THE INFLUENCE OF TENDON YOUNG'S MODULUS,
DIMENSIONS AND INSTANTANEOUS MOMENT ARMS
ON THE EFFICIENCY OF HUMAN MOVEMENT

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Abstract—The purpose of the study was to examine the influence of passive tendon work on the gross mechanical efficiency of human whole body movement.

Seven male subjects participated in the study. They performed repetitive jumps (like skipping) of three different intensities. Metabolic costs and work rates were recorded to obtain mechanical efficiencies. Net joint moments were calculated from film recordings using inverse dynamics.

A general stress-strain relationship for tendons was modelled using a quadratic function, including Young's elastic modulus of tendon tissue and tendon dimensions. Instantaneous tendon moment arms for the largest leg extensor muscles (m. triceps surae and m. quadriceps femoris) were calculated using joint angle-moment arm transfer functions obtained from the literature (cadaver studies) and the tendon work was calculated from the net joint moments.

Gross efficiency values of 0.65-0.69 and efficiency values of 0.77-0.80 at the approximate level of the muscle-tendon complexes were observed. The tendons performed 52-60% of the total work. The enhancement of the muscle-tendon efficiency over the maximal theoretical efficiency of the contractile machinery (0.30) could exclusively be explained by the contribution of the tendon work. A clear negative relationship between repetitive jumping with high mechanical efficiency and running economy at 12 km h⁻¹ was found.

Using model calculations the gross efficiency and the muscle-tendon efficiency were shown to be sensitive to tendon Young's modulus, dimensions and moment arms. The efficiencies were most sensitive to changes in the tendon moment arms. A 10% decrease in tendon moment arm results in a 13% increase in the gross efficiency. Optimization or minimization of the mechanical efficiency by changing the tendon variables 5% was followed by changes in mechanical efficiency of +14% and -10%, respectively.

INTRODUCTION

The energy transfers in biological 'machines' are complex although the efficiency of whole body movements and the muscle actions involved can be explained in rather simple terms.

The gross efficiency of movement (eG) is defined as the ratio between the mechanical power transfer from the body to the environment (PM) and the rate of production of chemical energy for body functions (Pi).

The muscle efficiency, at the level of the muscle fibres (eM) is defined as the ratio between the mechanical power output (eccentric and/or concentric) from the contractile machinery of the muscles (PJ) and the difference between PM and the power consumed by maintenance of other body functions (Pn) (definitions and symbols according to Ingen Schena and Cavanagh 1990).

The energy source for human movement is the chemical energy in food. Approximately a fraction of 0.70 of the chemical energy is lost as heat during the re-synthesis of ATP (Åstrand and Rohdal, 1977) and energy is further consumed for maintenance of the basic body functions (basic metabolism, stabilising muscle actions and the action of the heart and the digestive tract). The remaining part is available for the muscles to generate positive work on the surroundings or resist negative work. Therefore, eM during, e.g. force generation (concentric muscle action) will always be less than 0.5.

During whole body movements muscle work is lost through friction, plastic deformation of tissues within the body and during co-contractions, where the muscles work against each other. At the same time some of the mechanical energy generated (concentric action) or resisted (eccentric action) by the muscles is conserved due to work against the conservative forces of elastic structures in the body. This conserved energy may be used in a later phase of the movement. The net result of the above mentioned processes is the rate of mechanical work performed on the environment (PM). If no energy is conserved before concentric muscle action eM will be lower than eM, even when PM is subtracted from PM, but if considerable amounts of energy are conserved and reused, eM will eventually increase to levels higher than the muscle efficiency (Thys et al. 1975).

During concentric muscle action starting either after an isometric state or immediately after an eccentric muscle action, i.e. in a stretch-shortening cycle,
the muscle efficiency ($e_{\text{conc}}$) rarely exceeds 0.25 (Haan et al., 1989). At the level of the muscle–tendon complex the reported efficiencies ($e_{\text{mech}}$) during concentric muscle–tendon action range from 0.14 to 0.40 (for a review see Ingen Schenau and Cavanagh, 1990). When stretch-shortening cycles are involved in the muscle–tendon action, $e_{\text{mech}}$ nearly always exceeds 0.30, which indicates that some mechanical energy is conserved in the elastic structures of the muscle–tendon complex during the stretch and reused during the shortening.

The series elasticity of a muscle is the combined elasticity of the muscle fibres and tendinous structures, i.e. cross-bridges, actin/myosin filaments, Z-lines, aponeuroses and free tendons. When the efficiency during the concentric part of stretch-shortening cycles at the level of the muscle fibres ($e_{\text{conc}}$) fails to exceed 0.30, the ability of the active cross-bridges and other series-elastic structures in the muscle fibres to store and reuse elastic energy must be small compared to the elastic potential of the tendinous structures. This is supported by Alexander and Bennet-Clark (1977) who estimated the capacity of the cross-bridges to store elastic energy to be approximately 1% of the capacity of tendon tissue.

The stress–strain relationship for tendons is non-linear and which is a consequence of the organisation of the macromolecules in the collagen fibres (Vilarta and Vidal, 1989) and of the collagen fibres in the tendon (Abrahams, 1967). The amount of energy stored in and released from tendons during cyclic loading (i.e. the mechanical work performed by the tendon) can be determined by the area under the stress–strain relationship.

The shape of the stress–strain relationship for individual tendons varies (Abrahams, 1967; Ker, 1981; Riemersma and Schamhardt, 1985; Shadwick, 1990) but as an approximation this relationship can be described by a quadratic function (Ingen Schenau 1984). The elastic work performed by a given tendon can be calculated as the area under this function after a proper scaling of tendon variables obtained from the literature including the Young's modulus of the tendon tissue. Perhaps compensating for hysteresis and strain rate dependence (Zajac, 1989).

For a given muscle transfer of the linear force produced by the muscle fibres to joint moment (via the tendon) is determined by the length of the instantaneous tendon moment arm. In a given movement that requires a certain average level of joint moments, short tendon moment arms will increase the average tendon forces compared to the tendon forces acting during the performance of the same movement, but with longer tendon moment arms. The amount of energy that is stored in the tendons is a function of the tendon force and therefore, subjects with short tendon moment arms might take more advantage of elastic energy stored in and released from the tendons during movement, than subjects with longer moment arms.

As stated above, the elastic work of the tendinous structures in the muscle–tendon complex enhances the mechanical efficiency of movement. The combination of Young's modulus of the tendon tissue, the tendon dimensions and the length of the tendon moment arms determines the amount of work performed by the tendons during a given work task. Therefore, there might be a close relationship between the magnitude of these variables and the mechanical efficiency of the work performed by individual subjects. This relationship has never been demonstrated and consequently the purpose of the present study was to investigate the influence of tendon Youngs modulus, tendon dimensions and tendon moment arms on the mechanical efficiency of human movement.

**MATERIAL AND METHODS**

**Subjects and experimental procedures**

Seven medium to well-trained male subjects participated in the study. Age: 31 ± 5 yr, height: 1.80 ± 0.05 m and body weight: 76 ± 5 kg (mean ± S.D.) The subjects gave their informed consent before they participated in the study.

Approximately one month before the experiments the subjects were asked to practice with a skip rope for 15–20 min, 3 times a week in order to accustom themselves to repetitive jumping and to assure that the jumping could be performed under steady state conditions and without fatigue. None of the subjects had difficulties in learning and sustaining the work tasks during the following experiments.

The measurements were for practical reasons carried out on two different days.

The first day the subjects were asked to perform horizontal running at 12 km h⁻¹ on a treadmill, and three series of repetitive jumping (Fig. 1).

After 8 min of standing rest the subjects were asked to run for 8 min. Expired air was collected during the last 2 min of the resting and of the running period (steady-state conditions were assumed to be reached within 4–6 min of work). The air was collected in four successive 30 s intervals and analysed immediately (Jaeger, ErgOxyscreen). Then the subjects performed the three series of repetitive jumps on a force plate.

*Fig. 1. Small repetitive jumps. The stick diagrams represent every 15th picture from the film recording (200 frames s⁻¹). The vertical ground reaction force ($F_y$) (both feet) is superimposed. The peak force in the figure is 3450 N.*
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(AMTI OR6-5-1), barefoot, and with their hands on the hips. They jumped at a basic frequency of 2 Hz and the work intensity was changed by changing the contact time. A short contact time (SCT), a long (LCT) and the preferred (PCT) were used. The subjects were paced by a programmable tone generator. PCTs were paced by one tone. SCT and LCT were paced by two tones, a low-pitch tone signalling the time of touch down and a high-pitch tone signalling the time of take off. The high-pitch tone was set at 10% (SCT) and 70% (LCT) of the cycle time in all experiments. The sequence of the jumping tasks was chosen randomly. The subjects jumped in periods of 6 min. Expired air was sampled during the last 2 min and analysed as mentioned above. During the same period the vertical ground reaction force ($F_v$) was sampled (DT2801A) directly into a PC at 500 Hz. Two minutes after each work bout a blood sample was collected in a small glass tube directly from a finger tip in order to determine the concentration of blood lactate. The tube was sealed and stored on crushed ice and the blood samples were analysed immediately after each experiment (Analox P-LMS). At the beginning of each experiment the flowmeter of the ErgOxyscreen was calibrated with a known flow and just before each recording the O$_2$- and CO$_2$- analysers were calibrated with known gas concentrations in an air mixture analysed using the Scholander method.

On the second day the subjects performed the same jumping tasks as described above. The movements were filmed with a high-speed camera (TeleDyne DBM45) at 200 frames s$^{-1}$ from the right side in the sagittal plane. Markers were placed on the following anatomical landmarks on the right side in order to delimit the body segments and the angles between them: 5th metatarsal joint, tip of the lateral malleolus, lateral epicondyle of the knee, the top of trochanter major and the side of the neck at the level of 5th cervical vertebra. Each film sequence was recorded after 4 min of jumping and covered a minimum of 10 successive jumps. The subjects jumped on two force plates (AMTI OR6-5-1), one foot on each. The vertical ground reaction force ($F_v$), the sagittal reaction force ($F_s$) and the reaction moment around the frontal axis of the force plate ($M_z$) under the right foot and $F_v$ under the left foot were recorded. The ground reaction signals were sampled (DT2801A) directly into a PC. The analog signals and the film recordings were synchronized by simultaneously switching a LED on in the photographic field and sending a TTL pulse to a separate channel on the A/D-converter.

Data treatment and calculations

Film calculations. The high-speed films were transferred to video (Elmo TRV-166) and the coordinates of the markers were digitised automatically (Peak Performance Technologies ver 5.0). The coordinates were low-pass filtered at 6 Hz. The cutoff frequency was chosen from a residual analysis of the coordinates (Winter, 1990). The centre of pressure ($P_c$) was calculated as $\frac{1}{M_c} \int F_c(t) \cdot f_c(t) \, dt$. A four-link segment model of the body with lumped feet, shanks, thighs and head, arms, and trunk was used. Joint angles and angular velocities were calculated from the filtered coordinates and net joint moments at the right ankle, knee and hip joints were calculated using inverse dynamics incorporating $F_s$, $F_v$ and $P_c$.

Model calculations. The calculation procedure is illustrated in Fig. 2.

The 4-segment model was equipped with two big leg extensor muscles, a lumped quadriceps femoris muscle acting at the knee and a lumped triceps surae muscle at the ankles and the net joint moments at the ankles and the knees were used to calculate the tendon work. The work produced at the hip joints was neglected in the calculations (see discussion).

![Fig. 2. Flow diagram of the calculations (see text for further explanation).](image-url)
The stress–strain relation of the tendons was modelled using a quadratic function

\[ F_T = k \Delta l^2, \]

where \( F_T \) is the tendon force and \( k \) a constant. The constant \( k \) was calculated as described in a previous study (Voigt et al., 1994) as

\[ k = \frac{Y A_T (e_{max} - e_T) 10^2}{(e_{max} l_0)^2}, \]

where \( Y \) is the normalized tangent elastic modulus of the tendon (Young’s modulus of tendon tissue), \( A_T \) the cross-sectional area of the tendon, \( e_{max} \) ultimate strain or the ‘yield point’, \( e_T \) the length of the toe piece, defined as the intercept between the extrapolation of the linear part of the stress–strain curve and the abscissa in the stress–strain diagram and \( l_0 \) the resting length of the tendon.

The variables in equation (2) were obtained as literature data from in vitro experiments on human tendon specimens. The following values were used in the tendon model (see Voigt et al., 1994 for references): \( Y = 1.2 \text{ GPa}, e_T = 2\%, e_{max} = 6\%, l_0 = 0.364 \text{ m} \) (m. triceps surae) and \( 0.231 \text{ m} \) (m. quadriceps femoris) and \( A_T \) (one leg) = \( 0.625 \times 10^{-4} \text{ m}^2 \) (Achilles tendon) and \( 2.50 \times 10^{-4} \text{ m}^2 \) (quadriceps tendon). These values represent averages of the values reported for human tendons.

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The instantaneous moment arms (\( a_i \)’s) for the Achilles tendon and the quadriceps tendon were obtained from the data presented by Spoor et al. (1990) and Spoor et al. (1992). Least-squares polynomials were fitted to the reported relationships between the enclosed joint angle and moment arm length (Table 1).

The ankle and knee joint angles obtained from the film then served as input to the polynomials. The absolute values of \( a_i \)’s were obtained by applying the individual segment lengths in the calculations.

### Table 1. Least-squares polynomial coefficients for transfer functions between the enclosed joint angle (\( \Theta \)) and instantaneous tendon moment arms at the ankle joint (Achilles tendon) and the knee joint (rectus femoris part of the quadriceps tendon)

<table>
<thead>
<tr>
<th>Coefficients</th>
<th>Ankle</th>
<th>Knee</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a )</td>
<td>(-5.03442 \times 10^{-1})</td>
<td>(-8.36305 \times 10^{1})</td>
</tr>
<tr>
<td>( b )</td>
<td>(1.10351 \times 10^{9})</td>
<td>(3.46853 \times 10^{-1})</td>
</tr>
<tr>
<td>( c )</td>
<td>(-4.78432 \times 10^{-1})</td>
<td>(-4.4736 \times 10^{-2})</td>
</tr>
<tr>
<td>( d )</td>
<td>(-2.00026 \times 10^{-7})</td>
<td>(3.12694 \times 10^{-4})</td>
</tr>
<tr>
<td>( e )</td>
<td>(-7.15577 \times 10^{-7})</td>
<td>(-7.15577 \times 10^{-7})</td>
</tr>
</tbody>
</table>

Note: The least-squares polynomials had the form \( a + b \Theta + c \Theta^2 + d \Theta^3 + e \Theta^4 \). A 3rd order polynomial was used at the ankle joint and a 4th order polynomial was used at the knee joint. The resultant moment arms are expressed in percentage of the shank and the thigh lengths, respectively.

The tendon force \( (F_T) \) was calculated as the net joint moments (multiplied by 2) divided by the instantaneous tendon moment arm. The tendon length changes \( (\Delta l) \) were then calculated from equation (1) and the rate of length changes \( (r_T) \) was obtained by differentiating \( \Delta l \) in time. Finally the tendon work rate \( (P_T) \) was calculated as \( F_T r_T \). The average \( P_T \) (stretch also defined as positive) over 10 successive jumps was used for further calculations.

The influence of tendon strain rate on the elastic modulus is not evident for large tendons (Ker, 1981; Riemsma and Schamhardt, 1985) and the hysteresis of large mature tendons lies between 6 and 11% (Bennet et al., 1986; Ker, 1981; Riemsma and Schamhardt, 1985; Shadwick, 1990). The influence of these two factors on the tendon work rate calculations was considered to be small and therefore ignored in the calculations.

### Calculations of movement economy

#### Gross efficiency

The steady-state oxygen uptake \( (V_o) \) during a given work task was calculated as the mean of the four samples collected during the last two minutes of each work period. An energy equivalent of 20.93 kJ \( \text{1O}_2^{-1} \) (corresponding to an average respiratory quotient (RQ) of 0.8) was used for the calculation of the total energy expenditure \( (P_t) \) as

\[ P_t = \frac{20.93}{60} \times 10^3 V_o W. \]

where \( V_o \) was measured in l min \(-1\).

The \( F_z \) recorded simultaneously with the collection of expired air was used for calculating of the mechanical power or work rate \( (P_m) \). The average velocity of the mass centre of the body during ground contact was obtained as the average of the time integral of \( F_z \) after dividing by the body mass and subtracting the gravitational acceleration. The velocity was then multiplied by the average \( F_z \) and divided by the cycle time. Thereby the work rate during the downward movement of the mass centre of the body was also defined as positive and the work rate was calculated as the average work rate over the movement cycle and not exclusively during ground contact where it was produced. The average work rate over 40 successive jumps was used to determine \( P_m \) for a given jumping task.

The gross efficiency \( (e_g) \) could then be calculated as

\[ e_g = \frac{P_m}{P_t}. \]

#### Muscle efficiencies

The total work rate of the active muscle–tendon complexes \( (P_{m,tot}) \) during movement must always be the sum of the work rates of eccentric \( (P_{ecc}) \) and concentric \( (P_{conc}) \) muscle fibre actions and the tendon work rate \( (P_t) \), i.e.

\[ P_{m,tot} = P_{ecc} + P_{conc} + P_t \]

(note that the stretch and the shortening work in this equation have the same sign (positive)). When
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PM,mtc as defined above is used for the calculation of the mechanical efficiency it should be noted that the energy expenditure is not strictly related to the energy demanding work produced by the muscle fibres but also to the elastic and no-energy demanding tendon work. The total energy expenditure therefore can be expressed in the following way:

\[
P_{\text{M,mtc}} = \frac{PC_{\text{ecc}}}{e_{\text{ecc}}} + \frac{PC_{\text{conc}}}{e_{\text{conc}}} + P_T.
\]

where \( e_{\text{mtc}} \) is the mechanical efficiency of the muscle–tendon work and \( e_{\text{ecc}} \) and \( e_{\text{conc}} \) the mechanical efficiencies of eccentric and concentric muscle fibre work.

Equation (6) can only be applied to whole body movements, where the mechanical work is measured as work on the surroundings, if it is assumed that the work (or work rate) performed by the muscle tendon complex (PM,mtc) is transferred to the surroundings without a significant loss of mechanical energy, and when the energy expenditure that does not contribute to the generation of muscle–tendon work on the skeleton (PM) is subtracted from the total energy consumption (P1). This was assumed in this study and therefore we calculated \( e_{\text{mtc}} \) as

\[
e_{\text{mtc}} = \frac{P_{\text{M,mtc}}}{P_1 - P_{\text{m}}} = \frac{P_{\text{M,mtc}}}{P_{\text{I,mtc}}}.
\]

where \( P_{\text{I,mtc}} \) is the energy expenditure due to the muscle–tendon work generating the movement. \( P_1 \) was calculated from the oxygen consumption measured at standing rest according to equation (3).

During cyclic movements like horizontal walking and running, and repetitive jumping, the sum of the negative and positive work is zero and therefore the concentric and eccentric work rates were calculated as

\[
P_{\text{eco}} = P_{\text{conc}} = 0.5(P_{\text{M}} - P_T).
\]

The two unknowns \( e_{\text{eco}} \) and \( e_{\text{conc}} \) were obtained from the literature. Assuming an \( e_{\text{eco}} = 1.2 \) (Asmussen, 1952) \( e_{\text{conc}} \) was calculated, and assuming an \( e_{\text{cone}} = 0.25 \) (Haan et al., 1989) \( e_{\text{eco}} \) was calculated.

![Figure 3](image_url)

Fig. 3. A typical example of joint angles, angular velocities, net joint moments and net joint powers (right leg) from a subject performing repetitive jumping at 2 Hz with preferred contact time. The subject was filmed at 200 frames s\(^{-1}\). Each set of curves represents the right leg and was calculated as an average of 10 successive jumps (± 1 S.D.).
Running economy. Running economy was calculated according to its definition (Ingen Schenau and Cavanagh, 1990) as the oxygen uptake obtained during steady-state running divided by the body mass of the subject and expressed in ml O$_2$ min$^{-1}$ kg$^{-1}$.

Statistics

Changes were tested with the Friedman two-way analysis of variance by ranks and association was measured by the Spearman rank-order correlation coefficient ($r_s$) (Siegel and Castellan, 1988).

The critical level of significance was set at $p<0.05$.

RESULTS

No significant differences were found between the ground reaction forces under the left and right foot. The subjects were very good in maintaining the basic jumping frequency (2 Hz ± 4%), however, all subjects showed a considerable variation in kinematic and dynamic variables between successive jumps as exemplified in Fig. 3. Figure 4 shows typical differences in kinematic and dynamic variables between the three different jumping tasks.

The measured ground contact times were $0.297 \pm 0.034$ s (SCT), $0.359 \pm 0.059$ s (PCT) and $0.383 \pm 0.027$ s (LCT). SCT was significantly shorter than PCT and LCT. The mechanical work rates ($P_m$) were $585 \pm 59$, $517 \pm 78$ and $479 \pm 48$ W and the corresponding work rates of the tendons were 60%, 54% and 52% of $P_m$ respectively (Table 2). The average tendon strain rates in the modelled triceps surae during the loading phase were $65 \pm 14\% \text{ s}^{-1}$ (SCT), $36 \pm 10\% \text{ s}^{-1}$ (PCT) and $35 \pm 14\% \text{ s}^{-1}$ and

![Fig. 4. Joint angles, angular velocities, net joint moments and net joint powers (right leg) during repetitive jumping at 2 Hz with three different contact times corresponding to three different work rates. Short (x), long (o) and preferred (no mark). The data are from the same subject as shown in Fig. 3. The subject was filmed at 200 frames s$^{-1}$. Each curve is the average of 10 successive jumps.](image-url)
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Table 2. Measured oxygen consumptions during rest, running and repetitive jumping at 2 Hz, lactate levels, calculated mechanical work rates and efficiencies (seven subjects, mean and in parenthesis 1 S.D. expressed in percent of the mean)

<table>
<thead>
<tr>
<th></th>
<th>Standing rest</th>
<th>Horizontal running (12 km h⁻¹)</th>
<th>2 Hz jumping</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SCT</td>
<td>PCT</td>
</tr>
<tr>
<td>Oxygen uptake</td>
<td>0.33</td>
<td>3.35</td>
<td>2.45</td>
</tr>
<tr>
<td>(l min⁻¹)</td>
<td>(21)</td>
<td>(18)</td>
<td>(11)</td>
</tr>
<tr>
<td>Blood lactate</td>
<td>2.1</td>
<td>2.9</td>
<td>2.9</td>
</tr>
<tr>
<td>(mmol l⁻¹)</td>
<td>(34)</td>
<td>(40)</td>
<td>(31)</td>
</tr>
<tr>
<td>PM (W)</td>
<td>—</td>
<td>585</td>
<td>517</td>
</tr>
<tr>
<td>(W)</td>
<td>—</td>
<td>(10)</td>
<td>(15)</td>
</tr>
<tr>
<td>PT (W)</td>
<td>—</td>
<td>349</td>
<td>280</td>
</tr>
<tr>
<td>(2')</td>
<td>—</td>
<td>(26)</td>
<td>(26)</td>
</tr>
<tr>
<td>εₖ</td>
<td>—</td>
<td>0.688</td>
<td>0.662</td>
</tr>
<tr>
<td>(9)</td>
<td>(14)</td>
<td>(8)</td>
<td></td>
</tr>
<tr>
<td>εₑₑ</td>
<td>—</td>
<td>0.797</td>
<td>0.757</td>
</tr>
<tr>
<td>(8)</td>
<td>(14)</td>
<td>(8)</td>
<td></td>
</tr>
<tr>
<td>εₑₑ</td>
<td>—</td>
<td>0.193</td>
<td>0.211</td>
</tr>
<tr>
<td>(31)</td>
<td>(18)</td>
<td>(21)</td>
<td></td>
</tr>
<tr>
<td>εₑₑ</td>
<td>—</td>
<td>0.726</td>
<td>0.755</td>
</tr>
<tr>
<td>(93)</td>
<td>(55)</td>
<td>(60)</td>
<td></td>
</tr>
</tbody>
</table>

Note: The oxygen uptakes were significantly different from each other. The lactate level at rest was significantly lower than during work and the lactate levels during running and SCT was significantly higher than PCT and LCT. PM, εₖ and εₑₑ during SCT were significantly larger compared to PCT and LCT (P < 0.05).

37 ± 8% s⁻¹ (SCT), 26 ± 7% s⁻¹ (PCT) 20 ± 8% s⁻¹ (LCT) in the modelled m. quadriceps muscle.

The oxygen uptakes (Table 2) were significantly different from each other. The lactate level at rest was significantly lower than during work and the lactate levels during running and SCT were significantly higher than PCT and LCT. PM, εₖ and εₑₑ during SCT were significantly larger than during PCT and LCT.

The estimated efficiencies of both the eccentric and the concentric muscle actions (Table 2, εₑₑ and εₑₑ) did not show any significant differences between the jumping situations. However, there was a tendency towards an increase in both the εₑₑ and the εₑₑ with decreasing εₖ and εₑₑ.

The relationships between gross efficiency (εₖ) and running economy are shown in Fig. 5. A clear negative correlation (rₛ = -0.893, p < 0.01, N = 7) was found between running economy and εₖ from SCT (upper panel).

The effect on εₖ and εₑₑ of reducing or increasing l₀, A₁, Y and α₁ by 10% is shown in Table 3. The observed changes ranged between -4 and +13%. The largest effects were seen when the length of tendon moment arms was altered. Changes in the cross-sectional areas of the tendons and the normalised elastic modulus had exactly the same and the smallest effect on εₖ and εₑₑ.

DISCUSSION

The subjects worked under well approximated steady-state conditions while running and jumping due to the test protocol and we did not observe any lactate accumulation. The influence of anaerobic metabolism on the calculation of εₖ and εₑₑ was therefore considered to be negligible.
joints oscillated 180° out of phase with the muscle action in the hip extension during take off was an expression of co-contraction with the hip flexors, it could not be calculated. However, if the eccentric muscle action in the hip extensor muscles during hip flexion (eccentric hip flexor action). Therefore, if elastic energy was stored in the hip extensor muscles during hip flexion in co-contraction with the hip flexors, it could not be calculated. However, if the eccentric muscle action in the hip extension during take off was an expression of another transport of muscle power via m. rectus femoris due to a coactivation between m. glutaeus maximus and m. rectus femoris (Ingen Schenau et al., 1987). Muscle power generated by m. glutaeus maximus would appear at the knees. Therefore, this contribution would be included in the calculations and reduce the possible underestimation of \( P_t \).

Co-contraction. As mentioned above, one major drawback in the calculation of the tendon force from net joint moments is that co-contractions between agonist and antagonist muscles affect the results. The most important implications of co-contractions in the present study are (1) a lowering of the measured and assumed muscle–tendon efficiency \( (\varepsilon_{\text{mech}}) \) and (2) an underestimation of \( P_t \). The effect is an underestimation of \( \varepsilon_{\text{conc}} \) and \( \varepsilon_{\text{ecc}} \).

Co-contractions during the landings which stabilise the knee and ankle joints would tend to increase the load on extensor muscles and subsequently the amount of stored elastic strain energy in the tendons of the extensor muscles. This extra energy might contribute to the push off if the flexors were relaxed during this phase. Any extra load on the extensor tendons during landings due to co-contraction is not ‘seen’ by the net joint moments but it becomes ‘visible’ if the co-contraction ceases during the following take off. Coordinated co-contractions of this type would only decrease the possible underestimation of \( P_t \).

However, we believe that the level of co-contractions during natural submaximal movement is low, which is supported by the control calculations discussed below. Otherwise the movements would appear rigid and clumsy.

Dimensions of the tendon variables. Another and possibly even more critical problem in the calculation of tendon work rates is the selection of the source for the applied tendon moment arms. We have chosen the works of Spoor et al. (1990) and Spoor and Leeuwen (1992), because they measured instantaneous tendon moment arms (on cadavers) based on the relationship between tendon travel vs joint angle. This method is simple and very accurate, because it does not require any knowledge about the position of the instantaneous centre of rotation or assumptions about joint geometry (An et al., 1984). However, the measurements were only carried out on a few specimens and like in the inverse dynamic calculations, we had to use a standard set of data which again might obscure individual characteristics. It has not been shown that a normalization of tendon moment arm length to segment lengths brings the calculations closer to reality, however, in this way some biological variation in this variable is taken into account.

The dimensions of the tendons and the elastic modulus of the tendon tissue are also critical. Our knowledge about inter-individual variations in the tendon cross-sectional area and Youngs modulus in relation to body size, age and physical condition is scarce and again we were forced to apply a standard set of anatomical data on each individual. At the

<table>
<thead>
<tr>
<th>( \Delta \varepsilon_{\text{mech}} ) and ( \Delta \varepsilon_{\text{conc}} )</th>
<th>(-10%)</th>
<th>(+10%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( l_0 )</td>
<td>-6</td>
<td>+8</td>
</tr>
<tr>
<td>( A_t ) or ( Y )</td>
<td>+3</td>
<td>-4</td>
</tr>
<tr>
<td>( \alpha_{t} )</td>
<td>+13</td>
<td>-8</td>
</tr>
</tbody>
</table>
ankle joint only the cross-sectional area of the Achilles tendon was taken into account and the tendons of the deeper plantar flexors were ignored. This simplification might have introduced an overestimation of the tendon work rates at the ankle joints.

Finally, the definition of the anatomical tendon length (equivalent to our tendon resting length, $l_0$) is critical. Conventionally the anatomical tendon length is defined as the origin to insertion length of the muscle–tendon complex minus the muscle fibre length (Ker et al., 1988) and the whole length of this tendon is assumed to have a constant cross-sectional area which is measured on a piece of free tendon. In this way the aponeuroses are given the same mechanical properties as the free parts of the tendons. The free parts of the Achilles tendon and the quadriceps tendon are between 5 and 10 cm long and the rest of the tendinous structures are aponeuroses. The mechanical properties of aponeuroses in active muscles are a matter of dispute (Otten, 1988; Huijing and Ettema, 1989) and the free parts of the tendons and the aponeuroses might have significantly different contributions to $P_T$.

**Mechanical efficiencies**

In the calculation of the mechanical efficiency of muscle–tendon work ($e_{\text{mtc}}$) it was assumed that energy spent on the maintenance of the basic body functions and stabilization ($P_m$) was the same both during rest and work. However, it is more likely that $P_m$ increased during work due to increased temperature and increased demands on stabilization and inefficient movement of segments. By combining equation (6) and the expression (7) it can be deduced that an underestimation of $P_m$ gives an overestimation of $e_{\text{conc}}$ (or $e_{\text{ecc}}$) and an underestimation of $e_{\text{mtc}}$. However, we believe that the error on $P_m$ was small due to the optimization of the selected movement with respect to inefficient movements and optimization of the experimental protocol with respect to work intensity and fatigue. It was also assumed that the mechanical work rate of the muscle–tendon complexes ($P_{\text{m,mtc}}$) was equivalent to the rate of transfer of mechanical work to the surroundings ($P_m$). However, $P_m$ will always be lower than $P_{\text{m,mtc}}$ because some mechanical energy is lost as non-elastic deformations of soft tissues, to small movements in the frontal and sagittal planes and due to co-contractions. Therefore, the assumptions in the calculations must have introduced some underestimation of $e_{\text{mtc}}$ which can be seen in Table 2 where the estimated $e_{\text{conc}}$ in all cases is lower than 0.25. However, if $e_{\text{ecc}} = 1.20$ is too high, $e_{\text{conc}}$ would also be underestimated. Kaneko et al. (1984) found that the efficiency of body work dominated by eccentric contractions was more variable than the efficiency of concentric work. Therefore, we also calculated $e_{\text{ecc}}$ with a fixed $e_{\text{conc}}$ of 0.25 and found a larger variability of $e_{\text{ecc}}$ than of $e_{\text{conc}}$ (Table 2). The average $e_{\text{ecc}}$ became 0.80 ± 0.55 which is close the 0.85 ± 0.38 found by Kaneko et al. (1984.)

In eccentric muscle actions the muscles do not generate force but act as brakes and the efficiency of the work is the efficiency of controlling a brake. If cross-bridges attach and generate force without metabolic costs during eccentric muscle actions (Curtin and Davies, 1994) the costs of eccentric muscle action would mainly be due to the activation process, and therefore the mechanical efficiency would be very sensitive to the force level and the range of lengthening of the contractile component. This could explain the larger variation in $e_{\text{ecc}}$.

The rather good estimates of $e_{\text{conc}}$ and $e_{\text{ecc}}$ were taken as a validation of the model calculations.

In the three jumping situations 60%, 54% and 52% of the total mechanical work was performed by the tendons and the enhancement of $e_{\text{mtc}}$ above the theoretical maximal efficiency of muscle work (approximately 0.30) can be explained by the contribution of tendon work. Potentiation of the contractile machinery in stretch-shortening type of muscle actions described by Cavagna et al. (1968) is negligible due to the low energetic potential of this mechanism (Haan et al., 1989; Ettema et al., 1990).

However, another factor that influences the mechanical efficiency is the absolute length changes of the muscle fibres and thereby working range within their force–length–velocity relation (Ettema et al., 1990) which is determined by the joint positions and the timing of the muscle activation and the external loading of the muscle–tendon complex (Griffiths, 1991).

**Sensitivity to variation in tendon variables**

The physiological and biomechanical factors that have an influence on movement economy are numerous and no single factor or subset of factors can explain the large inter-individual variation in mechanical efficiency of movement or movement economy that has been observed in human movement (Cavanagh and Kram, 1985).

The sensitivity of $e_{\text{mtc}}$ (or $e_{\text{ec}}$) to changes in tendon variables and moment arms is shown in Table 2. The calculations were carried out on the data from one subject. The mechanical efficiency of muscle–tendon work ($e_{\text{mtc}}$) was calculated from equation (5) with $e_{\text{conc}} - 0.25$ and $e_{\text{ecc}}$ estimated as explained earlier. We found that increased length ($l_0$), decreased cross-sectional area ($A_x$), decreased Youngs modulus ($Y$) and decreased moment arm ($a_y$) in concert increased $e_{\text{mtc}}$ and vice versa. Changes in $a_y$ had the greatest influence on $e_{\text{mtc}}$ and changes in $A_x$ and $Y$ had the smallest effect. The same relative change in $A_x$ and $Y$ had exactly the same effect, which can be deduced from equation (2).

If $A_x$, $l_0$, $A_y$ and $Y$ were changed by 5% (which we from a biological point of view considered to be reasonable) in the direction of optimization of the mechanical efficiencies, these increased 14%. If the variables were changed by 5% in the opposite direction a decrease of 10% was found. This range of changes was equal to the range of inter-individual variation in
the measured $\varepsilon_{\text{mech}}$ (or $\varepsilon_{\text{SS}}$) shown in Table 2. Therefore, we believe that the above mentioned discrete set of variables is extremely important in determining the movement economy of an individual.

Mechanical efficiency and running economy

The correlation between running economy and $\varepsilon_{\text{mech}}$ became successively better with increasing contributions of tendon work in relation to the total work during repetitive jumping (Fig. 5, bottom to top) and this observation indirectly suggests that the tendon variables have a strong influence on the running economy of the individual. Therefore, we would expect to find the same pattern of correlation between the tendon work rates during repetitive jumping ($P_r$) and the running economy. However, we did not correlate any of the data calculated from the model (e.g. $P_r$) with actually measured data (e.g. running economy), because this would implicitly imply assumptions about equal relative body dimensions between the subjects and linear relationships between segment lengths and tendon moment arms. The use of body segment parameters and moment arms measured on other subjects (cadavers) rather than the actual subjects must obscure any existent correlation and therefore we find such correlations meaningless.

The angular velocities at the knee joints are comparable in running at 12 km h$^{-1}$ and SCT jumping (Bosco et al., 1987) and this might also explain some of the increased correlation.

The effect of physical training

Physical exercise or immobilisation has a significant influence on the mechanical properties of tendons due to changes in the tendon cross-sectional areas and Youngs modulus of the tendon tissue (Woo et al., 1980; Vilarta and Vidal, 1989). Woo et al. (1980) reported increases of 21% in the cross-sectional area and of 25% in Youngs modulus of the digital flexor tendons of pigs after 8 months of training (running on a dirt track). The data in Table 3 show that adaptations to exercise by increase in tendon cross-sectional area and Youngs modulus of the tendon tissue must tend to decrease the movement economy (assuming that all other variables are constant). This indicates that other factors than movement economy are optimised in response to exercise.

In this study the mechanical efficiency of movement was significantly increased by forcing the subjects to perform repetitive jumping at higher forces than they spontaneously preferred (Table 2). Both an increased cross-sectional area of the tendons and a movement pattern that keeps the tendon forces low will reduce the tendon stresses. Therefore, it might be factors that tend to minimise musculo-skeletal stress that are optimised in response to exercise. This is in accordance with the observations of Biewener (1990) who showed that the musculo-skeletal stresses in mammals during locomotion is kept constant with increasing body weight caused by changes in the limb postures (bent to straight legs) and by an increase in the so-called 'muscle mechanical advantage' (i.e. the relationship between muscle moment arm at a joint and the moment arm of the ground reaction force) in order to maintain an acceptable safety factor.

Conclusions

The enhancement of the gross mechanical efficiency during movements dominated by stretch-shortening cycles like repetitive jumping or running compared to the theoretical mechanical efficiency of positive muscle work can be explained by the contribution of tendon work.

The mechanical efficiency of whole body movement is very sensitive to changes in Youngs modulus of the tendon tissue, tendon length, tendon cross-sectional area, because the factors determine the amount of tendon work that is performed. Changes in the lengths of the tendon moment arms of the locomotor muscles had the most profound effect on the gross mechanical efficiency.

Inter-individual differences in the tendon variables can explain observed inter-individual differences in movement economy.

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REFERENCES

The influence of tendon young's modulus


