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ORIGINAL ARTICLE

Taija Finni · Paavo V. Komi · Vesa Lepola

In vivo human triceps surae and quadriceps femoris muscle function in a squat jump and counter movement jump

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Abstract An optic fibre method was used to measure in humans in vivo Achilles (ATF) and patellar tendon forces (PTF) during submaximal squat jumps (SJ) and counter movement jumps (CMJ). Normal two-legged jumps on a force plate and one-legged jumps on a sledge apparatus were made by four volunteers. Kinetics, kinematics, and muscle activity from seven muscles were recorded. The loading patterns of the tendomuscular system differed among the jumping conditions, but were similar when the jumping height was varied. Peak PTF were greater than ATF in each condition. In contrast to earlier simulation studies it was observed that tendomuscular force could continue to increase during the shortening of muscle-tendon unit in CMJ. The concentric tendomuscular output was related to the force at the end of the stretching phase while the enhancement of the output in CMJ compared to SJ could not be explained by increases in muscle activity. The stretching phase in CMJ was characterised by little or no electromyogram activity. Therefore, the role of active stretch in creating beneficial conditions for the utilisation of elastic energy in muscle was only minor in these submaximal performances. The modelling, as used in the present study, showed, however, that tendon underwent a stretch-shortening cycle, thus having potential for elastic energy storage and utilisation. In general, the interaction between muscle and tendon components may be organised in a manner that takes advantage of the basic properties of muscle at given submaximal and variable activity levels of normal human locomotion.

Key words Muscle mechanics · Tendon force · Muscle-tendon interaction · Power · Optic fibre

Introduction

In human movement studies standing jumps with and without a counter movement have been widely explored both experimentally (e.g. Asmussen and Bonde-Petersen 1974; Komi and Bosco 1978; Gollhofer et al. 1992; Fukashiro et al. 1995) and by computer simulation (e.g. Pandy and Zajac 1991; Bobbert et al. 1996). The performance itself, with regard to jumping height and movement kinematics, as well as to different aspects of neuromuscular function of the muscles involved in the tasks has been covered in the literature. For example, enhanced muscular performance during a counter movement jump (CMJ) as compared to a squat jump (SJ) has been attributed to increased myoelectrical activity (Bosco et al. 1982), recoil of elastic energy (Komi and Bosco 1978; Fukashiro et al. 1995), the time available for force development (Bobbert et al. 1996) and a high force at the end of the stretching phase (Zajac 1993). From these factors, recoil of elastic energy has been shown to be very important in economising muscular performance both in animal (Alexander and Vernon 1975; Morgan et al. 1978) and human locomotion (Thys et al. 1975). In accordance with these observations, Anderson and Pandy (1993) suggested that the elastic tissues improve the efficiency rather than jumping height of CMJ compared to SJ.

The complex multijoint nature of standing jumps raises difficulties when the function of individual muscles or muscle groups are of interest. Muscle modelling with inverse solutions has provided net joint moments (Fukashiro and Komi 1987) and estimated muscle forces

T. Finni (✉)
Department of Biology of Physical Activity,
University of Jyväskylä,
P.O. Box 35 (LL 227),
40351 Jyväskylä, Finland
e-mail: finni@pallo.jyu.fi
Tel.: +358-14-2602075; Fax: +358-14-2602071

T. Finni · P. V. Komi
Neuromuscular Research Center,
Department of Biology of Physical Activity,
University of Jyväskylä, 40100 Jyväskylä, Finland

V. Lepola
LIKES-Research Centre for Sports and Health Sciences,
40100 Jyväskylä, Finland

(Bobbert et al. 1986). While forward dynamics models rely on measured neuromuscular signals (Zajac 1993) experimental muscle force data are scarce due to the methodological challenges involved. If muscle forces can be directly recorded, one can avoid the often inaccurate estimation of changes in moment arms of a muscle during locomotion and its effect on calculated muscle forces. Furthermore, modelling studies usually simulate optimal performance while little is known about submaximal movements where one may observe individually different movement strategies with variability in activation patterns and movement kinematics, which make calculation of forces produced by a muscle group or a single muscle even more complex.

In the course of developing a force transducer for human studies, animal experiments provided a basis for applying the buckle force transducer in recording Achilles tendon forces in men (Komi et al. 1987). Later, the method was used to measure human tendomuscular forces in natural movements such as walking, running, cycling and jumping (Komi 1990; Gregor et al. 1991; Komi et al. 1992; Fukashiro et al. 1993, 1995). Recent development of an optic fibre technique (Komi et al. 1996) has opened up new possibilities for less invasive tendon force measurements in routine experiments (Finni et al. 1998). The fact that the insertion of an optic fibre is quick and virtually painless is a clear advantage over the more invasive buckle-type transducer technique. The optic fibre is inserted through the entire cross-section of the tendon and the tendon deformation during locomotion compresses the optic fibre inside the tendon. It has been shown that this compression can then be calibrated to represent the in vivo tendomuscular force (Komi et al. 1996).

In the present study, the optic fibre method was used to study triceps surae (TS) and quadriceps femoris (QF) muscle loading during SJ and CMJ. Different levels of submaximal jumping performance were used to examine how the output of TS and QF muscles is modulated to achieve greater jumping height. Instantaneous force-length and force-velocity relationships together with muscle activation are presented to examine the nature of muscle action and the relationship between muscle input and output. As length changes in the complete muscle-tendon complex may not correspond to the changes at the muscle fibre level, Achilles tendon and soleus muscle compartment interaction is also examined using modelling techniques.

Methods

Subjects

Four healthy subjects volunteered for this study [three women and one man whose body masses and heights were mean 63 (SD ± 3) kg, mean 167 (SD ± 4) cm, and 90 kg, 181 cm, respectively]. The subjects were informed of all the risks associated with the study and gave their written consent to participate. The subjects were free to stop the experiment at will. The recommendations contained in the Declaration of Helsinki were followed and the Ethics Committee of the Central Hospital of Central Finland approved the study.

Experiment protocol

Prior to the day of measurement the subjects were introduced to the jumping activities to be performed on the sledge apparatus that has previously been described (Kaneko et al. 1984) and on the force plate. Using the sledge the joint movements could easily be controlled and the contribution of the hip joint was limited because the subject's upper body was secured to the back of the chair of the apparatus. The purpose of these measurements was also to evaluate possible alterations in jumping performance due to the insertion of the optic fibre. Visual comparison of the electromyogram (EMG) and ground reaction force patterns showed that the presence of the optic fibre in the tendon did not cause any disturbances.

Isometric maximal voluntary ankle plantarflexions (90° angle) were performed on the ankle ergometer that has been described previously by Kyröläinen and Komi (1994) where torque around the rotational axes of the pedal was measured by a piezoelectric crystal transducer (Kistler, Winterhur, Switzerland). The torque applied to the pedal was converted to force under the point of force application. The distance from a 1-cm-wide bar under the first metatarsal head to the rotational axis was measured as the length of the pedal lever arm. Isometric maximal voluntary extensions of the knee (120°) were measured using the knee ergometer as has been described by Komi et al. (1999, in press). In this machine the lever arm was equipped with a strain gauge and the lever arm length could be read from an inbuilt ruler. The same knee and ankle ergometer settings were used in the calibration of the optic fibre force transducer.

On the measurement day, after the optic fibres had been inserted, the subjects made one-legged jumps on the sledge apparatus that had an inclination of 20° from the horizontal position. With one-legged jumps any possible bilateral differences could be avoided. Furthermore, the hip joint angular displacement was reduced and easily controlled compared to normal standing jumps. Two to five SJ and CMJ were performed with increasing effort, thus jumping a little higher each time. The amplitude of the sledge movement in each jump was predetermined and the subjects were provided with visual feedback of their performances from a monitor in front of them. On the force plate, SJ and CMJ were repeated as normal two-legged jumps.

Optic fibre technique

The transmitter-receiver unit used in the optic fibre method contained a light emitting diode and a PIN photodiode receiver (Hewlett Packard, USA). The light signal (wavelength 820 nm) travelled in the core of the plastic optic fibre and returned to the unit for conversion into an analogue signal which was sent telemetrically to the recording computer. The use of optic fibre as a transducer for tendomuscular forces is based on light intensity modulation. Tendomuscular loading has been shown to develop tensile stress within the tendon fibres (Butler et al. 1978). This stress compresses the plastic optic fibre inside the tendon. A linear relationship has been reported between an increasing loading of the tendon and the intensity of the light passing through the optic fibre (Komi et al. 1996; Arndt et al. 1998) even in maximal voluntary contractions (MVC; Finni et al. 1998).

The subjects arrived at the laboratory at least 1 h before the insertion of the optic fibre took place. First, a pad covered with an anaesthetic cream containing lidocaine-prilocaine was placed over the skin of the calcaneal and patellar tendons of the right leg and kept in place for at least 1 h. With the subject lying prone and with the ankle angle secured at 90°, a hollow 19 gauge needle was passed through the right Achilles tendon 2–3 cm proximal to the calcaneus. The direction of the needle was perpendicular to the tendon. Aseptic conditions were ensured during the insertion procedure. The optic fibre, sterilised using ethylene oxide at 37 °C, was then passed through the needle. By removing the needle the fibre remained in situ. After insertion, both ends of the fibre were carefully cleaned before being attached to the transmitter-receiver unit for the light intensity baseline correction.

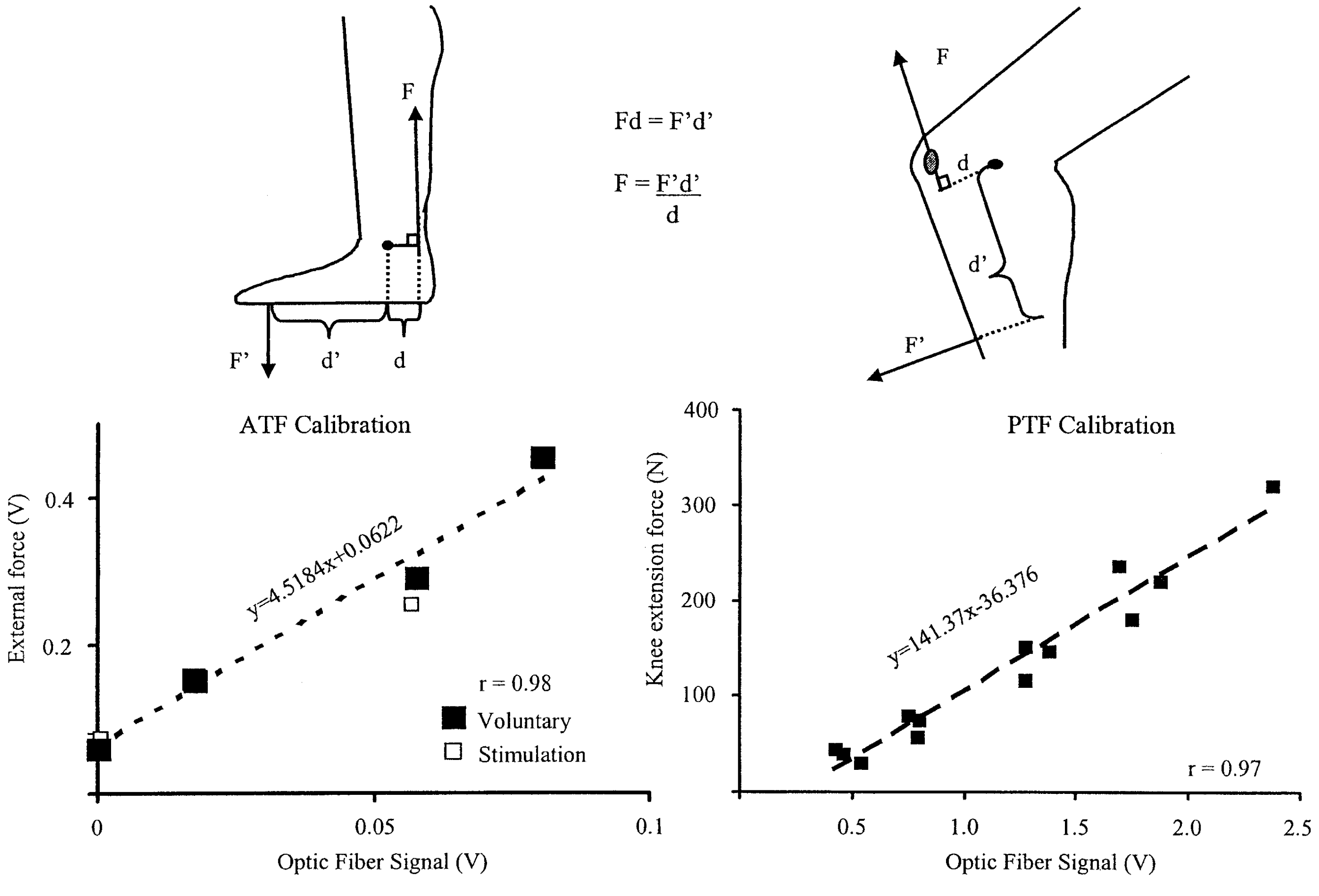
A similar procedure was used for the insertion of the optic fibre through the patellar tendon. During this procedure the subject was lying supine with the right knee at an angle of 120°.

Optic fibre calibration

The optic fibre was calibrated using an ankle ergometer (Achilles tendon) and the knee extension apparatus (patellar tendon) with approximately 10%, 20%, 30%, and 40% of MVC. In each condition, the subjects maintained the predetermined force levels for a few seconds. From the data recorded, the output of the optic fibre was related to the muscle force (F) that had been converted from the external force output (F') using the equation in Fig. 1. The optic fibre signal in volts was then converted into absolute force values according to the linear relationship for each individual. It was assumed in calibration using the simple model in Fig. 1 that the contribution of plantarflexor muscles other than the TS muscle could be neglected at low forces. To test this assumption the calibration was repeated using percutaneous stimulation (Neuropack Four MINI) in two subjects. Stimulating electrodes were placed over the proximal end of medial and lateral gastrocnemius muscles (anodes) and over the distal end of soleus muscle (cathode). Stimulation at three to four low stimulus intensities was used to quantify the contribution of the *other muscles* (flexor digitorum longus, flexor hallucis longus, peroneus, tibialis posterior muscles) to the plantarflexor moment. The stimulation and voluntary calibration linearities were found to be identical at low force levels (95% confidence interval). In the present and earlier pilot studies the two different calibration protocols have produced identical coefficients for all subjects with forces under 20% MVC and, in some cases, up to 40% MVC (Fig. 1). In the pilot studies, we observed the possibility of not having identical regressions in calibrations performed using voluntary and percutaneous stimulation protocols (Fig. 2). This difference was taken to be evidence that with voluntary effort the subject may activate *other plantarflexors* depending on the activation strategy used. Therefore, in the present calibrations the identical regression lines were taken as evidence that no *other muscles* were involved in plantarflexion at low levels of force (Gregor et al. 1991). Thus, the use of submaximal calibration minimises the overestimation of Achilles tendon force (ATF) caused by the other plantarflexor muscles. No stimulation protocol was necessary in the patellar tendon force (PTF) calibration since all the force produced by the knee extensors was transmitted to the skeletal system through the patellar tendon. The calibration for both ATF and PTF produced linear relationships ($0.864 < r < 0.986$).

One critical point in the calibration was the determination of the axis of rotation for ankle and knee joints. This was done both by using external landmarks and by rotating the distal segment of the corresponding joint on a marker table. Outlines of the leg around the ankle and knee joints were first projected on to the marker table at angles specific to the calibration while the subjects contracted their leg muscles isometrically. The proximal segment was kept in place while the distal segment, with markers attached, was rotated. Lines drawn by the distal segment markers were used to determine a fixed centre of rotation. The moment arm distances (d, Fig. 1) measured using anatomical landmarks were then confirmed by also measuring the distances from the images on the marker table.

Fig. 1 Measured forces and moment arms for the calibration of Achilles tendon force (*ATF*) and patellar tendon force (*PTF*). The optic fibre output was related to the muscle force (F) that had been converted from the external force output (F') using equation $Fd = F'd'$, where d = moment arm of tendon force and d' moment arm of the foot or leg



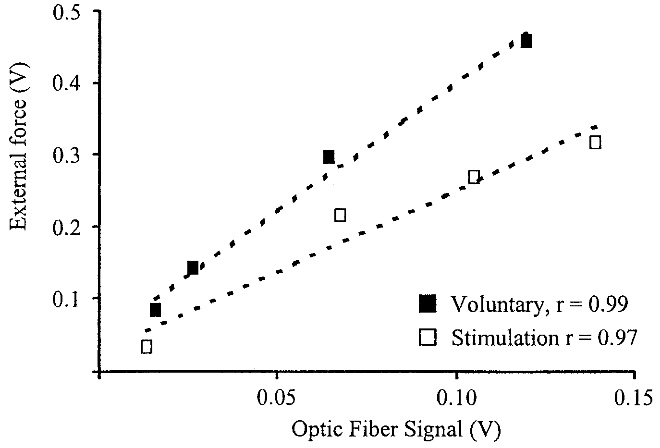


Fig. 2 An example of calibration from the pilot study. Depending on the strategy used by the subjects to activate their calf muscles during plantarflexion, it was possible that voluntary calibration would lead to overestimation of the triceps surae muscle force. The difference between the gradients of the regression lines can be attributed to the contribution of force from deeper plantarflexor muscles

The optic fibre as a force transducer has been tested both in animal preparations (Komi et al. 1996) and in human experiments (Arndt et al. 1998; Finni et al. 1998). During dynamic muscle work, the skin moves in relation to the tendon. To test for a possible artefact caused by skin movement in the measurement of tendon force, the skin was pulled along the tendon near to the site of insertion of the optic fibre. The measured effect of skin movement was calculated to be less than 2% of the peak forces recorded during locomotion. It is possible, however, that the effect of a movement artefact would become greater during full ankle plantarflexion when the skin is folded around the Achilles tendon. This potential problem is not present in the patellar tendon.

Data recording and processing

Reaction forces, sledge displacement and velocity were measured on the sledge apparatus. The sledge had an inclination of 20° and the seat on which the subjects sat had a mass of 30 kg. Forces and EMG were collected with Codas software (1 kHz) for further analysis. From the jumps on the force plate the vertical ground reaction forces (F_z) were measured and jumping height (h) $[h = (\mathrm{NI/m})^2/2\ \mathrm{g}]$ (where NI is net impulse) was determined from $\mathrm{NI} = \int[F_z(\mathrm{t}) - \mathrm{m} \cdot \mathrm{g}]\mathrm{d}t$.

Bipolar EMG electrodes (Beckmann miniature skin electrodes, Ill., USA) were placed on the tibialis anterior, soleus, gastrocnemius medialis, vastus lateralis and rectus femoris muscles of the right leg and on the soleus and vastus lateralis muscles of the left leg. The interelectrode distance of 20 mm used routinely in our laboratory conformed to the recent recommendation of SENIAM (Hermens and Freriks 1997). The electrodes were positioned according to the recommendations of SENIAM (Hermens and Freriks 1997). The EMG signals were amplified (Glonner Biomes 2000, Glonner Electronic GmbH, Munich, Germany) and sent telemetrically to the recording computer. The signals were high-pass filtered (20 Hz, before sampling) and full-wave rectified. The EMG signal was integrated (iEMG) separately for the breaking and push-off phases and the iEMG was divided by the integration time to obtain average EMG (aEMG). The aEMG values were normalized to the aEMG obtained in calibrations made during isometric contractions (40%) for each individual. Smooth activity patterns presented in the figures resulted from time normalisation and averaging of the jumps of the four subjects.

All jumps were videotaped at 200 Hz in the sagittal plane from the subject's right side. Reflective markers were placed on the following points: on the neck at the level of the fifth cervical vertebra, greater trochanter major, approximate centre of rotation of the knee, lateral malleolus, heel and fifth metatarsal head. These points were digitised from the video with Motus software (Peak Performance Technologies Inc., USA). The scaled co-ordinates were filtered with a 4th order Butterworth conditioner with a cut-off frequency of 8 Hz. An electrical pulse was used to synchronise the computer and video data. The length changes of the muscle-tendon complex (Δl) for QF and TS muscles were determined using the method of Hawkins and Hull (1990). No attempt was made to separate the loading of individual muscles contributing to ATF or PTF. A model where the detailed anatomy of a muscle (pennation angles, fibre lengths) or tendon (areas corresponding to each muscle) has not been taken into consideration provides a simple but, we feel, effective tool for examining muscle mechanics. Consequently, the QF muscle lengths correspond to averaged vasti muscles and the TS lengths represent the average of gastrocnemius and soleus muscles. Muscle-tendon velocities (v) were calculated by dividing the infinitesimal change in muscle length by the corresponding time (5 ms). Both instantaneous and average power outputs ($P = F \cdot v$) were calculated over eccentric and concentric periods.

Changes in length of the Achilles tendon were calculated according to the method of Voigt et al. (1995) who used quadratic tendon force function $\mathrm{ATF} = k(\Delta l)^2$, where Δl is change in tendon length and k is a constant which was derived from the following equation: $k = [\mathrm{YA}_{\mathrm{atf}}(\varepsilon_{\mathrm{max}} - \varepsilon_{\mathrm{t}})10^2]/[(\varepsilon_{\mathrm{max}} l_{\mathrm{o}})^2]$, where Y = Young's modulus (1.2 GPa used), $\mathrm{A}_{\mathrm{atf}}$ = Achilles tendon cross-section area, $\varepsilon_{\mathrm{max}}$ = maximal tolerable strain (6% used), ε_{t} = length of nonlinear part of load-deformation curve (2% used), and l_{o} = tendon rest length. Tendon rest lengths were obtained from Yamaguchi et al. (1990) and Achilles tendon cross-sectional areas were determined individually by ultrasonography according to Kallinen and Suominen (1994). Tendon length changes ($\Delta l = (\mathrm{ATF})/k^{1/2}$) were subtracted from changes in length of the muscle-tendon complex for determination of muscle compartment length changes.

As the jumping heights varied individually only the jumps with the greatest heights were averaged among the subjects. The modulation of tendomuscular loading with increased jumping height is presented as individual recordings.

Statistical analysis

Pearson's two-tailed correlation ($P < 0.05$) was employed to investigate the relationships between the variables measured. A Student's t-test for paired samples was used to test for differences in variable mean values between jumping conditions.

Results

Normal ground reaction force patterns (e.g. Gollhofer et al. 1992) were observed in each jumping condition. Increases in jumping height caused slight modulations in the tendomuscular force-time patterns but there was a tendency for greater peak forces to be reached later during the push-off of the higher jumping performance (Fig. 3). In one-legged jumps the inclination of the sledge caused smaller reaction forces, although ATF and PTF did not differ significantly from those recorded during jumps on the force plate (Table 1). In general, decreasing the hip joint angular movement (sledge condition) did not alter the TS and QF loading patterns from those observed on the force plate, although the time course of the jumps was longer in the sledge condition (0.66 s vs 0.42 s in SJ and 1.3 s vs 0.66 s in CMJ, $P < 0.001$). Therefore, the following results will focus on the normal two-legged jumps.

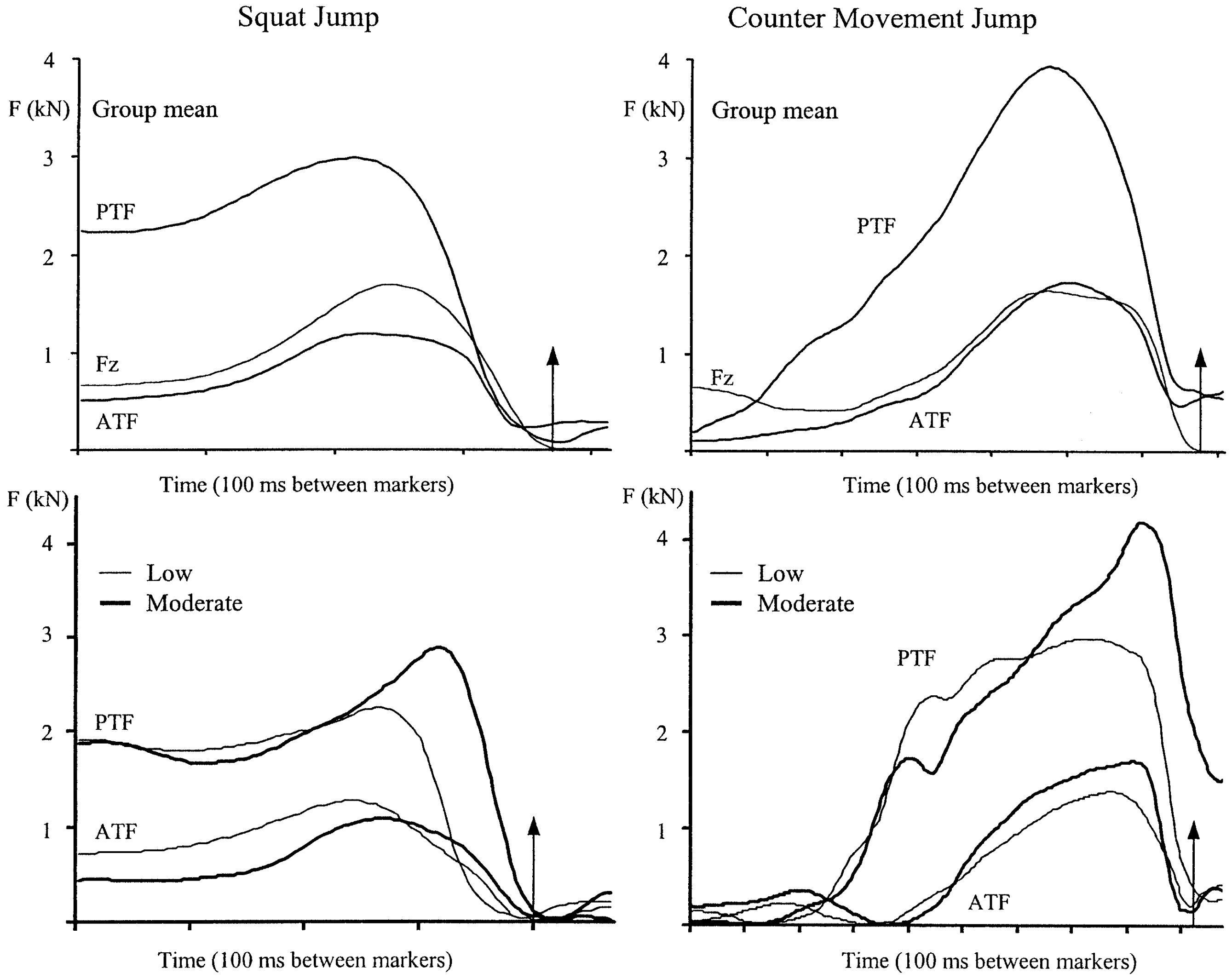


Fig. 3 Reaction forces (F_z), patellar tendon forces (*PTF*) and Achilles tendon forces (*ATF*) during squat jump and counter movement jump. Group mean values are shown in the *upper panel*. In the *lower panel*: a representative sample of loading patterns during low (*thin line*) and moderate intensity (*thick line*) jumps is shown. *Arrows* indicate the time of take-off

During the CMJ, the tendomuscular force-length relationships of the QF muscle show that the force increase occurred mainly during lengthening, but could continue during shortening – as seen for the subject in Fig. 4. The initial lengthening of the QF muscle occurred with very low EMG activity. This is illustrated in Fig. 5, where group mean EMG activities of the vastus lateralis muscle have been taken as a representative sample. The activity of the vastus lateralis muscle was greatest at long muscle lengths both during SJ and CMJ.

The force increase of the TS muscle occurred at relatively constant length both in SJ and CMJ, and coincided with EMG activity (Figs. 4, 5). Soleus and gastrocnemius muscle activity patterns were remarkably similar with only small inter- and intra-individual variation in the initiation of activation. The action of the TS muscle-tendon complex was further analysed by

Table 1 Group mean values of peak-to-peak forces from the highest jumps on the force plate and on the sledge. F_z Reaction force, *ATF* Achilles tendon force, *PTF* patellar tendon force, *h* vertical displacement of the centre of gravity, *SJ* squat jump, *CMJ* counter movement jump

	SJ								CMJ							
	F_z (N)		ATF (N)		PTF (N)		*h* (cm)		F_z (N)		ATF (N)		PTF (N)		*h* (cm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Force plate	1713	316	1305	811	3200	1463	16	4	1633	233	1855	780	4297	2147	18	5
Sledge	510	150	1200	832	2700	831	6	3	822	428	1570	869	3037	614	7	3

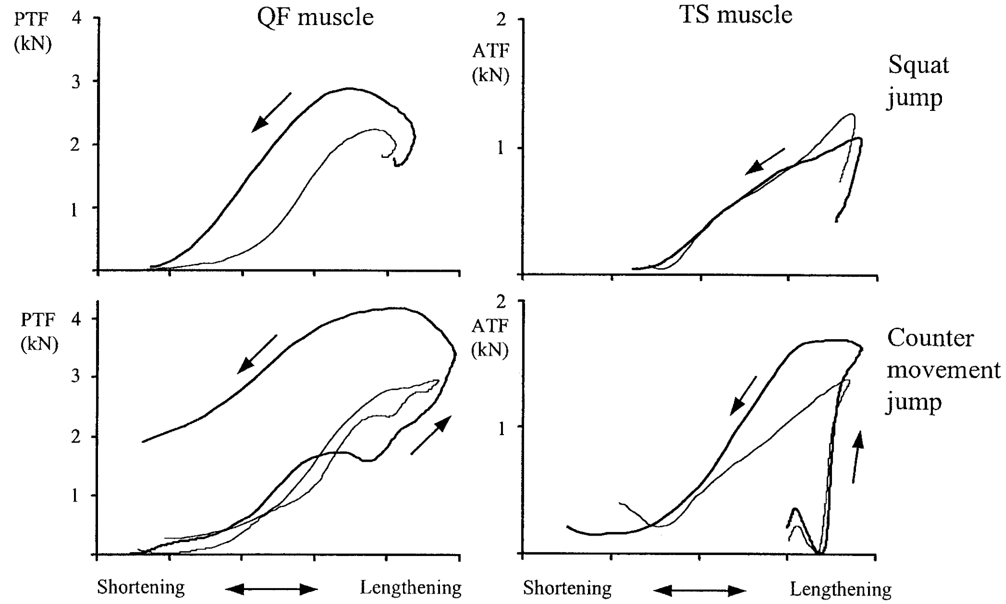


Fig. 4 Instantaneous force-length relationships for the quadriceps femoris (*QF*) and triceps surae muscles (*TS*) during squat jump and counter movement jump. Jumps with low (*thin line*) and increased effort (*thick line*) are shown. Note: different force scales for Achilles tendon force (*ATF*) and patellar tendon force (*PTF*). On the *x*-axis the change in length is marked in intervals of 1 cm

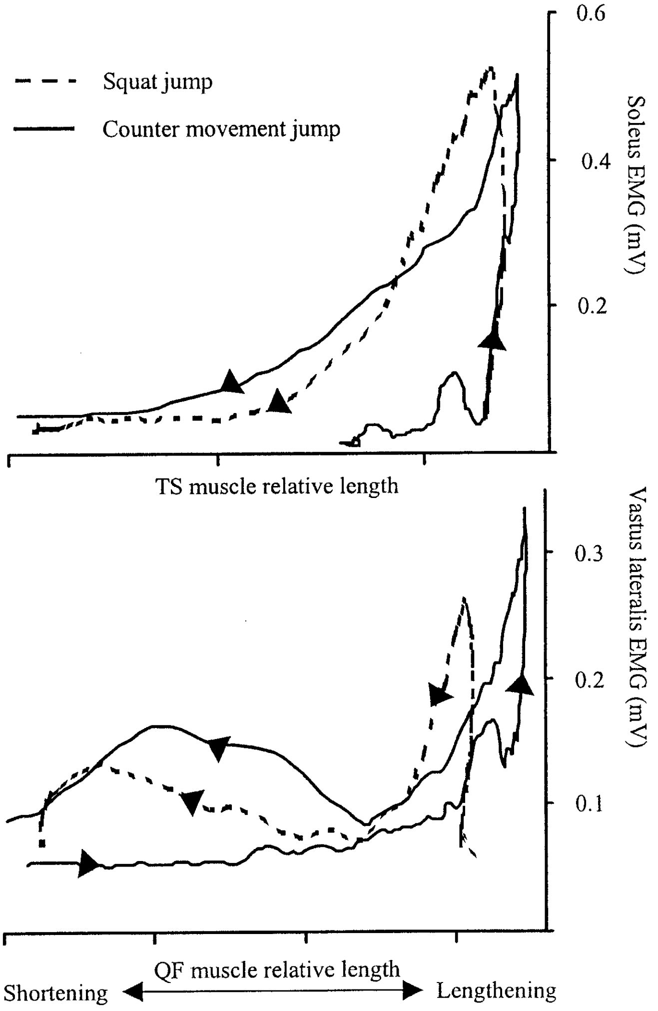


Fig. 5 The rectified and smoothed soleus (*upper panel*) and vastus lateralis muscle electromyogram (*EMG*) activities (*lower panel*) are plotted against the relative length change of the tendomuscle complex during squat jump and counter movement jump. Mean values of highest jumps. For other abbreviations see Fig. 4

modelling the length changes of the soleus muscle and tendon compartments. Figure 6 shows that during SJ the muscle itself shortened throughout the movement causing initial tendon lengthening. In the late push-off phase the tendon reached its maximal shortening velocity before the muscle ($P > 0.05$). During the early downward movement in CMJ, the soleus muscle was passively lengthened. While the tendon length was constant the change in muscle length was responsible for lengthening of the muscle-tendon complex. When the muscle became active the muscle compartment started to resist lengthening simultaneously, causing tendon elongation. During the push-off phase the length changes followed those seen during SJ.

The instantaneous force-velocity relationships (Fig. 7) illustrate how the concentric power output increased with increasing jumping height. Average concentric power was greater ($P < 0.05$) in CMJ than in SJ for the muscle groups examined although the range of muscle activity was similar in both jumping conditions (Fig. 8). An example of the TS and QF muscle power-time curves together with vertical ground reaction forces during SJ and CMJ are shown in Fig. 9. The timing of peak powers varied individually in these submaximal performances. The greatest peak powers produced by QF [1032 (SD 310) W] were found during CMJ. Tendomuscular forces at the end of the breaking phase correlated positively with peak powers in the following concentric phase of CMJ (Fig. 10).

Discussion

In the present study where SJ and CMJ were made with variable efforts the tendomuscular loading patterns changed in amplitude and duration when the jumping height was varied. The vertical ground reaction forces

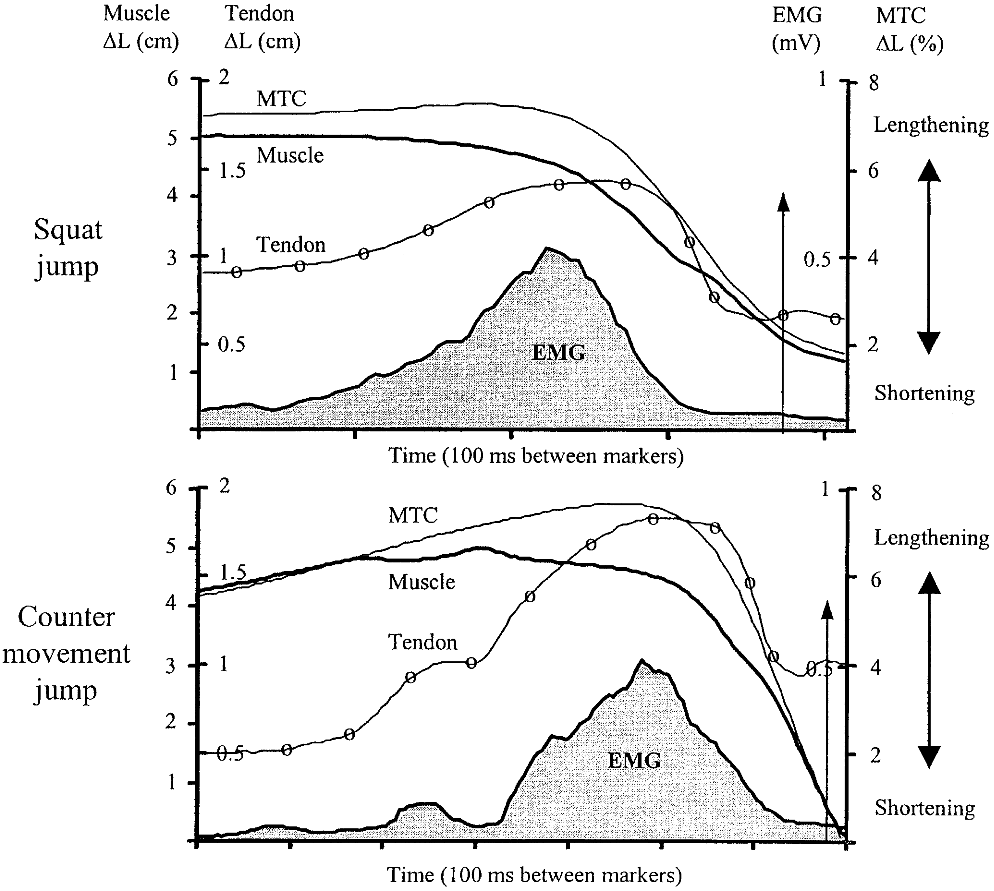


Fig. 6 Results of modelling changes in the soleus muscle-tendon complex (*MTC*), muscle, and Achilles tendon compartment lengths (Δl for length) during squat jump and counter movement jump. The rectified and smoothed muscle electromyogram (*EMG*) activities are shown. Mean values of the highest jumps. *Arrows* indicate the time of take-off

showed normally observed patterns and Achilles tendon loading was of similar magnitude to that recorded earlier with the buckle type force transducer (Fukashiro et al. 1995). The interindividual variation found in peak forces (Table 1) was not unexpected (Finni et al. 1998), and followed observations from animal experiments (e.g. Gregor et al. 1988).

Some simulation studies have indicated that while the force development in SJ occurs during shortening, the peak forces in CMJ are reached prior to the concentric phase. This observation has been made with the hip extensor muscles (Bobbert et al. 1996) and with the vastus lateralis muscle (Anderson and Pandy 1993). The present results show, however, that the force development can also continue during the shortening phase in CMJ as shown in Fig. 4. Van Ingen Schenau et al. (1997) have concluded that the time for force development prior to shortening can explain the difference in muscle output in these two jumping conditions. While this conclusion may be valid in maximal jumping, the present low level jumps may not necessarily follow the same mechanism. Naturally, the previous history of the muscle has an effect on the following concentric phase. For example, a high force prior to shortening favours concentric muscle output (Fig. 10), which has been referred to in several studies (Bosco et al. 1981; Bobbert et al. 1996; Takarada et al. 1997). The literature on human studies suggests also that an increased myoelectrical activity (Bosco et al. 1982; Walshe et al. 1998) and elastic recoil (Fukashiro et al. 1995) may be operative. The present results showed that with a given EMG a higher power output was achieved in the CMJ (Fig. 8). This suggests that enhancement of muscle output cannot be solely explained by increased muscle activation. Thus, elastic recoil may have also contributed to the tendomuscle performance in the present low level jumps.

The direct comparison of muscle performances in SJ and CMJ requires that the concentric phases are identical. In the present experiment the knee joint angle amplitudes tended to increase with increasing effort in the CMJ. This is especially seen for the QF muscle in the group mean values of the highest jumps (Fig. 5). As the length changes in TS muscle were comparable (for some subjects also in QF) the comparison is valid for that muscle group. Examination of Fig. 8 shows that for both TS and QF muscle groups concentric mean power output was greater in CMJ than in SJ although the range of EMG activities of the vastus lateralis muscle is slightly different between jumping conditions, a fact that may have been caused by different knee angular movement.

For the stretch shortening cycle (SSC) to be effective, active lengthening of the muscle is required. It has been shown that an active muscle, when lengthened, may

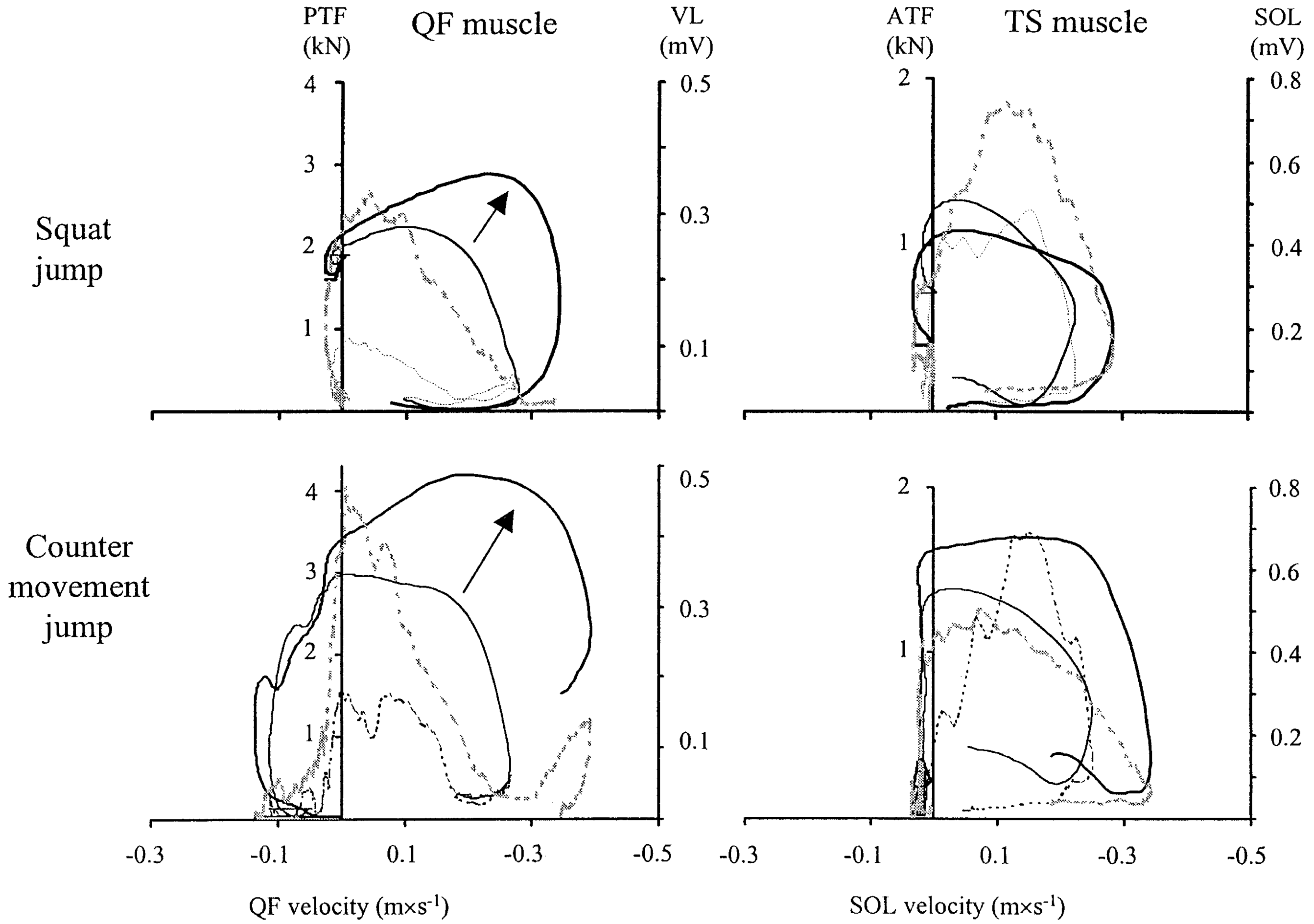


Fig. 7 Instantaneous force-velocity relationships for *QF* and *TS* muscle groups during low (*thin line*) and moderate intensity jumps (*thick line*). The rectified and smoothed muscle activity levels (*dashed lines*) are presented using a second y-axis on the right. *SOL* Soleus, *VL* vastus lateralis muscles. For other definitions see Fig. 4

sustain high forces and stretch the tendon sufficiently so that it can store elastic energy to be used in the late concentric phase when the muscle activity starts to decay (Alexander and Bennet-Clark 1977; Lou et al. 1999). In the present study, the results from modelling suggest that at least part of the muscle lengthening occurred without, or with low, EMG activity. Therefore, the following possibility can be considered to describe events in the muscle-tendon complex.

In CMJ, both ATF and PTF start to increase during the unweighting phase, due first to the passive stretch and then during the active breaking phase (Figs. 4, 5). According to Kawakami et al. (1998) and Narici et al. (1996) one may expect that the passive stretch applied would take up at least part of the slack in the tendon and that this passive stretch would also lengthen the muscle fibres as shown for the soleus muscle (Fig. 6). Thus the muscle length, hypothetically, could be positioned on the descending limb of the force-length curve prior to activation. Then, when activity starts, the muscle shortens and moves towards the plateau of the force-length curve. Consequently, the force-producing capability of the tendomuscular complex is increased in the beginning of the activation phase.

In other words, due to the counter movement of the body the muscles are being stretched, first passively and then actively when breaking the downward movement. This could imply that the procedure takes advantage of the force-length properties of the muscle. The result that the tendon reached maximal shortening velocity earlier than the muscle compartment during the late push-off (modelling experiment), further suggests that interaction of the two components created beneficial conditions for the muscle to act for longer in the middle part of the force-velocity relationship, thus having a greater force producing capacity. From the entire muscle-tendon unit point of view the tendon plays an important role in enhancing velocity and thus power in the push-off phase. As stated earlier, at least part of the increase in the QF output in the push-off phase of CMJ (Fig. 7) may be achieved by an effective tendon action. It must be emphasised, however, that more accurate reference to the contractile and tendon components in the force enhancement during the concentric phase may require more sophisticated measurements of the length and velocity changes of both components.

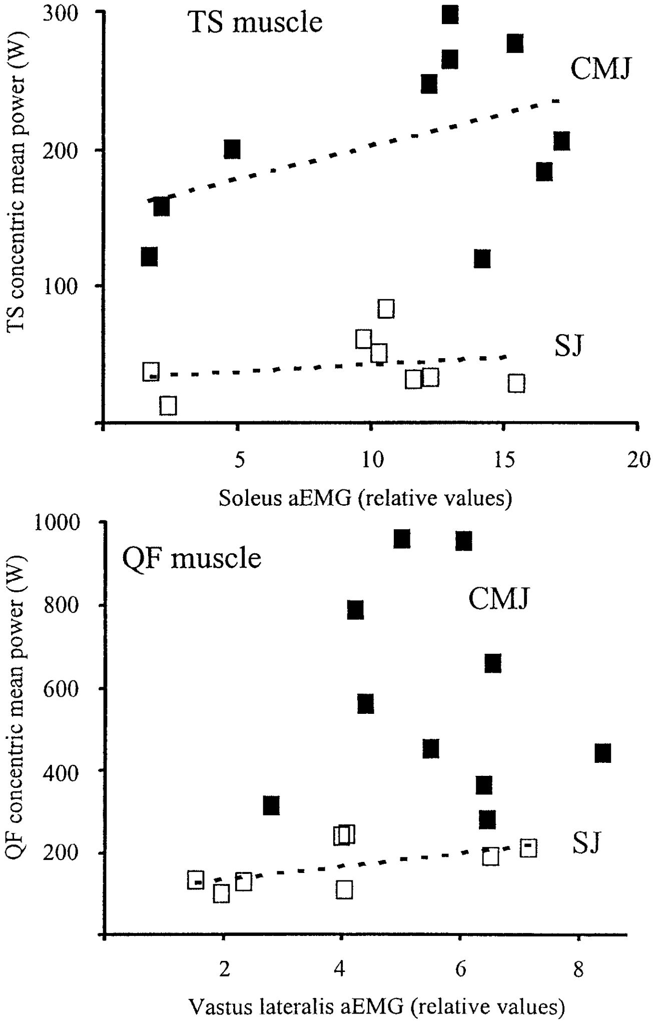


Fig. 8 Relationships between tendomuscular power output and averaged electromyogram (*aEMG*) in the concentric phase of squat jump (*SJ*) and counter movement jump (*CMJ*). The EMG was normalised to the average EMG obtained during calibrations using isometric contractions in each individual. The correlations were not significant and the *dashed lines* merely illustrate that within the same range of EMG the concentric tendomuscular power output was higher in *CMJ* than in *SJ*. For other definitions see Fig. 4

It has been shown that normally the peak powers of the joint and tendomuscular system are reached in the sequence of hip, knee and ankle (Fukashiro and Komi 1987; Bobbert and van Ingen Schenau 1988; Pandy and Zajac 1991; Prilutsky and Zatsiorsky 1994). However, in the present study QF peak power was not always reached earlier than TS peak power (Fig. 9). Here the jumps were very submaximal and possibly affected by loading differences between the two legs, and thus the common patterns of segmental rotations were not always achieved. Furthermore, a submaximal jump can be executed using various techniques and interpretation of the present results may not be generalised to maximal jumps.

When the jumping height increased the peak forces and shortening velocities tended to increase as well (Fig. 7). Thus, greater peak powers were reached in the higher jumps. As expected, the greatest PTF and peak QF powers were found during CMJ (Fig. 9). The present TS peak powers during SJ were similar to those reported by Fukashiro et al. (1995; 243 W) who measured in vivo ATF with the buckle-type force transducer. Tendomuscular powers during maximal (or optimal) SJ have also been estimated using muscle modelling. Prilutsky and Zatsiorsky (1994) reported muscle peak powers of 1000 W (knee extensor muscles) and 700 W (ankle extensor muscles) while Pandy and Zajac (1991) reported peak values of 1300 W (vasti muscles) and 600 W (gastrocnemius muscle). Comparison of these values with the present values of 749 W (QF) and 294 W

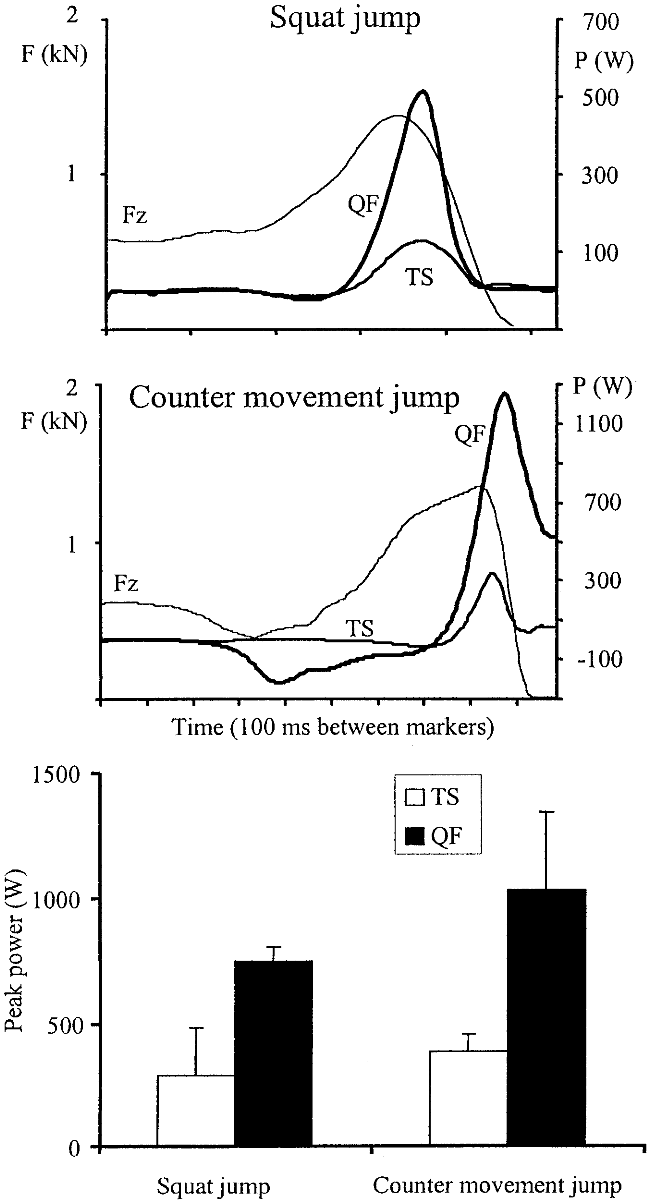


Fig. 9 Representative example of power-time curves during squat and counter movement jumps together with average (and SD) peak powers (*bottom panel*). *F* Force. For other definitions see Fig. 4

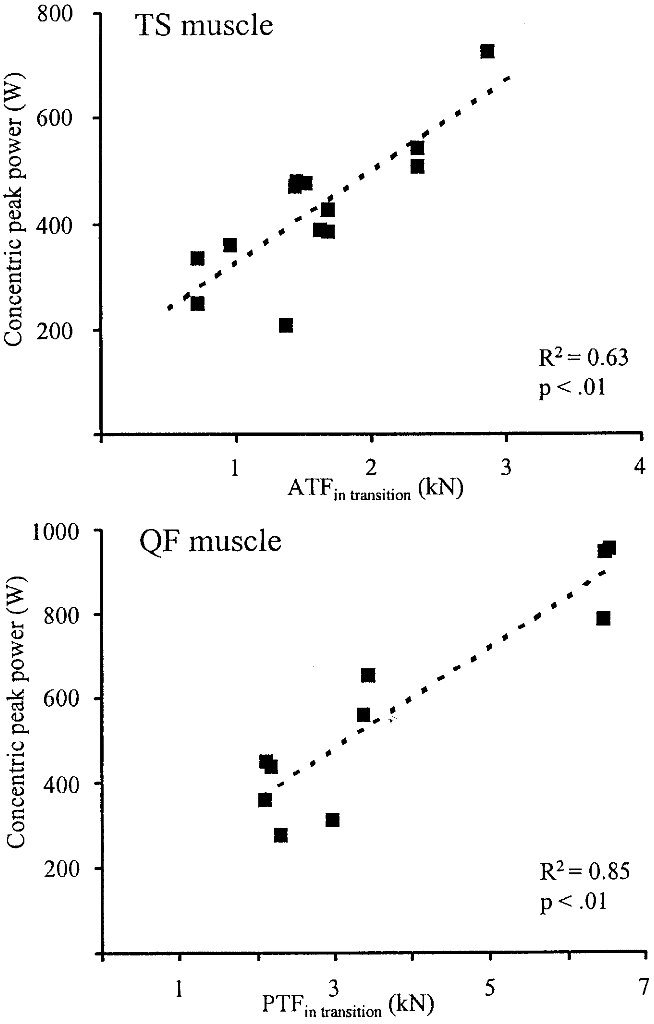


Fig. 10 Relationships between force at the end of the stretching phase ($ATF_{in\ transition}$, $PTF_{in\ transition}$) and tendomuscular power in the following concentric phase (*n* = 4). For other definitions see Fig. 4

(TS) may give an idea about the degree of muscle effort in the present submaximal SJ.

Conclusions

The present study where SJ and CMJ were made with variable efforts suggests that enhancement of tendomuscle output in the concentric phase of SSC cannot be solely explained by increases in muscle activity. The importance of active stretch in creating beneficial conditions for the storage and use of elastic energy within muscle may also be questioned in these submaximal jumps where little or no activity was present during the stretching phase. However, results from modelling indicate that the tendon undergoes SSC both in SJ and CMJ. Therefore the submaximal activation of normal locomotion may not be effective in allowing the stretch-induced enhancement of muscle force to play a significant role, but it is essential in creating conditions where the performance efficiency is improved by tendon action. In general, interaction between the muscle and tendon components in normal locomotion, where the level of activity is submaximal and varies considerably, must be taken into consideration before attributing the differences in tendomuscular output to any single factor.

References

Alexander RM, Vernon A (1975) The mechanics of hopping by kangaroos (Macropodidae). J Zool (Lond) 177: 265–303

Alexander RM, Bennet-Clark HC (1977) Storage of elastic strain energy in muscle and other tissues. Nature 265: 114–117

Anderson FC, Pandy MG (1993) Storage and utilization of elastic strain energy during jumping. J Biomech 26: 1413–1427

Arndt AN, Komi PV, Brüggemann G-P, Lukkariniemi J (1998) Individual muscle contributions to the in vivo achilles tendon force. Clin Biomech 13: 532–541

Asmussen E, Bonde-Petersen F (1974) Apparent efficiency and storage of elastic energy in human muscles during exercise. Acta Physiol Scand 92: 537–545

Bobbert MF, Ingen Schenau GJ van (1988) Coordination in vertical jumping. J Biomech 21: 249–262

Bobbert MF, Huijing PA, Ingen Schenau GJ van (1986) A model of the human triceps surae muscle-tendon complex applied to jumping. J Biomech 11: 887–898

Bobbert MF, Gerritsen KGM, Litjens MCA, Soest AJ van (1996) Why is countermovement jump height greater than squat jump height? Med Sci Sports Exerc 28: 1402–1412

Bosco C, Komi PV, Ito A (1981) Prestretch potentiation of human skeletal muscle during ballistic movement. Acta Physiol Scand 111: 135–140

Bosco C, Viitasalo JT, Komi PV, Luhtanen P (1982) Combined effects of elastic energy and myoelectrical potentiation during stretch-shortening cycle exercise. Acta Physiol Scand 114: 557–565

Butler DL, Grood ES, Noyes FR (1978) Biomechanics of ligaments and tendons. Exerc Sport Sci Rev 6: 125–181

Finni T, Komi PV, Lukkariniemi J (1998) Achilles tendon force during walking: measurements with the optic fibre technique. Eur J Appl Physiol 77: 289–291

Fukashiro S, Komi PV (1987) Joint moment and mechanical power flow of the lower limb during vertical jump. Int J Sports Med 8[Suppl]: 15–21

Fukashiro S, Komi PV, Järvinen M, Miyashita M (1993) Comparison between the directly measured achilles tendon force and the tendon force calculated from the ankle joint moment during vertical jumps. Clin Biomech 8: 25–30

Fukashiro S, Komi PV, Järvinen M, Miyashita M (1995) In vivo achilles tendon loading during jumping in humans. Eur J Appl Physiol 71: 453–458

Gollhofer A, Strojnik V, Rapp W, Schweizer L (1992) Behaviour of triceps surae muscle-tendon complex in different conditions. Eur J Appl Physiol 64: 283–291

Gregor RJ, Roy RR, Whiting WC, Lovely RC, Hodgson JA, Edgerton VR (1988) Mechanical output of the cat soleus during treadmill locomotion: in vivo vs. in situ characteristics. J Biomech 21: 721–732

Gregor RJ, Komi PV, Browning RC, Järvinen M (1991) A comparison of the triceps surae and residual muscle moments at the ankle during cycling. J Biomech 24: 287–297

Hawkins D, Hull ML (1990) A method for determining lower extremity muscle-tendon lengths during flexion/extension movements. J Biomech 23: 487–494

Hermens HJ, Freriks B (1997) The state of the art on sensors and sensor placement procedures for surface electromyography: a proposal for sensor placement procedures. Roessingh Research and Development, The Netherlands, pp 125–146

Ingen Schenau GJ van, Bobbert MF, Haan A de (1997) Does elastic energy enhance work and efficiency in the stretch-shortening cycle? J Appl Biomech 13: 389–415

Kallinen M, Suominen H (1994) Ultrasonographic measurements of the Achilles tendon in elderly athletes and sedentary men. Acta Radiol 35: 560–563

Kaneko M, Komi PV, Aura O (1984) Mechanical efficiency of concentric and eccentric exercises performed with medium to fast contraction rates. Scand J Sports Sci 6: 15–20

Kawakami Y, Ichinose Y, Fukunaga T (1998) Architectural and functional features of human triceps surae muscles during contraction. J Appl Physiol 85: 398–404

Komi PV (1990) Relevance of in vivo force measurements to human biomechanics. J Biomech 23[Suppl] 1: 23–34

Komi PV, Bosco C (1978) Utilization of stored elastic energy in leg extensor muscles by men and women. Med Sci Sports Exerc 10: 261–265

Komi PV, Salonen M, Järvinen M, Kokko O (1987) In vivo registration of Achilles tendon forces in man. I. Methodological development. Int J Sports Med 8[Suppl]: 3–8

Komi PV, Fukashiro MS, Järvinen M (1992) Biomechanical loading of Achilles tendon during normal locomotion. Clin Sport Med 11: 521–531

Komi PV, Belli A, Huttunen V, Bonnefoy R, Geyssant A, Lacour JR (1996) Optic fibre as a transducer of tendomuscular forces. Eur J Appl Physiol 72: 278–280

Komi PV, Linnamo V, Silventoinen P, Sillanpää M (2000) Force and EMG power spectrum during eccentric and concentric actions. Med Sci Sports Exerc (in press)

Lou F, Curtin NA, Woledge RC (1999) Elastic energy storage and release in white muscle from dogfish Scyliorhinus canicula. J Exp Biol 202: 135–142

Morgan DL, Proske U, Warren D (1978) Measurements of muscle stiffness and the mechanism of elastic storage of energy in hopping kangaroos. J Physiol (Lond) 282: 253–261

Narici MV, Binzoni T, Hiltbrand E, Fasel J, Terrier F, Cerretelli P (1996) In vivo human gastrocnemius architecture with changing joint angle at rest and during graded isometric contraction. J Physiol (Lond) 496: 287–297

Pandy MG, Zajac FE (1991) Optimal muscular coordination strategies for jumping. J Biomech 24: 1–10

Prilutsky BI, Zatsiorsky VM (1994) Tendon action of two-joint muscles: transfer of mechanical energy between joint during jumping, landing, and running. J Biomech 27: 25–34

Takarada Y, Hirano Y, Ishige Y, Ishii N (1997) Stretch-induced enhancement of mechanical power output in human multijoint exercise with countermovement. J Appl Physiol 83: 1749–1755

Thys H, Gavagna GA, Margaria R (1975) The role played by elasticity in an exercise involving movements of small amplitude. Pflügers Arch 354: 281–286

Walshe AD, Wilson GJ, Ettema GJC (1998) Stretch-shorten cycle compared with isometric preload: contributions to enhanced muscular performance. J Appl Physiol 84: 97–106

Voigt M, Simonsen EB, Dyhre-Poulsen P, Klausen K (1995) The influence of tendon Young's modulus, dimensions and instantaneous moment arms on the efficiency of human movement. J Biomech 28: 281–291

Yamaguchi GT, Sawa AGU, Morgan DW, Fessler MJ, Winters M (1990) A survey of human musculotendon actuator parameters. In: Winters JM, Woo SL-Y (eds) Multiple muscle systems. Springer, Berlin Heidelberg New York, pp 717–773

Zajac FE (1993) Muscle coordination of movement: a perspective. J Biomech 26[Suppl] 1: 109–124