Muscle fiber and tendon length changes in the human vastus lateralis during slow pedaling

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Received 17 October 2000; accepted in final form 6 July 2001

Muraoka, T., Y. Kawakami, M. Tachi, and T. Fukunaga. Muscle fiber and tendon length changes in the human vastus lateralis during slow pedaling. J Appl Physiol 91: 2035–2040, 2001—Muscle fascicle lengths of vastus lateralis (VL) muscle were measured in five healthy men during slow pedaling to investigate the interaction between muscle fibers and tendon. Subjects cycled at a pedaling rate of 40 rpm (98 W). During exercise, fascicle lengths changed from 91 ± 7 (SE) to 127 ± 5 mm. It was suggested that fascicles were on the descending limb of their force-length relationship. The average shortening velocity of fascicle was greater than that of muscle-tendon complex in the first half of the knee extension phase and was less in the second half. The maximum shortening velocity of fascicle in the knee extension phase was less than that of muscle-tendon complex by 22 ± 9%. These discrepancies in velocities were mainly caused by the elongation of the tendinous tissue. It was suggested that the elasticity of VL tendinous tissue enabled VL fascicles to develop force at closer length to their optimal length and kept the maximum shortening velocity of VL fascicles low during slow pedaling.

METHODS

Subjects. Subjects were five healthy men [age 24.6 ± 0.2 (SE) yr, height 171.4 ± 2.5 cm, mass 66.7 ± 2.8 kg, thigh circumference 48.4 ± 1.2 cm] who cycled between 40 and 60 rpm (96–168 W). Subjects were five healthy men [age 24.6 ± 0.2 (SE) yr, height 171.4 ± 2.5 cm, mass 66.7 ± 2.8 kg, thigh circumference 48.4 ± 1.2 cm].

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length 40.0 ± 0.7 cm). They were not cyclists and did not ride a bicycle as a part of their training regimen. The experimental protocol was explained to all subjects, and their informed consent was obtained.

**Cycling exercise.** Subjects cycled at a pedaling rate of 40 rpm at a power output of 98 W without toe straps on a cycle ergometer (model 814E, Monark, Varberg, Sweden). Because of limitations in the sampling rate of ultrasonography (30 Hz), it is not possible to obtain ultrasound images clear enough for latter analyses at higher pedaling rates. Preliminary experiments showed that, when cycling at the pedaling rate of 40 rpm, knee joint angle velocity was <160°/s and that fascicle length can be measured as shown by Ichinose et al. (15). Subjects kept constant pedaling rate of 40 rpm with the help of a metronome (model SQ-77, Seiko, Tokyo, Japan). The saddle height was adjusted to the distance between the greater trochanter and sole, a distance requiring the least oxygen consumption (25). The trunk was inclined forward 10–20° from the vertical (Fig. 1).

**Measurement of fascicle length.** Longitudinal images of VL in the right leg were obtained by a B-mode ultrasound apparatus (model SSD-2000, Aloka, Tokyo, Japan) at a sampling frequency of 30 Hz with an electronic linear array probe of 7.5 MHz. The probe was positioned 2 cm distal to the center of the thigh, which was defined by the greater trochanter proximally and the lateral condyle of the femur distally. To avoid movement of the probe, the probe was firmly placed on the dermal surface by double-sided adhesive tape (model NW-K25, Nichiban, Tokyo, Japan) and surgical tape (DERICLEAR2, Johnson & Johnson, Tokyo, Japan). In addition, an expanded polystyrene block that was also placed on the dermal surface adjacent to the probe limited the movement of the probe relative to the dermal surface. The cycle ergometer we used was equipped with the switch. While the subject was cycling stably in a given condition, the electrical signal triggered by the switch was transferred to the ultrasound apparatus at a crank angle of 260° [top dead center (TDC) of the crank was 0°]. This signal was also transferred to high-speed camera and recorded together with electromyograph (EMG) data for the synchronization (Fig. 1). Forty-two images preceding the signal that covered a range from 68° before TDC to 260° after TDC were stored in the computer memory of the ultrasound machine, before being printed on paper at ×1.12 magnification. Fascicle lengths were measured from these printed images using a curvimeter or map measurer (10, 14, 15, 17; Comcurve-8, Koizumisokki, Tokyo, Japan). Fascicle lengths were always measured along their path. Fascicle lengths were too long to be visualized over their lengths within one ultrasound image. Therefore, the directions of superficial and deep aponeuroses and fascicles were extended by straight lines (Fig. 2). Both parts around origin and end of fascicles were extended separately because fascicles were curved. However, when the fascicle curvature was unpredictable from one ultrasound image (Fig. 2; dotted lines), we could not obtain accurate fascicle lengths by this extrapolation method. Therefore, less curvature of fascicles, especially around their origin and end, was more desirable for measuring of fascicle lengths using the extrapolation method. In preliminary experiments, we found that the extent of fascicle curvature tended to increase at the extremity of muscle, especially at the proximal region, and that the probe position described above was the best position for the extrapolation method. To evaluate the validity of this extrapolation method, we compared the fascicle lengths determined using this method (\(L_{\text{cal}}\); Fig. 2B) with the fascicle lengths measured directly from three successive images that contained a whole fascicle (\(L_{\text{dir}}\); Fig. 2A) for three subjects during submaximal isometric knee extension (0 and 60 Nm) at several knee joint angles (30, 45, 60, 75, 90, and 105°; 0° corresponded to full knee extension). We obtained three images so that adjacent images have common parts, and their printed images were carefully superposed according to common parts. Additionally, reproducibility of measurements was tested by an expert examiner from the measurement for one subject performing twice.

Fascicle lengths during cycling were described effectively with a third-degree polynomial using a least squares method [correlation coefficient \((r) = 0.99–1.00\)]. Contraction velocities of fascicle were calculated by differentiating those regression curves.

**Measurement of EMG.** Electrical activity of VL was sampled at 1,000 Hz during the same cycle in which fascicle lengths were measured. After careful abrasion of the skin, bipolar surface Ag-AgCl electrodes (5 mm in diameter) were placed on the center of VL muscle belly in the right leg with an interelectrode distance of 3 cm. The ground electrode was placed over the patella. The electrodes were connected to a preamplifier (model 1272, San-ei, Tokyo, Japan; input impedance >200 MΩ, common mode rejection ratio >60 dB) and a differential amplifier having a bandwidth of 5 Hz to 1 kHz (1253A, NEC Medical Systems, Tokyo, Japan) to avoid electrical and mechanical noise. Records sampled from each cycle...
were full-wave rectified, integrated (integrated EMG) every 15° for crank angles from 0° to 255° or every 5° for knee joint angles from 40° to 115° and normalized to the highest value achieved in each cycle.

Calculation of length changes in MTC, fascicle, and tendinous tissue. All trials were filmed using a high-speed camera (MEMRECAM c2s, Nac, Tokyo, Japan) at a sampling frequency of 200 Hz. The camera was located perpendicular to the sagittal plane of the subject at a distance of 3.5 m. Markers were applied to the skin overlying the greater trochanter, the approximate center of rotation of the knee joint, and the lateral malleolus to determine the knee joint angles. The films were analyzed using a motion analyzer (FrameDIAS, DKH, Tokyo, Japan). The coordinates of the markers were filtered with a Butterworth fourth-order low-pass filter (zero lag; cut-off frequency, 15 Hz). The length change of VL was calculated using data from Visser et al. (31), who reported the relationship between knee joint angles and the length change of VL muscle that was determined from the experimental results on six legs of five human cadavers. They divided VL muscle into lateral and medial parts, so we used the average length changes of them. Additionally, markers were applied to the center of the crank and center of the right pedal to determine the crank position. The repeatability of the relationship between knee joint angles and the crank angles was tested by coefficient of variation (CV) at several crank angles (0, 45, 90, 135, 180, 225, and 260°), and the average CV for each subject was 0.7%.

Length changes of MTC and fascicles were expressed as length changes (ΔLf and ΔLmtc, respectively) from each reference length which was the average length in the crank angle from 196 to 260° where the EMG activity of VL was scarcely observed. The length change of the tendinous tissue (ΔLt) was calculated according to the following formula:

\[ ΔLt = ΔLmtc - (Lf × \cos θ0 - Lfo × \cos θ0) \]

where \( Lf, Lfo, θ0, \) and \( θ \) are fascicle length, the reference length of fascicle, the reference pennation angle of fascicle (average pennation angle in the crank angle from 196 to 260°), and the pennation angle of fascicle, respectively. The pennation angles were measured as angles between fascicles and deep aponeurosis (Fig. 2).

Statistics. Validity and reproducibility of fascicle length measurement were tested by regression analysis, CV, and Student’s t-test. The differences between fascicle and MTC in contraction velocity were tested by Student’s t-test. Significance was accepted at \( P < 0.05 \).

RESULTS

Validity and reproducibility of fascicle length measurement by extrapolation method. The values for \( r \) were 0.99 between \( Lf_{ext} \) and \( Lf_{dir} \) and were 0.98 and 0.99 between the first and the second measurement for \( Lf_{ext} \) and \( Lf_{dir} \), respectively. There were no significant differences in all three relationships. CV ranged from 0.0 to 3.7% between \( Lf_{ext} \) and \( Lf_{dir} \), and it ranged from 0.7 to 3.5 and from 0.1 to 2.0% between the first and the second measurement for \( Lf_{ext} \) and \( Lf_{dir} \), respectively.

Length changes of fascicle, MTC, and tendinous tissue. During slow pedaling, fascicle length changed from 91 ± 6 (SE) to 127 ± 5 mm for knee joint angles changing from 39 ± 3 to 114 ± 1° (0 degree = full knee
extension). $\Delta L_f$, $\Delta L_{mtc}$, and $\Delta L_t$ were expressed as a function of crank angle (Fig. 3A). In the knee extension phase, $\Delta L_t$ reached $10 \pm 1$ mm. Assuming that the slack length of VL tendonous tissue was 225 mm (13), the strain of VL tendonous tissue reached 4%. Reported values of strain of the tendon are 5% for human medial gastrocnemius muscle during 90% maximal voluntary contraction (24) and 3% for human tibialis anterior muscle during maximal torque development by electrical stimulation (22). Reported values of aponeurosis are 6% for human medial gastrocnemius muscle during 90% maximal voluntary contraction (24) and 7% for human tibialis anterior muscle during maximal torque development by electrical stimulation (22). Our result (4%) was within the range of previous results mentioned above, although the previous results were obtained at higher muscle forces. Fascicle lengths in the knee extension phase were shorter than those in the knee flexion phase at same knee joint angles (Fig. 3B).

**Contraction velocity of fascicle and MTC.** Contraction (shortening) velocity of fascicle and MTC in the knee extension phase was expressed as a function of crank angle (Fig. 4A) and knee joint angle (Fig. 4B). The shortening velocity of MTC gradually increased in most of the knee extension phase (73%; crank angle = −23 to 105°), but that of fascicle became maximal in the first half of the knee extension phase (P1; crank angle = 66°). The maximum shortening velocity of fascicle (62 ± 6 mm/s) in the knee extension phase was less than that of MTC by 22 ± 9% (80 ± 8 mm/s). In P1 (crank angle = −23 to 66°), the shortening velocity of fascicle (average 49 ± 4 mm/s) was greater than that of MTC (33 ± 2 mm/s) by a maximum of 25 ± 7 mm/s. In contrast, in the second half (P2; 66 to 150°), the shortening velocity of fascicle (average; 43 ± 6 mm/s) was less than that of MTC (62 ± 6 mm/s) by a maximum of 37 ± 7 mm/s.

**EMG.** The EMG activity of VL was limited mostly to the knee extension phase (Fig. 4A), though it could be observed in just start of the knee flexion phase when the electromechanical delay (EMD) of 89 ms (30) was taken into account. The EMG activity increased rapidly when the knee started to extend and reached its maximal value at the crank angles of 0–15° (the knee joint angles of 85–90°), followed by...
a gradual decrease up to the crank angles of 90–105° and a rapid decrease thereafter. When considering EMD, the maximal EMG value was obtained at the crank angles of 45–60° (the knee joint angles of 95–100°) and gradual decrease was observed up to the crank angles of 120–135°.

**DISCUSSION**

In this study, the directions of superficial and deep aponeuroses and fascicles were extended by straight lines to measure the fascicle length. Fascicles measured in this study were not always straight as suggested in previous papers (17, 34). If fascicle curvature was large around origin and end part of fascicles as shown in Fig. 2 (dotted lines), it would be difficult to predict the whole shape of the fascicle. However, fascicle curvature was small enough for us to obtain fascicle lengths accurately and reproducibly.

The EMG profile of VL with respect to crank position was similar across subjects (see Fig. 4), and our results were consistent with previously published results (26, 30). It can be said that VL is generally active in the knee extension phase and inactive in the knee flexion phase during cycling even if EMD was taken into account, and our results showed that fascicle lengths in the active phase were shorter than those in the inactive phase at the same knee joint angle (i.e., at the same MTC length) (Fig. 3B). This was consistent with previous findings in that contracting fibers elongated the tendinous tissue (10, 14, 17).

Force-length relationship of muscle fibers affects their capability of force development. Our results showed that fascicle length of VL changed from 91 to 127 mm during slow pedaling. Recently, Ichinose et al. (14) investigated the force-length relationship of VL fascicles (sum of the force-length relationship of each fascicle in VL) in human in vivo using ultrasonography. They found that, when the subjects performed their maximal voluntary knee extension exercise isometrically with the knee positioned at 70° of flexion, the maximal VL muscle force was obtained and VL fascicle length was 78 mm. The characteristics of subjects in the present study were similar with their study (present study vs. previous study (mean ± SD): height, 171.4 ± 5.5 vs. 168.5 ± 5.2 cm; mass, 66.7 ± 6.3 vs. 65.8 ± 5.7 kg). In addition, Wickiewicz et al. (32) showed that muscle length-to-fiber length ratios were generally consistent throughout the muscles. Taking these findings into account together with our results on fascicle length, it can be assumed that only the descending limb of the force-length relationship of fascicles was used during the cycling task in this study. Therefore, the position in which the knee is more extended, where the net knee joint moment changes to flexion moment (11), is better for the force production of VL fascicles in the low-intensity pedaling adopted in this study. When cycling against higher pedaling load that requires VL fascicles to produce larger forces, the middle of the knee extension phase where the net knee joint moment is large might be suitable for the force production of VL fascicles because of more lengthened tendinous tissue. In any case, the elasticity of the tendinous tissue allows VL fascicles to produce force at closer length to their optimal length.

Zuurbier and Huijing (33) have shown by animal experiments that there were differences in the length change and velocity between muscle fibers and MTC during isokinetic concentric contraction. Considering the elasticity of tendinous tissue, it is appropriate to assume that the shortening velocity of fibers is less (greater) than that of MTC because the fiber force decreases (increases) during MTC shortening, excluding the effect of pennation angle. The result of our experiment supported this, as shown in Fig. 4. In P1, the average shortening velocity of fascicle was greater than that of MTC by 50%. In contrast, the average shortening velocity of fascicle was less than that of MTC by 29% in P2. Bigland and Lippold (4) have shown that muscle force depends on its contraction velocity in accordance with force-velocity relationship even at submaximal excitation levels. Therefore, in terms of the force-velocity relationship, lengthening of VL tendinous tissue in P1 has a negative effect on the force producing potential of fascicles. In P2, VL tendinous tissue shortening enhances the force-producing potential of fascicles. Overall, the lengthening of VL tendinous tissue decreased the maximum shortening velocity of fascicles. This might allow fascicles to produce force during pedaling at faster rate.

Although we could not show the work accomplished by fascicles in P1 and P2 because the force developed by fascicles was unknown, it could be said that a part of the work accomplished by MTC in P2 was a part of the work accomplished by fascicles in P1. The elastic energy storage in VL tendinous tissue accounts for this phenomenon. When the elastic energy is released from the tendinous tissue, part is dissipated as a result of the viscosity of the tendinous tissue (3, 18). In future study, the dissipated energy should be shown by the measurement of the force applied to the tendinous tissue for better understanding of the role of the tendinous tissue in movements.

In conclusion, it was found through in vivo measurement of fascicle length that the length of VL tendinous tissue increased in P1 and decreased in P2 during slow pedaling. Fascicle length was on the descending limb of force-length relationship in the low-intensity cycling task adopted in this study. Because of the elasticity of tendinous tissue, the average shortening velocity of fascicles increased by 50% in P1 and decreased by 29% in P2 compared with that of MTC, and the maximum shortening velocity of fascicles less than that of MTC by 22%. It was suggested that the elasticity of VL tendinous tissue enabled VL fascicles to develop force at closer length of their optimal length and kept the maximum shortening velocity of VL fascicles small during slow pedaling.
REFERENCES


