European Journal of Sport Science, vol. 1, issue 1

In Vivo Behavior of Vastus Lateralis Muscle During Dynamic Performances

Taija Finni, Shigeki Ikegaw, Vesa Lepola, Paavo Komi

{PRIVATE}{PRIVATE}Length changes in vastus lateralis fascicles were measured in vivo using ultrasonography during one-legged squat jumps (SJ), counter movement jumps (CMJ), and drop jumps (DJ) in the sledge apparatus (n = 9). Patellar tendon forces were recorded simultaneously with an optic fiber technique from 4 subjects. Fascicle length changes were compared with muscle-tendon unit length changes calculated from kinematic recordings. In general, the tendomuscular and fascicle length changes demonstrated similar patterns. During SJ the fascicles showed shortening throughout the action while during CMJ and DJ they underwent stretch-shortening cycle. In DJ greater muscular activity in braking phase ($p < .001$) enabled fascicles to resist lengthening better and thus the length changes were smaller ($p < .001$) as compared to the CMJ. Because muscle-tendon unit length changes were of same magnitude in both DJ and CMJ, tendon stretching and shortening played more important role in DJ enhancing the velocity of entire muscle-tendon unit, especially during the push-off phase.

Key Words: vastus lateralis muscle, fascicle, tendon force, force-length relationship, jumping

{PRIVATE}Key Points:

1. In vivo length and force of human vastus lateralis muscle were measured during squat, counter movement, and drop jump performances.

2. In squatting jump both fascicles and muscle-tendon unit showed shortening while they underwent stretch-shortening cycle in the other two conditions.

3. Fascicles were stiffer in drop jump than in counter movement jump. While the change in muscle-tendon (MT) length was the same in both conditions, the results demonstrate the importance of tendinous tissue in enhancing velocity of the entire MT unit.

Introduction

Muscles can serve various purposes in locomotion. For example, they can act as force and power generators or absorbers depending on their anatomical factors as well as task related functions (6, 12). During natural human locomotion that can be characterized with submaximal, constantly varying activation, muscular function has been evaluated by means of modeling both force and length changes of given muscles (16, 32) but also with in vivo recordings of tendomuscular forces (8, 10, 13, 23) and measurement of fascicle (11) or sarcomere lengths (28). The pennation angle and length of muscle fascicles that run from aponeurosis to aponeurosis can be determined by non-invasive ultrasonograpic (US) method. The light striations seen in US images are generated by fat and connective tissue that runs between the fascicles (7). Although the orientation of fascicles is the same as muscle fibers, the fascicle length may not correspond to the muscle fiber length because muscle fibers may terminate mid-fascicularly (31). In spite of the fact that fascicle length measurements do not give accurate representation of fiber or sarcomere function due to inhomogenieties in sarcomere lengths in series and compliance of connective tissue, the ultrasonographic method can give more detailed information about muscular function in vivo as compared to the muscle-tendon unit length estimations alone.

Tendomuscular performance is greatly affected by tendon compliance that can have an effect on operating range and velocity of muscle fiber (29). Therefore, the muscle-tendon (MT) interaction may explain enhanced power output during natural locomotion as compared to the in situ experiments (14). This interaction has been the object of studies on both animal and human movements. Griffiths (1991) has reported muscle fiber shortening despite stretch of entire muscle-tendon complex of cat medial gastrocnemius muscle during slow walking. On the other hand, Roberts et al. (1997) have shown in running turkeys that during the ground contact phase the muscle fiber length changes only little while tendon stretches and recoils. Another example is pectoralis muscle of birds that lengthens mostly passively and does considerable amount of work while shortening (3).

In human studies, Hof et al. (1983) concluded by means of EMG to force processing that in natural locomotion, submaximal activation accompanied with concerted contraction might be an important factor for utilization of elastic energy and thus for efficient movement. While interaction of muscle and tendinous tissue has been directly measured in isometric (22) and isokinetic contractions (21), only preliminary results are available during natural locomotion (26). The objective of the present study was to examine MT interaction in different jumping conditions by measuring vastus lateralis (VL) muscle fascicle length changes with ultrasonography. From simultaneous in vivo recording of patellar tendon force, it was possible to examine vastus lateralis muscle length dependence of force during normal human movement. It was hypothesized that VL fascicle and MT length changes show similar patterns.

Methods Nine subjects volunteered for this study (7 males, 2 females, age 26.5 ± 4, height 179.9 ± 7 cm, weight 75.4 ± 8 kg). They were informed of all the risks associated with the study and gave their written consent to participate. They 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 use of in vivo tendon force transducer in the study. The subjects were tested for maximal isometric knee extension after which they performed submaximal one-legged jumping performances in the sledge apparatus.

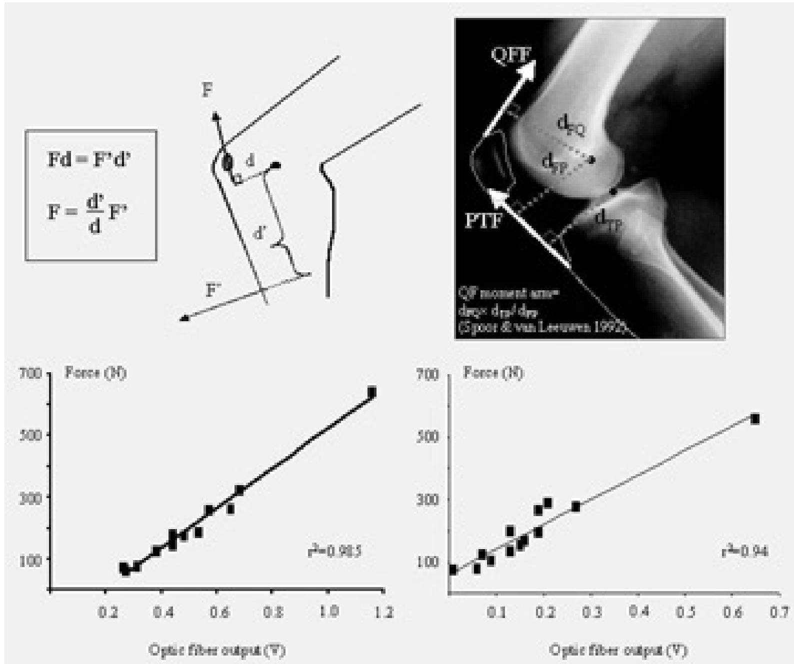
Four subjects repeated the sledge measurements after an optic fiber force transducer was inserted to their patellar tendons.

Isometric Measurements

At least two maximal isometric (MVC) knee extensions were measured while subjects were seated in a leg extension ergometer (25). The lever arm of the ergometer was equipped with strain gauge transducer, and lever arm length could be read from an inbuilt ruler. Measurements were repeated at knee angles of 90 ± 1, 120 ± 4, 138 ± 7, 151 ± 4 and 180° (full extension). For the subjects from whom patellar tendon force recordings were done, the leg extension ergometer was used also in calibration of the optic fiber force transducer.

The Optic Fiber Force Transducer

While the subjects were sitting in the leg extension ergometer with knee angle of 120°, a hollow 19-gauge needle was passed through their patellar tendon perpendicularly to the sagittal plane. The skin around the tendon had been anaesthetized with lidocain-prilocain cream pad. After the sterile optic fiber (PMMA, diameter: 0.5 mm) had been threaded through the needle, the needle was removed leaving the fiber in situ (AVI format, RealPlayer format). After insertion, the tips of the optic fiber were cleaned and attached to the transmitter-receiver unit (Hewlett Packard, USA). Tendon deformation during locomotion modulates the intensity of the light going through the fiber. The light signal detected by the receiver was converted to analogue signal and further to force using calibration curves and equation of balance of the moments (Figure 1). Changes in the light intensity have been shown to have linear relationship with the external force (see 2, 8, 9, 24 for further details of the method). In the present study the optic fiber was calibrated both before the sledge jumps with 10, 20, 30, and 40 % MVC and after the measurements when the calibration was continued until maximum effort. Linear relationship was maintained throughout the measurements (Figure 1).



{PRIVATE}Figure 1 — Tendon forces were calibrated using individual relationships between optic fiber output and knee extension force and equation of balance of the moments. Moment arms were determined from superimposed X-ray images with contracted knee extensor muscles at three different knee angles. The exemplary image was taken at 110°.

Moment Arms and Muscle Forces

Radiographs of the subject's right knee were obtained at three knee flexion angles (approximately 180, 120, and 60°). When lying on the right side on the X-ray table the subjects were asked to contract their knee extensor muscles while the images were taken (Figure 1). X-ray image scaling coefficient of 1.071 was confirmed with metal ruler. Images at different joint angles were superimposed to a transparency in order to determine the axis of rotation and moment arms for patellar and quadriceps tendons (35). Assessment of QF tendon moment arm as compared to the PT moment arm requires more parameters, thus increasing uncertainty of measurement. Furthermore, after the calibration of the fiber force transducer has been done at a certain joint angle, changes in moment arm do not affect the patellar tendon force values, thus eliminating one variable. Therefore, it was decided to use PTF values as tendon force instead of QFF because the difference in these two values was calculated to be less than 10%, but an error due to reading of the moment arm values only is 5.1 (relative error, 4.5) times greater for quadriceps moment arm. When calculating VL forces from the knee extension force recorded in the isometric conditions, individual moment arm changes due to knee angle change were taken into account. The relationship between patellar tendon moment arm and knee joint angle was quite similar to that reported by Visser et al. (1990) for medial portion of vastus lateralis muscle (Figure 3). The vastus lateralis force in the direction of fascicle was calculated by multiplying the tendon force with 34% and dividing it by cosine of the fascicle angle as done by Ichinose et al. (2000).

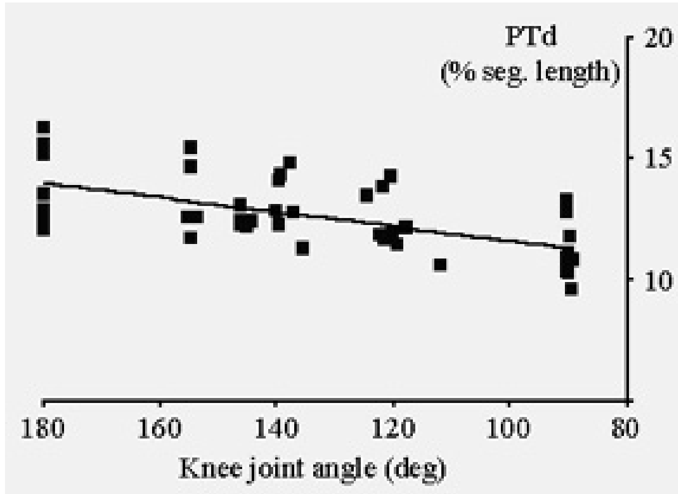
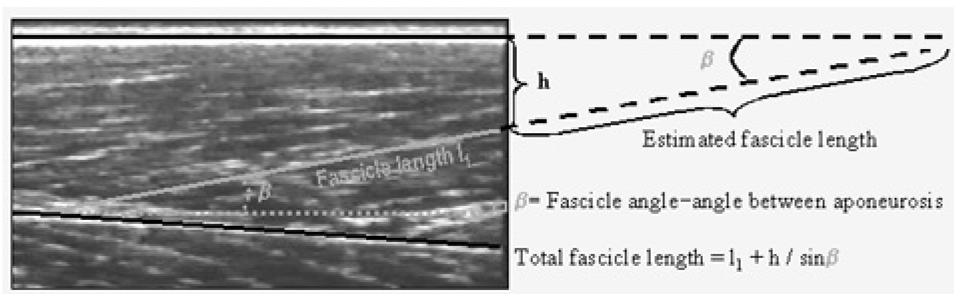


Figure 2 — Relationship between knee angle and patellar tendon moment arm as percentage of segment length.



{PRIVATE}

Figure 3 — Model used for VL fascicle length determination.

Sledge Performances

In the sledge apparatus (24.9° inclination from horizontal) (27) subjects repeated one-legged squat jumps (SJ), counter movement jumps (CMJ), and drop jumps (DJ) (AVI format, RealPlayer format)). Knee angle of 120° was the target for lowest position or initial position in SJ. Subjects were provided with visual feedback for the purpose to control their performances during the measurements.

Reaction forces, displacement, and velocity of the sledge and EMGs from soleus, tibialis anterior, vastus lateralis, vastus medialis, rectus femoris, and biceps femoris muscles were collected with frequency of 1,000 Hz with Motus software (Peak Performance Technologies, USA). EMG signals were amplified and sent telemetrically to the recording computer. The signals were high-pass filtered (20 Hz, before sampling), full-wave rectified and integrated separately for eccentric and concentric phases that were determined from MT length changes. Integrated EMG was divided by the integration time to obtain average EMG. Smoothed activity patterns presented in figures resulted from time normalization and averaging of the jumping performances of the 4 subjects. Performances were videotaped at 200 Hz in the sagittal plane from the subject’s right side. Reflective markers were placed on the neck at the level of the fifth cervical vertebra, greater trochanter major, approximate center of rotation of the knee, lateral malleolus, heel, and fifth metatarsal head. These points were digitized from video with Motus software. Joint angular data was used for calculation of length changes of the vastus lateralis muscle-tendon unit (17). MT velocities were calculated by dividing infinitesimal change in muscle length with corresponding time (5 ms).

Fascicle Length Measurements

Vastus lateralis fascicle lengths were imaged by Aloka SSD 2000 ultrasonographic device with frequency of 42 Hz. Images obtained at 50% of thigh length were recorded on videotape at 50 Hz. After the researcher had confirmed the visibility of echoes from VL fascicle interspaces, a linear array probe (8 cm, 7.5 MHz) was firmly secured to the subject's thigh with a special support devise. Visibility of echoes during contraction and movement were also tested carefully. A parallelogram model was used when the video image was digitized with Motus software. Same fascicle was followed throughout the motion. Because VL fascicle lengths go beyond the length of the probe used presently, total fascicle lengths were calculated as shown in Figure 3. When the aponeuroses were not parallel, the angle between them was subtracted from the measured pennation angle to make calculation possible. Patellar tendon cross-sectional area was also determined by ultrasonography for calculation of stress in the tendon.

An electronic pulse was used to synchronize the analog and video data. The data collected at different frequencies were combined at 200 Hz to allow multiple calculations. US image data collected with 50 Hz was extrapolated utilizing quintic spline function to correspond the frequency of 200 Hz.

Statistics

Mean, standard deviations, and Pearson's two-tailed correlations were calculated. *T* test or Anova model with Tuckey Post Hoc test were employed appropriately to reveal significant differences between eccentric and concentric phases or between variables in the three jumping conditions.

Results During one-legged squat jumps in the sledge apparatus, the fascicles showed shortening throughout the push-off phase whereas, during CMJ and DJ, they stretched prior to shortening (Figure 4). In drop jump, the magnitude of fascicle length changes during ground contact was smaller (1.6 cm, $p < .001$), while muscular activity was greater than in CMJ, especially in the eccentric phase ($p < .001$). Correlation analysis revealed inverse relationship between PTF and fascicle length in the concentric phase (Figure 5). For the subjects without in vivo tendon force measurements, similar relationship was found between maximum Fz and minimum fascicle length in the concentric phase. The fascicle lengths used in these jumping performances corresponded to those in the ascending limb of the force-length relationship measured in maximal isometric condition. This was also true when entire MT unit lengths were considered (Figure 6).

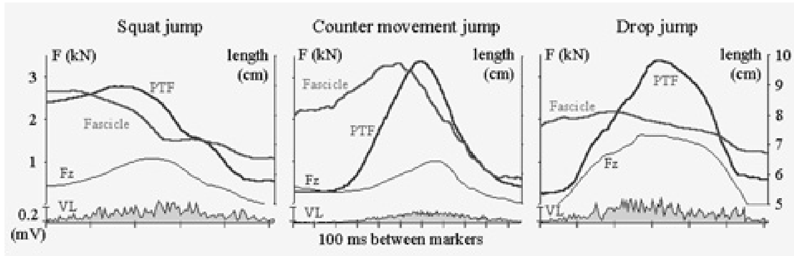


Figure 4 — Reaction forces (Fz), patellar tendon forces (PTF), fascicle length (fascicle), and vastus lateralis muscle EMG activity (VL) during one-legged SJ, CMJ, and DJ on the sledge apparatus. Average curves from 4 subjects.

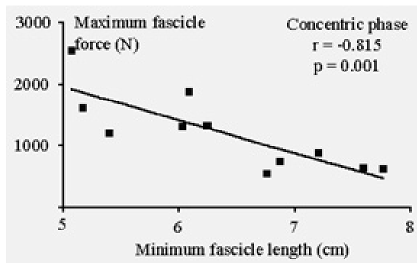


Figure 5 — Fascicle force and minimum length correlated negatively in concentric phase of jumping performances.

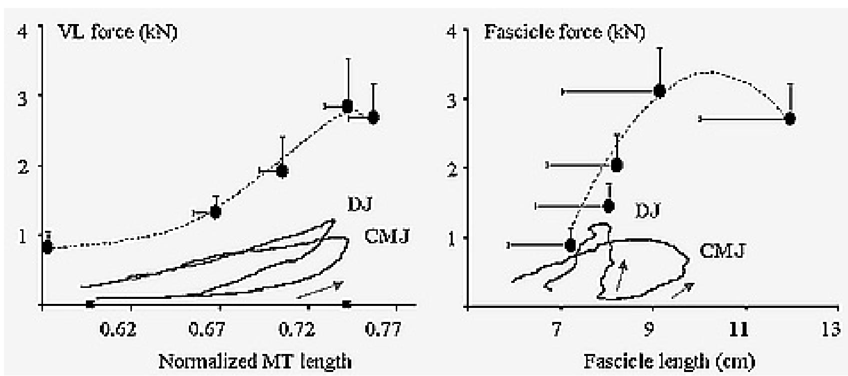


Figure 6 — Vastus lateralis muscle-tendon complex (left) and fascicle force-length relationships (right) in isometric (circles, n = 9) and stretch-shortening cycle conditions (lines). Curves during counter movement jump (blue) and drop jump (brown) are averaged across 4 subjects. Black squares indicate the operating range of the MT-complex during CMJ for subjects without in vivo tendon force measurements.

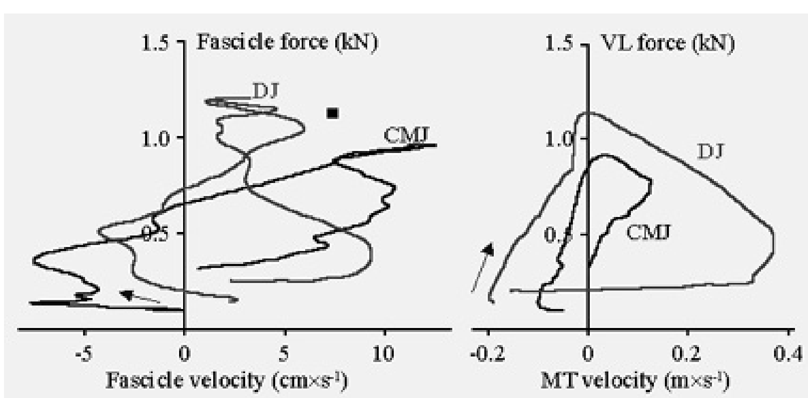


Figure 7 — Fascicle (left) and MT-complex (right) force-velocity relationships during CMJ and DJ. The black square indicates fascicle force produced at shortening velocity of $150° \cdot s^{-1}$, and is taken from ref. 21.

For the stretch-shortening cycle (SSC) performances the force-velocity curves for entire MT unit and fascicle showed distinct differences. While the peak forces were reached near transition phase for MT unit, fascicles reached their maximum forces during shortening (Figure 7).

Minimum knee angles reached during SJ, CMJ and DJ performances did not differ between conditions. Consequently the calculated MT lengths were also similar at the transition from braking to push off phase. For DJ, the take-off velocity ($p < .001$) and reaction forces ($p < .05$) were greater as compared to the CMJ.

Torques, forces, and patellar tendon moment arm values in 100% MVC are given in Table 1 as function of a knee angle. Average stress of 61 MPa in the patellar tendon was obtained during maximal isometric contractions whereas during jumping performances the average peak stress was 39 MPa.

{PRIVATE}**Table 1 — Mean (*SD*) Values of Knee Extension Torque, Tendon, and Fascicle Forces, and Moment Arm of the Patellar Tendon in Maximal Voluntary Contraction at Five Different Knee Angles**

Knee angle (°)	Torque (Nm)	F_{tendon} (N)	$F_{fascicle}$ (N)	d PT
90 (1)	318 (56)	6949 (1244)	2708 (495)	4.5 (0.3)
120 (3)	395 (72)	7816 (1476)	3106 (638)	5.1 (0.3)
137 (7)	303 (52)	5727 (979)	2054 (443)	5.3 (0.3)
151 (4)	226 (32)	4162 (669)	1445 (339)	5.4 (0.4)
180	148 (24)	2633 (467)	891 (237)	5.6 (0.4)

Discussion

Reaction forces and patellar tendon forces showed similar patters as observed earlier during one-legged sledge jumps as well as during normal jumping performances (9). The result that the fascicles shortened throughout the SJ and underwent SSC during CMJ also coincides with a modeling experiment in our earlier study for soleus muscle compartment (9). Although the fascicles behaved similar to the entire musculotendinous unit, the magnitude of lengthening and shortening was, however, different for fascicle and MT unit (Figure 6). This difference can be attributed to tendinous tissue elongation. Literature supports the idea that although strain in muscle fibers is much higher than in tendons or aponeurosis, the changes in tendon length may be responsible for the major proportion of the MT length change (18). It is, however, a matter of speculation how the interaction between muscle and tendon appears. It can be different depending on examined muscles and their functions, activity level, force, and overall MT length. Zajac (1989) has used tendon slack length to muscle fiber length ratio to characterize muscle-tendon unit properties. Vastus lateralis MT unit with ratio of 3 can be considered stiffer as compared to compliant plantarflexor muscles with ratios around 10. The present result that both MT unit and fascicles utilized the ascending part of the force-length relationship may be explained by nature of stiff MT unit that does not distort the force-length relationship to the right as much as for compliant actuators.

Average vastus lateralis muscle fiber length of 6.6 cm (38) is less than average fascicle length of approximately 9 cm. When this discrepancy is added to the fact that fiber lengths are not homogeneous within fascicle (31), it must be acknowledged that the length changes measured here may not reflect exactly the changes in fiber or sarcomere lengths. With this limitation in mind, the obtained results can have considerable importance. In the present study, fascicles were expected to operate more in the middle or descending part of the F-L relationship rather than in the shorter end of the curve as observed (Figure 6). However, no deep squatting positions where fascicles may be stretched more were used. Cutts (1989) has predicted that VL sarcomeres operate in the ascending and plateau region of the F-L relationship during walking. In the jumping conditions of the present study, the muscular activity is greater than in walking and, therefore, it may be reasoned that the sarcomeres work at shorter lengths as observed in the present study for fascicles. The inverse correlation between force and fascicle length also supports this view (Figure 5). In the present study, it is possible that fascicles did not utilize longer lengths because of the moderate knee flexion angles and performance intensity used. As hypothesized by Fukunaga et al. (1997), it is possible for VL fascicles to operate also in the descending limb of the F-L relationship in other tasks.

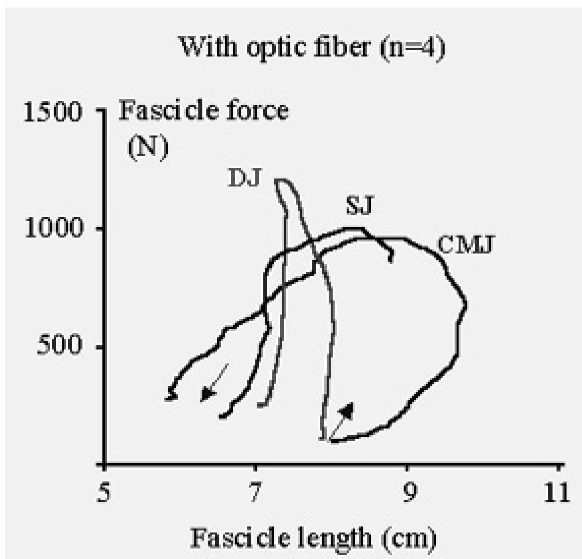


Figure 8 — Fascicle force-length relationships during SJ (black), CMJ (blue), and DJ (brown).

In the DJ performance, both maximum eccentric and takeoff velocities of the sledge were greater than in CMJ. It seems that in DJ, the programmed pre-landing activity was appropriate in order to achieve greater takeoff velocity as compared to that in CMJ (20). The greater EMG activity with narrower fascicle operating range emphasizes tendon function (Figure 6). The tendon lengthening was greater in DJ than in CMJ because entire MT-unit length changes did not differ between conditions. The greater EMG activity in DJ reduced both the magnitude and velocity of fascicle length change as compared to the CMJ (Figures 7 and 8). From the point of view of the entire tendomuscular unit, the higher shortening velocity was reached during DJ performance where take-off velocities were also greater than in CMJ. This clearly shows that the tendon function has dramatic effect on the velocity and thus on power in the present DJ condition. Greater stiffness in the contractile part (smaller fascicle length change with greater force) with effective tendon stretch and recoil has been shown to be beneficial to movement efficiency (1, 30, 37). However, it must be remembered that the reason for improved tendon function in the present conditions is also a greater EMG activity and thus greater energy consumption (4). In CMJ the downward movement is partly passive, as the gravity acts to lengthen the tendon. This is true also for DJ, but there is probably a stronger contribution from muscle activity to stretch the tendon. Therefore, besides looking at the efficiency that tendon action may bring about, focus should be given to how the tendon compliance affects muscle length. As stated earlier, tendon action has the possibility of creating beneficial conditions for muscle to work with slower velocities (29) and consequently with a possibility for high force production with lower energy cost (34).

The present measurements of fascicle lengths and velocities are similar to those of Ichinose et al. (21) and allow comparison of "classical" and instantaneous F-V relationships. Although the optimum fascicle lengths measured were slightly longer in the present study, the force-velocity comparison seems to indicate that even in submaximal jumping performances forces produced by fascicles reach close to that obtained in maximum "isokinetic" condition (150°/s point from Ichinose et al. [21, Figure 7] is attached to our Figure 7).

In our previous study (9), it was shown that tendomuscular force could continue to increase during the push-off phase of CMJ. In the present one-legged sledge performances, this was not as clear for the MT unit, but in the fascicle level it could be seen that peak forces were reached during shortening (Figure 7). This is a natural consequence of the phenomenon known from fixed-end contractions, where contractile component is required to produce force and stretch the tendon before external force can be observed. In the present CMJ, the activation in the beginning of downward movement is low, and tendon lengthen together with initially nearly passive muscle. Then, with gradually increasing activity, the fascicles start to resist lengthening, and eventually the shortening phase begins. After reaching a certain force level, shortening of the entire MT unit can be observed. In the DJ, the high muscular activity corresponded to smaller magnitude of lengthening. In this connection, the high pre-landing activity could have limited the length change during the ground contact phase even further. The clear prelanding activity sets already the conditions for smaller length change to follow.

Conclusions

In the present unilateral SJ, CMJ, and DJ conditions fascicles of the vastus lateralis muscle operated in the shorter end of the force-length curve. In SJ both fascicle and MT-unit showed shortening, whereas they underwent stretch-shortening cycle in CMJ and DJ. The observed differences in fascicle and muscle-tendon unit behavior between CMJ and DJ were attributed to greater EMG activity in DJ that resulted in greater force, smaller change in fascicle length, and effective tendon stretch and recoil. The tendon function was shown to be of great importance in enhancing the shortening velocity of the MT-unit thus enabling the contractile part to function in a low velocity and high force region of the force-velocity curve.

Acknowledgments

The authors would like to thank Ms. Pirkko Puttonen, Ms. Marja-Liisa Romppanen, Ms. Sirpa Roivas, Mr. Markku Ruuskanen and Mr. Jouni Kallio for their assistance in data collection and analysis. This study was supported by grant (119/722/99) from the Ministry of Education, Finland.

References

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

2. Arndt AN, Komi PV, Brüggemann G –P, Lukkariniemi J. 1998. Individual muscle contributions to the in vivo achilles tendon force. Clin Biomech 13:532-41.

3. Biewener AA, Corning WT, Tobalske BW. 1998. In vivo pectoralis muscle force-length behavior during level flight in pigeons columba livia.. J Exp Biol 201:3293-307.

4. Bigland-Richie B, Woods JJ. 1976. Integrated electromyogram and oxygen uptake during positive and negative work. J Physiol 260:267-77.

5. Cutts A. 1989. Sarcomere length changes in muscles of the human thigh during walking. J Anat 166:77-84.

6. Dickinson MH, Farley CT, Full RJ, Koehl MAR, Kram R, Lehman S. 2000. How animals move: an integrative view. Science 288:100-106.

7. Engstrom CM, Loeb GE, Reid JG, Forrest WJ, Avruch L. 1991. Morphometry of the human thigh muscle. A comparison between anatomical section and computer tomographic and magnetic resonance images. J Anat 176:139-56.

8. Finni T, Komi PV, Lukkariniemi J. 1998. Achilles tendon force during walking: measurements with the optic fiber technique. Eur J Appl Physiol 77:289-91.

9. Finni T, Komi PV, Lepola V. 2000. In vivo triceps surae and quadriceps femoris muscle function in a squat jump and counter movement jump. Eur J Appl Physiol. In print.

10. Fukashiro S, Komi PV, Järvinen M, Miyashita M. 1995. In vivo achilles tendon loading during jumping in humans. Eur J Appl Physiol 71:453-58.

11. Fukunaga T, Ichinose Y, Ito M, Kawakami Y, Fukashiro S. 1997. Determination of fascicle length and pennation in a contracting human muscle in vivo. J Appl Physiol 1:354-58.

12. Gans C, De Vree F. 1987. Functional bases of fiber length and angulation in muscle. J Morphol 192:63-85.

13. 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 5:287-97.

14. 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 9:721-32.

15. Griffiths RI. 1991. Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. J Physiol 436:219-36.

16. Gollhofer A, Strojnik V, Rapp W, Schweizer L. 1992. Behaviour of triceps surae muscle-tendon complex in different conditions. Eur J Appl Physiol 64:283-91.

17. Hawkins D, Hull ML. 1990. A method for determining lower extremity muscle-tendon lengths during flexion/extension movements. J Biomech 5:487-94.

18. Herbert RD, Crosbie J. 1997. Rest length and compliance of non-immobilised and immobilised rabbit soleus muscle and tendon. Eur J Appl Physiol 76:472-79.

19. Hof LA, Geelen BA, Van den Berg Jw. 1983. Calf muscle moment, work and efficiency in level walking: role of series elasticity. J Biomech 7:523-37.

20. Horita T. 2000. Stiffness regulation during stretch-shortening cycle exercise. [Ph.D. thesis] Jyväskylä, University of Jyväskylä. p. 56-57.

21. Ichinose Y, Kawakami Y, Ito M, Kanehisa H, Fukunaga T. 2000. In vivo estimation of contraction velocity of human vastus lateralis muscle during "isokinetic" action. J Appl Physiol 88:851-56.

22. Ito M, Kawakami Y, Ichinose Y, Fukashiro S, Fukunaga T. 1998. Nonisometric behavior of fascicles during isometric contractions of a human muscle. J Appl Physiol 4:1230-35.

23. Komi PV. 1990. Relevance of in vivo force measurements to human biomechanics. J Biomech Suppl. 1:23-34.

24. 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 72:278-80.

25. Komi PV, Linnamo V, Silventoinen P, Sillanpää M. 2000. Force and EMG power spectrum during eccentric and concentric actions. Med Sci Sp Exerc In print.

26. Kurokawa S, Yan H, Nagareda H, Funato K, Fukunaga T. 1997. Muscle fiber behavior of gastrocnemius during vertical jumping. XVIth Congress of the International Society of Biomechanics. Book of Abstracts.

27. Kyröläinen H, Komi PV. 1995. Differences in mechanical efficiency between power-and endurance-trained athletes while jumping. Eur J Appl Physiol 70:36-44.

28. Lieber RL, Loren GJ, Fridén J. 1994. In vivo measurement of human wrist extensor muscle sarcomere length changes. J Neurophysiol 3:874-80

29. Lieber RL, Brown CG, Trestik CL. 1992. Model of muscle-tendon interaction during frog semitendinosis fixed-end contractions. J Biomech 4:421-28.

30. Morgan DL, Proske U, Warren D. 1978. Measurements of muscle stiffness and the mechanism of elastic storage of energy in hopping kangaroos. J Physiol 28:253-61.

31. Ounjian M, Roy RR, Eldred E, Garfinkel A, Payne JR, Armstrong A, Toga AW, Edgerton VR. 1991. Physiological and developmental implications of motor unit anatomy. J Neurobiol 5:547-59.

32. Pandy MG, Zajac FE. 1991. Optimal muscular coordination strategies for jumping. J Biomech 1:1-10.

33. Roberts TJ, Marsh RL, Weyand PG, Taylor CR. 1997. Muscular force in running turkeys: the economy of minimizing work. Science 21:1113-15.

34. Ryschon TW, Fowler MD, Wysong RE, Anthony A-R, Balaban RS. 1997. Efficiency of human skeletal muscle in vivo: comparison of isometric, concentric, and eccentric muscle action. J Appl Physiol 3:867-74.

35. Spoor CW, van Leeuwen JL. 1992. Knee muscle moment arms from MRI and from tendon travel. J Biomech 25:201-206.

36. Visser JJ, Hoogfamer JE, Bobbert MF, Huijing PA. 1990. Length and moment arm of human leg muscles as a function of knee and hip-joint angles. Eur J Appl Physiol 61:453-60.

37. Voigt M, Simonsen EB, Dyhre-Poulsen P, Klausen K. 1995. Mechanical and muscular factors influencing the performance in maximal vertical jumping after different prestretch loads. J Biomech 28:293-307.

38. Wickiewicz TL, Roy RR, Powell PL, Edgerton VR. 1983. Muscle architecture of the human lower limb. Clin Orthop Rel Res 179:275-83.

39. Zajac FE. 1989. Muscle and tendon: Properties, models, scaling and application to biomechanics and motor control. Critical Reviews in Biomedical Engineering, CRC Press, Vol. 17, 4:359-411.