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Title: The expression of the skeletal muscle force-length relationship in vivo: a simulation study.

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1 **Abstract (298 words):** The force-length relationship is one of the most
2 important mechanical characteristics of skeletal muscle in humans and animals.
3 For a physiologically realistic joint range of motion and therefore range of
4 muscle fibre lengths only part of the force-length curve may be used in vivo, i.e.
5 only a section of the force-length curve is expressed. A generalised model of a
6 mono-articular muscle-tendon complex was used to examine the effect of
7 various muscle architecture parameters on the expressed section of the force-
8 length relationship for a 90 degree joint range of motion. The parameters
9 investigated were: the ratio of tendon resting length to muscle fibre optimum
10 length ($L_{TR} : L_{F.OPT}$) (varied from 0.5 to 11.5), the ratio of muscle fibre optimum
11 length to average moment arm ($L_{F.OPT} : r$) (varied from 0.5 to 5), the normalised
12 tendon strain at maximum isometric force (c) (varied from 0 to 0.08), the muscle
13 fibre pennation angle (θ) (varied from 0 to 45 degrees) and the joint angle at
14 which the optimum muscle fibre length occurred (ϕ). The range of values
15 chosen for each parameter was based on values reported in the literature for
16 five human mono-articular muscles with different functional roles. The ratios
17 $L_{TR} : L_{F.OPT}$ and $L_{F.OPT} : r$ were important in determining the amount of variability
18 in the expressed section of the force-length relationship. The modelled muscle
19 operated over only one limb at intermediate values of these two ratios
20 ($L_{TR} : L_{F.OPT}=5$; $L_{F.OPT} : r=3$), whether this was the ascending or descending limb
21 was determined by the precise values of the other parameters. It was
22 concluded that inter-individual variability in the expressed section of the force-
23 length relationship is possible, particularly for muscles with intermediate values

24 of $L_{TR} : L_{F.OPT}$ and $L_{F.OPT} : r$ such as the brachialis and vastus lateralis.

25 Understanding the potential for inter-individual variability in the expressed

26 section is important when using muscle models to simulate movement.

27

28 **Keywords:**

29 force-length, tendon, model, biomechanics

30

31 INTRODUCTION

32 The force-length relationship of muscle is a fundamental mechanical property of
33 muscle. It is also an important component of most biomechanical models of
34 movement since it determines the maximum isometric force that can be
35 produced at a given joint configuration. The force-length relationship has been
36 shown to consist of three regions at the sarcomere level (Gordon et al., 1966):
37 the ascending limb, the plateau, and the descending limb. However, in vivo
38 different skeletal muscles may operate over all or only some of these regions of
39 the force-length curve, that is over physiological joint ranges of motion only part
40 of the force-length relationship may be expressed (e.g. Herzog and ter Keurs,
41 1988; Lieber and Friden, 1998). The section of the force-length relationship that
42 a muscle operates over, given the physiological range of motion of the joints
43 crossed by the muscle, will be referred to as the expressed section. Previous
44 work has shown that there is a great deal of variability in the expressed section
45 for the rectus femoris (Herzog and ter Keurs, 1988; Winter, 2004) and the
46 hamstrings (Savelberg and Meijer, 2003). There is apparently not much
47 variability in the expressed section of the gastrocnemius (Herzog et al., 1991a;
48 Winter and Challis, 2008b). The reason for the different amount of variability in
49 the expressed section in different muscles has not been investigated. The
50 section of the force-length relationship that a muscle operates over affects the
51 pattern of force production across the range of motion. The change in muscle
52 force with muscle length must present a substantial challenge to the successful
53 control and co-ordination of movement. It is therefore of considerable interest
54 to investigate which factors determine the expressed section of the force-length

55 relationship in vivo, and to understand why some muscles show more variability
56 in this property than others.

57

58 There are several possible sources of the reported variation in the expressed
59 section of the force-length relationship. These are: anatomical differences, for
60 example in the distance of muscle insertion points from joint centres relative to
61 segment length; differences in tissue mechanical properties such as tendon
62 compliance; and differences in muscle architectural features, such as pennation
63 angle. These musculo-skeletal features are reflected in the parameters usually
64 included in muscle models, for example the muscle pennation angle is included
65 in many muscle models (e.g. Otten, 1988). In a previous study gastrocnemius
66 muscles operating over different sections of the force-length curve were
67 modelled in order to assess the ability of an in vivo testing method to accurately
68 reconstruct different sections of the force-length relationship (Winter and
69 Challis, 2008a). In formulating models for muscles operating over different
70 sections of the force-length relationship it was found that certain model
71 parameters affected the expressed section of the force-length relationship more
72 than others.

73

74 The purpose of this study was to undertake a more systematic examination of
75 the effect of anatomical, architectural and mechanical muscle-tendon complex
76 parameters on the expression of the force-length curve in vivo using a muscle
77 model. The model was initially formulated as a generalised mono-articular
78 muscle-tendon complex and then each parameter was systematically varied in

79 turn over ranges that reflect the range of parameter values reported in the
80 literature for several mono-articular muscles. It was hypothesised that varying
81 the ratio of resting tendon length to the muscle fibre optimum length
82 ($L_{TR} : L_{F.OPT}$) would have the greatest influence on the section of the force-length
83 relationship that was expressed (Winter and Challis, 2008b).

84

85

86 **METHODS**

87 ***Model Description***

88 The muscle model comprises a contractile component that models the
89 behaviour of the muscle fibres, and a series elastic component (Figure 1). The
90 force produced by the muscle model (F_M) is described by,

91

$$92 \quad F_M = q \cdot F_{MAX} \cdot F_L(L_F) \cdot F_V(V_F) \quad [1]$$

93

94 where,

95 q - current active state of muscle model,

96 F_{MAX} - maximum isometric force possible by the muscle model,

97 $F_L(L_F)$ - fraction of the maximum isometric force the model can produce given

98 its current fibre length (L_F),

99 and $F_V(V_F)$ is the fraction of maximum isometric force the model can produce

100 given its current fibre velocity (V_F).

101

102

<<Insert Figure 1 around here>>

103

104 The current active state of the model (q) represents the recruitment as well as
105 the firing rate, or rate coding, of the α -motor neurons. The value of q can range
106 from 0 to 1. In the simulations only maximal isometric conditions were
107 examined so the muscle fibres were assumed to have a velocity of zero, making
108 $q=1$ and $F_V(V_F)=1$. The value of F_{MAX} was always set to be 100 arbitrary units of
109 force.

110

111 The normalised force-length properties of the muscle were represented by
112 (Gallucci and Challis, 2002),

$$113 \quad F_L(L_F) = 1 - \left(\frac{L_F - L_{F.OPT}}{w \cdot L_{F.OPT}} \right)^2 \quad [2]$$

114

115 where:

116 $L_{F.OPT}$ is the optimum length of the muscle fibres, and

117 w is a parameter specifying the width of the force-length relationship (Figure
118 1A).

119

120 The muscle fibre optimum length is the length at which optimal overlap of actin
121 and myosin occurs and therefore maximum muscle force can be produced. The
122 value for w for single fibres in vitro has been reported as 0.56 (Gordon et al.,
123 1966).

124

125 In series with the contractile component is an elastic component. Although this
126 component reflects the behaviour of any elastic structure in series with the
127 contractile component, the series elastic component mainly reflects the
128 behaviour of the tendon. The model of this element assumes that the tendon
129 has a linear stress-strain curve (Figure 1B). The force-extension curve of this
130 element is represented by,

131

$$132 \quad L_T = L_{TR} + \frac{F_M \cdot c}{F_{MAX}} \cdot L_{TR} \quad [3]$$

133

134 where:

135 L_T is the current length of the tendon,

136 L_{TR} is the resting or slack length of the tendon, and

137 c is the extension of tendon under maximum isometric force as a fraction of
138 tendon resting length.

139

140 The length of muscle-tendon complex (L_{MT}) is the length from origin to
141 insertion. For a paralleled fibred muscle it is equal to the length of the muscle
142 fibres plus the length of the tendon (Equation 4),

143

$$144 \quad L_{MT} = L_F + L_{TR} \quad [4]$$

145

146 The muscle fibres can be pennate (Figure 1C). In a planar model of pennate
147 muscle it is assumed that the area of the muscle fibres remains constant, this is

148 equivalent to the constant volume assumption for actual muscle (Otten, 1988).

149 Given that the thickness (T) of the muscles must remain constant, the pennation

150 angle (θ) can be computed from,

151

$$152 \quad \cos(\theta) = \sqrt{1 - (T / L_F)^2} \quad [5]$$

153

154 where:

155 θ is the muscle fibre pennation angle in radians.

156

157 If the muscle is pennate then the force in the direction of the tendon is not equal

158 to the force in the muscle fibres (Figure 1C), instead the correction given in

159 Equation 6 has to be applied.

160

$$161 \quad F_T = F_M \cdot \cos(\theta) \quad [6]$$

162

163 where:

164 F_T is the force in the direction of the tendon.

165

166 The length of the muscle-tendon complex can then be computed from (Figure

167 1C),

168

$$169 \quad L_{MT} = L_F \cdot \cos(\theta) + L_T \quad [7]$$

170

171 For input into the model it was necessary to know the length of the muscle-
172 tendon complex (L_{MT}). In many muscle models (e.g. Out et al., 1996) the
173 length of the muscle-tendon complex is computed from the joint angle according
174 to an experimentally determined relationship (e.g. Grieve et al., 1978). The
175 muscle moment arm is then computed by taking the derivative of this muscle-
176 tendon complex length-joint angle relationship with respect to angle (An et al.,
177 1983). However, in order to examine the effect of the ratio $L_{F.OPT} : r$ on the
178 expressed section of the force-length relationship the value of r had to be
179 specified in advance, and the change in the length of the muscle-tendon
180 complex was therefore obtained by integration of the moment arm-joint angle
181 relationship. This ratio is important since it determines the length change that
182 the muscle must go through in order to move through the joint range of motion.

183

184 The reference length of the muscle-tendon complex (L_{MTR}) was specified
185 according to,

186

$$187 \quad L_{MTR} = L_{F.OPT} + L_{TR} \quad [8]$$

188

189 For each simulation there was a reference length of the muscle-tendon complex
190 which was always set to be 50 arbitrary units long. The lengths L_{TR} and $L_{F.OPT}$
191 were set according to the desired value for the ratio $L_{TR} : L_{F.OPT}$. The angle at
192 which this reference muscle-tendon complex length occurs (ϕ) was specified,
193 this parameter specifies the angle at which the reference length occurs and is

194 therefore important in determining the range of lengths used for a certain joint
 195 range of motion. The moment arm length at this reference angle (r_{REF}) was
 196 computed according to the desired value for $L_{F.OPT} : r$. The moment arm-joint
 197 angle relationship could be constant, increasing, or decreasing according to
 198 Equation 9. The range of motion for the joint was always 0 to 90 degrees. A 90
 199 degree range of motion was used since it is a typical range of motion for many
 200 joints (Pheasant, 1986).

201

$$202 \quad r = r_{REF} + r_{SLOPE}(\phi_{JOINT} - \phi) \quad [9]$$

203

204 where:

205 r_{SLOPE} is the slope of the moment arm-joint angle relationship, and

206 ϕ_{JOINT} is the current joint angle in radians.

207

208 For a constant moment arm r_{SLOPE} was set to zero.

209

210 The length of the muscle-tendon complex at the current joint angle was then
 211 computed by integrating the moment arm-joint angle relationship and adding the
 212 reference muscle-tendon complex length,

213

$$L_{MT} = L_{MTR} + r_{REF}(\phi_{JOINT} - \phi) + \frac{1}{2} r_{SLOPE}(\phi_{JOINT} - \phi)^2 \quad [10]$$

215

216 For a given joint angle the moment arm of the muscle was computed and

217 muscle-tendon lengths were computed. Given these muscle-tendon lengths the

218 maximum isometric force the muscle could produce was computed. The length
219 of the fibres was determined by an iterative procedure. First fibre length was
220 estimated by subtracting resting tendon length from the muscle-tendon length at
221 a given joint angle. This value was used to estimate muscle isometric force.
222 The tendon stretch under this force was then computed, and therefore a new
223 muscle fibre length was computed, and a new isometric force computed. This
224 sequence was continued until a consistent value for maximum isometric force
225 was produced, which was always achieved in 20 iterations or less.

226

227 ***Model Parameters***

228 The model parameters under investigation in the present study are: the muscle
229 fibre pennation angle (θ), the compliance of the tendon (c), the ratio of the
230 muscle fibre length to the size of the moment arm ($L_{F.OPT} : r$), the joint position
231 at which the reference muscle-tendon complex length occurs (ϕ), and the ratio
232 of resting tendon length to fibre optimum length ($L_{TR} : L_{F.OPT}$). The model was
233 formulated initially as a generalised mono-articular muscle-tendon complex and
234 then each parameter was systematically varied in turn over ranges that reflect
235 the range of parameter values found in a variety of mono-articular muscles.
236 Five mono-articular muscles were chosen to reflect a variety of anatomical and
237 architectural features. The muscles were: the soleus (SOL), vastus lateralis
238 (VL), the short head of the biceps femoris (SHBF), the brachialis (BR), and the
239 extensor carpi radialis brevis (ECRB). Although the ECRB arises partly from
240 the lateral epicondyle of the humerus it was treated as a mono-articular muscle
241 since it is only a weak elbow flexor (Ettema et al., 1998; Riek et al., 2000).

242 Table 1 shows the source and range of the values used for each muscle for
243 $L_{F.OPT} : r$, $L_{TR} : L_{F.OPT}$, c , and θ parameters. The intention in referring to these
244 parameter values is to ensure that the range of values investigated with the
245 model covers the range of parameter values typically found in vivo.

246

247 <<Insert Table 1 around here>>

248

249 The maximum normalised tendon strain is specified by c . The values for c were
250 directly specified for SOL by Magnusson et al. (2001) and for ECRB by Loren
251 and Lieber (1995) (Table 1). No information on either c or the tendon cross-
252 sectional area could be found for BR. For the VL and SHBF the values for c
253 shown in Table 1 were computed by taking the values for the tendon and
254 muscle cross sectional areas from Pierrynowski and Morrison (1985) and
255 Wickiewicz et al. (1983) and then using the relationship,

256

$$257 \quad c = \frac{PCSA \times ST}{TCSA \times E} \quad [11]$$

258 Where:

259 $PCSA$ is the physiological cross sectional area of muscle

260 ST is the specific tension of muscle (0.3MPa taken from Close, 1972)

261 $TCSA$ is the tendon cross sectional area, and

262 E is the Young's Modulus of tendon (1,500MPa taken from Alexander, 2002).

263

264 The reference muscle tendon length is equal to the resting tendon length plus
265 the optimum fibre length. The parameter ϕ , representing the joint angle at
266 which the reference muscle-tendon complex length occurs, was varied in order
267 to shift the optimum length to different points in the joint range of motion. The
268 joint angle at which the optimum length occurs is difficult to determine in vivo
269 since more than one muscle crosses each joint, and for this reason the
270 parameter ϕ was varied through the whole range of motion (0 to 90 degrees).
271 When the muscle is activated at the reference position the muscle fibres will
272 exert force and stretch the tendon, and the muscle fibres will shorten due to
273 tendon stretch. This means that the angle at which the optimum muscle fibre
274 length occurs under full activation will change if a compliant tendon is specified
275 in the model. For this reason a non-compliant tendon was used when
276 examining the effect of changing parameters $L_{TR} : L_{F.OPT}$, ϕ and θ .

277

278

279 **RESULTS**

280 It was not feasible to report all possible parameter set combinations, but based
281 on the data presented in Table 1, a representative range has been selected.
282 The combinations of parameter values used are reported in Table 2. The left
283 hand column shows which parameter was varied, the columns to the right show
284 the values of the fixed parameters, and the range of values used for the
285 parameter under investigation. The results are presented in the row order
286 shown in Table 2.

287

288

<<Insert Table 2 around here>>

289

290 Varying the ratio $L_{F,OPT} : r$ with $L_{TR} : L_{F,OPT}$ held constant affects how much of
291 the force-length relationship is expressed (Figure 2). This was the case
292 regardless of whether the moment arm was held constant over the range of
293 motion or whether the moment arm increased or decreased over the range of
294 motion. Under the model formulation with a constant moment arm the change
295 in the length of the muscle-tendon complex was equal to the length of the
296 moment arm multiplied by the change in joint angle from the reference position
297 in radians. This means that the amount of the force-length relationship used
298 also depends on the joint range of motion relative to the width of the force-
299 length relationship (w). Consequently the proportion of the force-length
300 relationship that is used (p) can be computed using the inverse of the ratio
301 $L_{F,OPT} : r$ and the joint range of motion (ROM),

302

303
$$p = \frac{r}{L_{F,OPT}} \cdot \frac{ROM}{2w} \quad [12]$$

304

305 Using Equation 12 it can be shown that the value of $L_{F,OPT} : r$ at which the
306 whole of the force-length relationship is used when there is a constant moment
307 arm, a width parameter of 0.56, and a 90 degree joint range of motion is around
308 1.4 for an inextensible tendon and slightly more if a compliant tendon is used.
309 In vivo, only values of $L_{F,OPT} : r$ above this will allow some variability in the
310 expression of the force-length relationship.

311

312

<<Insert Figure 2 around here>>

313

314 The effect of varying the value for $L_{TR} : L_{F.OPT}$ depended partly on the size of the

315 moment arm, r (Figure 3 and Figure 4). For relatively small moment arms (high

316 ratios of $L_{F.OPT} : r$) and low ratios of $L_{TR} : L_{F.OPT}$ the muscle always operated

317 over the plateau, regardless of the joint angle at which the optimum length was

318 set. The optimum length had to be set at non-physiological joint angles in order

319 to make the muscle operate over one of the limbs (ascending or descending) of

320 the force-length relationship. For large moment arms (low values of $L_{F.OPT} : r$)

321 and high values of $L_{TR} : L_{F.OPT}$ the whole range of the force-length relationship

322 may be used for low values of c and θ if ϕ occurs in the middle of the joint range

323 of motion. The muscle could only operate over just one limb of the force-length

324 relationship when both ratios ($L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$) were at high values, or

325 both were at low values, or both were at intermediate values.

326

327

<<Insert Figures 3 and 4 around here>>

328

329 The effect of varying ϕ throughout the range of motion was to shift the

330 expressed section of the force-length relationship from the descending limb (for

331 ϕ equal to zero degrees), to the plateau (for ϕ equal to 30 to 60 degrees), and

332 then to the ascending limb (for ϕ equal to or greater than 75 degrees) (Figure 5).

333

334

<<Insert Figure 5 around here>>

335

336 Tendon compliance means that the tendon stretches when the muscle is
337 activated and applies force to it, resulting in a shorter muscle fibre length at a
338 given joint angle with increasing compliance and so shifting the expressed
339 section to shorter muscle fibre lengths. This means that a muscle, with ϕ set to
340 45 degrees so that the optimum length occurs in the middle of the range of
341 motion, would operate over the plateau region if the tendon were considered
342 inextensible, but would shift to shorter lengths so that it operates over the
343 ascending limb for values of c close to 0.08 (Figure 6). Similarly a muscle with
344 ϕ set to 0 degrees would operate over the descending limb for values of c
345 between zero and 0.05, but the muscle would be shifted to the plateau region
346 for values of c above 0.06 (Figure 7). The effect of changing the parameter c
347 would be smaller for lower values of $L_{TR} : L_{F.OPT}$, since the tendon would be
348 considerably shorter. Note that Figures 3 and 4 show the effect of varying the
349 ratios $L_{TR} : L_{F.OPT}$ and $L_{F.OPT} : r$ while c is set to zero. When c was set at values
350 above 0.01 the expressed section was shifted to shorter lengths, which is
351 consistent with the trend shown in Figures 6 and 7.

352

353

<<Insert Figures 6 and 7 around here>>

354

355 The effect of varying the pennation angle of the muscle fibres (θ) was to shift
356 the expressed section to longer lengths, i.e. towards the descending limb
357 (Figure 8). This is because the fibre length at a given joint angle is inversely

358 proportional to the cosine of the pennation angle. As the pennation angle
359 increases, the cosine of the angle decreases and the fibre length at the
360 specified joint angle increases. However, the shift in the operating range was
361 not sufficient to change the expressed section from one limb to the other, i.e.
362 from the ascending limb to the descending limb. The maximum force in the
363 direction of the tendon decreased with increasing pennation angle, this would
364 be expected as the force in the direction of the tendon is only the cosine of the
365 pennation angle times the force in the muscle fibres. The cosine of 45 degrees
366 is 0.707, so the force in the direction of the tendon is only around two thirds of
367 that in the muscle fibre with such a high pennation angle. The value specified
368 for θ represents the pennation angle at rest; the pennation angle increases with
369 decreasing muscle length.

370

371 <<Insert Figure 8 around here>>

372

373 **DISCUSSION**

374 The model parameters that were most critical in allowing variability in the
375 expressed section of the force-length relationship were the ratios $L_{F.OPT} : r$ and
376 $L_{TR} : L_{F.OPT}$. For high $L_{TR} : L_{F.OPT}$ ratios, representing a long tendon and short
377 muscle fibres, the whole of the force-length relationship was used due to the
378 shortness of the muscle fibres. For very low ratios of $L_{TR} : L_{F.OPT}$ the expressed
379 section was always the plateau unless the optimum length was set at a joint
380 angle that was very far outside a physiologically realistic range of motion. The
381 effect of changing the value of $L_{TR} : L_{F.OPT}$, however, was modified by the value

382 of $L_{F,OPT} : r$. This is because for a fixed range of motion and a given value for
383 the width of the force-length relationship, the inverse of $L_{F,OPT} : r$ was
384 proportional to the fraction of the force-length relationship that was used
385 (Equation 12). For the range of motion and the width of the force-length curve
386 used here only values of $L_{F,OPT} : r$ above 1.5 resulted in only one limb of the
387 force-length relationship being expressed. For intermediate values of
388 $L_{TR} : L_{F,OPT}$ and $L_{F,OPT} : r$ the effect of increasing tendon compliance was to shift
389 the expressed section to increasingly shorter lengths and the effect of
390 increasing the pennation angle was to shift the expressed section to
391 increasingly longer lengths.

392

393 The width parameter used in the simulations was 0.56 (Gordon et al., 1966), but
394 due to variability in the number of sarcomeres per muscle fibre (Meijer et al.,
395 1998) it is likely that the width of the force-length relationship is broader in vivo
396 in whole muscle than it is in an isolated fibre preparation (Challis, 2000).

397 However, the effect of a higher value for a width parameter can be explored
398 using Equation 12. For example, with $L_{F,OPT} : r$ equal to 2, ROM equal to 90
399 degrees or $\pi/2$ radians and w equal to 0.56 the length change required would
400 be 0.7 times the range of the force-length relationship. Changing the width
401 parameter to 0.7 reduces the proportion of the force-length relationship used to
402 0.561.

403

404 While some muscles have constant moment arms throughout their joint range of
405 motion, others have a variable moment arm – joint angle relationship. For
406 variable moment arm muscles, the proportion of the force length relationship
407 used can still be calculated if the mean moment arm over the joint range of
408 motion is calculated and then substituted into Equation 12. Equation 12 can
409 also be used to adjust results for joints with restricted ranges of motion, either
410 due to joint anatomy or due to pathologies such as osteoarthritis, though such
411 pathologies would doubtless affect the value of other parameters in the model.

412

413 When only one limb of the force-length relationship is used, whether an
414 individual operates over the ascending or descending limb will depend on the
415 joint angle at which the optimum length occurs. In the model, varying the joint
416 angle at which the optimum length occurs (ϕ) caused a change in the length of
417 the muscle tendon complex at a given joint angle of around 10%. This inter-
418 individual variability in muscle-tendon complex lengths at a given joint angle
419 could be caused in vivo by inter-individual differences in attachment sites, and
420 therefore differences in the distance between origin and insertion sites. Such
421 inter-individual differences in attachment sites have been reported, for example
422 Duda et al. (1996) found that the coefficient of variation for the centroid of the
423 attachment site of various muscles arising from and inserting onto the femur
424 was 80%. Inter-individual variability in the limb of the force-length curve used
425 for a given muscle could also arise in vivo due to small variations in $L_{TR} : L_{F.OPT}$.
426 Variability in $L_{TR} : L_{F.OPT}$ would mean that muscle-tendon complex lengths at a
427 given joint angle may be similar between individuals but that differences in the

428 expressed section could occur due to inter-individual differences in the tendon
429 length or in the muscle fibre length at a given joint position. Different muscle
430 fibre lengths at a given joint angle could occur in different subjects as a result of
431 the addition or removal of sarcomeres. Evidence from animal studies (Lynn et
432 al., 1998) and human studies (Brockett et al., 2001) show such changes in
433 sarcomere numbers are possible.

434

435 Most models used in biomechanical analyses are of the phenomenological
436 'lumped single sarcomere' type used here. The intention of this study was to
437 discover the broad principles concerning the expression of the force-length
438 relationship when considering the behaviour of the muscle-tendon complex as a
439 whole. However, a complex three dimensional muscle architecture may be
440 seen in vivo (Huijing, 1998) that may introduce subtleties that cannot be
441 represented by the more simple model used here. For example, variability in
442 the curvature and length of individual fascicles can cause fascicle strains that
443 are not uniform throughout the muscle (Blemker et al., 2005). Nevertheless,
444 very few biomechanical models have attempted to include such detail and
445 indeed it may be that the amount of inter-individual variation in muscle
446 architecture when considered at this level prevents the drawing of general
447 conclusions about muscle-tendon complex behaviour in vivo.

448

449 A second consideration is that the model parameters are inter-related and this
450 means that changes in one parameter can affect the value of other parameters.
451 For example, when an elastic tendon is assumed (c equal to or greater than

452 0.01) then the absolute length change at maximum isometric force will depend
453 on the value of $L_{TR} : L_{F.OPT}$ since a long tendon extending by say 6% will extend
454 more than a short tendon extending by 6%. For this reason an inextensible
455 tendon was sometimes assumed when varying the other model parameters in
456 order to make clearer the effect of the parameter under investigation.

457

458 Some aspects of the generalised muscle model used here have been simplified
459 in order to allow a more straightforward examination of the parameters
460 considered. For example, non-linearity in the tendon length-extension
461 relationship was not modelled, similarly the model did not include a parallel
462 elastic component. Under maximal activation for most of the results the forces
463 are likely to be high enough for the non-linear toe region of the tendon length-
464 extension relationship not to have an effect. Some simulations do show
465 expressed sections that encompass the limits of the force-length relationship
466 where the forces would be low and the toe region may be expected to apply.
467 However, these results are included to illustrate the proportion of the force-
468 length relationship used. It may be anticipated that in vivo the expressed
469 section is actually shifted so that the limits of the force-length relationship would
470 not be reached for physiological joint ranges of motion. A parallel elastic
471 component could affect the load placed on the tendon, and therefore tendon
472 stretch, and may also affect the muscle fibre excursion. Both of these effects
473 would be joint angle dependent. Future work will address the influence of
474 additional more complex architectural features on the expression of the force-
475 length relationship.

476

477 The findings from this study allow some predictions to be made about the
478 amount of variability that may be expected in vivo for the five muscles
479 considered as sources for the range of parameter values considered. The short
480 head of the biceps femoris has a high value of 4.39 for $L_{F.OPT} : r$ and a low
481 value of 0.52 for $L_{TR} : L_{F.OPT}$ (Table 1), meaning that this muscle is likely to
482 operate entirely over the plateau region or one of the limbs of the force-length
483 relationship (Figure 9).

484

485 The value of $L_{TR} : L_{F.OPT}$ for SOL is high, and the value of $L_{F.OPT} : r$ is low, which
486 would indicate that most of the force-length relationship would be used.

487 However, there is a fairly high amount of variability in the values reported for
488 $L_{F.OPT} : r$ by Maganaris et al. (2006). For subjects at the lower end of the range
489 with a value of 0.5 for $L_{F.OPT} : r$ the maximum joint range of motion that would
490 be allowed by the force-length relationship assuming the width of the force-
491 length relationship is 0.56 would be 0.56 radians or 32 degrees according to
492 Equation 12. At the other end of the range, a subject with a value of 1.5 for
493 $L_{F.OPT} : r$, assuming an ankle joint range of motion of 60 degrees, would use
494 only 62% of the force-length relationship (these values are used for the soleus
495 in Figure 9). One of the problems with modelling the soleus is that pennate
496 muscle fibres have a long aponeurosis. The length of this aponeurosis is
497 included in the estimate of the tendon resting length given by Hoy et al. (1990),
498 yet the fact that the muscle belly extends along the series elastic component

499 instead of sitting on top reduces the effective value of $L_{TR} : L_{F.OPT}$. This would
500 mean that SOL would be likely to operate over only part of the force-length
501 relationship for most of the values of $L_{F.OPT} : r$ quoted by Maganaris et al.
502 (2006) (Figure 9). Whether the muscle operates over the ascending or
503 descending limb would be affected by the values of θ and c . Magnusson et al.
504 (2001) report values of 0.044 - 0.056 for c . Increasing tendon compliance
505 would shift the expressed section of the force-length relationship to shorter
506 lengths as is shown in Figure 9. Given the long Achilles tendon and its
507 relatively high strain value it would be expected that the majority of individuals
508 would operate over the ascending limb. Nevertheless, Figures 6 and 7
509 demonstrate that it is possible that individuals with long SOL muscle bellies, and
510 therefore lower effective values of $L_{TR} : L_{F.OPT}$, and tendons at the stiffer end of
511 the range could still use the descending limb.

512

513 The muscles ECRB, BR, and VL have intermediate values for $L_{F.OPT} : r$ and
514 $L_{TR} : L_{F.OPT}$, low tendon compliance and low to intermediate pennation angles
515 making it likely that these muscles operate over one limb or only the plateau
516 region of the force-length relationship. Lieber & Friden (1998) measured ECRB
517 sarcomere lengths using laser diffraction and muscle fibre lengths at different
518 joint angles, and calculated from results averaged across 12 subjects that, in
519 agreement with the present findings, the ECRB operated over only one limb of
520 the force-length relationship: the descending limb.

521

522 There are several implications of the finding that some muscles may operate
523 over different limbs of the force-length relationship in different subjects, but that
524 other muscles may not demonstrate variability. When using muscle models in
525 forward dynamics simulations of movement, researchers often use parameter
526 values taken from the literature. These may result in the modelled muscle
527 operating over one or other of the limbs of the force-length relationship.
528 However, in some muscles such as the brachialis the muscle could theoretically
529 operate over either limb or the plateau depending on the subject specific
530 anatomical features of the muscle-tendon complex. This implies that when
531 using Hill-type muscle models it would be sensible to consider whether the
532 muscles could potentially operate over different limbs since this may change the
533 optimal solution.

534

535 A second implication arises from the finding that some muscles may exhibit
536 sport-specific or functional specialisations, for example Herzog et al. (1991b)
537 and Savelberg and Meijer (2003). These studies showed that the expressed
538 section of the force-length relationship was different for runners and cyclists,
539 such that cyclists tended to be stronger at short rectus femoris lengths (i.e., they
540 exhibited a negative gradient to the force-length curve indicating that they
541 operated over the descending limb), whereas the runners were stronger at
542 longer rectus femoris lengths (i.e., they exhibited a positive gradient to the
543 force-length curve indicating that they operated over the ascending limb). It is
544 not known whether this specialisation arises from genetically controlled factors
545 such as tendon length, which would affect the ratio of tendon slack length to

546 fibre optimum length, or whether it arises from training induced adaptations
547 such as the addition or removal of sarcomeres to change the muscle fibre
548 optimum length or changes in tendon stiffness. Nevertheless, it would seem
549 that for muscles such as the soleus where the values of the $L_{F.OPT} : r$ and
550 $L_{TR} : L_{F.OPT}$ and c found for this muscle in vivo, that the scope for such
551 specialisation is limited. Conversely, for a muscle such as brachialis, with its
552 typically more moderate values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ and c , there would
553 be more scope for specialisation in which limb of the force-length relationship is
554 used.

555

556 Finally, the expression of the force-length relationship has implications for the
557 motor control of movement. For example, the equilibrium point hypothesis (e.g.
558 Feldman and Latash, 2005) relies on the assumption that muscle force
559 increases with muscle length, i.e. that all muscles work on the ascending limb of
560 the force-length relationship. However, the present results suggest some
561 muscles use the whole of the force-length relationship whereas others use only
562 the plateau region. Inter-subject differences in the expression of the force-
563 length relationship should also be considered when training or rehabilitating
564 muscle (Savelberg and Meijer, 2003), and when identifying candidates for
565 surgical procedures (Orendurff et al., 2002).

566

567 In conclusion, the values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ seem important in
568 determining the likely inter-individual variability in the expressed section of the
569 force-length relationship. High values of $L_{F.OPT} : r$ and low values of $L_{TR} : L_{F.OPT}$

570 result in a muscle that operates over the plateau section. Low values of
571 $L_{F.OPT} : r$ and high values of $L_{TR} : L_{F.OPT}$ result in a muscle that uses the whole
572 of the force-length relationship. Intermediate values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$
573 allow a muscle to operate over one or other limb of the force-length relationship.
574 Whether this is likely to be the ascending limb or the descending limb is then
575 determined by the exact values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ and the values of
576 the remaining parameters: ϕ , θ and c . It appears on the basis of values
577 reported for these parameters in the literature that there is scope for inter-
578 individual variation in the values of these parameters for different human
579 muscles, and that some inter-individual variability in the expressed section of
580 the force-length relationship is possible, particularly for muscles with
581 intermediate values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$.

FIGURES

Figure 1: The essential elements of the muscle model, including the A) series elastic component, B) force-length properties, and C) overall model structure. Where F_M – force produced by the muscle fibres, q - current active state of muscle ($0 \leq q \leq 1$), F_{MAX} - maximum isometric force possible by muscle, $F_L(L_F)$ - fraction of maximum isometric force muscle can produce at current length (L_F), L_T - the current length of the tendon, L_{TR} - the resting length of the tendon, c - extension of tendon at F_{MAX} expressed as fraction of tendon resting length, $L_{F.OPT}$ - optimum length of muscle fibre, w - parameter indicating width of force-length curve, T – thickness of muscle, L_{MT} – length of muscle-tendon complex, θ – pennation angle, and F_T is the force in the tendon.

Figure 2: The effect of varying ratio of optimum fibre length to moment arm length ($L_{F.OPT} : r$) for a moment arm that is constant through the range of motion.

Figure 3: The effect of varying the ratio $L_{TR} : L_{F.OPT}$ with ϕ equal to 75 degrees and $L_{F.OPT} : r$ equal to a) three, and b) five.

Figure 4: The effect of varying the ratio $L_{TR} : L_{F.OPT}$ with ϕ equal to 15 degrees and $L_{F.OPT} : r$ equal to a) three, and b) five.

Figure 5: The effect of varying the ϕ parameter throughout the range of motion. The ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ were set to 3, c and θ were set to zero.

Figure 6: The effect of varying tendon extension at maximum isometric force (c) from 0 to 0.08 for a muscle with ϕ set to 45 degrees. The ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ were set to 3, and θ was set to zero.

Figure 7: The effect of varying tendon extension at maximum isometric force (c) from 0 to 0.08 for a muscle with ϕ set to 0 degrees. The ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ were set to 3, and θ was set to zero.

Figure 8: The effect of muscle fibre pennation angle (θ) with the ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ set at 3, c set at 0 and ϕ set at a) 75 degrees, and b) 15 degrees.

Figure 9: The values from Table 1 for soleus and short head (SH) of biceps femoris have been used to plot the predicted expressed section of the force-length relationship. A range of motion of 60 degrees has been used for the soleus and 120 degrees for the short head of biceps femoris. The ϕ parameter for both muscles has been set at the mid-point of the range of motion, but the expressed section is shifted for the soleus due to its longer, more compliant tendon.

TABLES

Table 1: Model parameter values for the soleus (SOL), vastus lateralis (VL), short head of the biceps femoris (SH BF), brachialis (BR) and extensor carpi radialis brevis (ECRB).

Table 2: Values of fixed parameters and range of values used for the parameter under investigation for each simulation reported.

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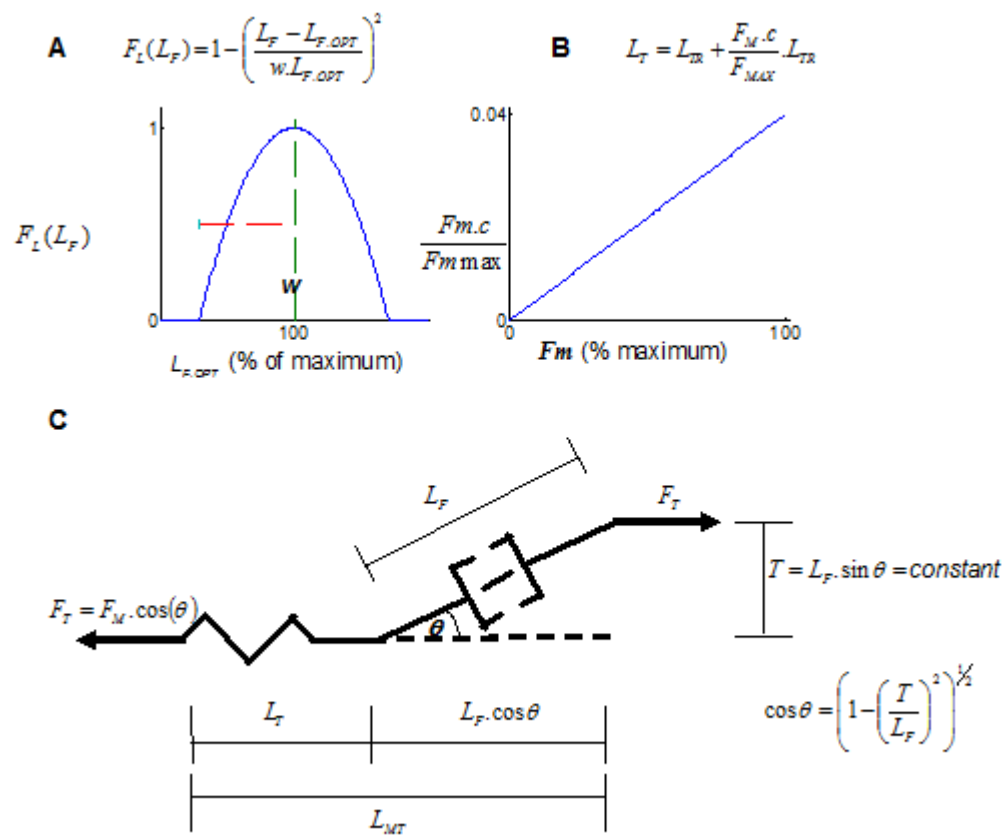
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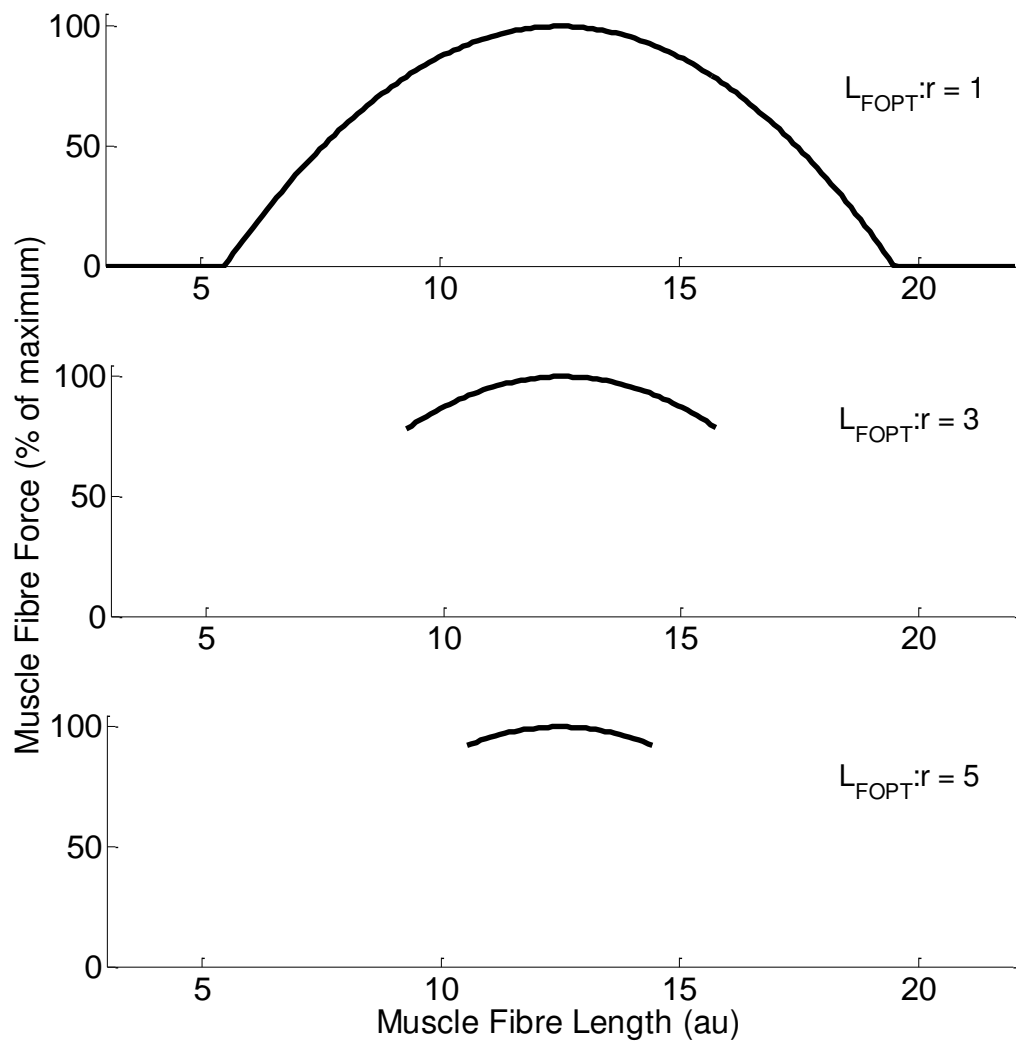
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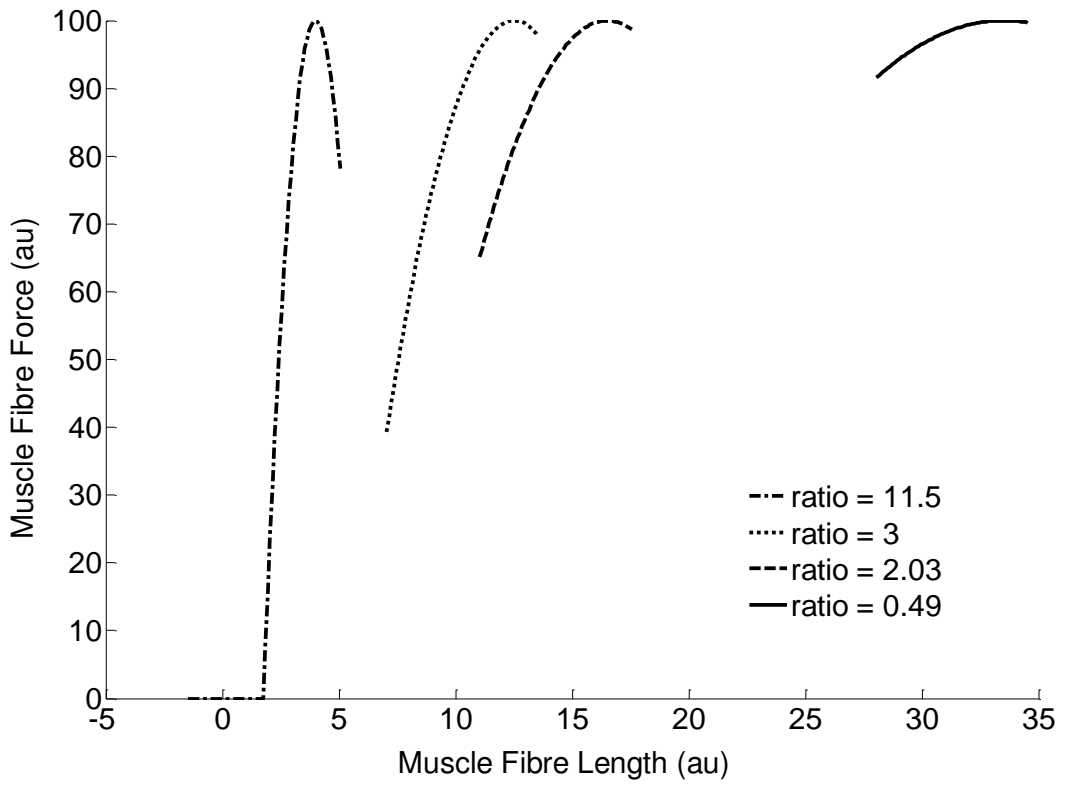
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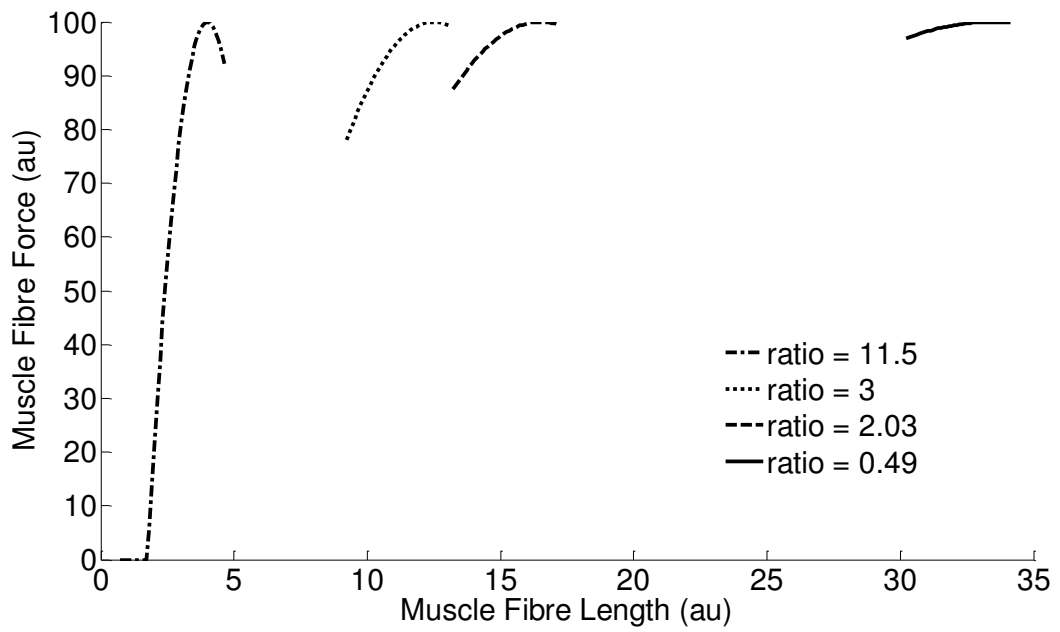




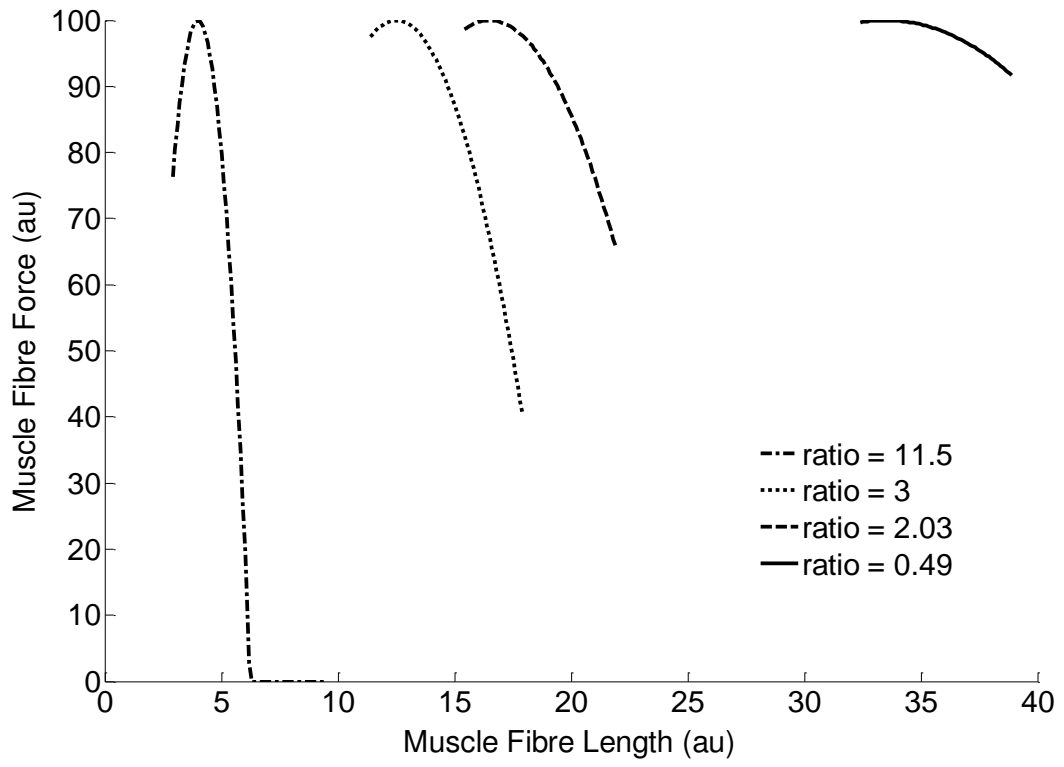
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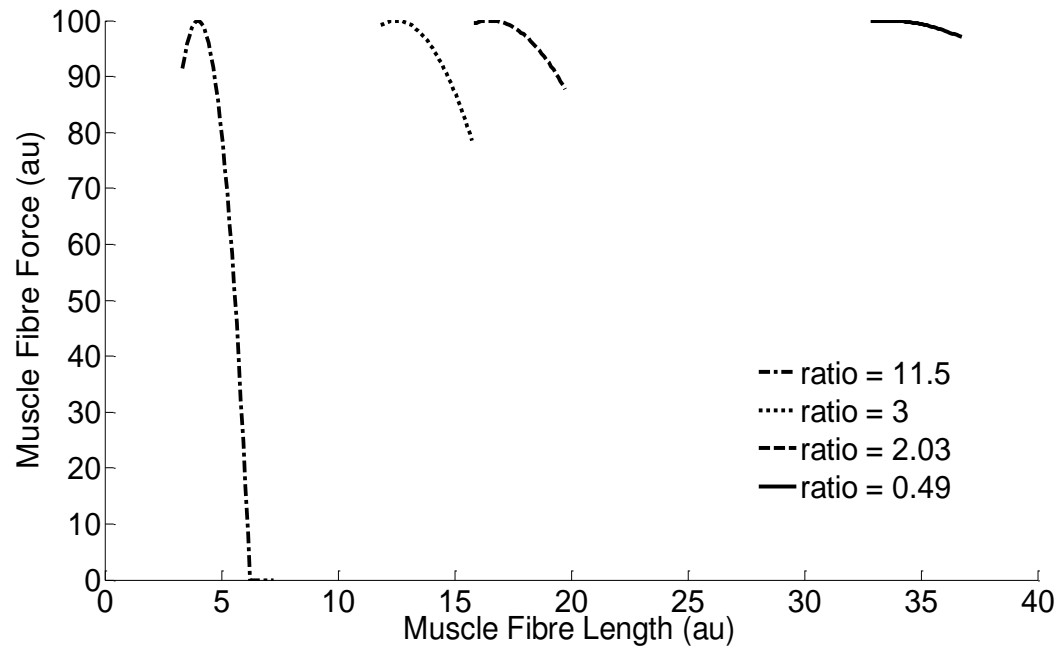
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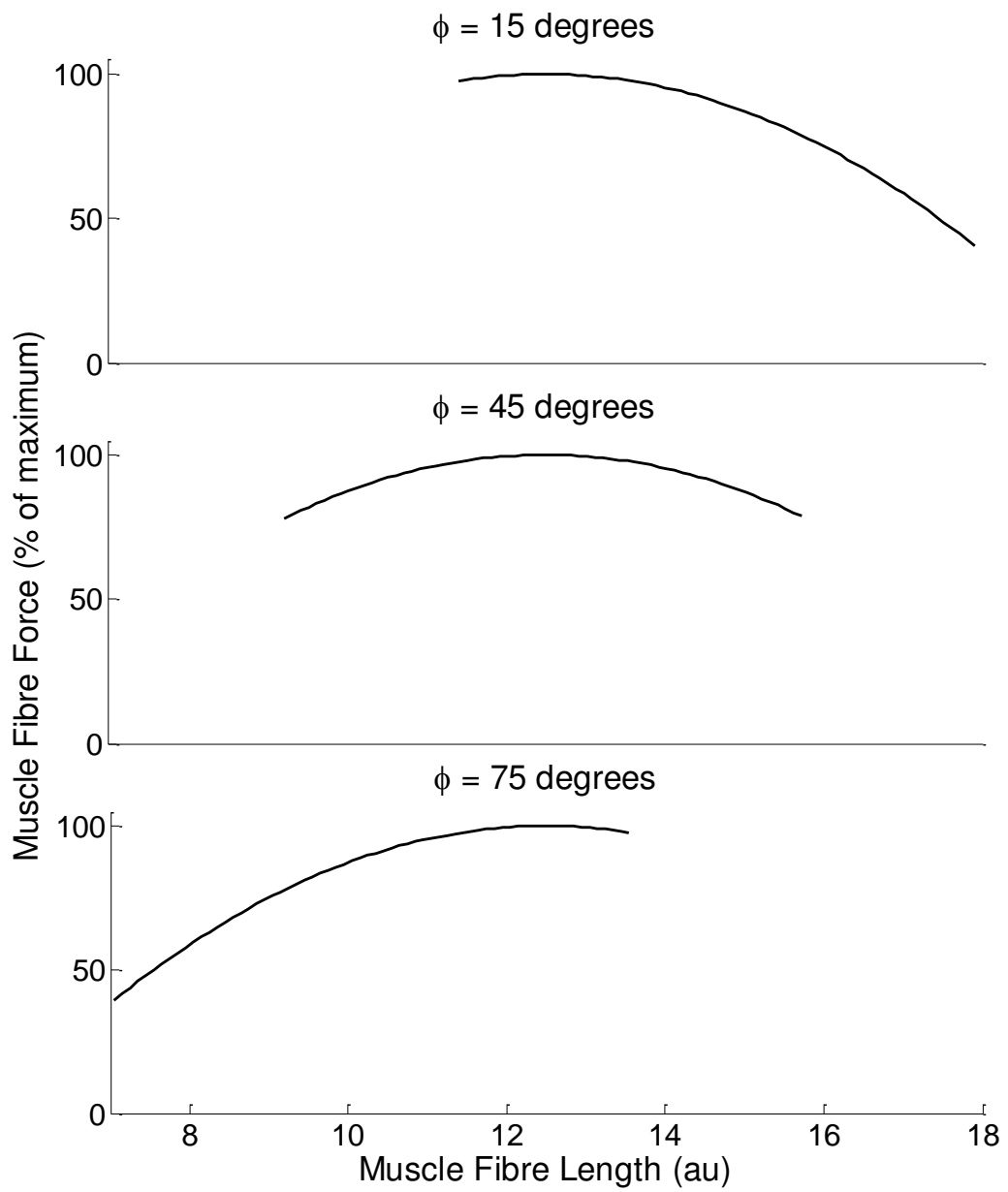


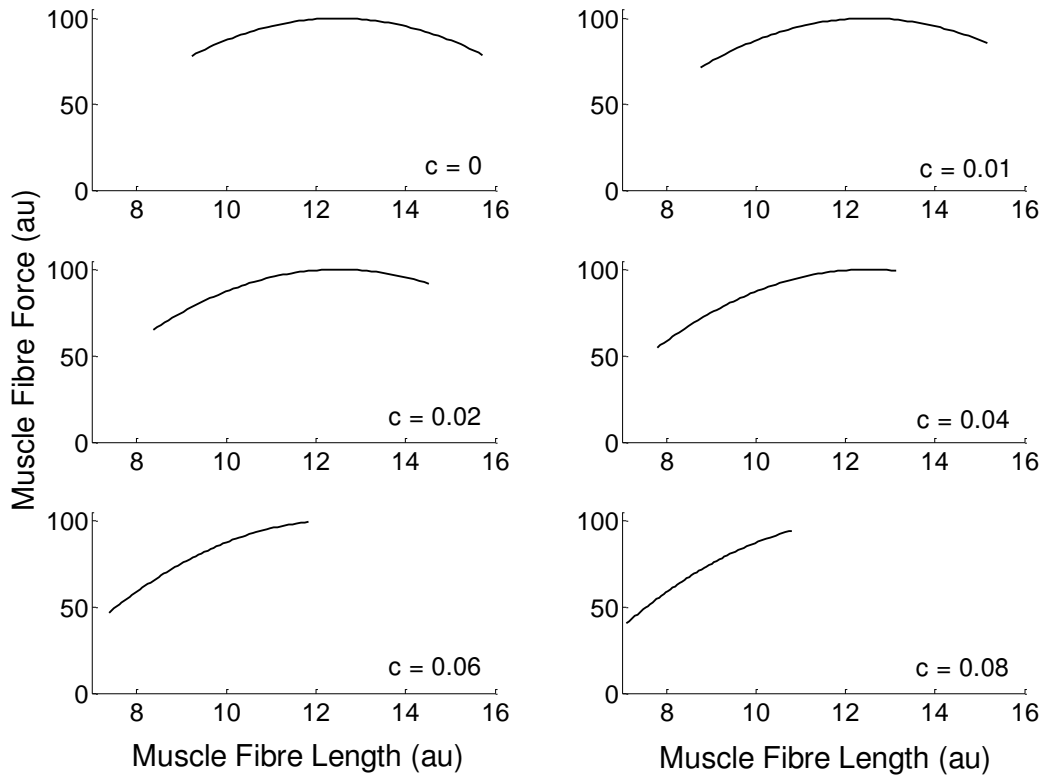
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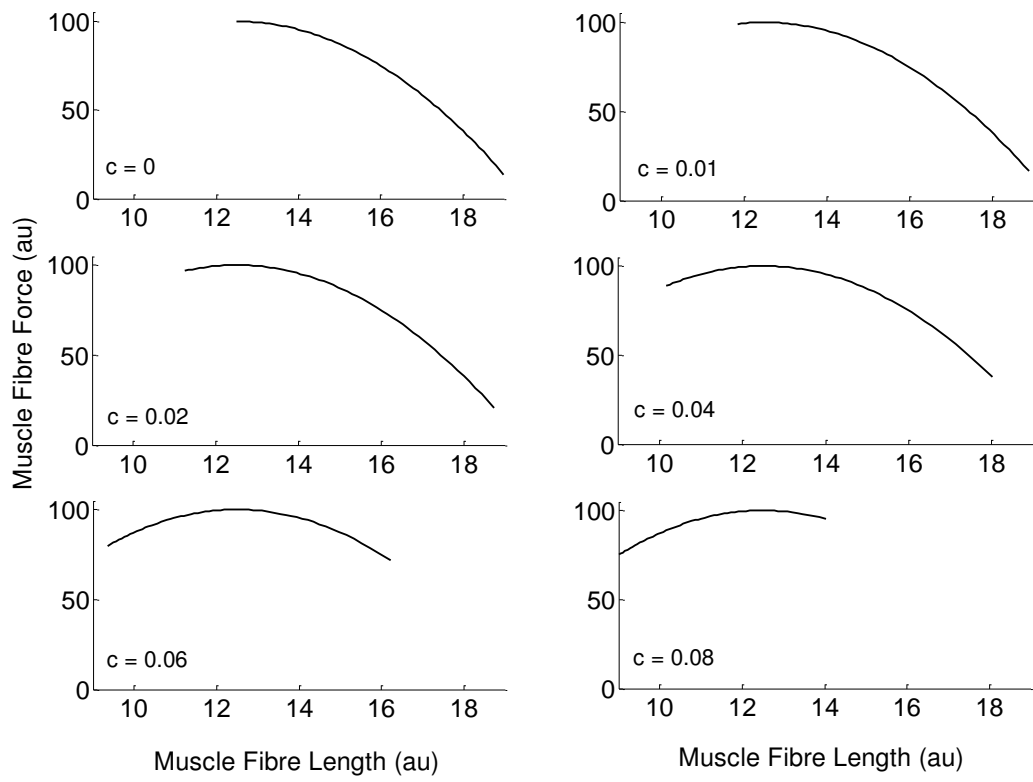


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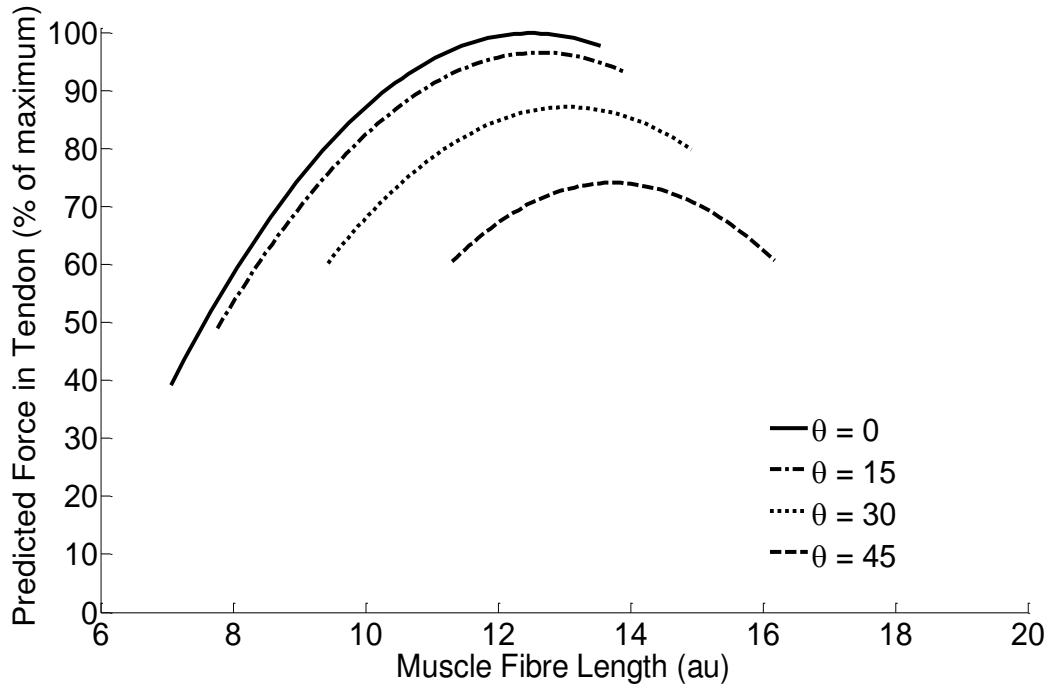




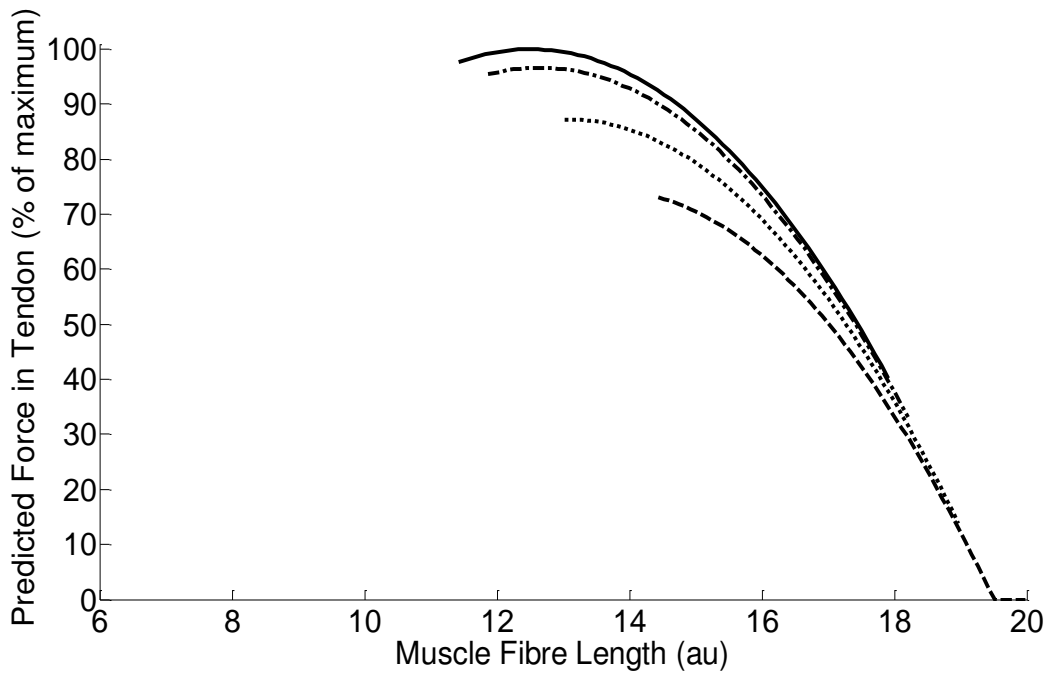




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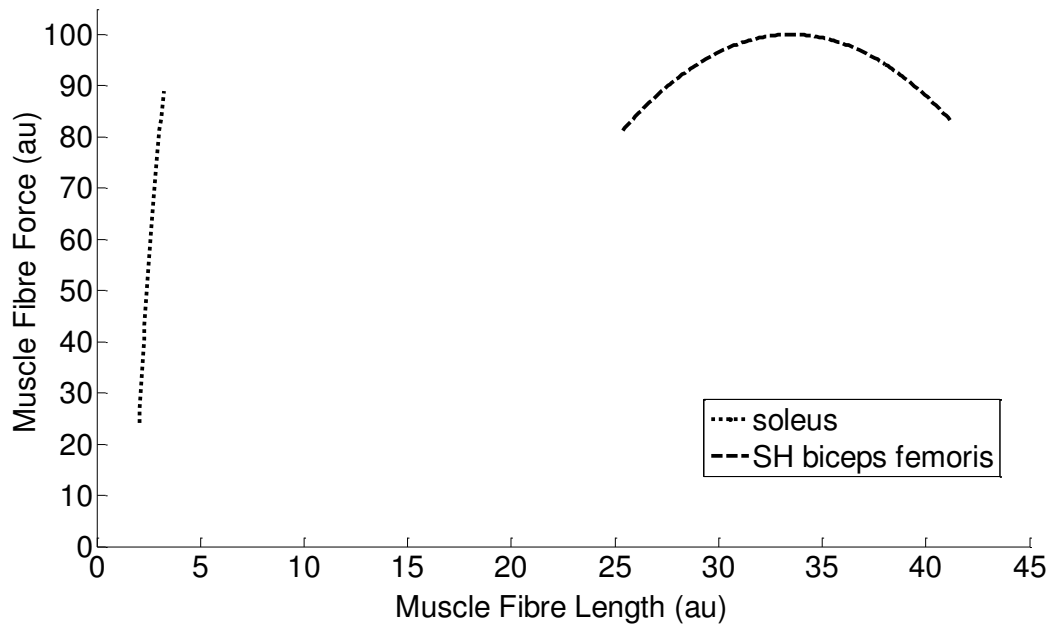


Table 1: Model parameter values for the soleus (SOL), vastus lateralis (VL), short head of the biceps femoris (SH BF), brachialis (BR) and extensor carpi radialis brevis (ECRB).

Parameter	Muscle	Range of parameter values used	Sources from which range of parameter values were taken
θ (degrees)	SOL	9-35	Morse et al. (2005)
	VL	7-33	Kawakami et al. (2006)
	SH BF	0 - 25	Alexander and Vernon (1975) & Wickiewicz et al. (1983)
	BR	6.5-12.9	Herbert and Gandevia (1995)
	ECRB	5-13	Lieber et al. (1990)
c	SOL	0.044 – 0.056	Magnusson et al. (2001)
	VL	0.01	Wickiewicz et al. (1983) & Pierrynowski & Morrison (1985)
	SH BF	0.01 – 0.02	Wickiewicz et al. (1983) & Pierrynowski & Morrison (1985)
	ECRB	0.0199	Loren & Lieber (1995)
$L_{TR}/L_{F.OPT}$	SOL	11.25	Hoy et al. (1990)
	VL	2.68	Hoy et al. (1990)
	SH BF	0.52	Hoy et al (1990)
	BR	3.0 5.87	Winters and Stark (1988) Garner and Pandy (2003)
	ECRB	2.89	Loren et al. (1996)
$L_{F.OPT}/r$	SOL	0.5-1.5	Maganaris et al. (2006)
	VL	1.5-2.4	Maganaris et al. (2006)
	SH BF	4.39	Hoy et al. (1990)
	BR	1.6-7.56	Ettema et al. (1998) & Garner & Pandy (2003)
	ECRB	3.62	Loren et al. (1996)

Table 2: Values of fixed parameters and range of values used for the parameter under investigation for each simulation reported.

Parameter varied	Relevant figures	Values used				
		$L_{F.OPT} : r$	$L_{TR} : L_{F.OPT}$	ϕ (degrees)	c	θ (degrees)
$L_{F.OPT} : r$	Figure 2	Varied from 0.5 to 5	3.0	45	0.04	0
$L_{TR} : L_{F.OPT}$	Figures 3 and 4	3 and 5	Varied from 0.49 to 11.5	15	0	0
ϕ	Figure 5	2	3	0 to 90 in steps of 15 degrees	0	0
c	Figures 6 and 7	3	3	45 and 0	Varied from 0 to 0.08	0
θ	Figure 8	3	3	15 and 75	0	0 to 45 degrees