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Fascicle shortening upon activation in voluntary human muscle contractions

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HIGHLIGHTS

- VL fascicle shortening as a function of activation/force depends crucially on muscle length.
- Fascicle shortening results from a compromise between the force generating potential of the muscle and muscle elasticity at different lengths.
- Fascicle kinematics cannot easily be estimated from joint angle and activation.

ABBREVIATIONS

EMG	Electromyography
MTU	Muscle tendon unit
MVC	Maximal voluntary contraction
RMS	Root mean square
VL	Vastus lateralis

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BACKGROUND: The dependence of fascicle length on complex interactions with joint angle and force challenges the interpretation of in vivo joint mechanics, muscle mechanical properties, contractile behavior, and muscle function.
AIM: The purpose of this study was to determine the complex interaction between muscle activation, joint angle, and fascicle length for isometric contractions of the human vastus lateralis muscle (VL).
METHOD: Knee extensor torques, joint angles, EMG activation, and fascicle lengths were determined in nine healthy subjects during maximal and submaximal isometric contractions.
RESULTS: Fascicle shortening during isometric contractions depended on muscle-tendon unit length/joint angle and activation, reaching a maximum between angles where VL had its maximum force potential and minimum resistance to fascicle shortening. Maximal fascicle shortening shifted to shorter muscle-tendon unit lengths with decreasing activation. **CONCLUSION:** Fascicle shortening upon activation depends crucially on the force generating potential and stiffness of the muscle and can reach 30% of the resting fascicle length. Not accounting for the complex interactions between muscle length, force potential, muscle structure, and muscle stiffness has led to erroneous interpretations of the function and properties of healthy and diseased muscles.

KEYWORDS: Series elasticity | Muscle properties | Isometric contraction | Force-length | Force-velocity | In vivo muscle function | Muscle work

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INTRODUCTION

Muscle tendon unit (MTU) length changes can be derived easily from joint angular excursion, if the instantaneous moment arm is known [1]. In contrast, length changes of fascicles and fibers depend heavily on complex interactions between muscle architecture, activation, and the force-dependent elongation of series elastic elements [2–6]. Muscle structure, such as the pennation angle and fascicle length, change during activation and force production, even when the contraction is “isometric” on the MTU level [7].

This dependence of fascicle length on complex interactions with several factors challenges the interpretation of in vivo joint mechanics, muscle mechanical properties, contractile behavior, and muscle function. One could make an argument that contraction types – concentric, eccentric and isometric - should be defined on the contractile element (fibre/fascicle) level since it is the contractile element’s conditions (length, rate of change in length, and history of length changes) that affect the basic muscle properties (force-length relationship [8], force-velocity relationship [9], and history-dependent relationships [10]).

A further complication in understanding fascicle mechanics during voluntary contractions is that activation, muscle length/joint angle, and series elasticity interact and affect fascicle lengths in a complex way. There are at least two factors that need to be considered when determining fascicle mechanics from joint kinematics: (i) the force potential of muscles, and therefore the capacity to stretch series elastic elements, depends on the joint angle [11–13], and (ii) the passive resistance to fascicle shortening also depends on joint configuration because of differences in stiffness and slackness of elastic elements across the operating range of the muscle [14–16].

However, despite the obvious importance of knowing fascicle, and thus contractile element lengths, little systematic work has been done to determine the interactions between muscle lengths/joint angle, force potential, muscle structure, and muscle stiffness that affect fascicle shortening properties and in vivo behavior.

The purpose of this study was to determine the interaction between EMG activation, joint angle, and fascicle length for in vivo isometric contractions of the human vastus lateralis muscle (VL). We hypothesized that a given level of activation produces different amounts of fascicle shortening depending on knee joint angle, and that the amount of fascicle shortening is greatest in the mid-range of knee motion, somewhere between the joint angles where VL force is greatest and resistance to fascicle shortening is smallest.

METHODS

Nine subjects (7 male and 2 female) took part in this study. Subjects gave written, informed consent to participate in this research, and all procedures were approved by the University of Calgary's Conjoint Health Research Ethics Board. The subjects were recreational athletes participating in sports such as running, swimming or soccer. Mean±SD age, height and weight were 27±3 years, 1.76±0.13 m and 69±15 kg, respectively. The maximal and submaximal fascicle force-length relationships obtained from this study have been published previously [11].

Knee extensor torques and knee joint angles were measured on a Biodex II dynamometer (Biodex Medical Systems, Inc., Shirley, NY). Subjects were seated with the back supported and the hip joint flexed at 80˚. Straps across the shoulders, waist and thigh were used to stabilize subjects and isolate the action of the knee extensor muscles. The lower limb was positioned until the knee joint rotational axis was aligned with the axis of the dynamometer arm throughout the entire range of motion. Full knee extension was defined as 180 degrees. The tibia was strapped to the dynamometer arm 3 cm proximal to the lateral malleolus.

Surface EMG was recorded from VL using bipolar electrodes (Norotrode 20™, inter electrode spacing 22 mm). The skin was shaved and cleaned with alcohol before placing the electrodes approximately two-thirds along a line from the anterior superior iliac spine to the proximal end of the patella. A ground electrode was placed on the tibial tuberosity. Skin impedance was checked and pronounced acceptable once it was less than 5 kΩ. EMG, torque and joint position were recorded at 1000 Hz using the Windaq data acquisition system (Dataq Instruments, Akron, OH).

VL fascicles were imaged at 37-49 Hz using a 12.5-MHz linear array ultrasound probe (50mm, Philips Envisor, Philips Healthcare, Eindhoven, The Netherlands). The ultrasound probe was attached to the skin on the lateral mid-thigh region using a custom-built holder and was supported by the examiner during testing. Probe orientation and location were adjusted until the best image of VL fascicles was obtained. An external function generator (B-K Precision 3010, Dynascan Corp., Chicago, IL) was used for synchronization of all signals.

Knee joint angle, VL EMG activity, and VL mid-portion fascicle lengths were obtained continuously. The ultrasound images were also used to determine the distance between the deep and superficial aponeuroses and the angle pennation using freely available software (MicroDicom version 0.7.8). When fascicles were not visible along their entire lengths, fascicle lengths (Fl) were calculated using standard trigonometry [11]. Fascicles were assumed to be straight lines and an error of 2-7% has been ascribed to this assumption [17–21].

Subjects executed a standard warm up consisting of ten submaximal knee extension and flexion repetitions. For the actual testing, subjects performed two maximum isometric knee extensor contractions at ten different knee angles (from 80° to 170° at 10° increments) in a randomized order, and the trial with the greater torque was used for analysis. Subjects were asked to build up to the maximal torque over 5 seconds and then hold the maximal torque for another 2 seconds. Verbal encouragement and visual feedback of the knee extensor torque were provided during all contractions. A rest period of at least 2 min was strictly enforced and was extended upon a subject's request.

Knee angle, EMG, fascicle length, and torque were exported to Microsoft Office Excel (Microsoft Corp. Redmond, WA) and analyzed using Matlab (Math-Works, Natick, MA). Root mean square values (RMS) of the EMG signal were calculated (100 ms window) throughout the entire contraction. Patellar tendon moment arms were calculated using the regression equation defined by Herzog and Read [22]. Knee extensor force was calculated by dividing torque by the patellar tendon moment arm. VL force was approximated by multiplying the total knee extensor force by 0.34 [23].

Fascicle lengths at 0 to 100% of maximum activation (in 10% increments, normalized to the maximum EMG at each knee angle), and at 10, 20, and 30% of the maximum force at optimal length were determined at all knee angles. Mean fascicle shortening as a function of activation and force was then calculated across all joint angles.

The interaction between activation and joint angle on fascicle lengths were analyzed based on a repeated measures ANOVA comparing fascicle shortening (passive – active) across the 10 different angles ($\alpha=0.05$). The effect of activation was further analyzed using regression analyses relating fascicle lengths and activation at long (80˚ knee angle), mid-range (130˚), and short muscle lengths (170˚).

RESULTS

Mean VL fascicle lengths ranged from 13.5±1.2 cm for passive VL at its longest position to 6.3±0.7 cm at maximum activation and its shortest position. VL maximal force production varied from approximately 523 N at 170° of knee extension to an optimal force production of 1588 N at 100° of knee extension. For contractions producing the same level of force, fascicle shortening was greater at more extended knee positions, and consequently shorter VL MTU, compared to more flexed knee positions and longer muscle lengths. The solid lines in Figure 1 show the mean values for fascicle shortening at 10% and 30% of MVC at the optimal knee joint angle. The dashed line shows the maximum VL force angle curve shape.

The effect of activation on fascicle length (passive – active) was significantly different across joint angles (F = 2.651; p = 0.048). For a given activation, fascicle shortening was greatest in the mid-range, decreasing towards the flexed and extended knee joint angles (Figure 1, columns).

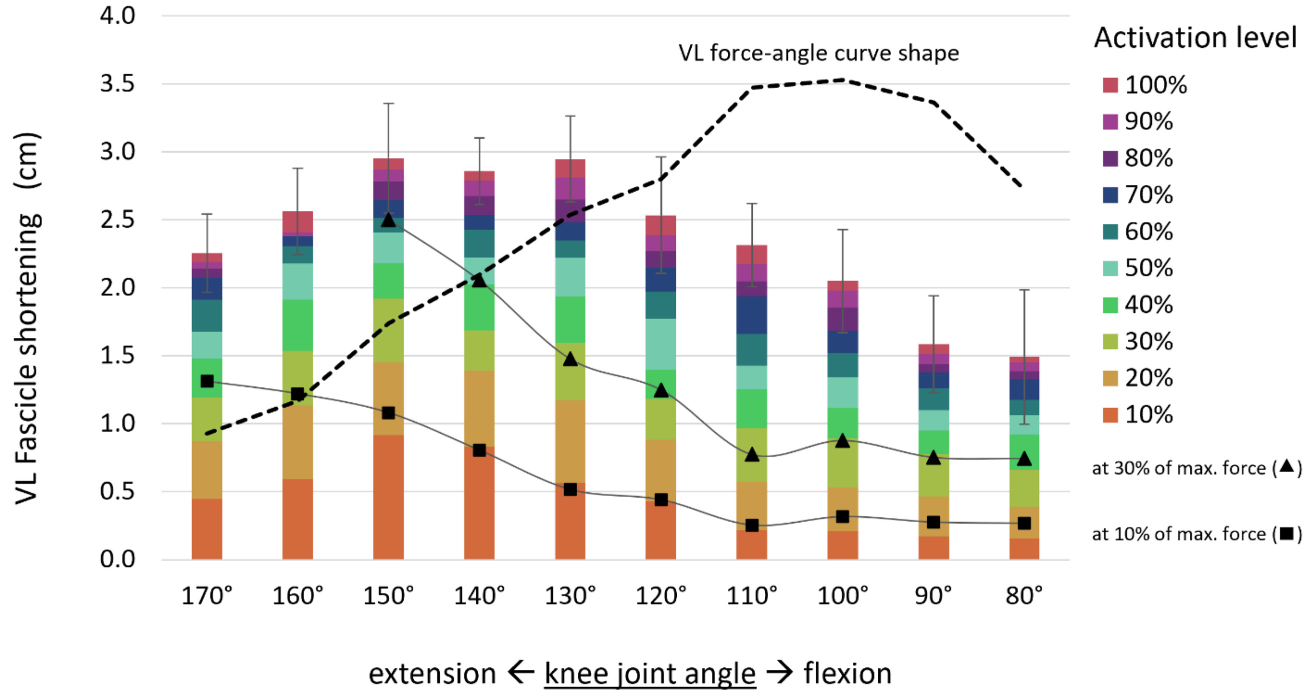

Figure 1. Fascicle shortening at different levels of activation and different knee joint angles (180° =full knee extension = shortest VL length). Fascicle shortening was greatest in the mid-range of knee joint angles because of the interaction between muscle force generating potential at the different joint angles/MTU lengths (illustrated by the VL force angle relationship - dashed line) and the decrease in resistance to fascicle shortening at more extended knee angles/short MTU Lengths (as illustrated by the increase in fascicle shortening for a given amount of force: solid lines, triangles = 30% of MVC force and squares = 10% of MVC force). In addition, fascicle shortening for 10% increments in activation were greater at low compared to high levels of activation, especially at the more extended knee positions/short MTU lengths. Values are means across subjects and error bars represent standard errors of the mean for the total fascicle shortening distances for the full activation conditions.

Fascicle lengths decreased at all joint angles as activation increased. Since the effect of activation on fascicle shortening was shown to depend on joint angle, regression analyses of activation-dependent absolute fascicle lengths were performed separately at an intermediate length (knee angle of 130°) and at the longest (80°) and shortest VL lengths (170°) (Table 1).

Table 1. Summary results of stepwise multiple regression analysis with normalized activation (0-100%) as a factor determining absolute fascicle length in cm for VL at an intermediate (130°), the longest (80°), and the shortest VL length (170°). △Predicted refers to maximum and minimum predicted values of fascicle length during isometric contractions at each angle. The constant value indicates the predicted values of VL fascicle length in the passive state.

Factor	80° KNEE ANGLE			130° KNEE ANGLE			170° KNEE ANGLE		
	R^2	B(SE)	β	R^2	B(SE)	β	R^2	B(SE)	B
Constant		12.7 (0.2) cm			10.1 (0.3) cm			8.4 (0.2) cm	
activation	**0.16**	-0.016 (0.004)	-0.392*	**0.27**	-0.028 (0.005)	-0.517*	**0.41**	-0.046 (0.010)	-1.330*
activation^2	non-significant p = 0.333			non-significant p = 0.084			**0.45**	2.36E-4 (9.3E-5)	0.715*
△Predicted	**[12.7 cm to 11.1 cm] 13% of max. shortening**			**[10.1 cm to 7.3 cm] 28% of max. shortening**			**[8.4 cm to 6.2 cm] 26% of max. shortening**		

* $p<0.05$ SE = standard error

From Table 1 the following equations can be used to relate activation and fascicle length (cm) at 80°, 130°, and 170° degrees, respectively.

$$I)\ Fl_{at\ 80^\circ} = -0.016\ (\%EMG_{max}) + 12.67$$

$$II)\ Fl_{at\ 130^\circ} = -0.028\ (\%EMG_{max}) + 10.10$$

$$III)\ Fl_{at\ 170^\circ} = 2.36 \times 10^{-4}(\%EMG_{max})^2 - 0.046 \times (\%EMG_{max}) + 8.44$$

A negative linear correlation was observed between activation and fascicle shortening at a knee angle of 80˚ and 130˚ with 16% and 27% of the absolute fascicle length variability explained by changes in activation (equation I, $p < 0.001$, equation II, $p<0.001$). For the most extended knee position, a quadratic relationship was obtained, indicating that changes in fascicle lengths upon activation were greatest for the lowest level of activation (from 0-10% of activation), and then decreased continuously with increasing activation. At this angle, 41% of the total variability in fascicle length was explained by changes in activation (equation III, $p = 0.013$).

DISCUSSION

Fascicle lengths and fascicle length changes in an activated muscle at a given joint angle/MTU length depend primarily on the force produced by fascicles and the resistance to fascicle shortening. We analyzed this relationship systematically for VL based on measurements of fascicle length and fascicle length change for the entire range of activation and for the physiologically relevant MTU lengths/joint angles. We also quantified the amount of fascicle shortening for a given absolute force across joint angles to determine the resistance to fascicle shortening – a measure of elastic element stiffness – as a function of muscle length.

Resistance to fascicle shortening is caused by muscle elastic elements that become stiffer with increasing MTU lengths. Therefore, for a given amount of force, one would expect fascicle shortening to be greatest at the shortest MTU length where resistance is lowest. This result was indeed obtained, with fascicle shortening for a force corresponding to 10% and 30% of the maximal isometric force at optimal length being 1.3±0.5 and 2.5±1.2 cm respectively at the shortest MTU lengths (Figure 1) and 0.3±0.3 and 0.7±0.6 cm, respectively at the longest (80˚) MTU length.

Fascicle force depends primarily on activation and on the length of the fascicle in accordance with the force-length relationship. For VL, the force generating potential (for maximal activation) reaches its maximum at knee angles of 100-110˚ (de Brito Fontana and Herzog [11] and Figure 1; 180 = full extension). Resistance to fascicle shortening increases continuously with VL elongation, therefore fascicle shortening upon full activation can be expected to be greatest somewhere between i) the knee angles where VL reaches its maximum force (100-110˚) and ii) the knee angles where resistance to fascicle shortening is smallest (170˚, Figure 1).

Indeed, fascicle shortening from the passive to the fully activated VL is greatest (2.9-3.0 cm) at knee angles ranging from 130-150˚ (Figure 1). At the longest VL length, fascicle shortening is a mere 1.5 cm because resistance to shortening is highest and the maximal VL force is only about 80% of its maximum at optimal length. At the shortest VL lengths, despite resistance to fascicle shortening being lowest, fascicle shortening is only 2.3cm because VL force is a mere 26% of the maximal force at optimal length. For optimal conditions, fascicles can shorten by nearly 30% of their resting length during an isometric contraction. Contractions at a knee angle of 130˚ appear to provide maximal muscle elastic element excursion, while at 100˚ - angle at which maximum force generating potential is achieved, the elastic elements are likely strained maximally. Maximizing the straining and sliding mechanisms that occur at the different structural levels of tendons during isometric contractions might be of interest in muscle rehabilitation to prevent the formation of connective tissue adhesions that are related to injury, aging, and age related diseases [24–27].

Our results demonstrate that resistance to fascicle shortening in voluntary contractions does not only increase with increasing muscle length (Figure 1), but also increases with muscle force at a given MTU length/knee joint angle (Table 1 and equation III). The shortening of fascicles for 10% increments in activation is greatest when the passive muscle is activated to 10% of its maximum (orange columns height, bottom, Figure 1), and smallest from 90% to 100% of its maximum (pink columns height, top, Figure 1). For example, at a knee angle of 150˚, fascicle shortening is 9 mm from passive to 10% activation, and then decreases for each 10% increment in activation until it becomes 1 mm when activation increases from 90 to 100% (Figure 1).

This non-linear effect of activation on fascicle length, observed primarily at the more extended knee positions, may result from two factors i) a non-linear relationship between activation and force production and ii) a decrease in compliance of the muscle as force increases. Increases in activation from 0-10% results in a greater increase in force than increases in activation from 90-100% [11]. This activation-force relationship tends to reduce the amount of shortening at activation levels close to maximum. However, changes in muscle compliance also play a role. This effect is observed when comparing fascicle shortening at constant force levels. For example, at a knee angle of 150 degrees, an increase in 10% in force from the passive condition led to 11 mm of fascicle shortening, while an increase from 20 to 30% of maximum force resulted in 6 mm of shortening only. This change in compliance was observed for short VL lengths corresponding to knee angles ranging from 130˚ to full extension. For longer VL lengths, elastic element compliance was constant for forces from 0 to 30% of the maximal force (Figure 1), suggesting that series elastic elements are taught at these knee positions and have entered the linear region of the force-elongation curve [28].

The complex interaction between joint angle, activation and fascicle length has not always been considered when determining the contractile properties and functions of healthy and diseased muscles (e.g. [29–31]). The force-length and force-velocity relationships are arguably the most important mechanical properties of skeletal muscles, and the key determinants of in vivo human muscle function. Both these properties depend crucially on the instantaneous length and velocity of the contractile elements which can be approximated by the instantaneous fibre/fascicle length and velocity [8,9]. Often, these instantaneous fibre/fascicle contractile conditions are represented by the joint angle or MTU length and velocity, despite strong evidence that this can lead to vast errors (e.g. [11,19,32,33]). This manner of estimating fascicle lengths may be a key reason why force predictions based on musculoskeletal models often fail to provide accurate results when compared to actual muscle force measurements in animal models [34–36].

The term “isometric”, used for contractions in which the MTU length is kept constant, cannot be assumed to reflect the contractile status of VL fascicles/fibres, as fibres under these conditions can shorten by as much as 30% of their passive length. The analysis of fascicle length during contractions in humans is typically performed using ultrasound imaging, since other medical imaging techniques (such as magnetic resonance imaging and computed tomography) cannot be used to measure dynamic changes in muscle architecture during contraction. Our findings are in agreement with the earliest ultrasound studies in the triceps surae muscles [37,38] and vastus lateralis [39], that demonstrated substantial shortening during maximal isometric contractions. They are also in agreement with a more recent systematic analysis on the tibialis anterior muscle, which showed that fascicle shortening during maximal contractions was greatest at an angle (0 degrees of ankle plantarflexion) that allowed the muscle to work on the ascending limb of the force-length relationship, where series elastic resistance is small. In the current study, we observed a similar behavior: maximal fascicle shortening occurred at a knee angle more extended (muscle shorter) than the optimal angle (MTU length) for force production: However, by exploring a wide range of muscle lengths on the ascending limb of the force-length relationship, we observed that maximal fascicle shortening occurred not at the shortest muscle length but was greatest in the mid-range (28% of fascicle shortening at a knee angle of 130°) and decreased towards more flexed (13% at 80°) and extended knee joint angles (26% at 170°).

The complexity of the relationship between fascicle length and muscle compliance discussed above for the vastus lateralis muscle increases dramatically when considering dynamic contractions [19,32,40]. In general, the relative velocity of fibre/fascicle shortening can be much greater when force increases compared to when force decreases during isokinetic testing. In the human VL, fascicle shortening velocities can exceed that of the MTU when force is increasing, and can be as low as 20% of the MTU shortening velocity when force is decreasing [32]. Future work should concentrate on investigating the interplay between muscle architecture, muscle compliance, and the dynamics of fascicles during contractions at various shortening and lengthening velocities. Exploring the concept of muscle gearing [6] can aid in differentiating between the effects of series elasticity within the tendon and the complex dynamics of the muscle belly on fascicle length. Conducting such studies in animal models that permit the measurement of individual muscles forces would also offer valuable insights into how muscles work and generate force when activated within a synergistic group [41].

The non-invasive investigation of muscle mechanics using the described setup has limitations that need to be kept in mind when interpreting our results [42,43]. We assumed that VL's relative force contribution to the total quadriceps force is constant. Also, antagonistic activation was not accounted for in the calculation of VL force. Although these factors might affect the magnitude, we would not expect them to affect the shape of the VL force-angle curve substantially, which is a main determinant of the fascicle shortening features discussed in this study. Fascicle shortening occurs in a 3D manner [44,45]. Even though the absolute values of fascicle shortening must be considered with this limitation in mind, we do not expect them to affect the fundamental results of this study, or the effect expressed in the regression equations.

CONCLUSION

We conclude from the results of this study that VL fascicle shortening as a function of activation/force depends crucially on muscle length and is not maximal at the angle where maximum force is achieved. Rather, the amount of fascicle shortening results from a compromise between the force generating potential of the muscle and the resistance to shortening imposed by muscle elasticity at different lengths. Consequently, force cannot easily be estimated from fascicle kinematics, and fascicle lengths should not be derived from passive measurements and muscle lengths alone.

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