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Influence of the mechanical properties of the muscle–tendon unit on force generation in runners with different running economy

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Abstract In earlier studies, we found more economical runners having a more compliant quadriceps femoris (QF) tendon at low force levels, and a higher contractile strength and stiffness at the triceps surae (TS). To better understand how these differences influence force generation economy and energy recovery, we simulated contractions using a Hill-type muscle model and the previously determined muscle properties as input parameters. For eight different activation levels, we simulated isovelocity concentric contractions preceded by an isovelocity stretch. The length changes and contraction velocities imposed to the muscle–tendon units (MTU) corresponded to those happening whilst running. The main results of the simulations were: (a) a more compliant tendon at low force levels (QF) led to an advantage in force-generation due to a decrease in shortening velocity of the CE, (b) a higher contractile strength and higher stiffness at the TS led to a disadvantage in force-generation at high activation levels and to an advantage at low activation levels. In addition at the high economy runners both MTUs showed an advantageous energy release during shortening, which at the QF was mainly due to a higher elongation of the SEE and at the TS mainly to the higher contractile strength. Especially at low activation levels both MTUs showed an advantageous force generation per activation and a higher energy release as compared to the low economy runners.

Although biomechanical studies could show that factors describing the body structure and running mechanics have the potential to influence running economy, the observed relationships are weak. For now no factor of critical importance has been identified (Cavanagh and Williams 1982; Heise and Martin 2001; Martin and Morgan 1992; Williams and Cavanagh 1987). It has been suggested that from a mechanical point of view, internal muscle–tendon properties related to the muscle force production are more suitable to explain differences in running economy than external mechanical factors (Martin and Morgan 1992). Consequently it has been pointed out that more research in this direction is needed (Heise and Martin 2001; Martin and Morgan 1992). Motivated by this, in an earlier study we examined the mechanical properties of the quadriceps femoris (QF) and triceps surae (TS) on 28 long distance runners by means of ultrasonography. A cluster analysis of their oxygen consumption identified groups having significantly different running economies. These groups revealed no differences in anthropometry or running kinematics. Concerning the properties of the muscle–tendon units (MTU), the QF of the more economical runners had a more compliant tendon at low force levels (<45% of the maximum voluntary contraction (MVC)), whereas the TS had a higher contractile strength and a higher tendon stiffness from 45% to 100% MVC.

Assuming that the observed differences effect running economy, there could be at least two mechanisms explaining this (Roberts 2002): (1) energy storage and recovery in the series elastic components (i.e. tendon and aponeurosis) (2) economy of force generation due to the force–length and force–velocity relationship. The literature (Alexander and Bennet-Clark 1977; Alexander 2002; Ettema 1996; Roberts et al. 1997; Roberts 2002) reports that the storage and recovery of mechanical energy in tendons is an important energy-conserving mechanism as it reduces the work a contractile element must do during running. Therefore it is necessary for a high efficiency (Ettema 2001). Both, a more compliant tendon and a higher exerted force contribute to a higher energy storage. The force generation due to the force–length and force–velocity relationship is dependent on the elongation of

1 Introduction

Many studies from different disciplines have tried to explain the interindividual variability in running economy in elite long distance runners (Daniels 1985; Saunders et al. 2004).

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the tendon and aponeurosis as they are operating in series with the contractile components. Thus a more compliant tendon reduces the shortening velocity of the muscle fibers and makes the force generation more economical due to the force–velocity relationship (Bobbert 2001; Ettema et al. 1990; Roberts et al. 1997; Roberts 2002). The effect of a more compliant tendon on force generation due to the force–length relationship, can be either positive or negative depending on whether it reduces or increases the difference to the optimum fiber length (Ettema et al. 1990). A higher elongation of the series elastic structures can be achieved by a more compliant tendon but also by a higher exerted force.

However, during running there is a complex interaction between all effects of the different examined properties of the MTU. They can both reinforce or counteract each other. As it is difficult to predict the behavior during a specific contraction, the purpose was to study the influence of the different experimentally examined mechanical properties on force generation by means of a model of the MTU applied to the TS and the QF. In order to do this we build a Hill-type muscle model, where the data pertaining to the high and low economy runners were used as input parameters. As we found significant differences in the force–strain relationship of the tendons for both MTUs and in force capability only for the TS, these parameters were adjusted for each group.

2 Method

2.1 Model of the muscle–tendon unit

The force production of the MTU was described by a Hill-type muscle model consisting of a series-elastic element (SEE) and a contractile element (CE), whose orientation with regard to the SEE is described by its pennation angle (α). The parallel elasticity of the MTU could be neglected because operations were performed only at the ascending limb of the force–length relationship. Following assumptions were done: Muscle thickness remains constant during contraction (Alexander and Vernon 1975; Epstein and Herzog 1998), and all muscle fibres are parallel and inserting at the same variable pennation angle on the tendon. As both elements are in series the following is valid for the forces:

$$F_{see}(t) = F_{ce}(t) \cos(\alpha(t)), \quad (1)$$

where F_{see} and F_{ce} represent the force in the series-elastic element and the contractile element, respectively. In a Hill-type muscle model the general form of the force produced by the contractile element is given by (Winters 1990)

$$F_{ce}(t) = q(t) f_{v_{ce}}(v_{ce}) f_{l_{ce}}(l_{ce}) F_{ce,max}, \quad (2)$$

where l_{ce} and v_{ce} are the time dependent length and contraction velocity of the CE, respectively; $f_{l_{ce}}$ is the normalized force of the CE due to the force–length relationship (force–length potential); $f_{v_{ce}}$ is the normalized force of the CE due to the force–velocity relationship (force–velocity potential); $q(t)$ is the active state; and the constant parameter $F_{ce,max}$ is

the maximum isometric force, which can be exerted at optimum CE length ($l_{ce,opt}$).

The force–length relationship of the whole CE was described by a parabolic model (van Soest and Bobbert 1993), with a parabola width (WIDTH) of 0.56 (van Soest and Bobbert 1993; Walker and Schrodt 1974) for all muscles. The force–velocity relationship of the CE was described by the classic Hill-Equation (Fung 1996; Hill 1938) for concentric contractions. For eccentric contractions a similar description was utilized (Spägle 1998). This latter assumes that for increasing lengthening velocities the force–velocity relationship converges to a value of $1.33 F_{ce,max}$. The ratio between the eccentric and concentric derivatives at $v_{ce} = 0$ (SLOPE-FACTOR) had a value of 2. The specific muscle parameters ($a_{rel} = 0.2175$ and $b_{rel} = 2.01$ Hz) are taken from van Zandwijk et al. (1996) and were the same for all muscles. The maximum shortening velocity can be calculated as $v_{ce,max} = (b_{rel} l_{ce,opt}) / a_{rel}$ utilizing $a_{rel} = a / F_{ce,max}$ and $b_{rel} = b / l_{ce,opt}$ (van Zandwijk et al. 1996) and $a / F_{ce,max} = b / v_{ce,max}$ (Fung 1996), where a and b are the parameters of the classical Hill-equation (Hill 1938).

The active state ($q(t)$) was described by the differential equation as proposed by Zajac (1989). Contrary to the original notation, we did not use an EMG signal as input. Instead we used a single rectangular pulse with a variable height and variable onset and offset times. Further in accordance to Hatze (1981) we defined a baseline activation $q_0 = 0.005$ in order to avoid numerical instability, so that $q(t)$ is of the interval $[q_0, 1]$. The value for the time constant $\tau_{act} = 0.012$ s was taken from Zajac (1989). No specific value for β was given. It was only stated, that the range for β has to be $0 < \beta < 1$. In accordance to Günther (1997), we set $\beta = 0.2$ for both muscles.

The behavior of the SEE is characterized by a force–strain relationship and its resting length ($l_{see,0}$). The force–strain relationship of the SEE includes all series-elastic components, e.g. tendon, aponeurosis and series-elasticity of contractile elements. Its behavior was described by a second-order polynomial:

$$F_{see}(\varepsilon) = k_1 \cdot \varepsilon + k_2 \cdot \varepsilon^2, \quad (3)$$

where ε stands for the strain. The parameters k_1 and k_2 are constants, which were estimated by fitting Eq. (3) to the experimental data.

Using the above information Eq. (1) was solved as an ordinary differential equation with the state variables $l_{ce}(t)$ and $v_{ce}(t) = \dot{l}_{ce}(t)$ by using the integration algorithm ‘ode45’ from the software Matlab (The Mathworks, Inc., Natick, USA).

2.2 Determination of the input parameters

The input parameters which have to be specified for the CE are the maximum isometric force ($F_{ce,max}$), the optimum CE length ($l_{ce,opt}$) and the optimum pennation angle (α_{opt}), which occurred at $l_{ce,opt}$. For the SEE the force–strain characteristic are specified by the constants k_1 and k_2 , and the resting length

($l_{\text{see},0}$). These parameters were determined experimentally. The used methods are only briefly explained. A detailed description can be found in Arampatzis et al. (2004, 2005a,b) and Stafilidis et al. (2005).

For the experimental determination of these parameters, the first duty was to find the joint configurations at which the exerted forces at the QF and TS are maximal. Therefore the athletes performed four maximal voluntary knee extending and three plantar flexing contractions. All joint angles are reported with respect to the anatomical neutral position (hip and knee extended and tibia perpendicular to the sole), where all joint angles are defined to be zero. The different joint positions for the knee extension were: hip flexed 40° and knee flexed 40° , 65° , 70° and 100° . For the plantar flexion the joint positions were: knee extended (0°) and ankle joint angles 10° dorsi flexed, in neutral position (0°) and 10° plantar flexed. The tendon forces were calculated by inverse dynamics for all positions. The lever arms of the Achilles and the Patellar tendons were determined using the data provided by Maganaris et al. (1998b) and Herzog and Read (1993).

Ultrasonography was used to determine optimum CE fascicle length, optimum pennation angle and tendon rest length of the gastrocnemius medialis (GM) and vastus lateralis (VL). The parameters describing muscle architecture (optimum fascicle length, optimum pennation angle) were measured directly during a MVC performed at the same joint configuration where maximum tendon force was achieved. These were defined as $l_{\text{ce,opt}}$ and α_{opt} . The pennation angle was 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 insertion of the fascicle into the upper and deeper aponeurosis. For the GM, the resting length of the tendon was defined as the length of the curved path between the tuberositas calcanei and the myotendinous-junction. For the VL, it was defined as the length between the tuberositas tibiae and the myotendinous-junction. They were both measured at a joint configuration, where passive joint moments were supposed to be minimized (Riener and Edrich 1999) in order to prevent any elongation of the tendon and aponeurosis. For the tendon of the GM, the ankle was plantarflexed 30° and the knee extended (0°). For the tendon of the VL, the hip and knee angles were flexed by 40° and 50° , respectively.

It should be considered that only the muscle and tendon properties of the VL and GM were determined experimentally. However, as the QF has four muscle bellies and the TS three, we estimated a mean muscle belly having a mean optimum fascicle length, a mean optimum pennation angle and a mean resting length. This was done using regressions calculated from data taken from the literature (Herzog et al. 1990; Hoy et al. 1990; Maganaris 2001, 2003; Narici et al. 1992; Out et al. 1996), weighted by the physiological cross-sectional areas (PCSA) which were also taken from the literature (Herzog et al. 1990; Out et al. 1996). This way for every specific muscle–tendon property $l_{\text{ce,opt}}$, α_{opt} and $l_{\text{see},0}$ we obtained the following respective factors: 1.014,

1.05 and 0.77 for the TS and 0.94, 1.27 and 1.23 for the QF. To obtain the mean muscle–tendon property the factors have to be multiplied by the corresponding experimentally determined property.

The maximum force the actuator can exert was calculated by using Eq. (1) and $\alpha = \alpha_{\text{opt}}$. To characterize the force–strain relationship, strain and tendon forces were identified and analyzed at 0, 15, 30, 45, 60, 80 and 100% of the maximum tendon force. The parameters for the force–strain relationship (k_1 , k_2) were estimated by a least square fit of Eq. (3) to the experimental data.

The above parameters were adjusted for the high and low economy runners according to the earlier study. Optimum fascicle length, pennation angle and the tendon rest length of the VL and GM as well as the maximum tendon force of the achilles and patellar tendon were measured directly. From these parameters the input values for the model were calculated as mentioned above. The values of all used input parameters are summarized in Table 1. The estimated force–strain relationship of both muscles and both groups is presented in Fig. 1. As we found no significant differences in the muscle architecture nor the tendon resting length between the groups, these were kept constant. Whereas the force–strain relation-

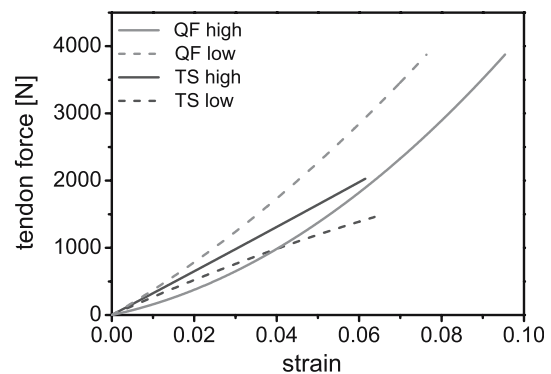


Fig. 1 The estimated force–strain relationship of the m. quadriceps femoris (QF) and m. triceps surae (TS) tendon of the high and low economy runners

Table 1 Parameter values for the m. triceps surae (TS) and m. quadriceps femoris (QF) muscle–tendon units adjusted to the high and low economy runners

	QF		TS	
	High	Low	High	Low
$F_{\text{ce,max}}$ [N]		4051	2342	1685
k_1 [kN/strain]	13.00	36.23	32.35	27.56
k_2 [kN/strain ²]	289.56	203.00	10.13	-73.24
$l_{\text{see},0}$ [m]		0.194		0.157
$l_{\text{ce,opt}}$ [m]		0.080		0.038
α_{opt} [$^\circ$]		17		34

The parameters are: The maximum isometric force of the CE ($F_{\text{ce,max}}$), the two constants describing the force–strain relationship (k_1 , k_2), the rest length of the SEE ($l_{\text{see},0}$), the optimum lengths of the CE ($l_{\text{ce,opt}}$) and the optimum pennation angles (α_{opt})

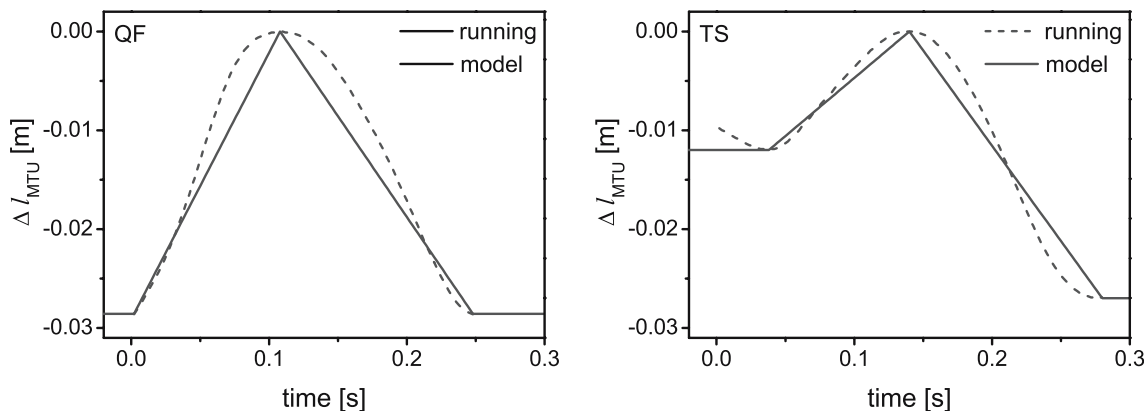


Fig. 2 Length of the m. quadriceps femoris (QF) and m. triceps surae (TS) muscle–tendon units during the contact phase in real running calculated from the kinematic data by using the regression of Hawkins and Hull (1990) (running) and the length used in the simulation model (model)

ship of the tendon was adjusted to the groups for both MTUs, muscle strength ($F_{ce,max}$) was adjusted only for the TS.

2.3 Simulations

We simulated isovelocity concentric contractions starting at optimum length of the MTU which were preceded by an isovelocity stretch. The optimum length of the MTU ($l_{MTU,opt}$) was defined as the length of the MTU at which the isometric muscle force is highest. As during running the TS and QF are working on the ascending limb of the force–length relationship (Herzog and Read 1991; Herzog 2000; Savelberg and Meijer 2003), the whole contractions take place at the ascending limb of the force–length relationship. The length changes and contraction velocities imposed to the MTUs correspond to those of the stretch-shortening cycle occurring during the stance phase of running (Fig. 2). Therefore the hip, knee and ankle joint angles were measured from 28 male long distance runners (body weight: 76.8 ± 6.7 kg, height: 182 ± 6 cm, age: 28.1 ± 4.5 years), whilst running on a treadmill at 3.5 m/s. There were no statistically significant ($p > 0.05$) differences between the high and low economy runners in ankle, knee or hip joint angles. Thus the mean from all subjects was used to obtain representative hip, knee and ankle joint angles during the stance phase of running. The lengths of the four individual muscles of the QF and the three individual muscles of the TS during the stance phase in running were calculated from these kinematic measurements and the regressions provided by Hawkins and Hull (1990). As we utilize a ‘mean’ MTU of the QF and TS, a mean time dependent length, weighted by the PCSAs was calculated. This method was already applied to compute the input parameters from the previous experimental data.

The parameters gained from the simulations were: the energy release of the SEE (E_{see-}), the force in the SEE (F_{see}), the force potential due to the force–length–velocity relationship ($f_{lce.vce} = f_{lce} \cdot f_{vce}$), the force potential due to the force–length relationship (f_{lce}) and the force potential due to the force–velocity relationship (f_{vce}). The comparison between

the high and low economy runners was limited to the shortening of the MTU. In order to compare F_{see} , $f_{lce.vce}$, f_{lce} and f_{vce} between groups, the integrals of each parameter against the time were calculated from the begin of shortening to the end of shortening. The difference between both groups for each examined parameter was expressed by the index I, as the percentage difference in relation to the low economy runners. A positive index indicates an advantage for the high economy runners.

The simulations were performed at eight different activation levels (30, 40, ..., 100%) and two different activation modes. Mode 1 (constant activation) having a constant activation level throughout the whole contraction and mode 2 (optimized activation) being identical to mode 1 but having an optimized switch off time. The switch off time was optimized in order to maximize the time integral of $f_{lce.vce}$ during the shortening of the MTU. The lengthening of the MTU always started from the equilibrium position. Exemplarily the time courses of the F_{see} from both MTUs calculated using the constant activation and representing the high economy runners are plotted in Fig. 3.

3 Results

Figure 4 shows the indices calculated for the energy release of the SEE (E_{see-}), the force of the SEE (F_{see}) and the force–length–velocity potential ($f_{lce.vce}$) for both MTUs obtained using the constant activation.

For the *m. quadriceps femoris*, all the three parameters showed positive indices for all activation levels (30–100%), i.e. an advantage in energy release and force generation for the MTU representing the high economy runners. However, these advantages decreased continuously with increasing activation levels (30–100%), the E_{see-} -indices decreased from 27.1 to 0.9%, the F_{see} -indices from 6.0 to 0.7% and the $f_{lce.vce}$ from 5.8 to 0.7%. As there were no differences in contractile strength for the QF between the high and low economy runners the F_{see} -indices and $f_{lce.vce}$ -indices were almost identical.

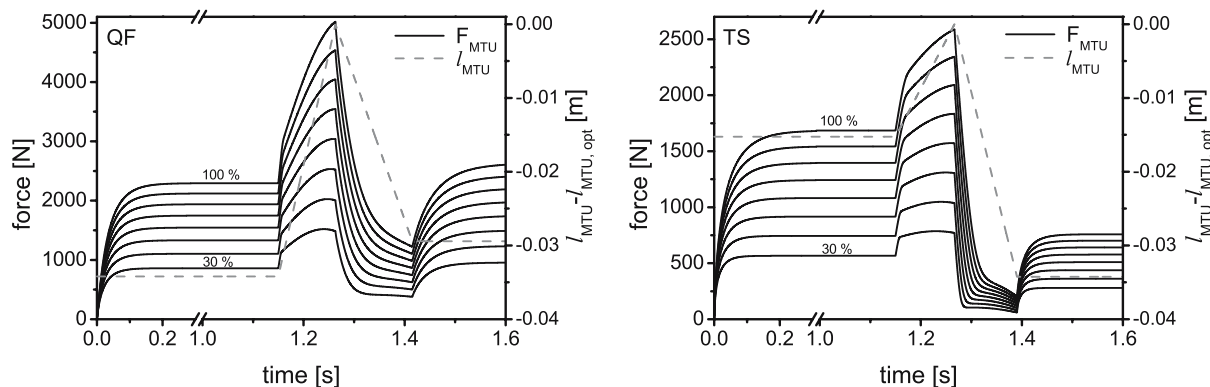


Fig. 3 Simulation results: force (F_{MTU}) in the m. quadriceps femoris (QF) and m. triceps surae (TS) muscle-tendon unit (MTU) at the examined activation levels (30 to 100%). The *dashed lines* are indicating the length of the MTU (l_{MTU}) with respect to its optimum length ($l_{MTU,opt}$)

For the *m. triceps surae*, the contractile strength of the high economy runners was 39% higher than that of the low economy runners. Therefore the behavior of the F_{see} -indices and the $f_{l_{ce}v_{ce}}$ -indices was obviously different. The MTU representing the high economy runners showed a great advantage for E_{see} - (54.0–17.8%) and F_{see} (46.1–25.0%) at all activation levels (30–100%). Same as for the QF this advantage decreased with increasing activation levels. The $f_{l_{ce}v_{ce}}$ -indices also decreased with increasing activation levels, but at 60% activation the values turned from positive into negative. Thus we found an advantage (5.1–1.9%) at low activation levels (30–50%) but a disadvantage (0.7–9.4%) at high activation levels (60–100%).

For the simulations at which the activation switch off time was optimized in order to maximize $f_{l_{ce}v_{ce}}$ during shortening, the deactivation started with or slightly after the onset of shortening for all calculations. At the QF the deactivation started 0.4–2.0 ms after onset of shortening for the high economy runners. For the low economy runners this happened 0.9–2.6 ms after onset, which was slightly later than for the high economy runners. However, this difference was below 0.7 ms for all activation levels. For the TS the deactivation started directly at the onset of shortening for the high economy runners. For the low economy runners it started directly at the onset of shortening for 30–50% activation and 0.1–0.8 ms later for 60–100% activation. Thus we obtained very similar results for both muscles and both groups. The calculations done for the low economy runners indicate only a slightly later deactivation onset. Concerning the calculated indices (Fig. 5), at the TS the values of all examined parameters were nearly the same as when using the constant activation for their calculation. In this case, for activation levels between 30% and 100%, the E_{see} -indices ranged from 54 to 17%, the force-indices from 49 to 23% and the $f_{l_{ce}v_{ce}}$ -indices from 5 to –10%. While at the TS both calculation modes led to the same results, at the QF the optimized activation enhanced the advantage for the MTU of the high economy runners in energy release and force production. At the QF the optimized activation led to higher E_{see} -indices (32–4%), higher F_{see} -indices (12–2%) and higher $f_{l_{ce}v_{ce}}$ -indices (12–7%) than the constant activation. Comparing

the F_{see} -indices and $f_{l_{ce}v_{ce}}$ -indices at the QF, it becomes evident, that the advantage for the high economy runners due to the force–length–velocity relationship was not completely transferred into force due to an earlier activation offset.

Table 2 presents the $f_{l_{ce}v_{ce}}$ -indices split up in their two components $f_{l_{ce}}$ - and $f_{v_{ce}}$ -indices for both muscles and both simulation modes. For *both muscles* the advantages or disadvantages due to the $f_{l_{ce}}$ remained nearly constant for all activation levels at a negligible low level (<1%), whereas the $f_{v_{ce}}$ -indices showed the same behavior and nearly the same values as the $f_{l_{ce}v_{ce}}$ -indices. Thus it becomes evident that the force–velocity relationship was the main responsible for the advantages and disadvantages due to the force–length–velocity relationship.

4 Discussion

We hypothesized that the different mechanical properties of the MTUs from the high and low economy runners are effecting running economy by means of the following two mechanisms: (1) energy storage and recovery in the series elastic components (i.e. tendon and aponeurosis), (2) economy of force generation due to the force–length and force velocity relationship. The results of the simulations support this hypotheses. At both muscles, the QF and the TS, we found a higher force potential due to the force–length–velocity relationship and a higher energy recovery, especially for submaximal contractions corresponding to those of running at velocities between 3.0 and 4.0 m/s.

4.1 M. quadriceps femoris: higher compliance of tendon and aponeurosis at low force levels

The simulations for the QF were performed with two different properties of the series-elastic component according to the experimental results. The series-elastic component, representing the QF tendon of the high economy runners, was more compliant than the one representing the tendon of the

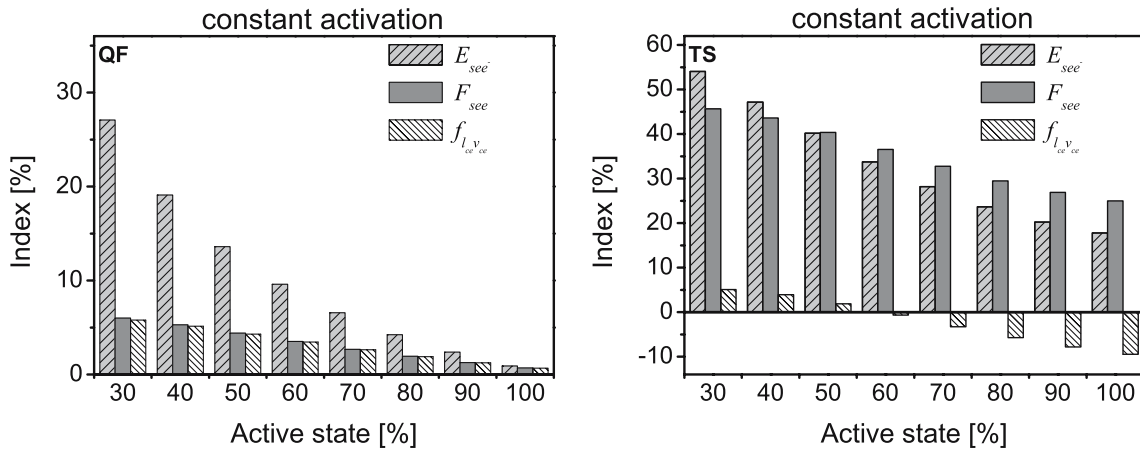


Fig. 4 Index values of the energy release (E_{see}), the force (F_{see}) and the force–length–velocity potential ($f_{l_{cc}v_{cc}}$) for the m. quadriceps femoris (QF) and m. triceps surae (TS) muscle–tendon unit obtained using a constant activation. The values represent the differences between high and low economy runners relative to the low economy runners

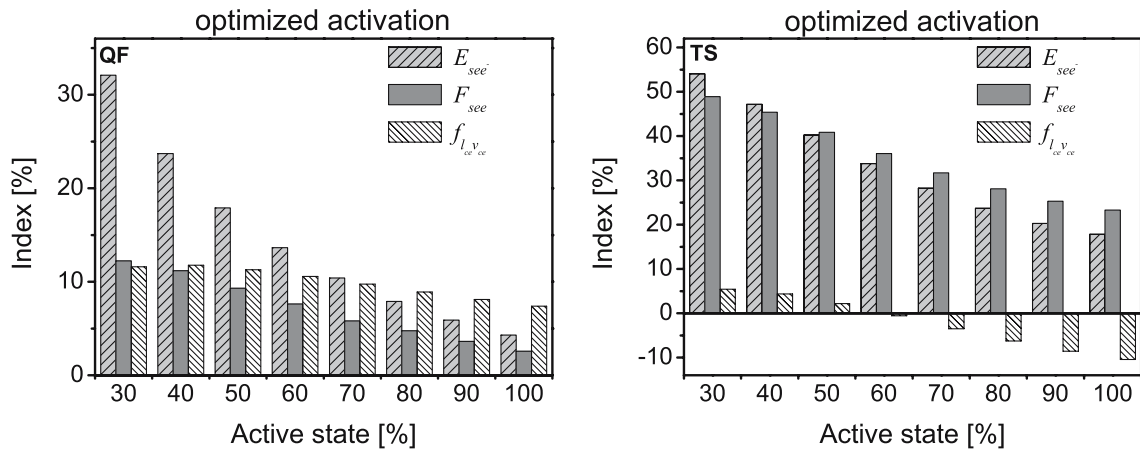


Fig. 5 Index values of the energy release (E_{see}), the force (F_{see}) and the force–length–velocity potential ($f_{l_{cc}v_{cc}}$) for the m. quadriceps femoris (QF) and m. triceps surae (TS) muscle–tendon units obtained using an optimized activation switch off time. The values represent the differences between high and low economy runners relative to the low economy runners

Table 2 Index values of the force–length relationship ($f_{l_{cc}}$) and force–velocity relationship ($f_{v_{cc}}$) of the m. quadriceps femoris (QF) and m. triceps surae (TS) muscle–tendon units obtained from the simulations

	Constant activation									Optimized activation							
	30	40	50	60	70	80	90	100	30	40	50	60	70	80	90	100	
QF	$f_{l_{cc}}$ [%]	0.5	0.6	0.5	0.5	0.4	0.3	0.3	0.2	0.6	0.8	0.9	0.9	0.9	0.9	0.9	0.8
	$f_{v_{cc}}$ [%]	5.4	4.6	3.8	3.0	2.3	1.7	1.1	0.6	11.6	11.8	11.3	10.6	9.7	8.9	8.1	7.4
TS	$f_{l_{cc}}$ [%]	-0.4	-0.5	-0.6	-0.7	-0.8	-0.9	-0.8	-0.7	-0.4	-0.4	-0.5	-0.6	-0.7	-0.7	-0.7	-0.6
	$f_{v_{cc}}$ [%]	4.8	3.8	2.2	0.2	-2.0	-4.2	-6.3	-8.1	5.0	4.1	2.3	0.0	-2.6	-5.1	-7.4	-9.4

The values represent the differences between high and low economy runners relative to the low economy runners

low economy runners. This higher compliance was limited to low force levels (0–45% MVC). The calculated stiffness of the quadriceps tendon from 0 to 45% MVC for the high and low economy runners was 29.8 and 43.4 kN/strain, respectively. Conversely these values were almost identical (57.5 and 58.8 kN/strain) for higher force levels (45–100% MVC).

The results from the simulations show advantages in force generation for the more compliant tendon. This is mainly

due to the force–velocity relationship. These results indicate that a more compliant tendon and aponeurosis would decrease the shortening velocity of the muscle fibres during running and lead to a higher force potential. The force potential is influenced by the force–velocity relationship and by the force–length relationship as well. The effect the more compliant tendon and aponeurosis has on the potential of the force–length relationship, seems not be relevant to the per-

formed contraction pattern. A higher force potential of the muscle fibers would decrease the volume of active muscle at a given force or a given rate of force generation. Consequently it would decrease the cost of force production as well. It is remarkable, that the effect of the more compliant tendon and aponeurosis is highest for submaximal contractions and almost vanishes for maximum contractions. Therefore it seems, that the higher compliance provides a specific advantage limited to low forces, i.e. to the demands of running at velocities from 3.0 to 4.0 m/s. This is further supported by the energy recovery of the quadriceps femoris tendon and aponeurosis. A higher energy recovery has been reported to be an important factor on running economy (Alexander and Bennet-Clark 1977; Alexander 2002; Ettema 1996; Roberts et al. 1997; Roberts 2002). We obtained a 1–27% higher energy recovery of the SEE for the more compliant condition. Again the highest advantages are obtained at submaximal contractions. The main responsible for the advantage in energy recovery, is the higher strain at the more compliant tendon. The higher force due to the higher force potential has only a marginal influence on the difference between both simulations in energy recovery (0–2%).

The simulations done with an optimized activation switch off time, lead to an enhancement of the advantage in both parameters: the energy recovery and the potential of the force–length–velocity relationship. It has been reported (Hof et al. 1983) that the activation pattern plays an important role in using the elastic energy and reaching a high efficiency. Studying the gastrocnemius muscle in rats in situ Ettema (1996) found that a stimulation cut off time well before the end of shortening is an important requirement for an optimal release of elastic energy. Our simulations support this although using an optimization criterion accounting only for the force potential. The results of these calculations suggest, that by considering only the simulations at constant activation, we may underestimate the effect of a more compliant tendon. A suited activation pattern would probably lead to a better utilization of the mechanical advantages.

4.2 M. triceps surae: higher contractile strength and higher stiffness

The simulations done for the TS were performed according to the experimental data, where we found a higher maximal contractile strength (about 39%) and a higher stiffness (30%). Consequently at the TS there are two factors affecting the energy storage capacity as well as the economy of force generation due to the force–length and force–velocity relationship.

The energy storage capacity is oppositely effected by these two factors. A higher force would contribute to a higher energy storage at identical stiffness values for the tendons. In contrast, a higher stiffness would contribute to a lower energy storage at a given force. When loading both SEE, representing the high and low economy runners, with the same percentage of their maximum tendon force, both SEE reach

Table 3 Strain in % of the SEE representing the high and low economy runners at forces from 30 to 100% of the maximum isometric force (F_{\max})

F_{\max} [%]	30	40	50	60	70	80	90	100
High	1.9	2.5	3.1	3.7	4.3	4.9	5.5	6.2
Low	1.7	2.3	2.9	3.5	4.2	4.9	5.6	6.4

similar strain values (Table 3). Thus the disadvantage due to the higher stiffness seems to be almost compensated by the higher forces. The advantages found in E_{see} for all activation levels are only due to the higher contractile strength of the high economy runners. Therefore it can be assumed that the effect of the higher force values in the examined groups is greater than the effect of the higher stiffness.

Concerning the economy of force generation also at the TS the effect of the force–length relationship on force generation is only marginal. Therefore an advantage in force generation can mainly be achieved by a reduction of the shortening velocity of the CE, which implies an increased velocity of the SEE. It has been reported in the literature that both factors, the stiffness of the SEE and the peak forces (Ettema et al. 1990), can influence the shortening velocity of the CE. A higher stiffness has been reported (Ettema et al. 1990; Roberts 2002) to lead to a higher shortening velocity for the same achieved forces and therefore to represent a disadvantage in the force–velocity potential. The effect a higher exerted force has on the velocity of the SEE cannot be easily predicted. Therefore we modified the inputs of the low economy runners in two different ways. First (higher F_{\max}) the only parameter adjusted to the high economy runners was F_{\max} . Second (higher stiffness) only the force–strain relationship of the SEE was adjusted. As we argued above, the higher stiffness of the SEE leads to a disadvantageous velocity of the CE at all activation levels (Fig. 6), whereas the higher F_{\max} leads to an advantageous velocity of the CE. Basing on these results it can be stated that both factors act oppositely with regard to the economy of force generation. The results of the simulations done for the TS, where both factors are combined, show higher shortening velocities of the CE expressed as disadvantages in the force–velocity relationship at high activation levels (60–100% MVC) and reduced shortening velocities of the CE at low activation levels (30–50% MVC). It can be assumed that at high activation levels the effects of the higher stiffness are dominant, whereas at low activation levels the effects of the higher peak force are dominant. These results support, that the functionality of the MTU is not only dependent on the stiffness of the SEE but also on the maximal strength of the CE. As we found almost no differences between the results of both activation modes, the above statements are valid for the constant activation as well as for the optimized activation.

4.3 Limitations

It is difficult to determine muscle properties in vivo. Therefore there are some aspects to be mentioned.

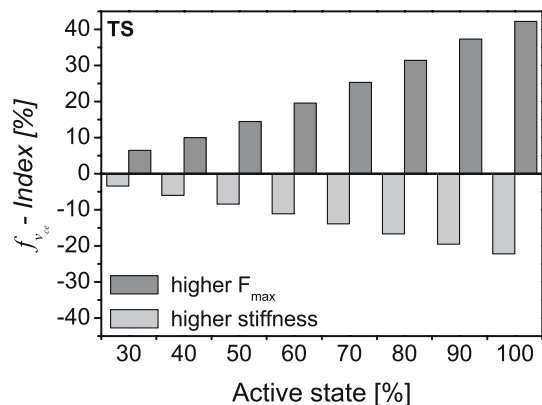


Fig. 6 Index values of the force–velocity potential ($f_{v_{ce}}$) calculated for MTUs having the low economy runners' properties but in one case higher F_{max} and in the other a higher SEE stiffness (both corresponding to the high economy runners). The values represent the relative differences in % to the low economy runners

The first aspect, which may influence the experimentally determined CE architecture, is that the individual muscles of the QF and TS reach their optimum fascicle lengths and therefore their force maximum at different joint angles (Herzog et al. 1990; Maganaris 2001, 2003). Thus the position, where maximum force is exerted, may differ from the position at which optimum fascicle length of the vastus lateralis (VL) or gastrocnemius medialis (GM) is reached. To minimize this influence we had chosen joint configurations for performing the MVCs, at which it is very likely that both muscles, the VL and GM, are acting at the plateau region or in its proximity at the ascending limb of the force–length relationship (Maganaris 2001, 2003; Savelberg and Meijer 2004). However, it is not possible to completely exclude any error. To estimate the influence the measured input parameters describing the muscle architecture may have on the model outputs and on the conclusions drawn from the results, we examined the sensitivity of the outputs of the used model to changes in the optimum pennation angle and the optimum fascicle length. The sensitivity was determined as described in Scovil and Ronsky (2005). It is defined as the normalized change in one model output from its original value due to a change in a model input parameter normalized to the unperturbed parameter value. For the TS each parameter was varied stepwise by $\pm 5\%$, $\pm 10\%$, $\pm 15\%$, $\pm 20\%$, $\pm 25\%$, and $\pm 30\%$. Thus the pennation angle was varied between 24° and 45° and the optimum fascicle length between 26 and 49 mm. These variations cover the ranges of fascicle lengths and pennation angles reported in the literature (Arampatzis et al. 2005c; Huijing 1985; Kawakami et al. 1998; Muramatsu et al. 2002; Out et al. 1996; Wickiewicz et al. 1983). In order to account for the range of reported QF muscle architecture (Herzog et al. 1990; Karamanidis and Arampatzis 2006; Wickiewicz et al. 1983), both parameters were varied up to $\pm 50\%$. This means a variation in pennation angle between 9° and 26° and in fascicle length between 40 and 120 mm. For the QF we found a sensitivity < 1 , which is considered to be small (Scovil and Ronsky 2005), for all analyzed outputs and the complete

range of perturbations. At the TS the sensitivity values are higher than for the QF, since the optimum pennation angle is bigger and the optimum fascicle length is smaller. In most of the cases the sensitivity remains below 1 for all analyzed outputs. Sensitivity values above 1 and below 25 are considered to be large (Scovil and Ronsky 2005). In some cases sensitivity values between 1 and 2 are found, just beyond the limit between small and large. Anyway, the conclusions drawn from the results are still valid for the complete range of perturbed pennation angles and fascicle lengths since only the absolute magnitudes of the advantages and disadvantages are changed. The range of obtained values for the different perturbations are given in Table 4.

Another aspect concerning the muscle architecture is, that to describe the behavior of the muscle–tendon unit, a so-called lumped-parameter model was used. This assumes that all fascicles have the same length and insert at the same pennation angle into the aponeurosis. There is experimental evidence for the TS that the fascicle length remains constant within the muscle (Maganaris et al. 1998a; Muramatsu et al. 2002). For the pennation angle Muramatsu et al. (2002) found that the proximal fascicles insert at smaller pennation angles than the remaining ones, whereas Maganaris et al. (1998a) did not find any significant differences. Muramatsu et al. (2002) investigated the fascicles more proximally than Maganaris et al. (1998a) did. From the above, it might be deduced that only the very proximal fascicles are different from the others and that the main portion of the muscle belly is almost homogenous. The differences reported by Muramatsu et al. (2002) were about $3^\circ - 4^\circ$ at rest and about 2° at MVC. This would correspond to a variation of about 6% in our model. Considering the results regarding the sensitivity of our model, such a variation should have only a very small influence on the outputs and consequently the conclusions drawn from the model calculations will remain unaffected. For the QF it can be supposed that they would have even a smaller influence on the results than at the TS, because of the smaller sensitivity due to the longer fascicles and the smaller pennation angles.

Concerning the determination of the maximum contractile strength, it is possible that the maximal isometric force of the QF and TS was not achieved during the MVCs. This can mainly be explained by muscle inhibition. In a study done with 12 subjects (22.9 ± 1.4 -years old) using the interpolated twitch technique Behm et al. (2001) found an average activation deficit value of 15.5% for the QF and of 5% for the plantarflexors. In his study only 7 from 12 participants were involved in a regular training program. Our subjects were all highly trained athletes from whom it can be assumed that the activation deficit is smaller than in normal trained subjects. Thus we may assume that the subjects from our study reached a higher voluntary activation level than that reported by Behm et al. (2001). Furthermore this would be a systematic error equally effecting both groups and should have no influence on the conclusions drawn from the results.

At last it has to be mentioned, that all conclusions and results presented in this paper are highly dependent on the simulated contraction patterns. We found that the influence of the force–velocity relationship is dominant over the influence

Table 4 Index values of the force–length–velocity relationship ($f_{l_{ce}v_{ce}}$), tendon Force (F_{see}) and energy release of the tendon (E_{see-}) of the m. quadriceps femoris (QF) and m. triceps surae (TS) muscle–tendon units

	$f_{l_{ce}v_{ce}}$			F_{see}			E_{see-}		
Perturbation [%]	–50	0	+50	–50	0	+50	–50	0	+50
QF $l\alpha_{opt}$ [%]	–12 to 7	–10 to 5	–5 to 5	–12 to 7	–10 to 5	–5 to 5	–12 to 7	–10 to 5	–5 to 5
QF $l_{ce,opt}$ [%]	–12 to 7	–10 to 5	–5 to 5	–12 to 7	–10 to 5	–5 to 5	–12 to 7	–10 to 5	–5 to 5
TS Perturbation [%]	–30	0	+30	–30	0	+30	–30	0	+30
TS $l\alpha_{opt}$ [%]	–12 to 7	–9 to 5	–5 to 5	23 to 48	25 to 46	27 to 43	17 to 57	18 to 54	20 to 51
TS $l_{ce,opt}$ [%]	10 to 13	–9 to 5	–9 to 3	24 to 54	25 to 46	26 to 43	20 to 62	18 to 54	17 to 52

The values represent the differences between high and low economy runners relative to the low economy runners

of the force–length relationship. However we only simulated contractions, at which the shortening started when the CE is near its optimum length. At this region the slope of the force–length relationship is low. It is at least probable that for other contractions the effects of the force–length relationship on force generation would be higher.

5 Conclusion

The present results show that both the QF and TS MTUs elicited a higher $f_{l_{ce}v_{ce}}$ especially for submaximal contractions corresponding to those occurring while running at velocities between 3.0 and 4.0 m/s. Therefore it can be inferred that (a) a more compliant tendon (QF) leads to an increase in $f_{l_{ce}v_{ce}}$ at low force levels, which is due to a decrease in shortening velocity of the CE; (b) a higher contractile capability and a higher stiffness in the TS influences not only the absolute force generation but also the $f_{l_{ce}v_{ce}}$. In addition both MTUs show a higher energy release. In the QF this was mainly due to a higher elongation of the SEE and in the TS it was mainly due to a higher contractile strength.

The higher $f_{l_{ce}v_{ce}}$ will allow the muscles to exert higher forces for a given activation level. If we assume that identical submaximal activation levels imply a similar activated muscle volume, it can be deduced that a higher $f_{l_{ce}v_{ce}}$ decreases the metabolic cost of force production, i.e. enhance the efficiency. In addition the lower shortening velocity does not only decrease the metabolic cost of force production through a higher force potential, but also through a lower shortening heat rate (Hill 1938). Furthermore, the elastic properties of tendons reduce the muscular mechanical work during each step in running (Roberts et al. 1997; Roberts 2002). Thus the higher $f_{l_{ce}v_{ce}}$ and the ability of a higher energy release in the high economy runners contribute to a higher muscular efficiency and hence reduce the metabolic cost of running compared to the low economy runners. This suggests that the observed differences in the mechanical properties of the MTUs at least partially explain the differences in running economy and supports the assumption that internal mechanical properties directly related to force production are suitable to explain differences in running economy.

The assumption that muscle volume is about the same in both groups is very likely for the QF, since both groups did not

show any differences in $F_{ce,max}$, muscle thickness, fascicle length and pennation angle. In the TS the lack of differences between the groups in fascicle length, muscle thickness, angle of pennation, tibia length and body mass points toward no differences in muscle volume as well. Factors at the level of cross-bridge interaction (D'Antona et al. 2003; Frontera et al. 2000) could be responsible for the differences in $F_{ce,max}$. However some uncertainties still remain and it is recommended for further studies to assess the entire muscle volume as well.

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