Recent *in vivo* studies investigating the mechanical and morphological properties of the MTU have demonstrated differences between athletes pertaining to different disciplines (Kawakami et al., 1993; Kawakami et al., 1995; Abe et al., 2000). Abe et al., for example, compared sprinters with long-distance runners, and found that the sprinters had longer fascicles and lower pennation angles in the mm. vastus lateralis and gastrocnemius (Abe et al., 2000). Longer muscle fascicles can exhibit higher shortening velocities and mechanical powers than shorter fascicles. In general, literature reports recognised a significant correlation between the fascicle lengths of the lower extremity muscles (vastus lateralis, gastrocnemii) and sprint performance (Kumagai et al., 2000; Abe et al., 2001).

While running the muscles acting around the ankle and knee joints (i.e. triceps surae and quadriceps femoris) contribute more than 70% of the total mechanical work (Winter, 1983; Sasaki and Neptune, 2005). Therefore it can be argued that they belong to the main muscles expending energy during sub-maximal running. Furthermore Sasaki and Neptune (Sasaki and Neptune, 2005) reported that during sub-maximal running the energy stored in the tendon and aponeurosis of the triceps surae and quadriceps femoris MTU is about 75% of the energy stored in all tendons of the muscoloskeletal system. Reports on the influence of the non-rigidity of the tendon and aponeurosis on the effectivity of muscle force production (Ettema et al., 1990a; Ettema et al., 1990b; Roberts et al., 1997; Hof et al., 2002) and

the effect of fascicle lengths on performance of sport activities (Kumagai et al., 2000; Abe et al., 2001) reveal the expectation that running economy may be affected by the mechanical and morphological properties of the triceps surae and quadriceps femoris MTUs. Basing on the above expectation it can be hypothesised that runners having different running economy would show differences in the mechanical and morphological properties of their MTUs in the lower extremities. Therefore we examined the mechanical properties and the architecture of the MTUs of the lower extremities from runners displaying different running economies, together with their running kinematics.

Materials and methods

Subjects

Twenty eight male long-distance runners (body mass 76.8±6.7 kg, height 182±6 cm, age 28.1±4.5 years), all regularly participating in running competitions locally, took part in the study. The runners gave their informed written consent to the experimental procedure complying with the rules of the local scientific board. All subjects performed endurance running training between 4 and 9 times per week. The training volume ranged from 40 to 120 km week^{-1}. None of the subjects had a history of neuromuscular or musculoskeletal impairments at the time of the study that could affect their running technique.

Oxygen consumption

After a warm-up period of 5 min at a running velocity of 3.0 m s^{-1} the subjects ran three different velocities for 15 min on a treadmill in the same order (3.0, 3.5 and 4.0 m s^{-1}) wearing their own running shoes. Oxygen consumption ($\dot{V}_{O_2}$; ml kg^{-1} min^{-1}) was measured during this 15 min period using a breath-by-breath spirometer (Jaeger Oxycon α, Hoechberg, Germany). The spirometer was calibrated before each session by means of a two-point calibration using environment air and a gas mixture (5.5% CO_2, 0% O_2, balance N_2). The volume sensor was calibrated by means of a manual 2 litre syringe. The accuracy values provided by the manufacturer were 0.01% for O_2 and CO_2 with a drift of 0.02% per hour, and ≤0.02% for volume. For each velocity the average value of the $\dot{V}_{O_2}$ was calculated from 4 min of running at steady state (Fig. 1, min 10–14). There were 10 min rests between running at each velocity test. Blood samples were taken from the earlobe directly after finishing each velocity test within the first 30 s of the rest to determine blood lactate concentration, which helps to identify differences in the anaerobic energy cost between the examined subjects that might occur.

Measurements of running kinematics

The kinematics of the runner's left leg were captured during the running on the treadmill at all three examined velocities using a high-speed digital camera (Kodak SR-500 C, San Diego, CA, USA) operating at 250 Hz. The video sequences were recorded between the fourth and the fifth minute of each
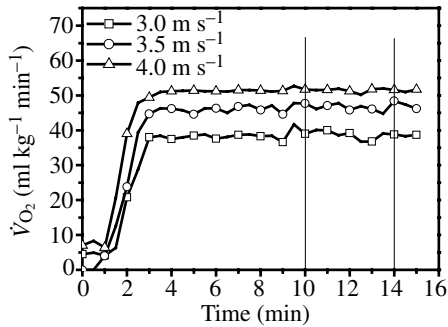
Fig. 1. Oxygen consumption ($\dot{V}_{O_2}$) of a runner at all three velocities. The two vertical lines delimit the period during which oxygen consumption was determined.

Table 1. *Eleven ankle–knee and knee–hip joint angle configurations used for the isometric maximal voluntary ankle plantarflexion and knee extension contractions*

Ankle plantarflexion (degrees)		Knee extension (degrees)	
Ankle joint	Knee joint	Knee joint	Hip joint
120	75	170	90
120	110	170	110
110	100	170	135
120	140	160	120
100	110	160	140
110	150	140	115
90	130	140	140
100	170	110	100
80	130	110	150
90	170	80	110
80	170	80	150

Tibia perpendicular to the foot-sole was defined as 90° ankle angle.

The fully extended trunk and knee were defined as 180° hip and knee joint angles, respectively.

examined velocity. This was done because in an earlier study we found that after 2–3 min running on a treadmill the running characteristics are very reproducible (Karamanidis et al., 2003). The camera axis was orthogonal to the plane of motion and was calibrated using a square frame (1 m×1 m). To improve the quality of the video analysis, five reflective markers (radius 10 mm) were used to mark joint positions. The markers were fixed on the following body landmarks (left side): metatarsal head V, lateral malleolus, lateral epicondylus, trochanter major and spina iliaca. The video recordings were digitised using the 'Peak-Motus' automatic tracking system and the two-dimensional coordinates were smoothed using a forth order low-pass Butterworth filter with an optimised cut-off frequency for each digitised point ('Peak Motus' Motion Analysis System; Centennial, CO, USA). One stride cycle from heel strike to the next heel strike of the same foot (left leg) was analysed for each running speed. The instants of touch-down and take-off were determined from the video sequences (250 Hz). The duty factor was defined as the proportion between contact time and total stride cycle duration (McMahon, 1985). The joint angles of the ankle, knee and hip were expressed relative to a reference position: tibia perpendicular to the sole corresponding to 90° ankle angle, fully extended knee and hip corresponding to 180° each.

Measurement of maximal isometric ankle and knee joint moment

The subjects performed isometric maximal voluntary ankle plantarflexion and knee extension contractions (MVC) of their left leg on two separate test days. The warm-up consisted of 2–3 min performing submaximal isometric contractions and three MVCs. Afterwards the subjects performed isometric maximal voluntary ankle plantarflexion or knee extension contractions at eleven different ankle–knee and knee–hip joint angle configurations, respectively (Table 1), on a dynamometer (Biodex Medical Systems. Inc., Shirley, NY, USA). Different joint angle configurations were chosen in order to examine triceps surae and quadriceps femoris muscle strength potential over the whole range of achievable MTU lengths. The different joint angle configurations were applied in random order. 3 min rest between contractions were allowed. The subjects were

instructed and encouraged to produce a maximal isometric moment and to hold it for about 2–3 s.

Before each MVC the axis of rotation of the dynamometer was carefully aligned with the axis of rotation of the ankle and knee joints. The axis of rotation of the ankle joint was defined to be parallel to the axis of the dynamometer and passing through the midpoint of the line connecting both malleoli. In the same way the axis of rotation of the knee joint was defined to be parallel to the axis of the dynamometer and passing through the midpoint of the line connecting the lateral and medial femoral condyles. During the contraction the axes clearly shifted away from each other. Therefore, kinematic data were recorded using a Vicon 624 system (Vicon Motion Systems, Oxford, UK) with eight cameras operating at 120 Hz to calculate the resultant joint moments. To calculate the lever arm of the ankle joint during ankle plantarflexion the centre of pressure under the foot was determined by means of a flexible pressure distribution insole (Pedar, Novel GmbH, Munich, Germany) operating at 99 Hz. The compensation of moments due to gravitational forces was done for all subjects before each ankle plantarflexion or knee extension contraction. The exact method for calculating the resultant joint moments has been previously described (Arampatzis et al., 2004; Arampatzis et al., 2005b).

The moments arising from antagonistic coactivation during the ankle plantarflexion and knee extension efforts were quantified by assuming a linear relationship between surface electromyography (EMG) amplitude of the ankle dorsiflexor or knee flexor muscles and moment (Baratta et al., 1988). This was established by measuring EMG and moment during one relaxed condition and two submaximal ankle dorsiflexion or knee flexion contractions at each joint angle configuration (Mademli et al., 2004). Therefore, in the text below, maximal knee and ankle joint moments refer to the maximal joint

moment values considering the effect of gravitational forces, the effect of the joint axis alignment relative to the dynamometer axis and the effect of the antagonistic moment on the moment measured at the dynamometer.

Measurement of EMG-activity during isometric contractions

Bipolar EMG lead-offs with pre-amplification (analogue RC-filter 10-500 Hz bandwidth, Biovision, Wehrheim, Germany) and adhesive surface electrodes (blue sensor; Medicotest, Ballerup, Denmark) were used to analyse muscle activity. Before placing the electrodes the skin was carefully prepared (shaved and cleaned with alcohol) to reduce skin impedance. The electrodes were positioned above the midpoint of the muscle belly as assessed by palpation, parallel to the presumed direction of the muscle fibres. The inter-electrode distance was 2 cm. The activation of the triceps surae muscle was assessed from the EMGs of the gastrocnemius medialis (GM), gastrocnemius lateralis (GL) and soleus (SOL). During knee extension the EMG-activities of the vastus lateralis (VL), vastus medialis (VM) and rectus femoris (RF) were analysed. The EMG signals were recorded at 1080 Hz by the Vicon system. Before starting the experiment, tests including submaximal and maximal isometric contractions for each muscle group were undertaken to determine whether an adequate signal was obtained from each muscle and to adjust the amplifier gains. The EMG signal from each muscle was checked online for artefacts due to mechanical causes by passively shaking the leg. Additionally, several functional tests (i.e. hopping in place) were undertaken to determine whether a good signal was obtained from each muscle. The preparation was renewed when such artefacts were observed. All isometric contractions at the knee or the ankle joint were performed within one testing session. No electrode replacement or re-adjusting of the EMG pre-amplification gain was done during the measurements.

The EMG-activity is described by the root mean square (RMS) of the raw signals for a time interval of 1000 ms at peak joint moment. The RMS from each muscle was normalised to the individual maximal RMS value of each muscle for each subject during the eleven isometric contractions. In order to determine the EMG-activity of the ankle plantarflexor and knee extensor muscles, the normalised RMS of the examined muscles were averaged and weighted by their physiological cross sectional areas (PCSA). For the TS, a PCSA ratio of 6:2:1 for the SOL, GM, GL (Out et al., 1996) and for the QF, a PCSA ratio of 0.92, 1.00 and 0.72 for the RF, VL and VM (Herzog et al., 1990) were assumed.

Measurement of tendinous tissue elongation

Tendon properties were determined on two additional test days. The subjects performed MVC ankle plantarflexion (ankle joint angle 90°, knee joint angle 180°) and knee extension (knee joint angle 115°, hip joint angle 140°) contractions with their left leg on a dynamometer. A 7.5 MHz linear array ultrasound probe (Aloka SSD 4000; 43 Hz) was used to visualise the distal tendon and aponeurosis of the gastrocnemius medialis (GM) and vastus lateralis (VL) MTUs (Fig. 2). The resolution of the ultrasound images was 0.7×0.4 mm. The ultrasound probe was placed above the respective muscle belly at about 50% of its length. It has been reported that during both maximal 'isometric' plantarflexion and knee extension efforts it is extremely difficult to completely prevent any joint rotation despite using external fixations (Magnuson et al., 2001; Muramatsu et al., 2001; Bojsen-Møller et al., 2003; Arampatzis et al., 2004; Arampatzis et al., 2005b). This joint rotation has a significant influence on the measured elongation of the GM and VL tendons and aponeuroses (Spoor et al., 1990; Muramatsu et al., 2001; Bojsen-Møller et al., 2003). To determine the elongation of th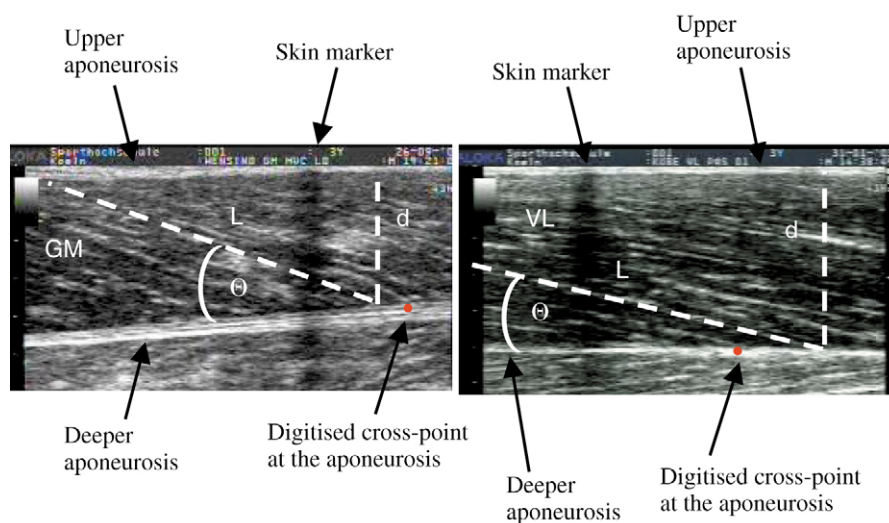e tendon and aponeurosis due to joint rotation, the motion of the GM and VL tendon and aponeurosis was captured by the ultrasound probe during a passive motion. This allowed the correction of the elongation obtained for the tendon and aponeurosis due to joint rotation for each maximal ankle plantarflexion or knee extension trial (Arampatzis et al., 2005a; Stafilidis et al., 2005). To estimate the resting (initial) length of the tendon and aponeurosis, following procedure was used: Before the main plantarflexion contraction, the subjects were seated on the Biodex dynamometer having a knee angle of 120° and an ankle angle of 110°. In a similar way, to estimate the rest length of VL, the subjects were seated on the dynamometer with hip and knee angles set at 140° and 115° respectively. In these positions the cross-points on the

Fig. 2. Muscle ultrasound images at rest. Left, gastrocnemius medialis (GM); right, vastus lateralis (VL). L, fascicle length; d, muscle thickness; Θ, pennation angle; digitalised cross-point, insertion of the fascicle into the deeper aponeurosis.

ultrasound images were identified and measured relative to the marker placed between the skin and the ultrasound probes. The length of the curved path from the tuberositas calcanei (defined as the origin of the Achilles tendon) to the markers was measured along the skin surface. Thus the resting length of the GM tendon and aponeurosis was defined as the length of the path between the tuberositas calcanei and the examined cross points identified on the ultrasound images. The resting length of the VL tendon and aponeurosis was defined as the length of the path between the tuberositas tibia (defined as origin of the patella tendon) and the cross point at the VL muscle belly. Again the distance of the curved path along the skin from the tuberositas tibia to the marker on the skin was measured using flexible measuring tape. The positions (120° knee angle, 110° ankle angle for the GM and 140° hip angle, 115° knee angle for the VL) were chosen because at these angles the passive moment is almost zero (Riener and Edrich, 1999), which prevented an elongation of the tendon and aponeurosis at the resting state.

The tendon force was calculated by dividing the ankle or knee joint moment by the corresponding tendon moment arm. The tendon moment arms of the Achilles tendon and the patellar tendon were calculated using the data provided by Maganaris et al. (Maganaris et al., 1998) and Herzog and Read (Herzog and Read, 1993), respectively. The stiffness of the tendon and aponeurosis was calculated by means of linear regression equations. The stiffness (normalised) represented the relationship between the tendon force and the strain of the tendon and aponeurosis between 45% and 100% of the maximal tendon force. We used the normalised stiffness because the amount of elongation of a tendon at a given exerted force depends on the rest length of the tendon. *In vitro* studies examining the elongation of the tendon used the same rest lengths. *In vivo* it is very difficult to do this, because of the differences in the anthropometrical characteristics of the subjects and also the differences in the localisation of the ultrasound probe (it is practically impossible to place the ultrasound probe exactly at the same position at all experiments). Differences in the rest length would influence the calculated stiffness (relationship between tendon force and elongation) of the tendon and aponeurosis (Rack and Westbury, 1984; Muramatsu et al., 2001; Arampatzis et al., 2005a; Stafilidis et al., 2005). This fact makes it difficult to compare the stiffness between different subjects or groups. Recently it has been reported that the strain measured at the myotendinous junction and at the muscle belly is similar (Muramatsu et al., 2001; Arampatzis et al., 2005a; Stafilidis et al., 2005), so the choice of the cross-point does not effect the calculated strain. Therefore in the present study we used the normalised stiffness. The linearity between tendon force and strain was checked using the coefficient of determination (r^2). The coefficients of determination were reasonably high (r^2=0.98 to 0.99). The energy storage capacity of the tendon and aponeurosis during the maximal voluntary contraction was calculated as the integral of the tendon force over the tendon strain.

Measurement of muscle architecture

The muscle architecture of the GM and VL (fascicle length, angle of pennation, and thickness) was determined at three different lengths for each muscle–tendon unit. Following ankle–knee joint angle combinations were chosen for the GM: Position 1: ankle angle 90°, knee angle 180°; Position 2: ankle angle 110°, knee angle 160°; Position 3: ankle angle 120°, knee angle 110°. The corresponding knee–hip joint angle combinations for the VL were: Position 1: knee angle 80°, hip angle 140°; Position 2: knee angle 115°, hip angle 140°; Position 3: knee angle 170°, hip angle 140°. All measurements were done on the relaxed muscle at the cited positions. The pennation angles of the GM and VL were measured as the angle of insertion of the muscle fascicles into the deep aponeurosis. The fascicle length was defined as the length of the fascicular path between the insertions of the fascicle into the upper and deeper aponeurosis (Fig. 2). The muscle thickness was defined as the distance between the deeper and upper aponeurosis.

Statistics

The examined runners were divided into groups by means of a cluster analysis, based on their oxygen consumption (ml kg^{-1} min^{-1}) at all three velocities (3.0, 3.5 and 4.0 m s^{-1}). The cluster analysis revealed three relatively homogeneous groups (group 1: high running economy, *N*=10; group 2: moderate running economy, *N*=12; group 3: low running economy, *N*=6). All parameters (running kinematics, mechanical and morphological properties of the lower extremity MTUs) were checked for differences between groups using one-way analysis of variance (ANOVA) and Tukey *post-hoc* comparisons. The level of significance was set to *P*=0.05.

Results
Metabolic parameters

The runners of the three groups showed statistically significant differences (*P*<0.05) in their $\dot{V}_{O_2}$ at all examined velocities (Table 2). Group 1 was the most economical, followed by groups 2 and 3. No differences between groups in body mass, body height or lactate concentration at each running velocity were found (Table 2).

Running kinematics

Fig. 3 shows the average ankle, knee, and hip angles at 3.0, 3.5 and 4.0 m s^{-1} for all three groups. The shape of the curves, as well as the angular and temporal parameters at all velocities, showed no statistically significant (*P*>0.05) differences between groups (Table 3). For all three velocities the average duty factor ranged from 36% to 39% and did not show any statistically significant (*P*>0.05) difference between groups (Table 3).

Triceps surae and quadriceps femoris muscle–tendon units

The maximal calculated tendon force, maximal plantarflexion moment, normalised stiffness and energy storage capacity during the MVC of the triceps surae tendon and

Table 2. *Anthropometric (body mass, body height) and performance (oxygen consumption, lactate concentration) characteristics for the three groups against the examined velocities*

Parameter	Velocity 1 (3.0 m s⁻¹)			Velocity 2 (3.5 m s⁻¹)			Velocity 3 (4.0 m s⁻¹)		
	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)
Body mass (kg)	80.5±7.8	75.1±5.7	74.0±4.2	–	–	–	–	–	–
Body height (cm)	185±6	180±5	180±5	–	–	–	–	–	–
Oxygen consumption (ml kg⁻¹ min⁻¹)	37.42±1.86	39.86±1.75*	44.38±1.94*,†	43.59±1.34	45.71±1.62*	49.85 ±2.51*,†	48.93±2.01	51.98±1.47*	58.93±1.48*,†
Lactate concentration (mmol l⁻¹)	1.39±0.49	1.54±0.37	1.78±0.77	2.35±1.30	2.29±1.05	3.58±1.49	4.56±2.41	5.01±1.80	5.86±1.87

Group 1, high running economy. Group 2, moderate running economy. Group 3, low running economy.

Values are means ± s.d.

Statistically significant differences *between group 1 and the other two groups (P<0.05), †between group 2 and group 3 (P<0.05).

aponeurosis were highest (P<0.05) for group 1 (Table 4). In contrast, the maximal strain of the tendon and aponeurosis showed no significant (P>0.05) differences between the groups (Table 4). The three examined groups showed significant

differences (P<0.05) in their mechanical properties of the quadriceps femoris tendon and aponeurosis (Table 5). Although the maximal knee extension moment, the maximal calculated tendon force, and the normalised stiffness showed no significant differences (P>0.05), the maximal strain and the energy storage capacity of the tendon and aponeurosis during the MVC were highest (P<0.05) for group 1 (Table 5). Furthermore, the normalised stiffness of the quadriceps tendon and aponeurosis of the group 1 runners was significantly lower (P<0.05) at low level forces (up to 45% MVC) compared to the other two groups (Fig. 4). The calculated stiffness of the quadriceps tendon and aponeurosis from 0 to 45% MVC for all the three groups was: 29.5±4.8 kN strain⁻¹, 42.5± 6.2 kN strain⁻¹ and 38.1±5.9 kN strain⁻¹, respectively.

As expected, on account of the length of the GM MTU at the examined ankle–knee angle combinations, the fascicle length of the GM decreased and the angle of pennation increased from position 1 to position 3 (Table 6). The thickness showed nearly constant values for all three examined positions. The morphological parameters: fascicle length, ratio (fascicle length/tibia length), angle of pennation and thickness (Table 6) showed no statistically significant differences between groups at any position (P>0.05). Similar to the results obtained for the GM, while the fascicle length of the VL decreased and its angle of pennation increased from position 1 to position 3, its thickness showed nearly constant values (Table 7). The comparison of all three groups, as for the GM, revealed no significant (P>0.05) differences in fascicle length, ratio (fascicle length/femur length), angle of pennation or thickness at any examined position (Table 7).

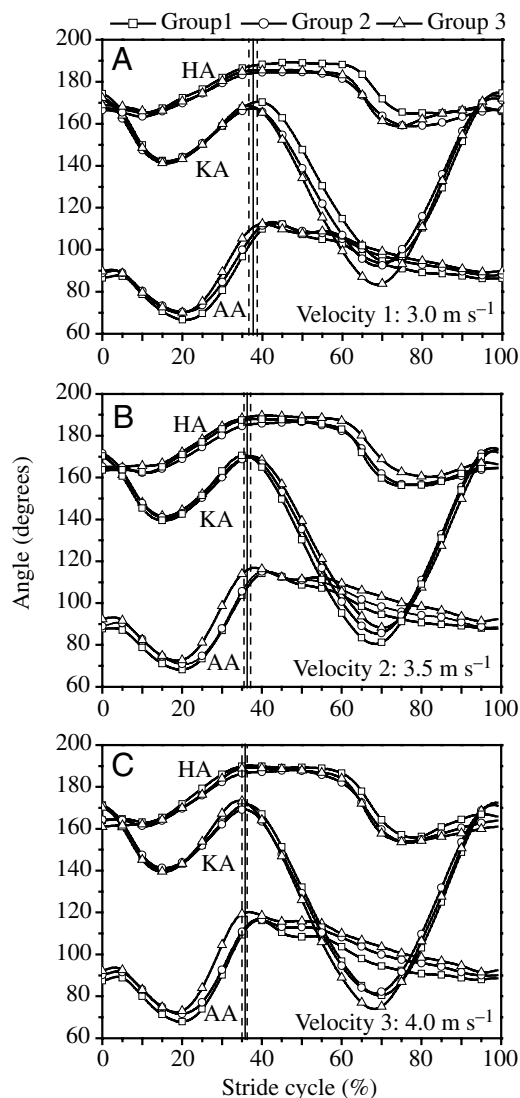The maximal plantarflexion moment was significantly higher

Fig. 3. Average values of the ankle (AA) knee (KA) and hip (HA) angles during running for all velocities and groups. The *x*-axis is normalised to the stride cycle (from heel strike to the next heel strike of the same foot). The vertical lines separate the contact and swing phases (mean ± 1 s.d.). Group 1, high running economy (*N*=10). Group 2, moderate running economy (*N*=12). Group 3, low running economy (*N*=6). (A) Velocity 1 (3.0 m s⁻¹), (B) velocity 2 (3.5 m s⁻¹), (C) velocity 3 (4.0 m s⁻¹).

Table 3. *Duration of the contact and swing phases, duty factor, stride frequency and range of motion of the joints of the lower extremity during contact phase for the three groups and the three examined velocities*

Parameter	Velocity 1 (3.0 m s⁻¹)			Velocity 2 (3.5 m s⁻¹)			Velocity 3 (4.0 m s⁻¹)		
	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)
Contact time (ms)	292±21	268±23	276±35	266±25	254±16	262±23	252±20	240±19	252±23
Swing time (ms)	455±20	445±18	455±45	441±28	436±24	441±43	443±27	431±21	449±30
Duty factor (%)	39.1±1.7	37.6±2.2	37.5±1.9	37.7±2.4	36.9±1.8	37.2±1.3	36.4±1.3	35.9±1.5	35.9±1.4
Stride frequency (Hz)	1.34±0.06	1.40±0.06	1.35±0.14	1.42±0.08	1.45±0.07	1.38±0.11	1.44±0.08	1.49±0.06	1.39±0.11
Range of ankle dorsi-flexion (degrees)	20.3±5.5	18.8±3.9	19.8±7.2	20.1±5.3	18.3±4.2	20.0±4.8	20.0±5.0	18.9±5.5	19.9±5.6
Range of ankle plantar flexion (degrees)	41.3±5.7	36.2±7.3	38.8±11.3	42.9±5.8	38.9±7.4	43.9±9.4	44.3±4.4	40.6±8.8	47.5±7.6
Range of knee flexion (degrees)	32.3±4.7	29.1±6.7	31.3±9.6	29.0±5.8	29.8±7.2	31.0±8.4	30.9±4.5	30.1±7.2	30.7±7.4
Range of knee extension (degrees)	29.1±4.5	26.5±4.4	28.4±7.5	30.5±4.2	28.2±4.9	32.2±6.3	32.4±4.1	28.9±4.6	35.1±5.9
Range of hip extension (degrees)	20.1±3.7	17.8±3.9	16.5±6.1	25.2±4.3	22.3±7.5	24.1±4.5	23.3±5.6	22.3±3.5	28.1±4.5

Group 1, high running economy. Group 2, moderate running economy. Group 3, low running economy.
Values are means ± s.d.

Table 4. *Maximal strain of the tendon and aponeurosis (Strain), maximal plantarflexion moment (Moment), maximal calculated tendon force (Force), energy storage capacity of the tendon and aponeurosis (Energy), normalised stiffness of the tendon and aponeurosis (Stiffness), and resting length of the tendon and aponeurosis (Rest length) for all three groups at the triceps surae muscle–tendon unit during the maximal voluntary contraction*

Parameter	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)
Strain (%)	6.2±1.2	6.4±1.7	5.4±1.7
Moment (Nm)	153.4±23.1	117.4±24.9*	107.2±13.2*
Force (N)	2028±379	1572±488*	1432±546*
Energy (J m⁻¹)	62.3±21.1	46.1±22.5*	42.2±16.9*
Stiffness (kN strain⁻¹)	34.4±6.6	23.7±9.6*	20.6±6.6*
Rest length (mm)	290±76	284±68	286±82

Group 1, high running economy. Group 2, moderate running economy. Group 3, low running economy. Values are means ± 1 s.d.; ankle angle, 90°; knee angle, 180°.
*Statistically significant differences between group 1 and the other two groups ($P<0.05$).

Table 5. *Maximal strain of the tendon and aponeurosis (Strain), maximal plantarflexion moment (Moment), maximal calculated tendon force (Force), energy storage capacity of the tendon and aponeurosis (Energy), normalised stiffness of the tendon and aponeurosis (Stiffness), and resting length of the tendon and aponeurosis (Rest length) for all three groups at the qudriceps femoris muscle–tendon unit during the maximal voluntary contraction*

Parameter	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)
Strain (%)	10.0±1.9	7.0±2.1*	7.4±1.7*
Moment (Nm)	209.5±52.8	175.4±51.8	161.5±44.1
Force (N)	4190±754	3556±1037	3330±881
Energy (J m⁻¹)	163.7±17.8	111.1±30.4*	116.1±31.5*
Stiffness (kN strain⁻¹)	66.9±7.3	57.8±16.6	58.4±9.4
Rest length (mm)	322±63	319±80	325±93

Group 1, high running economy. Group 2, moderate running economy. Group 3, low running economy.
Values are mean ± 1 s.d.; knee angle, 115°; hip angle, 140°.
*Statistically significant ($P<0.05$) differences between group 1 and the other two groups.
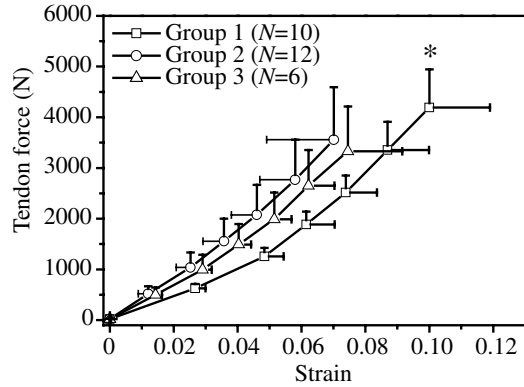
Fig. 4. Force–strain relationship of the quadriceps femoris tendon and aponeurosis during maximal knee extension effort for the three groups (mean ± 1 s.d.). Group 1, high running economy; Group 2, moderate running economy; Group 3, low running economy. *Statistically significant differences in maximal tendon strain between group 1 and the other two groups ($P<0.05$).

($P<0.05$) for group 1 at seven of the eleven examined positions (Fig. 5). However at four positions (i.e. pronounced ankle plantarflexion and knee flexion combinations) there were no differences between the three groups. Comparison of the EMG-activity during the maximal plantarflexion effort revealed no significant differences between groups at any ankle/knee joint combination ($P>0.05$) (Fig. 5). All three runner groups exhibited similar knee extension moments and EMG-activity in the quadriceps femoris muscles at all knee/hip angle combinations ($P>0.05$) (Fig. 6).

Discussion

The main findings of this study were that the most economical runners showed (i) a higher contractile strength of the triceps surae muscle tendon unit, (ii) a higher compliance of the quadriceps tendon and aponeurosis at low level forces, (iii) a higher energy storage capacity during MVC in both the triceps surae and the quadriceps muscle–tendon units, (iv) no differences in the muscle
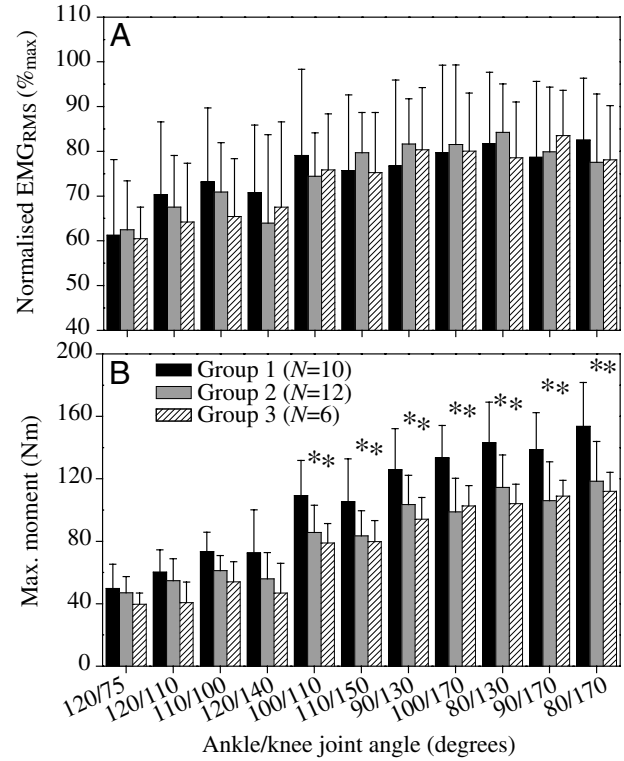

Fig. 5. Normalised RMS values of the EMG signal (A) for the triceps surae muscle (gastrocnemius medialis, gastrocnemius lateralis and soleus) and ankle joint moment (B) during isometric maximal voluntary ankle plantarflexion contraction at 11 different joint angle configurations for the examined groups (means ±1 s.d.). RMS values from each subject were normalised to the highest RMS value measured over all joint angle configurations. Group 1, high running economy; Group 2, moderate running economy; Group 3, low running economy. *Statistically significant differences between group 1 and the other two groups ($P<0.05$).

architecture of the GM and VL and (v) no differences in the kinematic characteristics of running.

It is noteworthy, however, that although groups 2 and 3 (moderate and low economy runners) showed clearly different

Table 6. *Fascicle length, ratio (fascicle legth/tibia length), angle of pennation and thickness of the gastrocnemius medialis muscle for the three groups against the examined positions*

Parameter	Position 1 (ankle angle 90°, knee angle 180°)			Position 2 (ankle angle 110°, knee angle 160°)			Position 3 (ankle angle 120°, knee angle 110°)		
	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)
Fascicle length (mm)	69.3±14.6	72.3±14.8	69.9±14.3	49.9±12.7	50.4±14.3	49.5±13.8	44.7±15.7	41.1±7.2	37.3±10.4
Ratio (fascicle length/tibia length)	0.167±0.025	0.172±0.031	0.171±0.042	0.121±0.018	0.121±0.025	0.120±0.019	0.108±0.016	0.099±0.021	0.091±0.022
Angle of pennation (degrees)	20.2±3.3	20.2±3.3	19.6±3.2	28.3±7.4	25.2±5.9	24.8±5.7	32.6±8.2	29.5±7.6	31.2±8.5
Thickness (mm)	19.2±3.3	20.1±2.9	21.3±1.3	18.8±4.4	17.2±3.3	17.7±4.1	17.6±3.5	16.1±4.2	17.0±4.5

Group 1, high running economy. Group 2, moderate running economy. Group 3, low running economy.
Values are mean ± 1 s.d.

Table 7. *Fascicle length, ratio (fascicle length/femur length), angle of pennation and thickness of the vastus lateralis muscle for the three groups against the examined positions*

Parameter	Position 1 (knee angle 80°, hip angle 140°)			Position 2 (knee angle 115°, hip angle 140°)			Position 3 (knee angle 170°, hip angle 140°)		
	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)	Group 1 (N=10)	Group 2 (N=12)	Group 3 (N=6)
Fascicle length (mm)	121.2±13.3	121.1±21.5	131.2±15.3	103.5±14.4	103.6±24.8	108.4±24.0	90.1±11.7	85.8±16.2	99.6±25.6
Ratio (fascicle length/ femur length)	0.269±0.032	0.275±0.049	0.295±0.051	0.230±0.037	0.233±0.041	0.244±0.049	0.200±0.029	0.195±0.037	0.223±0.035
Angle of pennation (degrees)	10.0±2.2	9.2±2.7	8.3±1.2	10.3±1.9	10.4±2.1	10.2±1.8	13.7±1.2	13.8±2.9	12.1±1.7
Thickness (mm)	23.0±5.5	22.4±4.3	21.8±2.0	22.6±2.4	21.7±2.8	20.8±1.2	22.1±5.4	22.2±3.3	19.7±2.2

Group 1, high running economy. Group 2, moderate running economy. Group 3, low running economy.
Values are mean ± 1 s.d.

oxygen consumptions at all three examined velocities they did not show differences in the mechanical (maximal joint moment, maximal calculated tendon force, maximal strain, normalised stiffness, energy storage capacity) properties of either the triceps surae or the quadriceps femoris MTUs. Thus
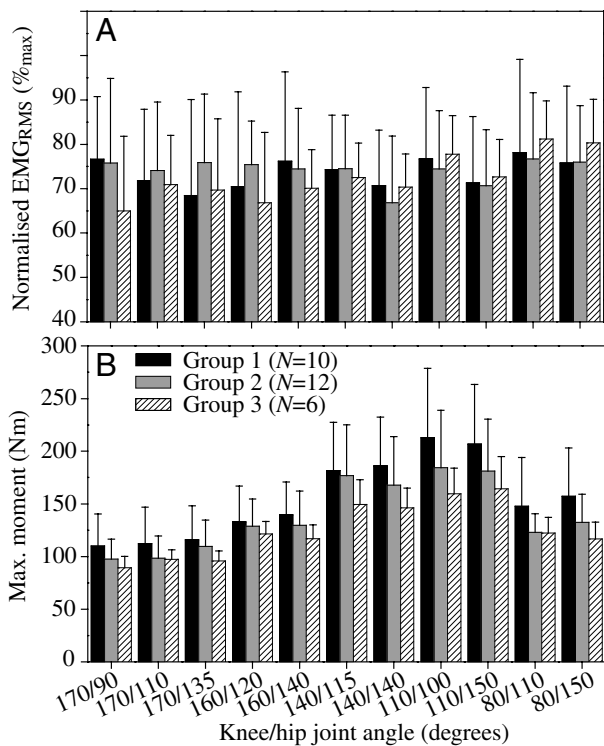

Fig. 6. Normalised RMS values of the EMG signal (A) for the quadriceps femoris muscles (vastus lateralis, vastus medialis and rectus femoris) and knee joint moment (B) during isometric maximal voluntary knee extension contraction at 11 different joint angle configurations for the examined groups (means ± 1 s.d.). RMS values from each subject were normalised to the highest RMS value measured over all joint angle configurations. Group 1, high running economy; Group 2, moderate running economy; Group 3, low running economy. *Statistically significant differences between group 1 and the other two groups ($P<0.05$).

the results demonstrate that the differences found in the mechanical properties alone between the three groups, cannot entirely explain the differences in running economy for all examined subjects and support the opinion (Williams and Cavanagh, 1987; Lake and Cavanagh, 1996; Kyrölainen et al., 2001) that a global explanation of running economy is very complex; many variables may affect the existing differences in running economy between individuals. In the present study, however, the most economical runners showed differing values in important mechanical properties at the triceps surae as well as in the quadriceps femoris MTUs. The different mechanical properties found in the lower extremities of the most economical runners may affect intrinsic muscle properties for force and energy production (i.e. force–length–velocity relationship, activation and energy storage and return during the running task) and may contribute to running economy.

Another point that should be discussed is that the examined runners showed a wide range of training volumes (4–9 times per week, 40–120 km week^{-1}). Although some studies reported no differences in running economy between trained and untrained subjects (Dolgener, 1982), or no relationship between running economy and training volume (Pate et al., 1992; Weston et al., 2000), others revealed that trained subjects are more economical than untrained subjects and elite runners more economical than sub-elite runners (Morgan et al., 1995). Therefore to examine whether the training volume of the examined runners could have an effect on the differences found in running economy we compared the training volumes (km week^{-1}) among the runner groups. No significant differences in training volume between the groups could be found ($P>0.05$) (group 1: 76.0±28.3 km week^{-1}, group 2: 74.1±13.4 km week^{-1}, group 3: 72.5±20.6 km week^{-1}) indicating that training volume was not responsible for the differences in running economy observed at our subject groups. Furthermore there was no relationship between training volume and $\dot{V}_{O_2}$ at all examined velocities (r^2=0.08–0.09, $P>0.05$).

Kinematic characteristics

There were no detectable differences between groups in contact time, swing time, duty factor or stride frequency at any

running velocity. Furthermore, the range of motion of the lower extremity's joints during running at all three examined velocities showed no statistically significant differences between groups. These data suggest that the differences in running economy between the three groups are not related to different stride frequencies or to different kinematic characteristics. Similar conclusions were reported in earlier studies examining kinematic parameters in runners with different running economies (Williams and Cavanagh, 1987; Kyrölainen et al., 2001). In summary, the findings of the kinematic analysis show that in a homogeneous group of runners, differences in running economy are not related to their kinematic parameters. As the effective mechanical advantage was not examined in the present study it is not possible to glean any information regarding this parameter for the three groups. However, it is unlikely that groups of runners showing no differences in running kinematics and body mass would show differences in the effective mechanical advantage during running.

Higher compliance of tendon at low level forces in the quadriceps femoris

The maximal strain of the quadriceps tendon and aponeurosis was higher (about 38%) in the high running economy group (group 1) compared to the other two groups. However at higher exerted forces the normalised stiffness showed no significant differences between the groups (45–100% of the MVC). This means that the quadriceps tendon and aponeurosis of the group 1 runners are more compliant at low level forces (up to 45% MVC) in comparison to the other two groups (Fig. 4).

No significant differences in joint kinematics between the three groups could be identified at any running velocity. Thus it can be argued that the velocities of the triceps surae and quadriceps femoris MTUs would not show significant differences between groups either. While running, during the first part of the contact phase the triceps surae and quadriceps femoris MTU are lengthening and so does the tendon and aponeurosis due to the developed forces (Hof et al., 2002; Sasaki and Neptune, 2005). During the second part of the contact phase the shortening velocity of the muscle fibres (contractile element, CE) is lower than the shortening velocity of the MTU due to the additional shortening of the tendon and aponeurosis (Roberts, 2002; Hof et al., 2002). Therefore at submaximal running intensities (velocities from 3.0 to 4.0 m s^{-1}) a more compliant quadriceps tendon and aponeurosis at lower force levels will increase the elongation of the series elastic element (SEE) during the first part of the contact phase and consequently decrease the shortening velocity of the CE during the second part of the contact phase (Biewener and Roberts, 2000; Bobbert, 2001). This way the CE increases its force potential due to the force–velocity relationship. A higher force potential of the CE would decrease the volume of active muscle at a given force or a given rate of force generation and consequently would decrease the cost of force production as well (Crow and Kushmerick, 1982; Roberts et al., 1997; Roberts et al., 1998a; Roberts et al., 1998b).

The VL muscle morphology (fascicle length, angle of pennation, muscle thickness) at rest did not differ between the runner groups. This suggests that the working range (width of the force–length relationship) of the VL is similar for all groups. Furthermore the maximal knee extension joint moments were similar at all analysed knee/hip joint angle configurations for the three groups of runners. The activation level during the maximal voluntary knee extension seems not to influence the above findings regarding the knee extension moments because the EMG-activities of the quadriceps femoris muscles did not differ between groups. The lack of differences in VL muscle architecture as well as in the maximal joint moments at different lengths of the quadriceps femoris MTU therefore supports the tenet that the other heads of the quadriceps femoris will also display similar fascicle lengths at all three groups. Thus we can conclude that the morphological properties of the quadriceps femoris muscles were not responsible for the differences in running economy in the examined runners.

It is well known from animal experiments that tendons reduce the mechanical work done by their muscle fibres in each step as a result of their elasticity (Biewener and Baudinette, 1995; Biewener et al., 1998; Biewener and Gillis, 1999) and reduce the metabolic cost of locomotion. During the loading phase, part of the mechanical energy coming from the mammal's body is stored as strain energy in the tendon and converted again into mechanical energy of the mammal's body in the following shortening phase (Biewener and Baudinette, 1995; Biewener and Roberts, 2000). Sasaki and Neptune reported that during submaximal running the energy stored in the SEE of the quadriceps femoris MTU is about 15% of the energy stored in all SEEs of the musculoskeletal system together (Sasaki and Neptune, 2005). Further the total mechanical work done (negative plus positive) by the quadriceps femoris CEs is about 42% of the total mechanical work done by all other CEs of the human system (Sasaki and Neptune, 2005). From this, 42% of the total mechanical work of the quadriceps femoris CE, approximately 70% is negative mechanical work (Sasaki and Neptune, 2005).

The above reports demonstrate that the mechanical work done by the CE and the energy conversion in the SEE of the quadriceps femoris MTU can contribute considerably to the metabolic energy consumption during running. The higher strain at similar exerted tendon force results into a higher energy storage in the tendon of the quadriceps femoris MTU in group 1. Fig. 7 shows the energy storage capacity of the tendon and aponeurosis and the percentage differences between the low/moderate economy and the most economical runners as a function of the tendon force. The values are calculated by fitting a second order polynomial equation to the experimental data in Fig. 4. Concerning the force–strain relationship of the tendon and aponeurosis at the quadriceps femoris we found that the groups 2 and 3 showed similar values. Therefore we considered these two groups together. For comparison of the energy storage capacity of the tendon and aponeurosis (Fig. 7), we presented the values of the high running economy *versus*
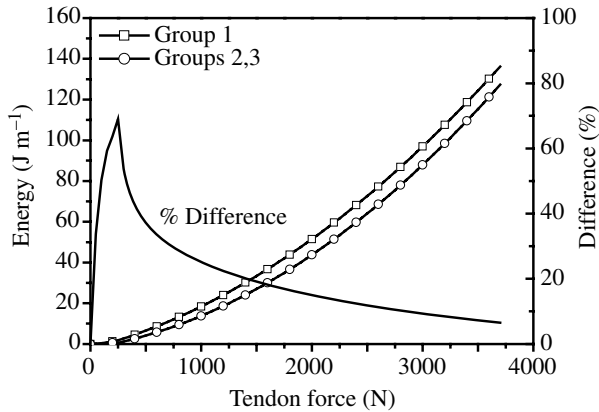
Fig. 7. Energy storage capacity of the tendon and aponeurosis as function of the tendon force between the runners of group 1 (high running economy) and the runners of groups 2 and 3 (moderate and low running economies), and percentage differences relative to group 1 in the quadriceps femoris muscle–tendon unit (as statistically significant differences in the force–strain relationship were found only between group 1 and both other groups, groups 2 and 3 have been considered together).

the moderate and low running economy runners. The percentage differences between the high economy group of runners and the other two groups in the energy storage capacity at medium and lower tendon forces (i.e. submaximal contractions) are higher than those at maximal forces. The higher ability of the most economical runners to store energy in their tendon and aponeurosis may increase the energy conversion in the SEE and at the same time decrease the negative and positive mechanical work done by the CE of the quadriceps femoris MTU. Therefore it is reasonable to assume that the ability of the most economical runners to achieve a higher energy conversion in the SEE could be an important issue causing the differences in running economy.

Higher contractile strength and tendon stiffness at the triceps surae

At the triceps surae MTU, group 1 shows a higher maximal contractile strength (about 36% higher ankle joint moments and calculated tendon forces) as well as a higher normalised stiffness relative to the other two groups. The higher plantarflexion moments of group 1 were observed at most of the analysed joint angle configurations (Fig. 5) indicating that the contributions of the different heads of the triceps surae to the total moment were similar for the three studied groups. The lack of differences in maximal ankle joint moments at short lengths of the triceps surae MTU (i.e. ankle plantarflexed and at the same time knee flexed positions) can be explained as follows. (1) Because of the parabolic curve of the force–length relationship of the triceps surae muscles (SOL, GM, GL) the group-related differences in plantarflexion moment would be reduced at short fascicle lengths. (2) The active insufficiency of the gastrocnemii at pronounced knee flexed positions, i.e. at short muscle lengths (Cresswell et al., 1995; Miaki et al., 1999)

would also reduce the group-related differences in the joint moments. At flexed knee-joint positions the gastrocnemii reach a critical shortened length at which, due to the force–length relationship, the torque output cannot be increased and therefore the gastrocnemii decrease their activation level (Cresswell et al., 1995; Kenedy and Cresswell, 2001). In accordance with these findings the examined runners decrease the EMG-activity of the triceps surae muscles at the more pronounced plantarflexion and knee flexion angles (Fig. 5).

The higher stiffness of group 1 (most economical runners) does not favour the muscle force generation based on a reduction of the shortening velocity of the muscle fibres nor the energy storage and return in the tendon at a given tendon force. However, a higher force would contribute to a higher energy storage and return at identical stiffness values of the tendons. This means that the energy storage capacity is oppositely affected by these two factors. Therefore from the present study, it is difficult to isolate the influence of the higher stiffness and higher maximal contractile strength of the triceps surae MTU on differences in running economy observed between the examined groups. Hof et al. used an inverse dynamics approach to study the triceps surae MTU at submaximal velocities (3.63 and 3.93 m s^{-1}) comparable to those in the present study (Hof et al., 2002). They showed that during running the subjects adapted to their own tendon stiffness values. Although the range of ankle joint motion was similar, the maximal muscle forces at the triceps surae during running were higher for the subject with the stiffer tendon (Hof et al., 2002). Unfortunately we don't have any data describing the ankle joint moments during running from our subjects. Therefore we can only speculate about possible adjustments in joint kinetics. From the results of the present study (higher contractile strength and higher tendon stiffness at the triceps surae for the most economical runners) and the reports from the literature (Hof et al., 2002) it seems that the functionality of the MTU at submaximal running is not only dependent on the stiffness of the SEE but also on the maximal strength of the CE.

Limitations

We measured the oxygen consumption of the whole body during running at three different velocities. We examined the mechanical and morphological properties of the triceps surae and quadriceps femoris MTUs, however, and argued that the differences found in the mechanical properties of these two MTUs may be responsible for the differences in running economy between the examined runners. This means that we assumed that the triceps surae and quadriceps femoris muscles are the main contributors to the energy expenditure while running. Earlier studies (Winter, 1983; Arampatzis et al., 2000) analysing submaximal running on the basis of inverse dynamics reported that the main contributors to the total mechanical work during running are the muscles acting around the ankle and knee joints (>70%). Similar studies based on forward dynamic simulations of running using a musculoskeletal model (Sasaki and Neptune, 2005) found that the mechanical work done by the CEs of the triceps surae and

quadriceps femoris muscles is about 68% of the mechanical work of all muscles CEs. In addition they reported (Sasaki and Neptune, 2005) that the energy storage in the SEEs of the triceps surae and quadriceps femoris MTUs is about 75% of the energy stored in the SEEs of the whole body. Based on all these studies, which rely on inverse dynamic analyses as well as on forward simulations, it is reasonable to assume that the triceps surae and quadriceps femoris MTUs may be representative of the energy expenditure of submaximal running.

In the present study we calculated tendon forces using tendon–moment arm data taken from the literature (Herzog and Read, 1993; Maganaris et al., 1998). It cannot be excluded that individual differences in the anatomical moment arms between groups could exist and could influence the calculated tendon forces. To estimate this potential source of error we analysed the ratio between tendon and aponeurosis displacement and ankle/knee joint angular rotation during a passive condition.

In order to do this we utilised the values from the correction of the tendon and aponeurosis elongation due to joint rotation (see Materials and methods). The average ratios were 0.55–0.69 mm deg.$^{-1}$ for the ankle joint and 0.42–0.54 mm deg.$^{-1}$ for the knee joint. There were no differences between groups in this ratios. Consequently it is likely that there were no differences between groups in the moment arms either. So a major influence of possible differences in lever arms between groups can be excluded.

Conclusions

All groups of runners (high, moderate and low running economy) showed similar kinematic characteristics during submaximal running, supporting earlier reports, which found that kinematic parameters cannot explain the complexity of running economy (Williams and Cavanagh, 1987; Martin and Morgan, 1992; Kyrölainen et al., 2001). The mechanical properties of the tendon and aponeurosis at the triceps surae and quadriceps femoris MTUs of the most economical runners showed clear differences from those of the moderate and low running economy groups. The quadriceps femoris of the most economical runners had a more compliant tendon at low force levels (< 45% of the MVC), whereas the triceps surae had a higher contractile strength and a higher tendon stiffness from 45% to 100% MVC. It is suggested that the more compliant quadriceps tendon and aponeurosis at low level forces will increase the force potential of the muscle while submaximal running and therefore would decrease the volume of active muscle at a given force generation. Further, we suggest that the efficiency of the triceps surae muscle contraction at submaximal running not only depends on the stiffness of the tendon and aponeurosis, but also on the maximal muscle strength.

List of symbols and abbreviations

CE	contractile element
EMG	electromyography
GL	gastrocnemius lateralis
GM	gastrocnemius medialis
MTU	muscle–tendon unit
MVC	maximal voluntary contraction
PCSA	physiological cross-sectional area
QF	quadriceps femoris
RF	rectus femoris
RMS	root mean square
SEE	series elastic element
SOL	soleus
TS	triceps surae
VL	vastus lateralis
VM	vastus medialis
$\dot{V}_{O_2}$	rate of oxygen consumption

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