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In vivo muscle mechanics during locomotion is dependent on movement amplitude and contraction intensity

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Abstract

Effects of movement amplitude and contraction intensity on triceps surae and quadriceps femoris muscle function were studied during repetitive hopping. In vivo forces from Achilles and patellar tendons were recorded with the optic fibre technique from eight volunteers. The performances were filmed (200 Hz) for determination of changes in muscle-tendon unit length and velocity. In hopping with small amplitude (23° knee flexion during the ground contact phase) Achilles tendon was primarily loaded whereas patellar tendon forces were greater in large amplitude hopping (56° knee flexion). In spite of the different magnitudes of stretch in quadriceps femoris muscle the stretching velocity and activity patterns of the quadriceps muscle were similar in both conditions. Simultaneously performed EMG recordings revealed that preferential preactivation of gastrocnemius muscle was evident in both jumping condition. The triceps surae muscle was strongly active in the eccentric phase of the small amplitude hopping. Results from hopping with small knee joint displacement suggest that there may be a certain frequency and jumping height where the elastic bouncing is best utilised and simultaneously the concentric phase is most economical. Results also support earlier observations that the economy of the shortening phase must be compromised at some point in order to produce more power and jumping height.

Key words: hopping, tendon force, muscle activity, economy, optic fibre

Introduction

Neuromuscular behaviour in bouncing jumps has been extensively studied in search for mechanisms of movement control (Moritani et al. 1991; Voigt et al. 1998), role of elasticity in locomotion (Fukashiro et al. 1995; Komi and Bosco 1978; Voigt et al. 1995), and neuromuscular adaptation to variable conditions (Avela et al. 1994; Gollhofer and Kyröläinen 1991; Farley et al. 1998). Hopping is often considered as a performance where stretch-shortening cycle (SSC) muscle function is effectively utilised (Komi and Gollhofer 1997). In SSC, referring to length changes in the entire muscle-tendon unit (from now on the word muscle refers to the muscle-tendon unit), function of muscle groups may differ depending on the changes in joint angular displacements, contact times, jumping height and frequency of hopping. Literature shows that changes in hopping height and frequency follow those in the timing of activation (Moritani et al. 1991) and stiffness of the leg spring (Farley et al. 1991). Farley et al. (1999) further showed that ankle joint function primarily determines the changes in the stiffness of the leg spring. Therefore, the behaviour of the triceps surae (TS) muscle group is of special interest in hopping. In submaximal multijoint movement, however, changes in the displacement of the centre of the mass (i.e. movement amplitude) during the ground contact phase can modulate the stretch, loading and activity patterns of TS muscle-tendon unit. In fact, the movement amplitude has been shown to affect the positive work as well as the efficiency of exercise (Thys et al. 1975). The amplitude can easily be modified with knee flexion, which in turn affects the magnitude of stretch in both quadriceps femoris (QF) and TS muscles.

In the present study submaximal hopping was used as exercise model when effects of stretch of different magnitudes on neuromuscular behaviour of QF and TS muscles were

studied. Changes in muscle function with gradually increasing jumping height were also examined. Load shearing between QF and TS muscles and changes in activation patterns were of special interest. Movement kinematics, muscle activity and in vivo Achilles and patellar tendon forces with the optic fibre method (Komi et al. 1996) were measured simultaneously.

Methods

Total of nine young adults volunteered for this study (5 females, 4 males). They 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 ethical committee of the Central Hospital of Central Finland approved the study.

The subjects arrived at the laboratory at least one hour before the insertion of the optic fiber took place. First, an anaesthesia cream pad containing lidocain-prilocain was placed over the skin of the calcaneal and patellar tendons of the right leg and maintained there at least for one hour. During the insertion procedure the ankle angle was secured at 90° and knee angle at 120°. A hollow 19-gauge needle was passed through the right Achilles tendon two to three centimetres proximal to calcaneus. The direction of the needle was perpendicular to the sagittal plane. Aseptic conditions were ensured throughout the insertion procedure. The optic fibre, sterilised with 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 (Hewlett Packard, USA) for the light intensity baseline correction.

A similar procedure was used in the insertion of the optic fibre through the patellar tendon. Further details of the optic fibre method as a transducer for tendomuscular forces are given elsewhere (Finni et al. 1998; Finni et al. 2000; Komi et al. 1996).

The optic fibre was calibrated against externally measured force with approximately 10, 20, 30, and 40 % of maximum voluntary contraction with similar procedure as reported earlier (Finni et al. 2000). In each condition, the subjects maintained the predetermined force levels for few seconds. From the recorded data, the optic fibre output 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 individual linear relationship ($0.86 < r < 0.99$). In case of Achilles tendon force calibration the percutaneous stimulation procedure (Finni et al. 2000) was used to confirm that other muscles than *m. triceps surae* (*flexor digitorum longus*, *flexor hallucis longus*, *peroneus*, *tibialis posterior*) do not contribute to the plantarflexor moment (Fig. 1). In addition, the calibration procedure was repeated after the performances to ensure the stability of tendon force calibration. For the subjects who performed hopping with different intensities, calibration was also repeated after every other hopping series using two low force levels as shown for knee extension in Fig. 1. In few cases, after the high intensity performances the ATF calibration was unstable due to deformation of the optic fibre caused probably by high tendomuscular forces. In those cases the ATF data was not included in the analysis.

In the calibration procedure the axes of rotations for ankle and knee joints were determined beforehand both using external landmarks and rotating the distal segment of the corresponding joint on a marker table. First, outlines of the leg around ankle and knee

joints were projected to the marker table at an angle specific to calibration while subjects contracted their leg muscles isometrically. The proximal segment was kept in place while the distal segment with attached markers 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 utilising anatomical landmarks were then confirmed by measuring the distance also from the image in the marker table.

After calibration one subject performed first repetitive hopping with 50-degree knee joint angular movement during the contact phase (large amplitude hopping) and then hopping with minimal (20° degrees) knee angular movement while gradually increasing jumping height (small amplitude hopping). In addition, four of the subjects performed large amplitude hopping only, and the remaining four subjects hopped with minimal knee angular movement. The latter group was given an instruction “jump a little higher next time” after each set of jumps having the freedom to choose their hopping frequency, contact time and target height. For purpose of control the subjects were provided with visual feedback of their knee angular displacement during the performances. For the entire subject group the knee joint angular movements during the ground contact were 23° (SD 10, $n = 5$) and 56° (SD 13, $n = 5$) for small and large amplitude hopping, respectively.

Vertical ground reaction forces (force plate by Raute Oy, Lahti, Finland), tendon forces and EMG were collected with Cudas software (1 kHz) for further analysis. The jumping height ($h = (v_o)^2 / 2g$) was determined from the take-off velocity (v_o) of the centre of mass. Stiffness of the leg spring (leg stiffness) was determined from the ratio of the peak vertical ground reaction force (F_z) to the vertical displacement of the centre of mass during the

contact phase (Farley et al. 1991; McMahon and Cheng 1990). Hopping frequency was calculated from consecutive touchdowns divided by the corresponding time (hop/s).

Bipolar EMG electrodes (Beckmann miniature skin electrodes, Illinois, USA) were placed on the tibialis anterior, soleus (SOL), gastrocnemius medialis (GA), vastus lateralis (VL) and rectus femoris muscles of the right leg and on the soleus and vastus lateralis muscle of the left leg. The positioning of the electrodes was chosen according to the recommendations of SENIAM (Hermens and Freriks 1997). The EMG signals were amplified (Glonner Biomes 2000, Glonner Electronic GmbH, München, 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 eccentric and concentric phases and the iEMG was divided by the integration time to obtain average EMG (aEMG). The EMG recordings were reduced to 200 Hz to allow combination of activity patterns with kinematic data. This procedure together with averaging acted as a low pass filter and resulted in smooth patterns seen in figures in the results section.

All performances 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 5th cervical vertebra, greater trochanter major, approximate centre of rotation of the knee, lateral malleolus, heel and 5th metatarsal head. These points were digitised from the video with Motus software (Peak Performance Technologies Inc., USA). The scaled coordinates 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 the QF and (TS) muscles were determined

using the method of Hawkins and Hull (1990). The QF muscle lengths correspond to averaged vasti muscles and the TS lengths represent the averaged gastrocnemius and soleus muscles. Muscle-tendon velocities (v) were calculated by dividing infinitesimal change in muscle length with corresponding time (5 ms). Average tendomuscular power outputs ($P = \text{tendon force times velocity of muscle-tendon complex}$) were calculated over eccentric and concentric periods.

The jumping performances with different knee joint angular displacements were averaged separately; in small amplitude hopping “medium” height performances were averaged. The modulation of tendomuscular loading with increased jumping height is presented in figures as individual recordings unless otherwise specified. This was considered to be appropriate because of noticeable inter-individual differences in jumping heights, peak forces and activation strategies. Pearson’s two-tailed correlation ($P < 0.05$) was employed to reveal the relationships between measured variables. Mann Whitney U-test was used to test differences in variable mean values between small and large amplitude jumps. Effect of increased jumping height on variables was tested with Friedman’s two way ANOVA. Paired samples t-test was employed to test differences between eccentric and concentric phases.

Results

Effects of movement amplitude. Group mean values of peak patellar tendon forces were greater than Achilles tendon forces (2810 vs. 1367 N, $P < 0.05$) in submaximal hopping with large knee joint displacement (Fig. 2) whereas the Achilles tendon forces were greater in small amplitude hopping (1017 vs. 605 N, for ATF and PTF, respectively). Peak

stretching velocities of TS muscle were greater in small amplitude hopping (0.45 vs. 0.37 $\text{m}\times\text{s}^{-1}$, $P < 0.05$) while they were similar for QF muscle in both conditions (0.33 vs. 0.36 $\text{m}\times\text{s}^{-1}$ for small and large amplitude, respectively). Average EMG of VL muscle was greater ($P < 0.05$) in the eccentric phase as compared to the concentric phase in both hopping conditions (Fig. 3). For SOL and GA there were no significant differences in aEMG between eccentric and concentric phase in large amplitude hopping but in small amplitude hopping major activity was observed in the eccentric phase ($P < 0.005$). Contact times were greater in the large amplitude hopping as compared to the small amplitude condition (347 vs. 221 ms, $P < 0.05$).

Effects of intensity. In small amplitude hopping the jumping height correlated positively with leg stiffness ($r = 0.75$, $P < 0.001$) and negatively with hopping frequency ($r = -0.88$, $P < 0.001$). Average hopping frequency was 2.5 hops/s in lowest jumps and 1.5 hops/s in highest jumps the major factor for this change being increased time in the flight phase. The contact times varied from 186 to 345 ms. Friedman's two-way ANOVA indicated that peak stretching and shortening velocities and power outputs of TS and QF muscles increased with jumping height ($P < 0.05$). Peak ATF and PTF showed also tendency to increase with jumping height (Fig. 4, individual recordings) as shown by positive correlation ($r = 0.6$, $P < 0.05$). A linear relationship ($r = 0.42$, $P < 0.05$) was found between concentric EMG-to-ATF ratio and hopping height. When this result was looked more closely, it was noted that an optimum could be found in low jumping heights (<16 cm) where parabolic relationship gave best fit ($r = 0.69$). Consequently, the relationship between EMG-to-ATF ratio and hopping height is best represented by J-pattern (Fig. 5).

Examples in figure 6 illustrate how the changes in the EMG-to-ATF ratio can occur. When jumping height was increased from “low” to “medium” height a dramatic increase of SOL and GA activity was seen in the eccentric phase but not in the concentric phase. Increasing the height even further the EMG increase occurred mostly in the concentric phase.

Discussion

Effects of movement amplitude. The present results show that the amplitude of knee joint angular displacement has an effect on relative loading between TS and QF muscles. The QF muscle was preferably loaded in hopping with large knee joint displacement whereas opposite was true in small amplitude performance. For the QF muscle the eccentric activity was dominant in both jumping conditions (Fig. 3). Although the magnitude of QF stretch and force were different, the stretching velocity and EMG patterns were similar in small and large amplitude hopping indicating that the control strategy of QF muscle was similar in these tasks.

Preferential preactivation of GA muscle was evident in both jumping conditions with major activity of GA and SOL occurring in eccentric phase of small amplitude hopping. Moritani et al. (1991) tried to explain the absence of concentric EMG activity by the presence of electromechanical delay (EMD). However, as the EMD is very short (10-15 ms) as measured with the optic fibre technique (Nicol and Komi 1999) this could not be a factor in these jumps. The decreased demand for neural input may arise from interaction between active muscle and tendon (Finni et al. 2000). The observed preactivation, high eccentric activity and high stretching velocity in the TS muscle with simultaneous increase in force creates beneficial conditions for storage of elastic energy (Cavagna 1997). With

shorter contact time and consequently shorter transition between eccentric and concentric phases the elastic energy may be utilised in the following concentric phase (Aura and Komi 1987; Bosco et al. 1981), thus decreasing the demand for muscular activity in the concentric phase. Furthermore, as the concentric muscle action is more energy consuming than eccentric one (Bigland-Ritchie and Woods 1978; Ryschon et al. 1997) it is logical to minimize the activity during shortening and use the energy from recoiling elastic components to achieve the required output. The present observations are in accordance with those of Thys et al. (1975) who monitored oxygen consumption and calculated higher efficiency during small amplitude as compared to large amplitude hopping.

As a limitation of the present study it must be noted that all the performances were submaximal and may not be generalized to maximal or optimal performances. Furthermore, in comparison of small and large amplitude hopping only one subject performed both tasks. However, the results of this subject were consistent with the remaining subjects in either group although it must be emphasised that differences may partly stem from individual differences in movement strategy and neuromuscular control.

Effects of intensity. In the study, where the ground contact time was kept constant while altering the frequency, Moritani et al. (1991) observed that the eccentric muscle activity in SOL and GA muscles dominated in high frequency, low-height hopping whereas the concentric activity increased in maximum-height hopping. In the present study where the subjects were able to choose preferred contact time the eccentric activity increased with simultaneous decrease in hopping frequency (Fig 7). However, depending on the jumping height and produced power, EMG activity increased also in the concentric phase. As shown in the example in Fig. 6, an increase from low to medium height hopping caused a

dramatic increase in eccentric EMG activity while concentric activity increased only slightly. Consequently, the lowest EMG-to-force ratio was found during the concentric phase of medium hopping. When the hopping height was increased even further, still being quite submaximal, the increase in EMG occurred mostly in the concentric phase. If we can consider the measure of EMG-to-force ratio as an indicator for economy, this example may imply that the economy of the shortening phase must be compromised at some point in order to produce more power and jumping height.

This can be evaluated further looking at the relationship between EMG-to-ATF ratio and jumping height. In hopping heights lower than 16 cm a parabolic line shows best fit between these variables indicating an optimum where the concentric output is most economical (Fig. 5). This observation was confirmed by looking the data points individually that followed J-pattern. Linear regression showed significant relationship when all the performances were included in the analysis with heights up to 27 cm that was achieved by a subject who was a national level high jumper.

Conclusion that optimising conditions for power production compromises efficiency has been presented earlier in animal studies. With variable duty cycle of stimulation and range of movement frequencies Curtin and Woledge (1996) found out that the highest efficiency was reached with brief stimulation bursts but maximum power output required long activation times. In the present study medium height hopping was performed with frequency of 2.0 Hz (see example in Fig. 6) that is reportedly close to preferred frequency of hopping (Melville Jones and Watt 1971). In addition to the concept of optimal frequency (Taylor 1985) the present observations also suggest that there may be a certain

jumping height (Fig. 5) where the elastic bouncing is best utilised and simultaneously the concentric phase is most economical.

The present positive relationship between hopping height and leg stiffness is in line with Farley et al. (1991; 1998; Farley and Morgenroth 1999) who have studied the concept of leg stiffness in detail. Farley et al. (1991) have also pointed out that at preferred hopping frequency the body behaves as a simple spring with minimal cost of generating muscular force by taking advantage of recoiled elastic energy.

The present interpretations are limited by the amount of performances at different intensities, and, with a small subject group. Obtaining more data from larger subject group would be necessary for general conclusions; however, the present results clearly demonstrate some possibilities how the neuromuscular system functions in the examined conditions.

Conclusions. Submaximal hopping can be executed in several different ways that affects the stretch, relative loading and activity patterns of muscles involved emphasising the used jumping technique. During hopping with 56-degree knee flexion QF muscle was predominantly loaded but forces in TS muscle were greater when knee joint angular displacement was minimized. While QF muscle control strategy did not differ dramatically when small and large amplitude hopping was compared, TS muscle showed several possibilities in this regard. The present observations with in vivo force measurements are in accordance with earlier literature suggesting that in bouncing jumps naturally selected jumping frequency and appropriate input to muscles are important factors for movement economy.

Figures

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

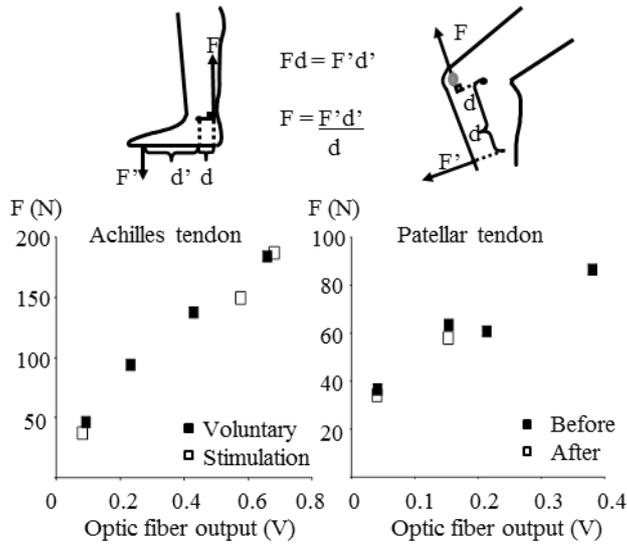


Fig. 2. Group mean values of tendon loading patterns during large amplitude hopping (left). In the other two panels Achilles (ATF, right) and patellar (PTF, middle) tendon forces are presented as function of triceps surae (TS) or quadriceps femoris (QF) muscle velocity. EMG activity patterns of rectus femoris (RF), vastus lateralis (VL), soleus (SOL) and gastrocnemius (GA) muscles illustrate that for knee extensors the activity was dominant in the eccentric phase while there was no significant difference between eccentric and concentric activity levels in the TS muscle. Arrow in the left panel indicates initial ground contact.

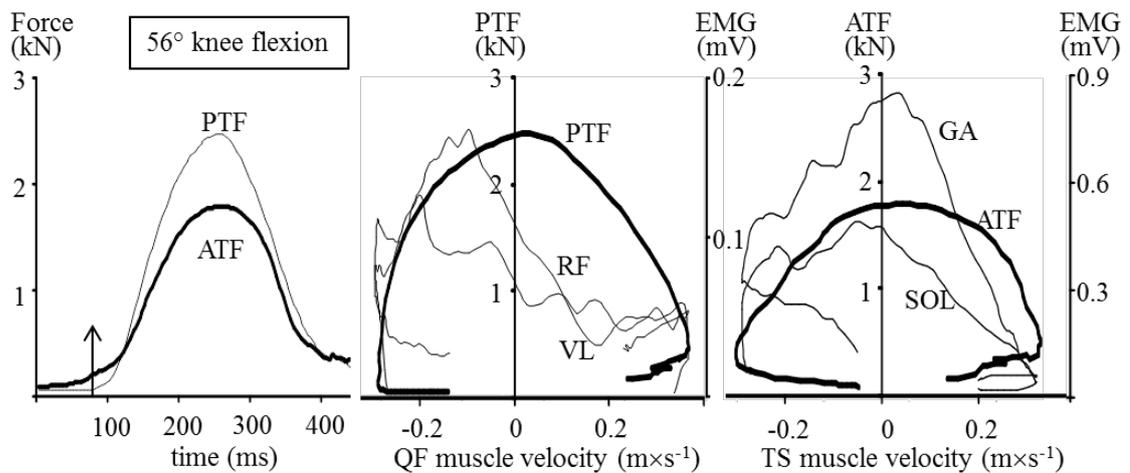


Fig. 3. Force-length (upper panel) and EMG-length relationships (lower panel) for quadriceps femoris muscle in small amplitude (solid line) and large amplitude hopping (dashed line). The upward and downward arrows indicate stretching and shortening, respectively.

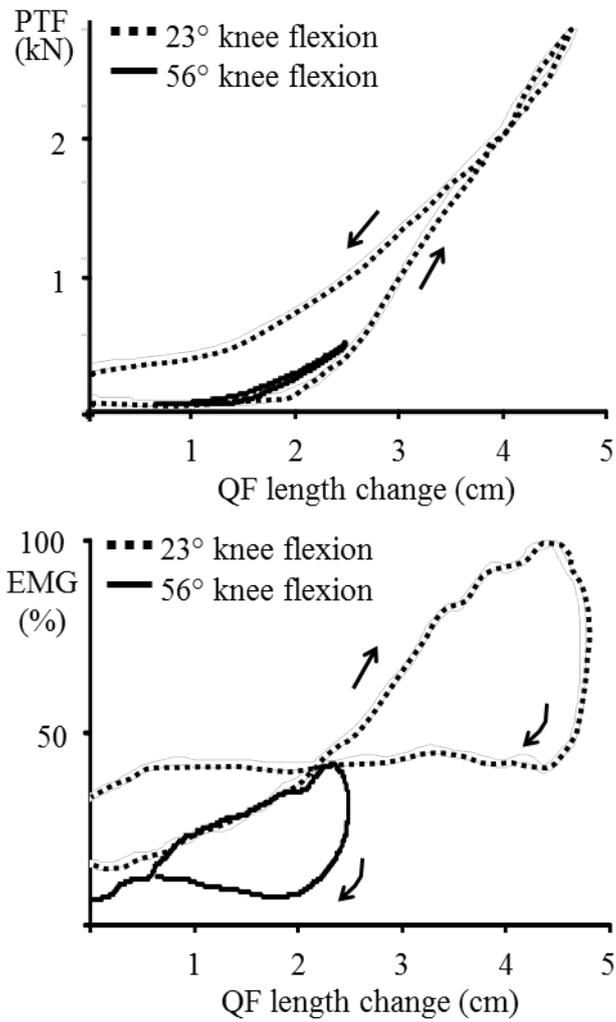


Fig. 4. Peak tendon forces increased when the hopping height was increased. The two representative examples show that the Achilles tendon (thick line) was always predominantly loaded when the knee joint angular displacement was small (26°).

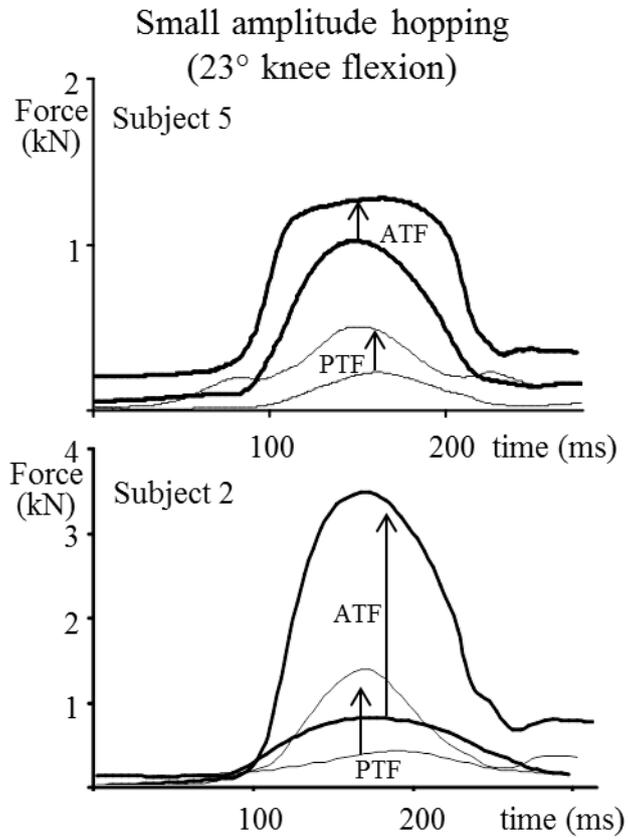


Fig. 5. Relationship between concentric EMG-to-ATF ratio and jumping height indicating that the concentric output is most economical with approximately 10 cm jumping height. Data from small amplitude hopping with different intensities.

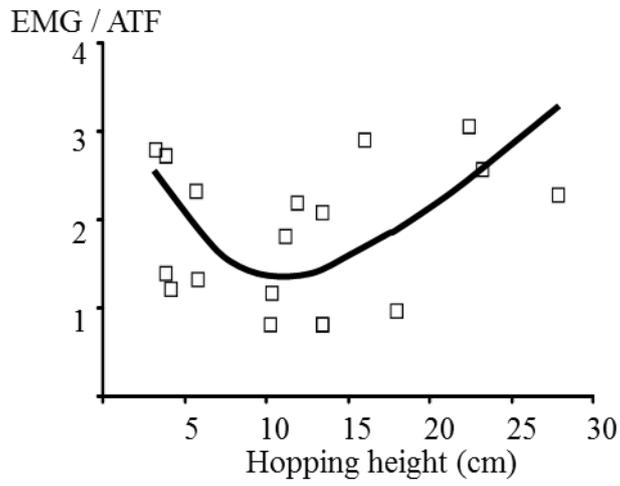


Fig. 6. Force-velocity (left) and EMG-velocity (right) relationships for triceps surae muscle during small amplitude hopping. Notations of low, medium (med.) and high refer to the increased jumping height. In this comparison the knee joint angular movement was same in each case [18° (SD 3)].

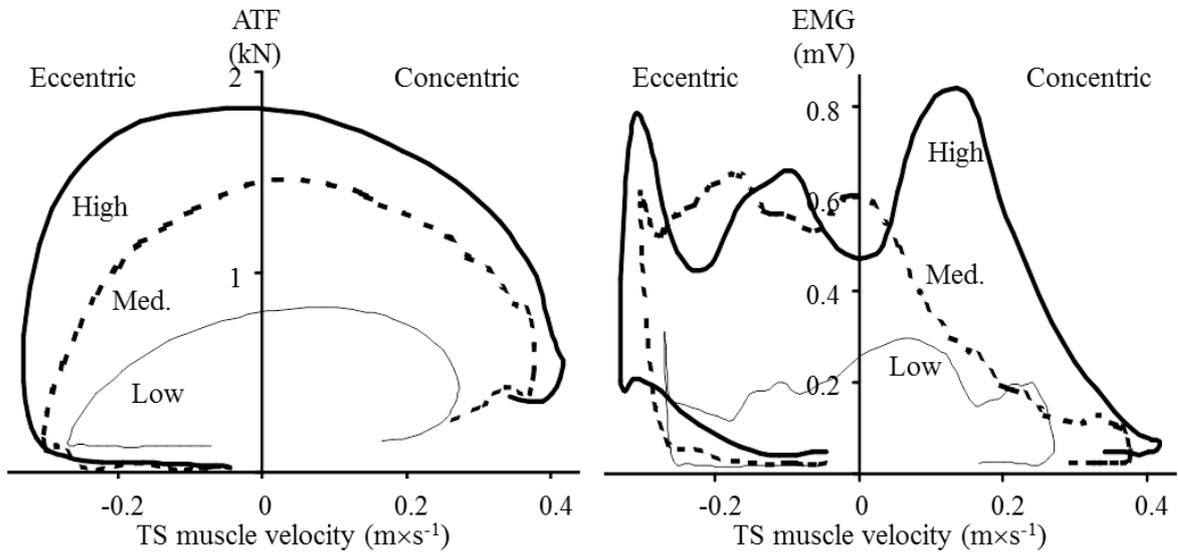
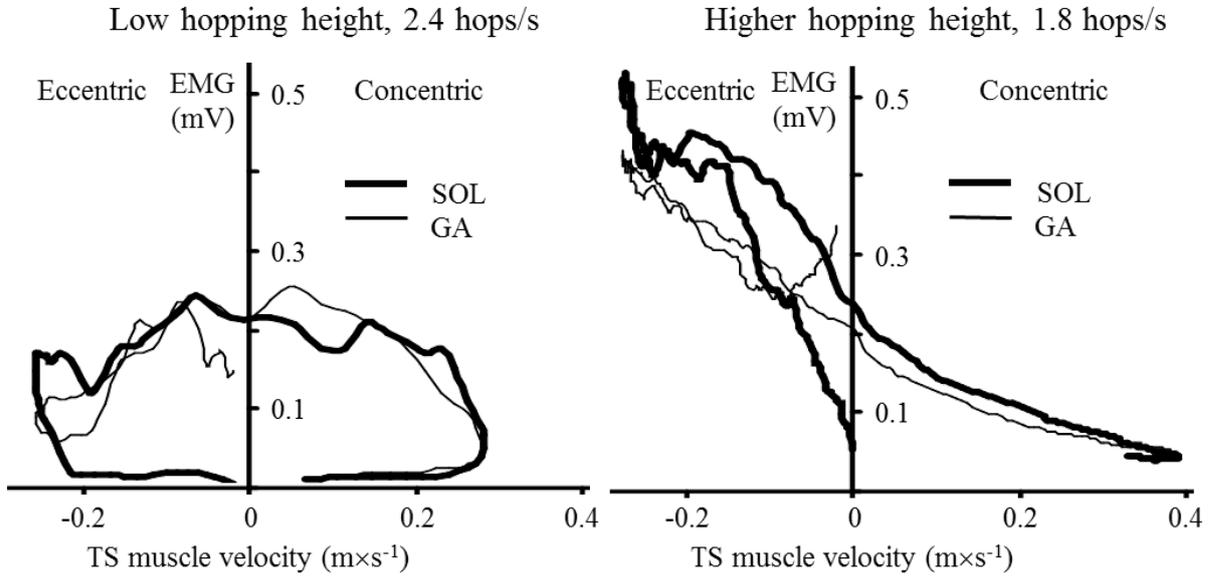


Fig. 7. In small amplitude hopping the decrease in hopping frequency (simultaneous increase in jumping height) was accompanied with dramatic increase in eccentric activity. Example from one subject.



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