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Age-related differences in vastus lateralis fascicle behavior during fast accelerative leg-extension movements

Evelien Van Roie[1] | **Stijn Van Driessche**[1] | **Christophe Delecluse**[1] | **Benedicte Vanwanseele**[2]

[1]Department of Movement Sciences, Physical Activity, Sports and Health Research Group, KU Leuven, Leuven, Belgium

[2]Department of Movement Sciences, Human Movement Biomechanics Research Group, KU Leuven, Leuven, Belgium

Correspondence
Evelien Van Roie, Department of Movement Sciences, Faculty of Movement and Rehabilitation Sciences, Physical Activity, Sports and Health Research Group, KU Leuven, Tervuursevest 101, 3001 Leuven, Belgium
Email: evelien.vanroie@kuleuven.be

Abstract

Leg-extensor rate of power development (RPD) decreases during aging. This study aimed to identify the underlying mechanism of the age-related decline in RPD during a fast acceleration in terms of in vivo vastus lateralis (VL) fascicle shortening behavior. Thirty-nine men aged between 25 and 69 years performed three maximal isokinetic leg-extensor tests with a fixed initial acceleration of 45° knee extension in 150 ms until 340°/s knee angular velocity. RPD, VL activity, and ultrasound images were recorded to assess (relative) fascicle shortening and mean shortening velocity for the phases of electromechanical delay, pretension, and acceleration. Our findings show that fascicle shortening and mean shortening velocity during a fast action increase with aging (0.002 per year, $P = .035$ and 0.005 s^{-1} per year, $P = .097$, respectively), mainly due to a higher amount of shortening in the phase of electromechanical delay. The ratio of VL fascicle length over upper leg length at rest showed a negative correlation ($r = -.46$, $P = .004$) with RPD/body mass, while pennation angle at rest showed a trend toward a positive correlation ($r = .28$, $P = .089$). To conclude, our findings indicate that the ability to reach high VL fascicle shortening velocities in vivo is not reduced in older men while performing preprogrammed fast accelerations. The greater amount of fascicle shortening in old age is probably the result of age-related differences in the tendinous properties of the muscle-tendon complex, forcing the fascicles to shorten more in order to transmit the muscle force to the segment.

KEYWORDS

explosive strength, fascicle shortening velocity, force-velocity relationship, knee extensors, rate of power development

Evelien Van Roie and Stijn Van Driessche contributed equally to the manuscript.

1 | INTRODUCTION

Impaired maximal leg-extensor strength is an important delimiter of functional capacity at older age, which can lead to increased fall incidence.[1] In addition, to prevent falling, muscle strength should also be developed extremely fast (<200 ms)[2] and at a certain movement velocity, resulting in power production. Fast dynamic muscle actions can be represented by the rate of power development (RPD). Recently, we showed that RPD of the leg extensors is decreased during aging and significantly more at high accelerations compared to lower accelerations.[3] In order to counteract these age-related deteriorations in muscle function, a better understanding of the physiological mechanisms behind the age-related decline in RPD at fast accelerations is warranted.

Muscle force generation is influenced by many factors. In particular, rapid force production is influenced by motor unit recruitment and discharge rate, next to muscle fiber type composition.[4] In addition, the larger decline in leg-extensor RPD with aging at higher compared to lower accelerations is accompanied by a reduction in neural drive.[3] At fiber level, it is well known that the length and shortening velocity of muscle fibers have a predominant influence on the magnitude of maximal force production.[5] For in vitro muscle fibers, the force-velocity relationship shows that the higher the shortening velocity is, the lower the force output at that given velocity.[6] Maximal shortening velocity of in vitro muscle fibers has been shown to decline because of age.[7] This causes a leftward shift in the force-velocity relationship, which in turn results in lower force production at high shortening velocities. However, to the authors' knowledge, the effect of aging on in vivo fiber shortening velocity of the leg extensors during fast actions has not yet been investigated.

As an alternative, many studies have focused on whole muscle force-velocity characteristics in aging research.[8] Similar to the in vitro fiber level, knee-extensor muscle strength and maximal contraction velocity have been reported to be reduced during maximal dynamic contractions, inducing a shift in the force-velocity relationship during aging.[9] Moreover, whole muscle maximal contraction velocity has been shown to decline significantly during aging[10] and was suggested to be a key component in the onset of functional difficulties in the elderly.[11,12] However, these findings may not be representative for in vivo human muscle fibers.[13] In vivo human muscle fiber shortening velocity depends on fiber geometry, muscle force, and compliance of the series elastic components.[14] Regarding the leg extensors, previous findings represent whole vastus lateralis (VL) muscle-tendon unit (MTU) shortening velocity, which is linearly related to knee joint angular velocity.[15] In particular, the shortening velocity of the MTU has been shown to respond differently to changes in joint angular velocity compared to the fascicles.[16,17] Yet, the effect of aging on in vivo VL fascicle shortening velocity during fast actions remains elusive.

Therefore, this cross-sectional study investigated the age-related differences on in vivo VL fascicle shortening behavior and its relation with RPD in multi-joint leg-extensor tests. We hypothesized that fascicle shortening velocity during fast actions is lower in older versus younger adults and is related to RPD.

2 | MATERIALS AND METHODS

2.1 | Subjects

Forty-nine men aged between 20 and 70 years (~ ten per decade) were recruited through advertisements and oral communications.[3] Subjects completed a short medical history and physical activity questionnaire and were excluded in case of a cardiovascular disease or acute thrombosis, recent surgery, neuromuscular disease, infection or fever, diabetes, and systematic participation in strength or endurance training (ie, progressive increases in volume and/or intensity) in the prior 6 months. Occasional engagement in physical activity, such as cycling, walking, and running, was allowed. After thorough examination of power output, electromyography (EMG) signals and ultrasound images and after exclusion of incomplete test samples because of measurement failure of one or more measurements, complete data of thirty-nine healthy subjects aged between 25 and 69 years were used for further analyses. All subjects provided written informed consent. The study was approved by the Medical Ethics Committee UZ KU Leuven/Research in accordance with the declaration of Helsinki.

2.2 | Power measurements

Power measurements and signal analysis procedures have been previously described.[3] Briefly, an isokinetic leg press machine was developed to measure multi-joint neuromuscular function of the leg extensors at a sampling frequency of 1000 Hz. The seat and lever arm were adjustable to allow for standardized range of motion (ie, knee joint angle of 90° to 160° and hip joint angle of 70° to 115°). Measurements were performed unilaterally on the right side. The right foot was fully supported and fixed to the foot plate using a solid strap with the lateral malleolus aligned with the point of force application, provoking a heel thrust to minimize the influence of lower-leg muscles and ankle movement. Movement of the lever arm was initiated by surpassing a cutoff torque of 20% of maximal isometric single-joint strength inducing a low level of pretension (ie, 20-70 Nm) as previously recommended.[18] This single-joint strength test was performed on a Biodex Medical System 3 dynamometer prior to the multi-joint test. Subjects performed four maximal isometric voluntary contractions of the knee extensors at 90° knee joint angle. They were instructed to push as hard as possible for 5 seconds, separated by a 20-second rest period.[19] Isometric peak torque was used to set the level of pretension in the multi-joint test.

Subjects performed two test sessions separated by a rest day to avoid fatigue. In the first session, familiarization with the protocol was performed. The second session was performed at the same time of day. Participants started with a warming-up on a cycle ergometer at a self-determined submaximal resistance for 10 minutes. For the leg-extensor test, lever arm angular acceleration was preprogrammed using a real-time control program (Simulink, The Mathworks Inc) at a high acceleration of 3200°/s^2 until an isokinetic lever arm velocity of 540°/s was reached. This lever arm angular acceleration corresponds to an extension of 45° in the knee in 150 ms until an isokinetic knee angular velocity of 340°/s is reached. The test was performed three times with a 30-second rest period in between. The subjects were clearly instructed to push as fast and as hard as possible.

2.3 | Electromyographic activity

EMG activity of vastus lateralis (VL) was collected during the multi-joint leg-extensor tests according to previous procedures.[3] Surface electrodes were positioned following the European Recommendations for Surface Electromyography (SENIAM) after careful preparation of the skin (ie, shaving and cleaning with alcohol) to keep skin impedance low. EMG signals were recorded using wireless EMG electrodes (KINE®, KINE Ltd., Hafnarfjördur, Iceland) with an input impedance of 10 GΩ, a common mode rejection ratio of 110 dB, a signal-to-noise ratio of 60dB, a differential detection mode, and a built in A/D converter of 10 bit with a range of 4 mV, resulting in a sensitivity of 4 µV. EMG signals were sampled at 1600 Hz. An extra electrode unit was used to catch a trigger pulse from the real-time control program at the start of the leg-extensor test to enable synchronization of the EMG signals and the power output. Onset of activation was determined as > 3 SD of the baseline signal[20] (Figure 1).

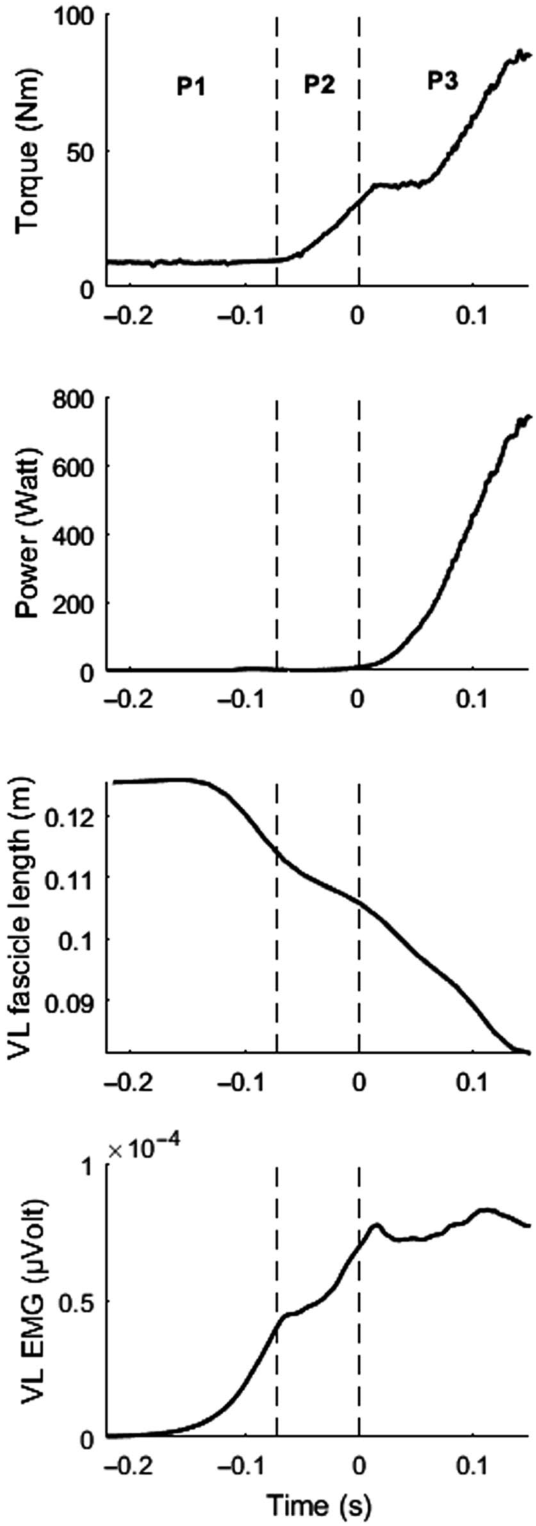

FIGURE 1 Representation of torque, power, and vastus lateralis (VL) fascicle length and electromyographic activity (EMG) of a random subject: (P1) phase of electromechanical delay, (P2) phase of pretension, (P3) phase of acceleration

2.4 | Ultrasound measurements

B-mode ultrasound images of VL muscle were obtained at 60 Hz using a Telemed Echoblaster 128 CEXT system (UAB Telemed, Vilnius, Lithuania). A 128-element linear transducer (LV 7.5/60/128Z-2, UAB Telemed, Vilnius, Lithuania) with a 60-mm field of view was used at 8 MHz.

The ultrasound probe was securely fixed to the skin on the lateral mid-thigh of the right leg (ie, 50% of the distance between the lateral femoral condyle and the trochanter major) using a semi-flexible holder, elastic bandage, and wrapping tape. The probe was oriented in a way to get the best image quality and as parallel as possible to the deep aponeurosis (Figure 2). The start of the ultrasound recordings was used as a trigger pulse and sent to the real-time control program to allow synchronization with EMG and power output (Figure 1).

2.5 | Signal processing

All signals were processed off-line using a commercial software package (Matlab R2016b, The MathWorks Inc). Torque signals were filtered using a fourth-order low-pass Butterworth filter with a 20 Hz cutoff frequency. Instantaneous power (watt) was calculated as the product of torque (Nm) and velocity (rad/s). Peak torque (Nm) and peak power (watt) were defined as the highest value of the torque-time and power-time curve, respectively, during the acceleration phase (ie, from the start of the movement, determined as the point where the cutoff torque was reached, until the isokinetic velocity was reached). The rate of power development (RPD, watt/s) was calculated as the linear slope of the power-time curve during the acceleration phase. Reliability of RPD in our laboratory was excellent (ICC: 0.96; SEM(%): 7.3).

The ultrasound images were processed by tracking three lines representing the superficial aponeurosis, the deep aponeurosis, and the orientation of the muscle fascicles with a semi-automated algorithm.[21] We linearly extrapolated these lines and calculated fascicle length as the distance between the two aponeuroses parallel to the muscle fascicles and the pennation angle as the angle between the muscle fascicles and the deep aponeurosis.[22] This method for estimating fascicle length when the whole fascicle is not visible has been used and validated in a number of studies.[23-25] All data were anonymized to avoid bias within and between individuals. The ultrasound data were filtered using a 4th-order low-pass Butterworth filter with a cutoff frequency of 10Hz. Fascicle length (mm) and pennation angle (°) at rest in the starting position of the leg-extensor test (ie, knee joint angle of 90° and hip joint angle of 70°) were analyzed. In addition, relative fascicle length was calculated by dividing it by upper leg length, measured as the distance between the lateral femoral condyle and the trochanter major.

Fascicle lengths during the leg-extensor test were normalized to the fascicle length at rest in the starting position of the test. Fascicle shortening was calculated as the difference between minimum and maximum fascicle length in the different phases: (a) from the onset of VL activation till the start of torque production (ie, phase of electromechanical delay—P1), (b) from the start of torque production till the moment the cutoff torque was reached (ie, phase of pretension—P2), (c) from the moment the cutoff torque was reached till the end of the acceleration phase (ie, acceleration phase—P3), and (d) from the onset of VL activation till the end of the acceleration phase (ie, complete test) (Figure 1). Fascicle shortening velocity (s^{-1}) was calculated at the first derivative of the fascicle length to the time. Mean shortening velocity (s^{-1}) was calculated over

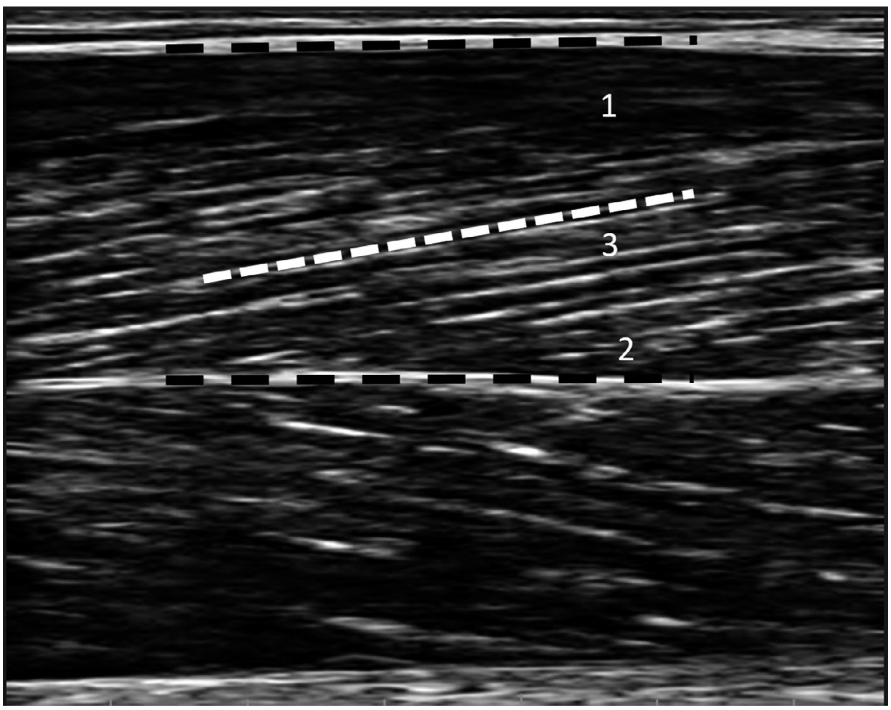

FIGURE 2 Example of the tracking procedure of an ultrasound image of the vastus lateralis. The black broken line represents the superficial aponeurosis (1) and deep aponeurosis (2), and the white broken line represents the muscle fascicle orientation (3)

TABLE 1 Subject characteristics, leg-extensor rate of power development, and vastus lateralis fascicle shortening behavior by age group

		25-40 y	40-55 y	55-70 y
	n	15	12-13	11
	Age (y)	29.7 ± 4.6	47.3 ± 4.5	62.5 ± 4.9
Anthropometrics	Body mass (kg)	79.8 ± 12.0	83.8 ± 10.8	82.0 ± 13.6
	Body height (cm)	180.9 ± 5.6	181.2 ± 5.7	174.8 ± 4.0
	BMI (kg/m^2)	24.4 ± 3.4	25.5 ± 2.6	26.7 ± 5.1
Muscle performance[a]	Peak torque	105.5 ± 20.4	94.1 ± 23.9	81.0 ± 16.1
	Peak power	996.1 ± 191.9	884.1 ± 231.4	754.2 ± 157.3
	RPD (watt/s)	6137 ± 1245	5700 ± 1228	4580 ± 1003
	RPD/BM (watt/(s.kg))	77.2 ± 11.4	66.4 ± 11.2	56.2 ± 10.7
At rest	Fascicle length (mm)	131 ± 24	139 ± 30	168 ± 38
	Fascicle length (mm)/upper leg length (mm)	0.30 ± 0.05	0.32 ± 0.07	0.37 ± 0.09
	Pennation angle (°)	10.4 ± 1.6	9.5 ± 2.2	8.0 ± 2.3
Complete test	Fascicle shortening (mm/mm)	−0.34 ± 0.08	−0.39 ± 0.07	−0.41 ± 0.10
	Mean shortening velocity (s^{-1})	−0.93 ± 0.24	−1.06 ± 0.24	−1.09 ± 0.23
	Duration (s)	0.368 ± 0.053	0.370 ± 0.043	0.362 ± 0.044
Phase 1—electromechanical delay	Fascicle shortening (mm/mm)	−0.09 ± 0.06	−0.10 ± 0.06	−0.13 ± 0.09
	Mean shortening velocity (s^{-1})	−0.77 ± 0.55	−0.77 ± 0.48	−0.96 ± 0.61
	Duration (s)	0.137 ± 0.048	0.146 ± 0.041	0.143 ± 0.042
Phase 2—pretension	Fascicle shortening (mm/mm)	−0.11 ± 0.05	−0.11 ± 0.05	−0.11 ± 0.06
	Mean shortening velocity (s^{-1})	−1.23 ± 0.53	−1.36 ± 0.64	−1.48 ± 0.62
	Duration (s)	0.090 ± 0.019	0.085 ± 0.013	0.076 ± 0.018
Phase 3—acceleration	Fascicle shortening (mm/mm)	−0.13 ± 0.04	−0.17 ± 0.04	−0.15 ± 0.06
	Mean shortening velocity (s^{-1})	−0.95 ± 0.30	−1.22 ± 0.32	−1.03 ± 0.42
	Duration (s)	0.142 ± 0.005	0.139 ± 0.006	0.143 ± 0.002

Abbreviation: BM, body mass; BMI, body mass index; RPD, rate of power development.

[a]Muscle performance outcomes represent values from the acceleration phase of the movement.

the different time phases. The error in the estimation of fascicle length using this method has been reported to be 2%-7%.[26] We tested our intra-rater reliability of the ultrasound processing by non-consecutively tracking the same images twice for six older subjects (ICC: 0.96-0.98; SEM(%): 4.9-7.9). For all data, the mean of the three trials was used for further analyses.

2.6 | Statistical analyses

All statistical analyses were performed using R software, version 1.0.153. Descriptive statistics were represented as means and standard deviations. For this purpose only, subjects were divided into three age categories (25-40 years, 40-55 years, 55-70 years). To study the effect of age on fascicle length and pennation angle at rest, fascicle shortening and mean shortening velocity (of the complete tests and the three different phases separately), we built linear models using the function lm. Age was entered as fixed effect into the model and was used as continuous variable. Statistical significance was set at $P < .05$ for all analyses.

Pearson's correlation coefficients were calculated to examine the association of fascicle length and pennation angle at rest, fascicle shortening, and mean shortening velocity with RPD normalized to body mass.

3 | RESULTS

Descriptive statistics are presented in Table 1. The RPD value of one subject (age 53.9 years) was deleted in the analyses, as he was considered an outlier (defined as a value lower than the lowest quartile minus 1.5 times the interquartile range).

At rest, absolute VL fascicle length and fascicle length relative to the upper leg length were significantly higher in older adults (increase of 0.80 mm per year, $P = .025$ and 0.002 per year, $P = .005$, respectively), while pennation angle at rest was significantly lower (decrease of −0.07° per year, $P = .002$).

For the complete test from the onset of VL activation till the end of the acceleration phase, more VL fascicle shortening, that is, about 0.002 mm/mm per year (P = .035), was shown in older adults. Similarly, mean shortening velocity was higher in older adults (increase of 0.005 s^{-1} per year, P = .097) (Figure 3A,B).

Subdivision of the complete test in successive phases of electromechanical delay (P1), pretension (P2), and acceleration (P3) revealed more fascicle shortening in older adults in P1, that is, an increase of on average 0.002 per year (P = .043), but not in P2 and P3 (P = .853 and P = .592). Furthermore, mean shortening velocity did not differ with age in either P1 (P = .478), P2 (P = .324) or P3 (P = .616).

In relation to RPD/body mass, VL fascicle length and the relative fascicle length to upper leg length at rest showed a negative correlation (r = −.36, P = .026 and r = −.46, P = .004), while pennation angle at rest showed a trend toward a positive correlation (r = .28, P = .089) (Figure 4). However, correlation coefficients between normalized RPD

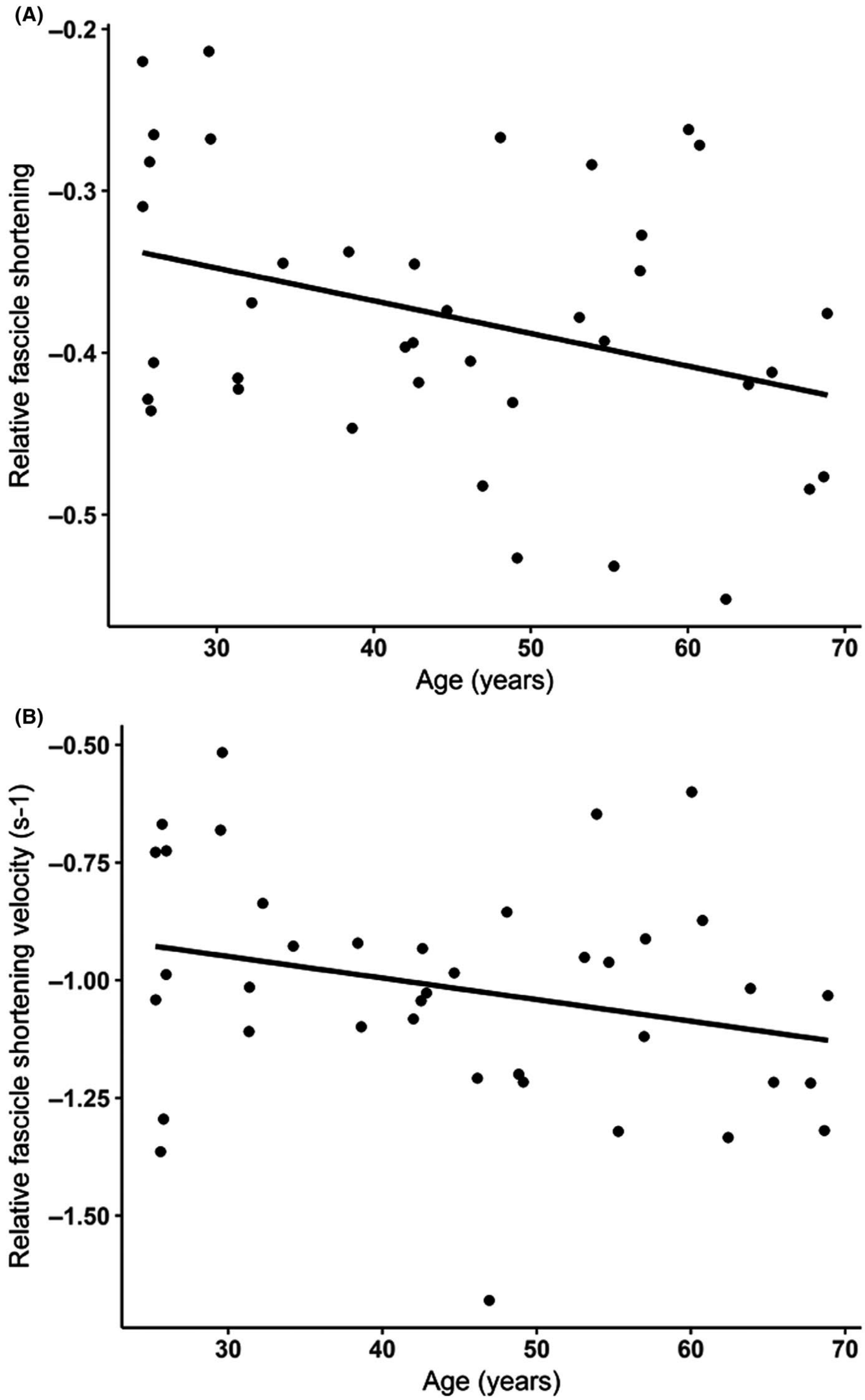

FIGURE 3 Age-related increase in vastus lateralis relative fascicle shortening (A) and relative mean fascicle shortening velocity (B) across 39 subjects (aged 25 to 69 y) during the leg-extensor test

and VL fascicle shortening ($r = .14$, $P = .391$) or mean shortening velocity ($r = .055$, $P = .743$) over the complete test were not significant.

4 | DISCUSSION

This study aimed at identifying the underlying mechanisms of age-related differences in leg-extensor RPD in response to fast accelerative actions in terms of VL fascicle shortening behavior. Our findings provide experimental evidence that in vivo fascicle shortening and shortening velocity during fast actions are higher in older adults compared to younger adults, mainly due to a higher amount of shortening in the phase of electromechanical delay. This higher amount of shortening at older age coincides with longer VL fascicle lengths and smaller pennation angles at rest. Moreover, both fascicle length and pennation angle are

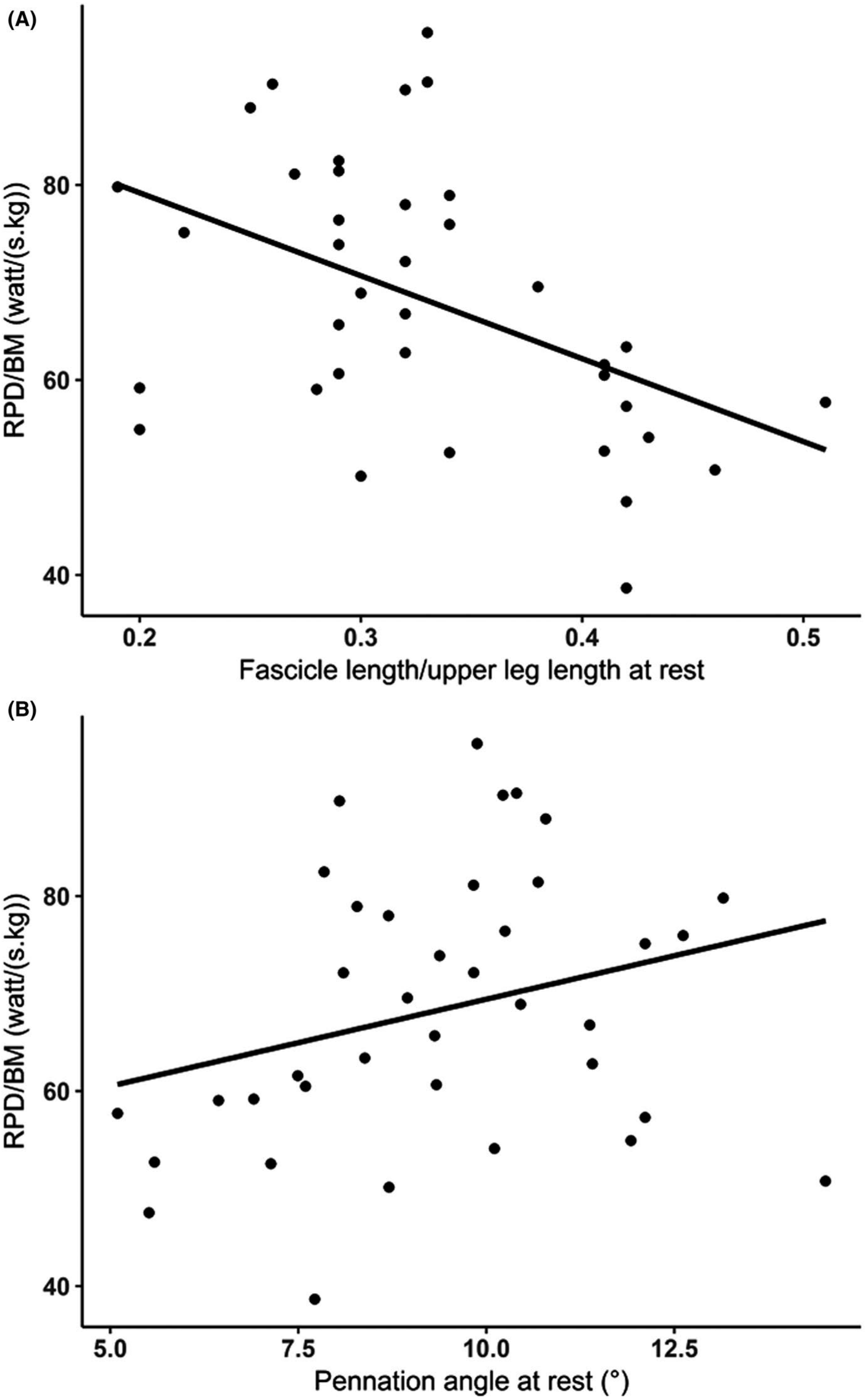

FIGURE 4 Association between the rate of power development (RPD) and relative vastus lateralis fascicle length to upper leg length at rest ($r = -.46$, $P = .004$; A) or pennation angle at rest ($r = .28$, $P = .089$; B) across 38 subjects (aged 25 to 69 y) during the leg-extensor test. RPD is normalized to body mass (BM)

associated with RPD, while fascicle shortening velocity is not related to RPD.

In contrast with our first hypothesis, in vivo VL fascicle shortening velocity is higher in older versus younger adults when performing fast actions. Although this might seem to contradict the age-related decline in maximal contraction velocity at the in vitro fiber level,[7] one should realize that a condition of unloaded shortening does not exist during in vivo leg-extension movements. Our test was not unloaded, considering that a pre-load of 20% of the isometric maximal strength was used to ensure a limited amount of pretension of the muscles before the start of the movement. Peak torques developed during the subsequent acceleration phase were up to 55% of peak torques at slow isokinetic velocity (data not shown). To conclude, the ability to produce force at fixed high accelerations is not necessarily related to in vitro maximal contraction velocity of fibers. In addition to the muscle fibers, we have measured the muscle fascicles in a muscle-tendon complex where the tendon plays an important role in the rate of force development.[4]

Similarly, it is difficult to compare our data to previous findings on whole muscle level,[11,27] as we used an approach in which accelerations were controlled instead of torque production (ie, an isotonic approach). This approach with preprogrammed acceleration was chosen to ensure a fast and challenging movement in all individuals, as older adults might be limited to produce such high velocities in voluntary isotonic actions.[12] Isotonic approaches did show a reduction in contraction velocity of the whole leg-extensor muscles with aging.[11,27] Whether this coincides with a reduced fascicle shortening velocity remains to be investigated in isotonic setups. Of note, studies have shown that the muscle-tendon unit response can differ from VL fascicle shortening behavior during concentric knee-extension movements.[17,28]

The higher fascicle shortening velocity combined with a greater amount of fascicle shortening at older age is related to age-related differences in muscle architecture properties such as VL fascicle length and pennation angle at rest. In agreement with previous research, VL pennation angle was greater in young than in older men.[29-31] In addition, VL fascicles were longer in older versus younger men, even after correction for upper leg length, although positioning (and corresponding joint angles) of subjects was identical. Previous findings regarding age-related differences in vastus lateralis fascicle length are inconsistent, with reports showing either no difference in absolute[30] or relative fascicle length (to limb length) between younger and older men[29,32] and young and older women,[33] longer relative fascicle lengths in older women compared to young,[29] or longer absolute fascicle length in young compared to older adults.[31,34]

The greater amount of fascicle shortening is not fully explained by greater starting lengths at rest, given that relative fascicle shortening was significantly greater in older adults, more specifically in the phase of electromechanical delay (P1). The similar amount of fascicle shortening during the pretension (P2) and acceleration phase (P3) in young and older adults suggests that the fascicles of older adults can act similarly to those of younger adults as soon as the electromechanical preparation phase is finished. The greater fascicle shortening at older age during P1 coincided with an increase in the duration of the phase of electromechanical delay, although this increase was not significant. The phase of electromechanical delay has previously been observed to be prolonged, and this was accompanied by an increase in compliance of the patellar tendon in older individuals.[35] During this electromechanical delay phase, slack in the muscle and tendon is taken up. Therefore, tendon slack will influence the duration and amount of shortening in the fascicle during this phase. Our results indicate that in older adults more slack needs to be taken up. Although data on tendon slack in an aging population are still lacking, multiple reports consistently demonstrated decreases in tendon stiffness with advancing age.[32,36] The underlying mechanisms of this age-related difference are not yet fully understood, but might be linked to changes in tendon dimensions, hydration status, glucosamine concentration, elastin content, cross-linking, or collagen content contribute.[37,38] Taken together, the higher compliance and potentially slack length of the tendon at older age could have forced the fascicles to shorten more in order to transmit the muscle force to the segment.

In previous research, the stiffness of VL tendon-aponeurosis complex was positively related to isometric knee-extensor rate of torque development and maximal vertical jump performance in healthy competitive volleyball players and cyclists.[39] In addition, reduced tendon stiffness has been suggested to contribute to the reduced rate of torque development in healthy older men.[37] However, in the current study, we did not observe a significant relationship between fascicle shortening and RPD, although more fascicle shortening at old age as a consequence of reduced tendon properties can result in fascicle lengths that are less optimal for force production based on the force-length relationship of skeletal muscles.[40] RPD was negatively related to normalized fascicle length and positively related to pennation angle at rest. The effect of muscle architecture on rapid force production is currently poorly understood (for a review, see Maffiuletti et al[4]). More pennation allows for a greater muscle cross-sectional area for a given muscle volume and therefore greater absolute rate of force rise.[4] Theoretically, muscles with longer fascicles have an increased shortening velocity potential, but could also exhibit a slower force rise because of a greater tendon compliance.[4,41] Taken together, our results seem to indicate that RPD at fixed high accelerations is more influenced by tissue compliance and pennation angle than by the fibers' shortening velocity potential. Other factors that may negatively influence the ability to rapidly produce force and power at old age are decreased neural excitation rate,[3,42] greater shortening-induced torque depression,[43] decreased potential to use variable gearing in the muscle,[44] and changes in muscle size and fiber properties.[4,45,46]

The following limitations should be kept in mind when interpreting our findings. First, age-related changes were based on cross-sectional findings, which may be confounded by inter-individual differences and may be divergent from longitudinal findings. Next, fascicle shortening was analyzed in the VL only, whereas other muscles contribute to leg-extensor movements. Furthermore, although some muscle deformation may only be visible in 3D, fascicle measurements were based on two-dimensional ultrasound images. For the analysis, it was assumed that fascicles are represented by straight lines, although it has been shown that this may result in an underestimation of absolute lengths of 2%-7%.[26] However, absolute length differences between groups are not the main focus of this study. The main findings are based on length changes (shortening and velocity), which, according to Brennan et al,[47] are not largely affected by the straight-line interpolation. Image quality can vary with age and can also influence the reliability of the data analysis. We carefully checked the quality of the images and also performed our reliability test on the older age group. The used ultrasound sampling frequency of 60 Hz might have been relative low to investigate fast accelerations. However, the total duration of the leg-extensor test is approximately 370 ms and the average time of the acceleration and electromechanical delay phase is approximately 150 ms. This means that on average 21 images for the whole test and 9 images per phase were analyzed. In addition, good reliability of the method was shown and our fascicle shortening velocities are very similar to those reached during isolated high-velocity knee extensions using ultrafast ultrasound.[28]

5 | PERSPECTIVES

Our findings indicate that the ability to reach high VL fascicle shortening velocities in vivo is not reduced in older men while performing preprogrammed fast accelerations. The greater amount of fascicle shortening in old age is probably the result of reduced stiffness of the patellar tendon, forcing the fascicles to shorten more in order to transmit the muscle force to the segment. Taken together, the rate of power development at fixed high accelerations seems more influenced by tendon compliance than by the fibers' intrinsic capacity to shorten fast. Exercise programs in older adults should therefore also target improvements in stiffness of the muscle-tendon unit.

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CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

ORCID

Evelien Van Roie https://orcid.org/0000-0002-4547-589X

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