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1 **Title**

2 The effect of muscle-tendon unit vs fascicle analyses on vastus lateralis force
3 generating capacity during constant power output cycling with variable cadence

4

5 **Abbreviated title**

6 Effects of muscle analysis level on muscle force in cycling

7

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22

23 **Keywords**

24 muscle mechanics, muscle tendon unit, fascicle, vastus lateralis

25

26 **Abstract**

27 The maximum force capacity of a muscle is dependent on the lengths and velocities
28 of its contractile apparatus. Muscle-tendon unit (MTU) length changes can be
29 estimated from joint kinematics, however contractile element length changes are more
30 difficult to predict during dynamic contractions. The aim of this study was to compare
31 vastus lateralis (VL) MTU and fascicle level force-length and force-velocity
32 relationships, and dynamic muscle function while cycling at a constant submaximal
33 power output (2.5 W/kg) with different cadences. We hypothesized that manipulating
34 cadence at a constant power output would not affect VL MTU shortening, but
35 significantly affect VL fascicle shortening. Furthermore, these differences would affect
36 the predicted force capacity of the muscle. Using an isokinetic dynamometer and B-
37 mode ultrasound (US), we determined the force-length and force-velocity properties
38 of the VL MTU and its fascicles. In addition, three-dimensional kinematics and kinetics
39 of the lower limb, as well as US images of VL fascicles were collected during
40 submaximal cycling at cadences of 40, 60, 80 and 100 RPM. Ultrasound measures
41 revealed a significant increase in fascicle shortening as cadence decreased (84%
42 increase across all conditions, $p < 0.01$), whereas there were no significant differences
43 in MTU lengths across any of the cycling conditions (maximum of 6%). The MTU
44 analysis resulted in greater predicted force capacity across all conditions relative to
45 the force-velocity relationship ($p < 0.01$). These results reinforce the need to determine
46 muscle mechanics in terms of separate contractile element and connective tissue
47 length changes during isokinetic contractions as well as dynamic movements like
48 cycling.

49

50

51 **New & Noteworthy**

52 We demonstrate that vastus lateralis (VL) muscle tendon unit (MTU) length changes
53 do not adequately reflect the underlying fascicle mechanics during cycling. When
54 examined across different pedaling cadence conditions, the force generating potential
55 measured only at the level of MTU (or joint) overestimated the maximum force capacity
56 of VL compared to analysis using fascicle level data.

57 **Introduction**

58 The characteristic force-length relationship of muscle demonstrates that the greatest
59 force production occurs at a specific length, defined as the optimal fiber length (L_0)
60 (18). At shorter or longer lengths, the maximum capacity of the fiber to produce force
61 is reduced due to a reduction in the effective overlap of its contractile proteins (23, 24).
62 The maximum force producing capacity of muscle fibers is also influenced by the
63 velocity that they shorten or lengthen at during a contraction. At slow shortening
64 velocities, muscles are still capable of producing relatively large forces (22). However,
65 as the velocity of shortening increases, there is an exponential decrease in the
66 maximum force producing capacity of the muscle until reaching its maximum
67 shortening velocity (V_{max}). The length and velocity properties of muscle therefore
68 constrain the way animals produce force, which subsequently influences their ability
69 to generate the mechanical power that is essential to move the body during cyclical
70 movement tasks such as walking, running and cycling (5).

71

72 Estimates of muscle tendon unit (MTU) lengths have been relatively easy to ascertain
73 from kinematic modelling of limb motion. A limitation of using estimates of MTU length
74 changes to infer contractile dynamics of muscle is that this approach does not account
75 for the effects of series elasticity in connective tissues like the aponeuroses and
76 tendons. Recent advances in ultrasound imaging have allowed length changes of the
77 contractile tissue to be measured in human muscle, which now allows for more
78 accurate representations of muscle fascicle length changes and estimates of intrinsic
79 contractile properties. Muscles like the human gastrocnemius and soleus have a long,
80 compliant tendon attached to much shorter muscle fibers (40) giving rise to a large
81 tendon length:muscle fiber length ratio (L_T/L_F) and significant energy recycling within

82 the tendon during locomotion. Those elastic interactions are particularly important for
83 locomotion, as the stretch and recoil of elastic tissues will affect the muscle's power
84 production and overall efficiency (29). This has been shown in walking and running
85 where the compliance of the series elastic tendon uncouples the length changes of
86 the contractile tissue from the MTU during periods of the gait cycle (28).

87

88 While walking and running involve stretch-shortening cycles that enhance muscle and
89 tendon function (25, 30), other repetitive movements like cycling involve primarily
90 concentric work of the lower limb muscles (11). Cycling is particularly interesting in
91 this regard, as it is possible to achieve the same overall power output while utilizing a
92 wide range of gearing and cadence combinations. Maintaining a constant power
93 output at different cadences has little impact on joint range of motion during seated
94 cycling, particularly for the knee (7, 12). The MTU length changes are likely to be
95 similar regardless of cadence because of the constraint that the pedals place on the
96 kinematics. Therefore, MTU velocity should predictably increase with cadence (37).
97 While the MTU length changes are predictable, the muscle forces and activations are
98 less predictable for individual muscles. For instance, there is little change in
99 neuromuscular activity of the vastus medialis or lateralis in response to cadence
100 manipulation for a given power output (38). However, the force-velocity relationship
101 would predict a decrease in force capacity as cadence increases, and therefore an
102 increase in activation to achieve a required submaximal muscle force. It is possible
103 that the discrepancies between shortening velocity, force and activation are linked to
104 the interaction between muscle and tendon and how this influences the length and
105 velocity of the contractile tissue, particularly with different force requirements under
106 varying cadence conditions.

107

108 Even at slow pedal rates (40 RPM) and relatively low power outputs (98 W) there can
109 be discrepancies between the length changes of the muscle fascicles and the
110 associated connective tissues (32). For instance, at low cadences the quadriceps
111 muscles will experience low MTU velocities. However, as the quadriceps contract and
112 force increases they will stretch the series elastic tissue and hence muscle fascicles
113 must shorten at greater velocities than the MTU to increase force output (32).
114 Conversely, as quadriceps force decreases later in the pedal cycle the series elastic
115 tissue will recoil at higher velocity than the fascicles (32). The magnitude of the
116 required forces also affects the stretch of series elastic elements and therefore the
117 operating length of the fascicles. For a given cadence, there is increased fascicle
118 shortening as power output is increased because of the greater force requirements
119 (3), illustrating that fascicle operating length is not only dependent on the knee angle
120 / MTU length, but also on fascicle force. As such, the forces, cadence and the degree
121 of series elastic compliance within the muscle will have a substantial effect on the
122 operating lengths and velocities of the contractile tissue.

123

124 The aim of this study was to explore the operating lengths and velocities of VL at the
125 MTU and fascicle levels during cycling at a constant power output at a range of
126 cadences and to determine how this influences the predicted force generating capacity
127 of the VL muscle. We first characterized the force-length and force-velocity properties
128 of the VL MTU and fascicles using an isokinetic dynamometer and a mono-articular
129 knee extension protocol with synchronous measurement of fascicle length using B-
130 mode ultrasound. We then determined the operating lengths and velocities of the VL
131 MTU and fascicles during cycling relative to those measured using the isokinetic

132 dynamometer. The MTU level analysis is analogous to basing optimum lengths and
133 velocities on joint kinematics alone, which ignores the potential effect of series
134 elasticity on contractile dynamics. We hypothesized that VL MTU shortening
135 magnitude would not be significantly different across the different cycling cadences,
136 while fascicle analyses would reveal significant differences in length changes across
137 cadences. Furthermore, we predicted that VL MTU velocities would increase linearly
138 with increased cadence due to the greater crank angular velocity, whereas fascicle
139 shortening velocities would not increase with the same magnitude due to the effects
140 of series compliance.

141

142 **Methods**

143 Eleven participants provided informed consent to participate in the study (age 27 ± 4.5
144 years, height 178 ± 5.7 cm, mass 73.6 ± 6.8 kg). The study was approved by an
145 institutional ethics committee. Each participant completed two experimental sessions
146 to firstly collect VL force-length and force-velocity data using an isokinetic
147 dynamometer (HUMAC NORM, CSMi Inc., Stoughton, MA, USA), and secondly, using
148 a cycling ergometer (Lode Excaliber Sport, Lode B.V., Groningen, Netherlands) to
149 collect motion data. Fascicle data for one participant was excluded from the analysis
150 because it could not be adequately tracked across all of the trials.

151

152 *Dynamometer Protocol*

153 A familiarization session was performed 1 to 2 days prior to the experimental data
154 collection to make sure the participants could perform consistent maximal voluntary
155 knee extensor efforts. Participants were seated in the dynamometer with a hip angle
156 of 80° and the dynamometer attachment was adjusted to align with the

157 rotation axis of the left knee. A 60-s isotonic warm up protocol was then performed
158 using the interactive capacity of the dynamometer, where the participant performs
159 repeated knee extensions to move a cursor within the target pathway presented on
160 screen. The resistance was self-selected; the participant was instructed to select a
161 torque value that corresponded to approximately 50% of their maximal voluntary effort.
162 Subsequently, an isometric protocol was implemented that consisted of randomized
163 blocks of three maximal voluntary isometric efforts from 50{degree sign}-100{degree
164 sign} of knee flexion at 10{degree sign} increments. The isometric angles were
165 selected to include the optimal angle of the torque-angle relationship, and the knee
166 angle range of motion during cycling. A fully extended knee was defined as 0{degree
167 sign}. For each contraction participants were instructed to perform a ramp contraction
168 up to their maximal effort over a 3-s period then hold the maximal effort for 1-s before
169 relaxing. Two minutes of rest was given between efforts to avoid any potential fatigue
170 effects. An isokinetic protocol was then implemented where participants performed
171 randomized blocks of three maximal effort knee extensions from 100{degree sign}
172 flexion to full extension at five angular velocities (50{degree sign}/s, 100{degree
173 sign}/s, 200{degree sign}/s, 300{degree sign}/s, and 400{degree sign}/s). A pre-
174 loading torque was used to reduce the effects of varying activation and series
175 compliance stretch across different isokinetic velocities (26). A torque threshold was
176 set to 90% of the maximum isometric torque at 100{degree sign} to control when the
177 dynamometer began moving (15).

178

179 *Dynamometer measurements*

180 Knee extensor torque and joint angle were sampled from the analogue output of the
181 dynamometer using a CED Micro 1401 A/D converter (2 kHz) and recorded in Spike

182 2 software (Cambridge Electronic Design Ltd., Cambridge, England). The torque
183 signal was filtered using a 10 Hz, first-order, low-pass, bi-directional Butterworth filter
184 in Matlab (MathWorks Inc., Natick, MA, USA). Knee extensor torque was gravity
185 corrected using the resting torque at 0{degree sign} (42). Passive torque was
186 calculated as the difference between the resting torque and gravity corrected torque
187 prior to the contraction. The best two-out-of-three trials based on maximal torque were
188 analyzed for each joint angle. For the isokinetic trials, the mean torque and muscle
189 shortening velocity was taken over only the constant angular velocity portion of the
190 movement. This removed any inertial effects on measured torque that would be
191 present during the acceleration periods at the start and end of the movement.

192

193 *Ultrasound measurements*

194 Measurements of VL fascicles were made using two ultrasound units that enabled the
195 use of two flat ultrasound transducers (LV7.5/60/96Z, TELEMED, Vilnius, Lithuania)
196 that were held end-to-end by a custom made frame. The arrangement enabled the
197 end-to-end visualization of fascicles that could not be similarly seen by either of the
198 transducers individually. A custom Matlab script was written to concatenate the two
199 individual images. A 22 mm gap between the visual fields of the two images occurred
200 as a result of the shape of the transducers, which was accounted for in the
201 concatenation process. The frame was placed at mid-thigh length, following a straight
202 line between the greater trochanter and the superior patella insertion. A self-adhesive
203 compression bandage was used to secure the frame and transducers to the thigh. The
204 central frequency of the transducers was set to 5 MHz, image depth 50 mm, and the
205 sampling rate to 80 Hz. A logic pulse from the first ultrasound unit triggered data
206 capture by the second ultrasound unit, which also produced its own logic pulse. The

207 two logic pulses were recorded by the A/D board to determine any delay between the
208 onsets of image collection that could be corrected. A semi-automated tracking
209 algorithm was used to measure fascicle length (13, 17). Fascicle lengths were
210 calculated as the distance between the origin of the fascicle in the proximal image and
211 the distal insertion with the deep aponeurosis in the distal image. Markings were made
212 around the location of the ultrasound transducers with a permanent marker so their
213 position could be matched between the dynamometer and cycling sessions.

214

215 *Dynamometer derived muscle relationships*

216 Quadriceps force was calculated by dividing the measured torque by the angle specific
217 moment arm from each individual scaled musculoskeletal model (9). VL fascicle length
218 was measured from the ultrasound data. VL MTU length was measured as the angle
219 specific MTU lengths from each individual scaled musculoskeletal model. The
220 musculoskeletal model was scaled using measurement-based scaling in OpenSim
221 software, using the anatomical markers placed to collect the kinematic data during
222 cycling.

223

224 A fascicle force-length curve and MTU force-length curve was produced for each
225 participant, based on a physiologically appropriate model (4).

$$226 \quad F_{active} = e^{-|(L^b-1)/s|^a}$$

227 where F is force, L is length (fascicle or MTU), a is roundness, b is skewness, and s
228 is width of the curve. The curve fit was optimized in Matlab using a nonlinear least
229 squares method. The predicted optimum fascicle length (L_{0_F}) and optimum MTU
230 length (L_{0_MTU}) was constrained to within the range of measured lengths. The b and s
231 coefficients were constrained to a range of 0-4 and 0-2 respectively. The a coefficient

232 was constrained to a value of 2. These values were selected to achieve force-length
233 curves similar to the characteristic sarcomere force-length relationship (18) and hence
234 ensure that the curve fits were physiological.

235

236 A fascicle force-velocity curve and MTU force-velocity curve was also produced for
237 each participant using a physiological model (8) that utilized the optimal length (L_{0_F}
238 or L_{0_MTU}) and isometric force (F_{max}) values from the isometric curve fit data.

239

$$240 \quad F = ((1 - (V/V_{max})) \div (1 + ((V/V_{max}) * G))) \times F_{max}$$

241

242 Where V is shortening velocity, V_{max} is the maximum shortening velocity, G is
243 curvature, and F_{max} is the maximum force capacity. For both relationships we allowed
244 a curvature of $3 < G < 9$ and a maximum shortening velocity of $4 < V_{max} < 12 L_0/s$,
245 which are reasonable boundaries based on animal models (10, 27).

246

247 The force-length and force-velocity properties for the VL MTU were computed for each
248 individual using the same approach as for the fascicles, however the MTU lengths
249 were used for each joint angle or angular velocity tested. The same curve fitting
250 parameters used in the fascicle analysis were used to construct an MTU force-length
251 relationship for each participant. Fascicle curves were normalized to the predicted L_{0_F}
252 and F_{max} . MTU curves were normalized to the predicted L_{0_MTU} and F_{max} . The force-
253 velocity relationship was constructed by using the mean fascicle or MTU shortening
254 velocity over the isokinetic period. The MTU velocities were normalized to the
255 respective L_{0_MTU} .

256

257 *Cycling measurements*

258 A six camera motion analysis system (Qualysis, Gothenburg, Sweden) was used to
259 capture, at 200 Hz, the locations of 23 passive, reflective markers positioned on
260 anatomical landmarks on the left thigh, left shank and pelvis. Scaling markers were
261 placed on anatomical landmarks of the anterior and posterior superior iliac spines (left
262 and right), greater trochanter, medial and lateral epicondyles of the femur, medial and
263 lateral malleoli, calcaneus, 1st and 5th metatarsal heads and most distal point of the
264 toes on the left leg. The calcaneus, 1st and 5th metatarsal head, and toe markers were
265 placed on the cycling shoes. Clusters of 4 markers on rigid plates were used for
266 dynamic tracking of the shank and thigh segments. The remaining markers were
267 placed on the iliac crest and sacrum for tracking the pelvis in dynamic movements.
268 The calibration markers on the shoe were used for dynamic tracking of the foot
269 segment. A static calibration capture was recorded as the subject stood with feet
270 shoulder width apart and arms crossed to opposite shoulder. A modified version of the
271 OpenSim gait 2392 model (only pelvis and left limb) was scaled using measurement-
272 based scaling based on the static calibration capture. An inverse kinematics analysis
273 was performed in OpenSim, using a weighted least squares fit between the model
274 markers and experimental markers at each time point. The inverse kinematics analysis
275 was used to measure joint angle, VL MTU length, and subsequently calculate MTU
276 velocity as the time differential of MTU length. Seat height was normalized to 100%
277 trochanter length (6, 33, 34). Participants cycled at a constant power output of 2.5
278 W/kg body mass, at predetermined cadences of 40 RPM, 60 RPM, 80 RPM and 100
279 RPM in a randomized order. Shimano SPD-SL pedals and R078 cycling shoes
280 (Shimano Inc., Osaka, Japan) were used for all conditions. Kinematic data was
281 exported for analysis using Matlab and OpenSim. Muscle fascicle length changes

282 were measured during cycling using the same ultrasound location and technique as
283 the dynamometer section.

284

285 *Analyses*

286 Statistical analysis was performed in Graphpad Prism 7 (GraphPad Software Inc., La
287 Jolla, CA, USA). The goodness of fit between the measured data points and curve
288 fitting results were measured using R^2 and standard error of the estimate (SEE). The
289 SEE values are reported relative to the individual F_{\max} to demonstrate the error relative
290 to the force-length and force-velocity curves. Curve fit coefficients were compared
291 between MTU and fascicle data using a paired t-test.

292

293 Fascicle and MTU lengths were filtered using a 5 Hz, 2nd-order, low-pass, bi-directional
294 Butterworth filter. The magnitude of muscle shortening was calculated as the
295 difference between the maximum and minimum length during the knee extension
296 phase. Muscle shortening velocities were calculated as the time differential of MTU
297 length and fascicle length. Peak shortening velocities during cycling were calculated
298 as the maximum shortening velocity of the MTU and fascicles during the knee
299 extension period. Mean shortening velocities were calculated as the average
300 shortening velocity during the knee extension period. Magnitude of shortening, mean
301 and peak velocity were compared across both analyses level (MTU vs fascicle) and
302 cadence using a two-way repeated measures ANOVA. Multiple comparisons were
303 made across cadences within each level of analysis, with corrections made using the
304 Holm-Sidak test. A one-way repeated measures ANOVA was used to compare the
305 effect of cadence on joint range of motion. The operating lengths represent the MTU
306 and fascicle lengths while the knee is extending (i.e. the push phase of the pedal

307 cycle). To determine the capacity for force production across conditions, we calculated
308 a *force index* for each participant from their individual force-length and force-velocity
309 relationships, and lengths and velocities recorded across all cycling conditions for the
310 same participant (2). The length-based and velocity-based force index values were
311 equal to the fraction of F_{\max} that could theoretically be produced by a maximally
312 activated muscle at the normalized length or velocity for each time point. For example,
313 if at a single time point the fascicle was active at a length of $1.2 L_0$ it could have a
314 length-based force index of approximately 0.6 (depending on the individual force-
315 length curve). That would mean at that time point the fascicles would have a maximum
316 force capacity of 60% F_{\max} based on length data. The mean force index values were
317 then computed as the average of all the time points during the knee extension period.
318 The same process was applied to the velocity-based force index. The total force index
319 was equal to the length-based force index multiplied by the velocity-based force index
320 and represents the total force generating capacity. The mean force index was
321 compared across level of muscle analysis (MTU vs fascicle) and cadence using a two-
322 way repeated measures ANOVA, with multiple comparisons across cadence. An alpha
323 of 0.05 was set to achieve significance for all tests, with corrections for multiple
324 comparisons. Data shown in text are mean \pm standard deviation.

325

326 **Results**

327 *Dynamometer force vs length relationships*

328 The range of absolute lengths spanned the upper end of the ascending limb, plateau
329 and descending limb of the force-length curve (Figure 1 a,b). The group mean (\pm SD)
330 R^2 values between the measured lengths and predicted curve were 0.84 ± 0.15 for the
331 MTU force-length relationship compared to 0.70 ± 0.16 for the fascicle force-length

332 relationship. The SEE was equal to 0.04 ± 0.02 for the MTU force-length curve fit and
333 0.07 ± 0.02 for the fascicle force-length curve fit. The optimal MTU length was
334 observed at 0.26 ± 0.01 m and the optimal fascicle length was 0.11 ± 0.01 m.
335 Normalizing the individual force-length curves to their respective optimal length
336 showed the data was spread across normalized lengths of $0.8 - 1.4 L_0$ (Figure 1 c,d).

337

338 *Dynamometer force vs velocity relationships*

339 The group mean (\pm SD) R^2 values were 0.82 ± 0.15 for the MTU force-velocity curves
340 and 0.78 ± 0.17 for the fascicle force-velocity curves. The group mean SEE values
341 were 0.09 ± 0.05 for the MTU force-velocity curves and 0.09 ± 0.04 for the fascicle
342 force-velocity curve fits. The isokinetic data showed that the fastest MTU shortening
343 velocities were observed at 45 ± 7 cm/s and fastest fascicle shortening velocities at
344 13 ± 3 cm/s. This resulted in normalized MTU shortening velocities of approximately
345 $2.0 L_{0_MTU}/s$ for the $400 \text{ } \{\text{degree sign}\}/s$ joint velocity (Figure 2a). The curvature of the
346 force-velocity fits was significantly different between analysis types ($p = 0.03$). The G
347 coefficient, representing the curvature of the relationship, for the MTU data was 7.39
348 ± 1.81 compared to 8.85 ± 0.46 for the fascicle data.

349

350 *Muscle-tendon unit and fascicle length changes during cycling*

351 When analyzing the cycling data, there were significant main effects of muscle
352 analysis and cadence on MTU and fascicle length changes ($p < 0.01$). The knee joint
353 ROM was not significantly different across the range of cadences ($79.0 \pm 6.3 \{\text{degree}$
354 $\text{sign}\}$ at 40 RPM, $76.3 \pm 4.0 \{\text{degree sign}\}$ at 100 RPM), which resulted in similar MTU
355 length changes across cadences ($0.21 L_{0_MTU} \pm 0.06$, $p = 0.07$). Fascicle length
356 changes significantly decreased with increasing cadence ($p < 0.01$), from 0.31 ± 0.07

357 L_{0_F} at 40 RPM to $0.16 \pm 0.05 L_{0_F}$ at 100 RPM. There was also a significant interaction
358 between factors ($p < 0.01$), further illustrating that length changes across cadences
359 did not show the same pattern for both the MTU and fascicle analysis.

360

361 VL MTU and fascicle lengths, over a crank cycle, were plotted against the respective
362 VL force-length curves to determine their operating range. The VL MTU lengths
363 covered the optimum of the force-MTU length curve (Figure 3a), operating across the
364 same range for all cadences ($0.90 \pm 0.02 - 1.07 \pm 0.02 L_{0_MTU}$, $p = 0.10$). VL fascicles
365 started each cycle at similar relative operating lengths ($1.2 \pm 0.02 L_{0_F}$) on the
366 descending limb of the force-length curve for all cadences, and shortened by greater
367 relative magnitudes at slower cadences compared to faster cadences (Figure 3b).

368

369 There was a significant effect of cadence and analysis on peak shortening velocity (p
370 < 0.01), with a significant interaction between cadence and analysis ($p < 0.01$). The
371 peak MTU shortening velocity predictably increased with cadence by 50%, 99% and
372 144% as cadence increased from 40 to 60, 80 and 100 RPM respectively (Table 1).
373 The peak fascicle shortening velocity increased with cadence by 28%, 46% and 52%
374 respectively as cadence increased from 40 to 60, 80 and 100 RPM. The absolute
375 fascicle shortening velocities were faster than the absolute MTU shortening velocities
376 during the early pedal cycle across all cadence conditions (Figure 4). For the 40 and
377 60 RPM conditions, there was both a higher peak fascicle velocity and an earlier
378 occurrence of peak shortening velocity compared to the MTU (Table 1). For the 80
379 and 100 RPM conditions the peak absolute MTU velocity was higher, but the
380 occurrence of peak fascicle shortening velocity was approximately 15% earlier in the
381 pedal cycle. There was also significant effects of cadence and analysis level on mean

382 fascicle shortening velocity ($p < 0.01$) with a significant interaction between factors (p
383 < 0.01). The multiple comparisons test showed the mean MTU shortening velocity
384 significantly increased between all cadence conditions ($p < 0.01$). However, the
385 average fascicle shortening velocity plateaued between the 80 RPM and 100 RPM
386 conditions (8.6 ± 2.7 and 8.5 ± 2.1 cm/s). For both the MTU and the fascicle analyses
387 there was a clear pattern for higher peak relative shortening velocities as cadence
388 increased (Figure 5, $p < 0.01$).

389

390 The group mean force indices during the knee extension phase showed that
391 shortening velocity had a greater influence on the capacity for force production
392 compared to the operating length for both the MTU and fascicle data. The mean
393 length-based force index (force-length index) was not significantly affected by the
394 analysis type ($p = 0.68$) or cadence ($p = 0.07$), maintaining a mean value across
395 conditions of 75% and 78% maximum force capacity for the MTU and fascicles
396 respectively (Figure 6a). The mean velocity-based force index (force-velocity index)
397 was significantly affected by both analysis method and cadence ($p < 0.01$) with a
398 significant interaction effect ($p = 0.01$). The MTU force-velocity index was overall
399 higher and decreased consistently with increased cadence. The fascicle force-velocity
400 index decreased with increasing velocity, however the slope of this relationship was
401 reduced with increasing velocity and plateaued between 80 RPM and 100 RPM
402 (Figure 6b). The mean force index based on length and velocity (total force index) was
403 significantly affected by both analysis and cadence ($p < 0.01$) with no significant
404 interaction effect ($p = 0.42$).

405

406

407 **Discussion**

408 This study investigated the effect of analyzing the length changes of the VL MTU
409 versus VL fascicles on the predicted force potential while cycling with a constant power
410 output and different cadences. The force index values represented the capacity for
411 force production during cycling relative to that which could theoretically be produced
412 by a maximally activated muscle at the normalized length or velocity. The results
413 showed that considering only the MTU length changes to predict force generating
414 capacity, and ignoring the effect of series elastic contributions, does not adequately
415 reflect how the contractile dynamics change with increasing cadence. The MTU
416 analysis resulted in consistent length changes across cadence conditions because of
417 the kinematic constraints, whereas the fascicle analysis was able to detect the force-
418 related differences in shortening as cadence was manipulated. MTU shortening
419 velocity increased progressively with cadence, whereas the fascicle velocity did not
420 increase at higher cadences and therefore the VL muscle likely maintained force
421 generating capacity at higher cadences. As such, using a joint kinematics or MTU
422 length measurement to predict muscle performance across different cycling conditions
423 is unlikely to yield valid information about optimal cycling technique or posture.

424

425 *Muscle-tendon unit and fascicle length changes during cycling*

426 The interaction between muscle fibers and series elastic tissues are important when
427 applied to dynamic movements like cycling. During cycling, the overall movement
428 pattern remains relatively constant in relation to the crank position, while the muscle
429 forces and velocities vary with different gearing and cadence combinations. The
430 constraints of the bicycle resulted in predictable MTU length changes because the
431 knee joint angular displacement is relatively unaffected by cadence. Thus, we did not

432 observe significant changes in MTU shortening across cadence conditions, and it
433 resulted in consistent force-length index values. However, the elasticity of the tendon
434 may augment the length changes of the fascicles to different degrees depending on
435 the force requirements dictated by maintaining a constant power output across
436 different cadences. The amount of fascicle shortening was affected by cadence (unlike
437 the MTU shortening), with greater fascicle shortening at low cadences because of the
438 increased force requirements and corresponding strain on the series elastic tissues.
439 Despite the increased fascicle shortening at low cadences, the greater range of
440 operating lengths did not reduce the fascicle force-length index. While these effects
441 did not translate to a significant difference in the capacity for force production, based
442 on the force-length index, they may be important in terms of separating fascicle and
443 tendon work throughout the pedal cycle.

444
445 The consistent decrease in the MTU force-velocity index as cadence increased was
446 not observed for the fascicles. The slope of the relationship between fascicle force-
447 velocity index and cadence reduced with increasing cadence and plateaued at the
448 highest cadences (80-100RPM). At low cadences the pedal forces are greater, which
449 imposes a greater strain on the series elastic tissues. Early in the pedal cycle, while
450 quadriceps force is rising, the absolute fascicle shortening velocity exceeds the
451 absolute MTU shortening velocity in order to stretch the tendon before it recoils during
452 force decline (32). At 40 RPM the peak fascicle shortening velocity is greater than the
453 peak MTU shortening velocity and occurs approximately 5% earlier in the pedal cycle
454 (Table 1). As cadence increased, the required pedal forces are reduced to maintain
455 constant power. The lower forces and higher velocity resulted in a disproportionate
456 increase in peak MTU shortening velocity compared to the fascicles (144% vs 52%
457 from 40 – 100 RPM), and a much earlier occurrence of peak fascicle shortening

458 velocity compared to the MTU, which maintained consistent timing relative to the pedal
459 cycle. The MTU analysis does not detect the force related differences in absolute
460 shortening velocity of the fascicles and series elastic tissues while cycling at different
461 cadences (Figure 4, Table 1). These findings show that an MTU analysis results in a
462 higher predicted maximum force generating capacity during cycling, because the MTU
463 velocities during cycling (even at 100 RPM) are low relative to the maximal shortening
464 velocity of the muscle (20). However, the MTU analysis also predicted a decrease in
465 force generating capacity across the range of cadences tested, whereas this
466 relationship was non-linear when considering fascicle dynamics. Fascicle level
467 analyses showed that force generating capacity plateaued at higher cadences and
468 this can be explained by the high velocity shortening late in the pedal cycle being
469 performed by the series elastic tissue.

470

471 *Dynamometer measurements for predicting force generating capacity*

472 The interaction between muscle fibers and tendon can affect the mechanical
473 performance of the muscle during contractions, and therefore influence predictions of
474 muscle force capacity (19, 31). Despite the constant angular velocity of the movement,
475 the force capacity of the muscle is crucially dependent on the length changes of the
476 fascicles because they represent the contractile apparatus. The fascicle shortening
477 velocity can be slower or faster than the MTU depending on the forces produced (15,
478 20). These force dependent length changes between contractile tissue and elastic
479 tissue impact our predictions of muscle force capacity if there is not an appropriate
480 differentiation between the two tissues. We have measured similar fascicle velocities
481 across the range of joint angular velocities investigated compared to similar isokinetic
482 and isotonic studies (15, 20). However, due to the contribution of the series elastic

483 tissue to overall shortening during high velocities (e.g. quick-release experiments –
484 Hauraix et al. 2017), it is unlikely that our data would be able to predict maximum
485 shortening velocities for the MTU. In this study, the MTU data was normalized to the
486 optimal MTU length rather than traditionally normalizing to L_{0_F} . This would have the
487 effect of reducing the magnitude of the relative velocities, but does not influence the
488 trends in shortening velocity across conditions.

489

490 In addition, the use of a pre-activation in our protocol may influence the prediction of
491 MTU force-generating capacity. It has been reported that the force-velocity
492 relationship measured using dynamometry is sensitive to the activation of the muscle
493 (26) and hence undertaking isokinetic tests with no pre-activation could result in
494 different F-V curves, particularly at higher speeds where activation levels may vary
495 (20). However, having a pre-activation should provide us with an estimate of the
496 maximum force producing capacity of the muscle when close to maximum activation.

497

498 *Limitations*

499 Knee extensor torque was measured as an indication of the VL force during isometric
500 and isokinetic contractions. While approximations of force generation from the VL can
501 be made based on the relative volume of the VL (1), there are changes in the relative
502 activation of the different quadriceps muscles throughout the knee joint range of
503 motion (36, 41), which may influence force estimations. In addition, three dimensional
504 muscle deformation may affect measurement of quadriceps fascicle lengths, which
505 has been shown in the gastrocnemius (21) and tibialis anterior (35). Fascicles and
506 aponeuroses were assumed to be straight lines to estimate fascicle length, which has
507 been found to result in a 2-7% underestimation when using a single transducer method

508 (14). However, the dual-transducer method used here should have reduced the
509 underestimation error in tracking the distal insertion of the fascicle, and it is less likely
510 to affect fascicle shortening velocities in the repeated measures design used in this
511 study. Finally, we did not examine the full range of isometric joint angles or very high
512 joint angular velocities (16, 20, 39), which means the prediction of the isometric force
513 capacity and maximal shortening velocity may be improved by measurement of data
514 approaching these extremities. However, the range of joint angles and velocities
515 examined here was within the range experienced during the relevant cycling
516 conditions (eg. 100 RPM equals approximately 400 {degree sign}/s). Our estimates of
517 force generating capacity should be consistent within the range tested, while our
518 estimates of V_{\max} may be susceptible to errors in curve fitting across the more narrow
519 velocity range; particularly if the series elastic tissue contribution increases at greater
520 MTU shortening velocities.

521

522 **Conclusions**

523 Analyzing muscle mechanics at a MTU level (or joint level) versus fascicle level can
524 have significant implications for interpretations of muscle mechanics during cycling.
525 Changes in force with cadence influence the instantaneous velocities of the fascicles
526 in relation to the MTU. The fascicles may be shortening faster, similarly, or at a slower
527 velocity than the MTU, depending on the instantaneous kinematic and force
528 requirements. Our results showed that the estimated force capacity of the VL relative
529 to the force-length relationship was not significantly affected by the type of muscle
530 analysis used. However, the estimated force capacity relative to the force-velocity
531 relationship was lower for fascicles compared to the MTU analysis, and in contrast to
532 the MTU analysis, did not consistently decrease as cadence increased (especially at

533 higher cadences). Thus, examining either MTU length changes or joint kinematics will
534 not provide a good indication of the force generating capacity of muscle across
535 cadence and gearing conditions. The results emphasized that either joint position or
536 MTU length measures may not be very useful to determine the conditions which may
537 maximize muscle force generating capacity during the cycling movement, particularly
538 at higher cadences. Further examination into how changes in power or cycling posture
539 (e.g. seat height) might influence force generating capacity are also warranted.

540

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543

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546

547 **Disclosures**

548 The authors have no financial or intellectual conflict of interest to declare.

549

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666

667

668 **Figure legends**

669 Figure 1. Absolute and normalized force-length curves at the MTU and fascicle level.
670 The absolute MTU lengths (a) and fascicle lengths (b) were consistent with the
671 reported L_0 values in the literature. Horizontal axis represents the absolute (a, b) VL
672 muscle tendon unit (MTU) and VL fascicle length, and (c, d) normalized to the
673 individual optimal lengths (L_{0_MTU} and L_{0_F}). Vertical axis shows the absolute
674 quadriceps force (a, b) and (c, d) normalized to the predicted maximal force (F_{max}).
675 Each cross represents an individual data point for each trial, across all participants.

676

677 Figure 2. Individual force-velocity curves for the isokinetic measurements. The
678 decrease in force as shortening velocity increased was less pronounced for the VL
679 muscle tendon unit (MTU) data (a) compared to the VL fascicle data (b). Each cross
680 represents an individual data point for each trial, for all participants. Data points are
681 normalized to the corresponding individual's maximum force (F_{max}) and optimal length
682 (L_{0_MTU} or L_{0_F}). The horizontal axis has been cropped to a maximum of 3.0 L_0 's for
683 clarity.

684

685 Figure 3. Vastus lateralis (VL) muscle tendon unit (MTU) and fascicle length changes
686 during cycling. The operating lengths of the MTU (a) and fascicles (b) are plotted
687 against the respective group mean force-length curves. The muscle begins actively
688 shortening just prior to top-dead-center (TDC), extending the knee until approximately
689 45% of the pedal cycle, then relaxing near bottom-dead-centre (BDC) and passively
690 lengthening to return to the upper operating length. (a) The range of operating lengths
691 spanned the plateau region of the MTU data, without a consistent trend across
692 cadence conditions. (b) The fascicle data started at longer normalized lengths and

693 shortened by a significantly smaller magnitude as cadence increased. The vertical
694 lines represent the upper and lower limits of the MTU and fascicle operating lengths
695 for each cadence condition. The circular arrows represent the pattern of length
696 changes as the muscle shortens (TDC-BDC, large arrow) and passively lengthens
697 (BDC-TDC, small arrow). Shaded regions represent -1 SE below the minimum and +1
698 SE above the maximum of the 40 RPM and 100 RPM conditions to demonstrate
699 variability.

700

701 Figure 4. Group mean MTU and fascicle shortening velocity waveforms across
702 cadence. The magnitude of (a) MTU shortening velocity predictably increased as
703 cadence increased whereas (b) the fascicle shortening velocity appeared to plateau
704 at high cadence. The red lines represent the start and stop of the knee extension
705 phase (approximately 95% - 45% of the pedal cycle). The shaded area represents the
706 knee flexion phase that was not included in the analysis. The vertical axis represents
707 muscle velocity normalised to the respective (a) MTU and (b) fascicle L_0 values. The
708 horizontal axis is expressed as a time normalized percentage of the pedal cycle from
709 the vertical crank position.

710

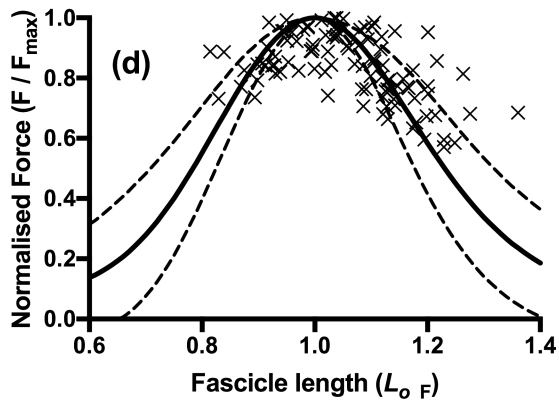
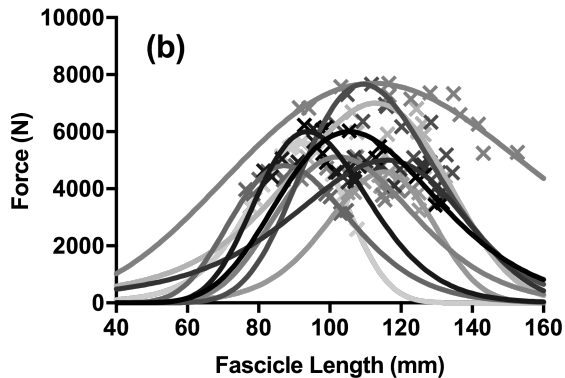
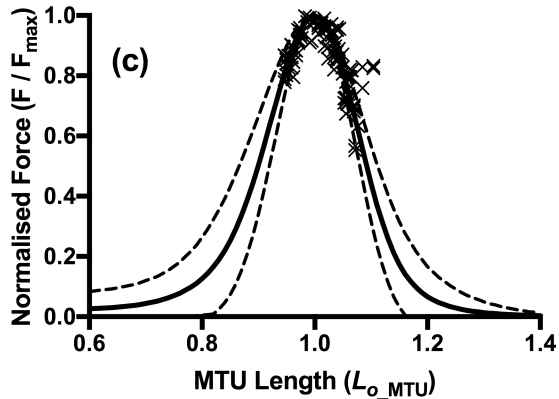
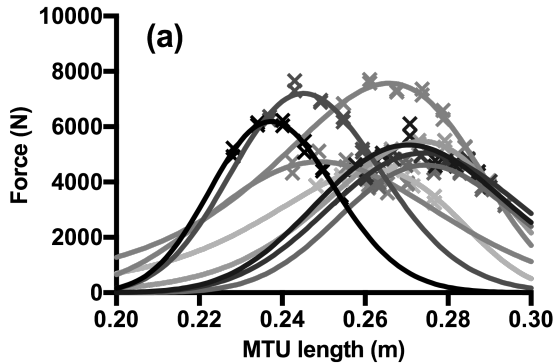
711 Figure 5. Range of vastus lateralis (VL) muscle tendon unit (MTU) and fascicle
712 shortening velocities (relative to optimum) during cycling. The peak velocities of the
713 (a) MTU and (b) fascicles are plotted against the respective group mean force-velocity
714 curve. The range of shortening velocities across cadences was lower for the MTU
715 relative to the compared to the fascicle shortening velocity (b). At the start of the push
716 phase the VL fascicles and MTU are close to isometric and start to shorten
717 immediately prior to top-dead-center (TDC). The vertical lines show the mean peak

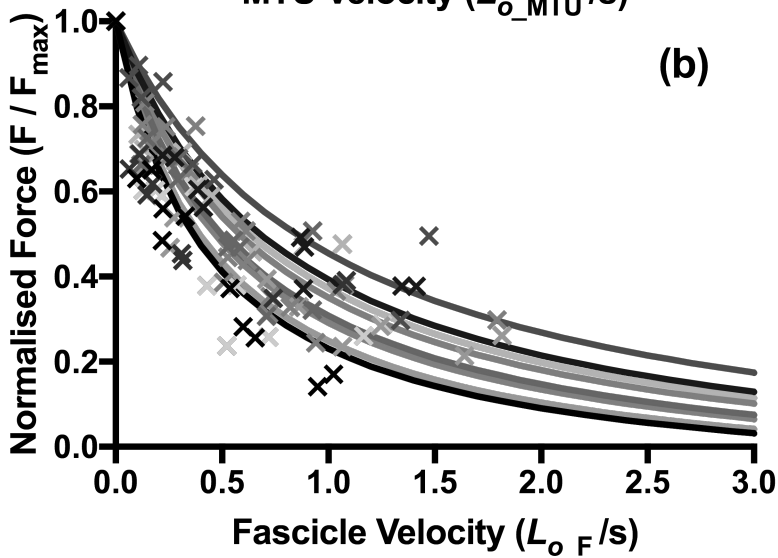
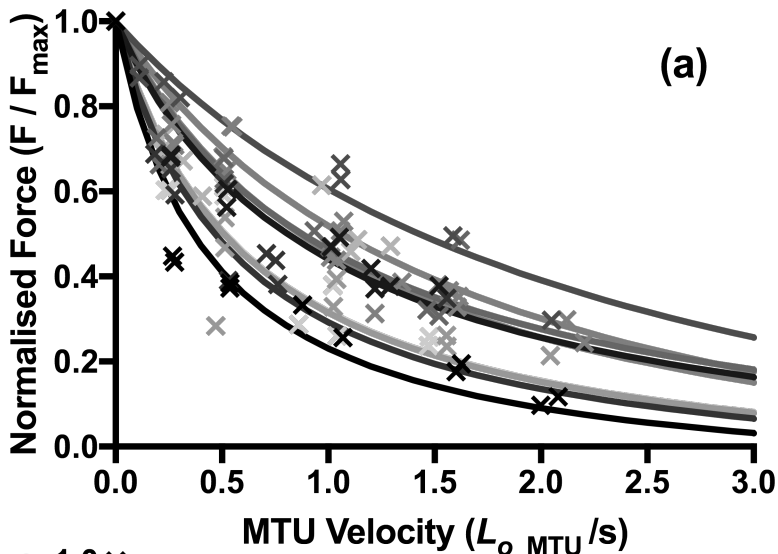
718 shortening velocities for each of the four cycling cadences. Shaded areas represent
719 ± 1 SE of the 40 RPM and 100 RPM conditions. Error markings are omitted for the 60
720 RPM and 80 RPM conditions for clarity.

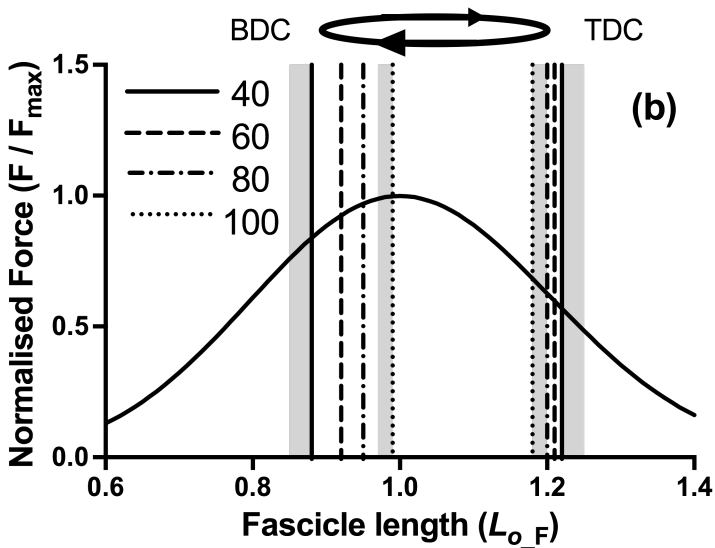
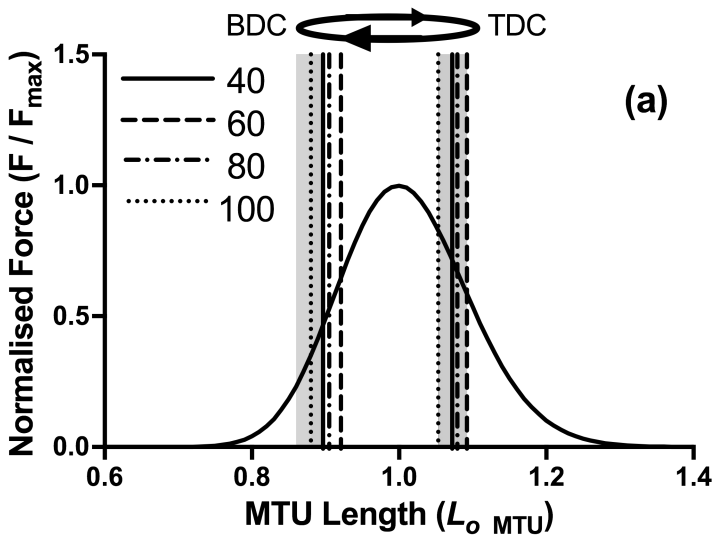
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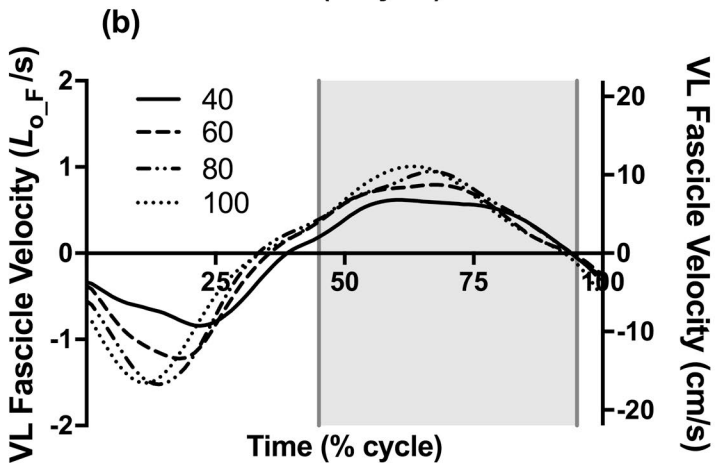
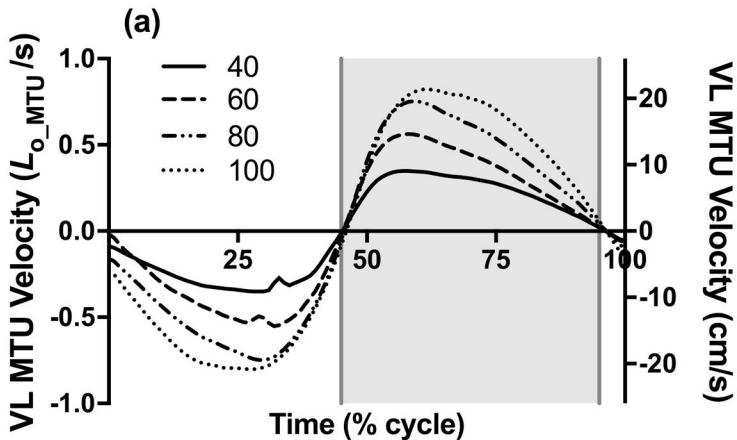
722 Figure 6. Mean force indices for the vastus lateralis muscle tendon unit (MTU) and
723 fascicle analysis methods relative to cadence. There was no significant difference in
724 the force-length index (a) values between analyses or cadences. The force-velocity
725 index (b) at the MTU decreased linearly with increased cadence, and was always
726 greater than the force index of the fascicles. The total force index was greater in the
727 MTU analysis than fascicle analysis, with a linear decrease as cadence increased.
728 Data shown are mean \pm SD. Data are offset relative to cadence for clarity between
729 overlapping points and error bars.

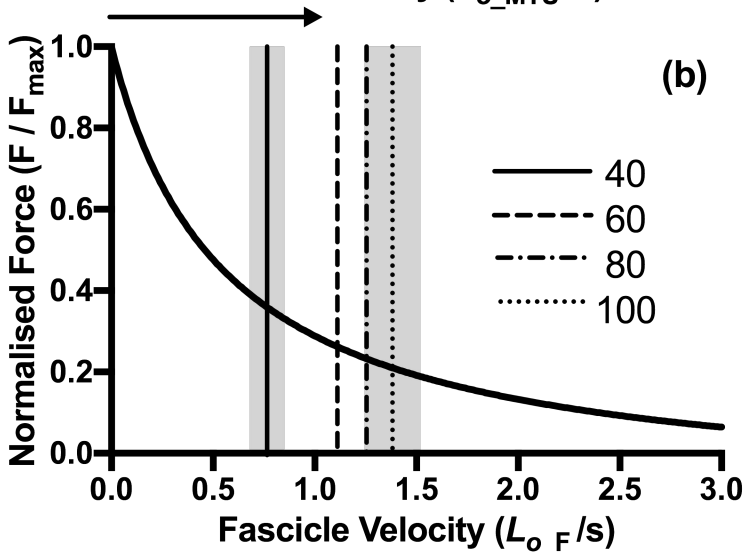
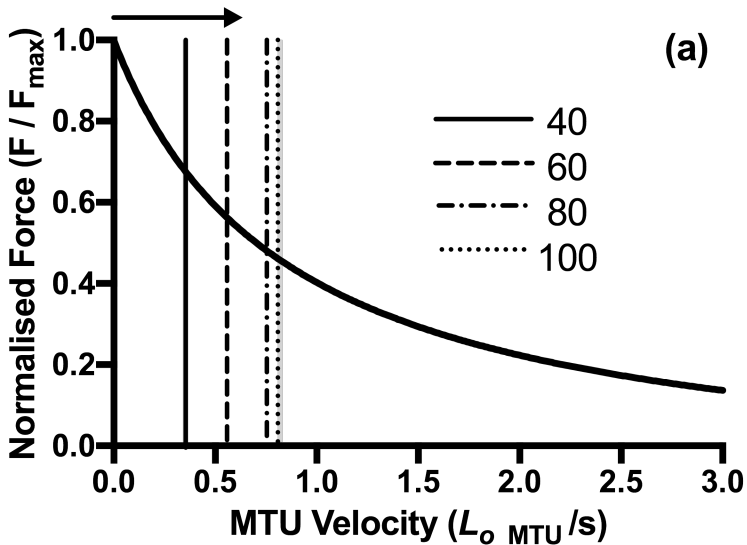
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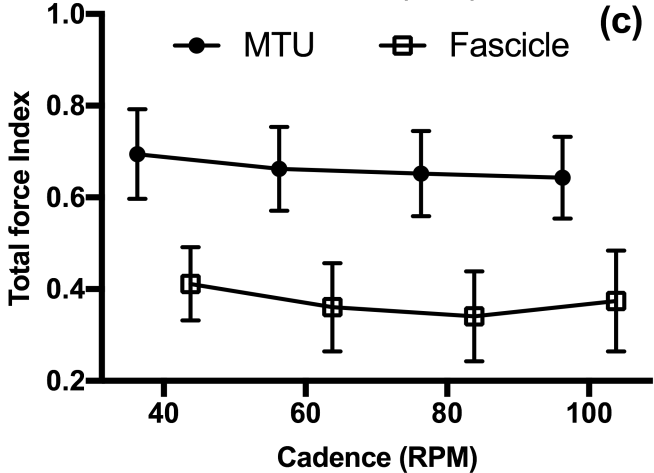
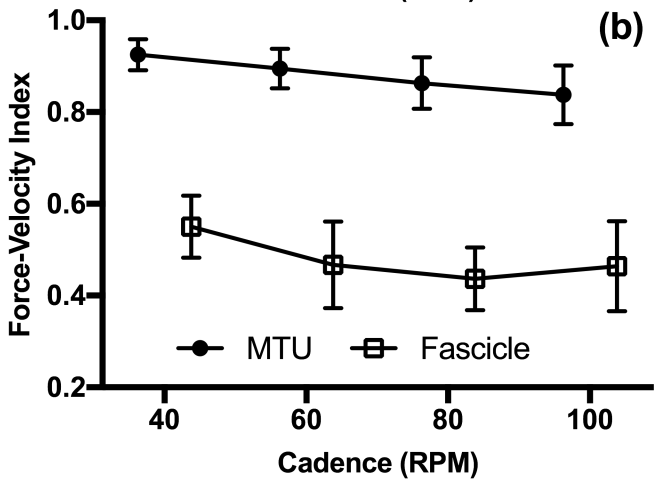
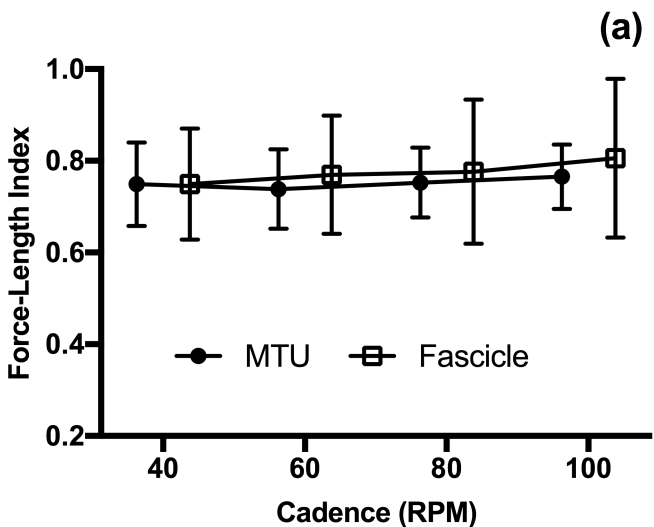


Table 1. Mean and peak absolute shortening velocities of the MTU and fascicles during cycling.

Cadence	MTU		Fascicle	
	mean shortening velocity	peak shortening velocity	mean shortening velocity	peak shortening velocity
40	6.6 ± 0.7	10.1 ± 1.1 (31 ± 4)	5.2 ± 0.9	12.0 ± 2.7 (25 ± 5)
60	9.4 ± 1.3	15.2 ± 1.6 (32 ± 3)	7.6 ± 1.7	15.3 ± 3.6 (18 ± 4)
80	13.3 ± 1.2	20.1 ± 2.1 (30 ± 2)	8.6 ± 2.7	17.5 ± 4.9 (15 ± 4)
100	16.0 ± 2.4	24.6 ± 2.5 (30 ± 4)	8.5 ± 2.1	18.2 ± 5.3 (14 ± 6)

Values for the MTU and fascicles are shown as mean ± SD in cm/s. Values in brackets represent the occurrence of peak velocity as a percentage of the pedal cycle (mean ± SD). There was a significant main effect of cadence and analysis level on mean and peak shortening velocity of both the MTU and fascicles ($p < 0.01$) with a significant interaction. All cadence conditions were significantly different for both the mean and peak MTU shortening velocity. The mean fascicle shortening velocity at 40 RPM was significantly different to the 60, 80 and 100 RPM conditions. The peak fascicle shortening velocity at 40 RPM was significantly different to 100 RPM.