

1           **Original Article**

2           **The mechanics of agonistic muscles**

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20           **Abstract:**

21           **Introduction:** In this study, we tested two assumptions that have been made in  
22 experimental studies on muscle mechanics: (i) that the torque-angle properties are similar  
23 among agonistic muscles crossing a joint, and (ii) that the sum of the torque capacity of  
24 individual muscles adds up to the torque capacity of the agonist group. **Methods:** Maximum  
25 isometric torque measurements were made using a specifically designed animal knee  
26 extension dynamometer for the intact rabbit quadriceps muscles (n = 10) for knee angles  
27 between 60 and 120 degrees. The nerve branches of the vastus lateralis (VL), vastus medialis  
28 (VM) and rectus femoris (RF) muscles were carefully dissected, and a custom made nerve  
29 cuff electrode was implanted on each branch. Knee extensor torques were measured for four  
30 maximal activation conditions at each knee angle: VL activation, VM activation, RF  
31 activation, and activation of all three muscles together. **Results:** With the exception of VL,  
32 the torque-angle relationships of the individual muscles did not have the shape of the torque-  
33 angle relationship obtained when all muscles were activated simultaneously. Furthermore, the  
34 maximum torque capacity obtained by adding the individual torque capacities of VL, VM and  
35 RF was approximately 20% higher than the torques produced when the three muscles were  
36 activated simultaneously. **Discussion:** These results bring into question our understanding of  
37 in-vivo muscle contraction and challenge assumptions that are sometimes made in human and  
38 animal muscle force analyses.

39           **Key words:** intermuscular pressure, torque-angle relationship, force-length  
40 relationship, muscle function, muscle properties, intermuscular force transmission, muscle  
41 coordination, distribution problem, muscle redundancy, quadriceps femoris

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45           The mechanics of agonistic muscles

46           When analyzing the mechanics of agonistic muscles crossing a joint, some basic and  
47 simplifying assumptions are often made implicitly, especially in experimental studies. These  
48 include that: (i) the torque-angle properties of agonistic muscles crossing a joint are similar in  
49 shape, and (ii) that the sum of the torque capacity of individual muscles adds up to the torque  
50 capacity of the agonist group. Despite the appeal of these assumptions, and their use in the  
51 literature, their validity remains unknown (Epstein and Herzog, 1998; Herzog, 2017;  
52 Sandercock and Maas, 2009; Tijs et al., 2014).

53           Regarding the first assumption, the relative contribution of each agonist muscle to the  
54 total muscle group torque is often thought to be independent of joint angle in experimental  
55 studies. Force contributions are primarily calculated based on a muscle's physiological cross-  
56 sectional area (e.g., de Brito Fontana et al., 2014; Finni et al., 2003; Ichinose et al., 2000,  
57 1997; Ishikawa et al., 2003; Kawakami et al., 1998). However, there are multiple factors that  
58 may influence the contribution of a muscle to the maximum isometric torque at a given joint  
59 angle, for example: the force-length relationship, the length-dependent activation, and the  
60 relationship between changes in joint angle, muscle tendon unit length and fascicle length  
61 (Gordon et al., 1966; Lieber and Fridén, 2000; Lutz and Rome, 1994; Rassier et al., 1999;  
62 Vaz et al., 2012). These factors may change differently for the individual muscles comprised  
63 in an agonistic group, thereby affecting the torque potential of a muscle relative to the torque  
64 potential of the agonistic group.

65           On the other hand, in theoretical models of the human musculoskeletal system,  
66 physical and biological parameters, such as muscles' anatomy, fascicle lengths, tendon slack  
67 lengths, and electromyographic activity, are often used to account for differences in the force-  
68 length properties of individual muscles during forward simulations and inverse dynamics  
69 approaches (Delp et al., 1990; Erdemir et al., 2007; Fidelus, 1969; Hatze, 1977; Hoy et al.,

70 1990). Although neuromusculoskeletal modeling and simulation has proliferated in the  
71 biomechanics research community over the past 25 years, there is still a lack of verification  
72 and validation standards, and experimental data regarding individual agonistic muscle  
73 properties are necessary for proper calibration and validation of models (Hicks et al., 2015).

74         Regarding the second assumption, it is important to consider that muscles are, in their  
75 natural anatomical situation, intimately interconnected and packed within connective tissues,  
76 such as the epimysium and fascia (Maas and Sandercock, 2010; Purslow, 2008). Upon  
77 contraction, muscles deform and exert pressure on each other. These deformations for a given  
78 muscle may depend on the activation and force produced by the other muscles within the  
79 anatomic confines of an agonistic group and may, in turn, affect the force potential of  
80 muscles (Maas and Sandercock, 2010; Purslow, 2010; Raiteri et al., 2016; Reinhardt et al.,  
81 2016). Since muscle properties are typically evaluated in maximally activated muscles, it  
82 seems relevant that these interactions are also evaluated in the fully active state. During  
83 submaximal contractions, inter-muscular pressures are likely low and may not be sufficient to  
84 affect force generating potential of individual muscles (Tijs et al., 2014).

85         If indeed the torque generating potential of a muscle stimulated in isolation is  
86 different from that of the same muscle when activated simultaneously with the muscles of its  
87 agonistic group, then the resulting discrepancy may need to be accounted for in experimental  
88 and theoretical studies of human movement. While great advances have been made in our  
89 comprehension of muscle properties in isolated muscles, fibres, myofibrils, and sarcomeres  
90 (Abbott and Aubert, 1952; Edman et al., 1982; Gordon et al., 1966; Hill, 1938; Joumaa and  
91 Herzog, 2010; Leonard et al., 2010; Rack and Westbury, 1969; Rassier and Herzog, 2004),  
92 our understanding of muscle properties and functions of individual muscles within their  
93 agonistic group remains limited (Jarc et al., 2013; Maas and Sandercock, 2010; Tijs et al.,  
94 2014).

95           The purpose of this study was to analyze systematically the torque-angle relationship  
96 of muscles within an agonistic group. Specifically, we tested two hypotheses related to the  
97 assumptions introduced above: i) that the torque-angle curves of all muscles (normalized to  
98 their peak torque) are similar, and ii) that the sum of the isometric torque capacity of the  
99 individual agonist muscles activated in isolation adds up to the torque capacity of the entire  
100 group activated simultaneously. These hypotheses were tested for the specific case of the  
101 rabbit knee extensor muscles where we used individual nerve stimulation of the vastus  
102 lateralis (VL), vastus medialis (VM) and rectus femoris (RF) muscles in isolation or in  
103 combination of all three.

#### 104 **Methods**

105           Experiments were performed on the right quadriceps muscles of 10 skeletally mature  
106 New-Zealand white female rabbits (average mass 4.0 kg; range 3.0 - 5.4 kg, Covance Inc.,  
107 headquartered in Princeton, NJ, US). Approval for all procedures was obtained from the  
108 University's Animal Ethics Committee.

109           Rabbits were tranquilized with 1ml/kg Atravet (25 mg/ml; Vetoquionol NA. Inc.,  
110 Lavaltrie, QC, Canada) and held under anesthesia with a 2 % isoflurane/oxygen mixture.  
111 After the experiment, animals were euthanized with an overdose injection of Euthanyl (MTC  
112 Pharmaceuticals; Cambridge, ON, Canada) into the lateral ear vein.

113           The branches of the femoral nerve responsible for the innervation of VL, VM, and RF  
114 were carefully dissected. One custom nerve cuff electrode was placed on each of the three  
115 branches, allowing for electrical stimulation of the three muscles individually or together.  
116 Then, Kwik-Cast (World Precision Instruments, Saraota FL, USA) was injected around the  
117 nerve cuffs. Rabbits were fixed supine in a stereotaxic frame (Sawatsky et al., 2012) with the  
118 pelvis and femoral epicondyles pinned to keep the hip angle at 130-140° (180°, full extension  
119 of the hip) and to stabilize the proximal segment of the knee. The knee center of rotation

120 (lateral epicondyle) was carefully aligned with the rotational axis of a servomotor (Parker  
121 Hannifin Corporation, Irwin, PA, USA) which controlled (Motion Planner, Rohnert Park,  
122 CA, USA) the angle of the tibia in relation to the femur. Passive knee flexion and extension  
123 was performed to verify that the servomotor and knee joint axes remained aligned throughout  
124 the entire range of motion tested. Knee joint moments were acquired using Windaq data  
125 collection software (Dataq Instruments, Akron) and a customized MATLAB program (The  
126 MathWorks, Natick, MA, USA) (Leumann et al., 2015). Stimulation of the nerves was given  
127 through a dual output stimulator (Grass S8800, Astro/Med Inc., Longueuil, QC, Canada),  
128 which was synchronized with the servomotor. Torque-angle curves of the quadriceps group  
129 and the individual quadriceps muscles were obtained for knee angles ranging between 60 to  
130 120 degrees (0°, full extension of the knee). Kinematic analysis of rabbits hopping in  
131 unrelated experiments indicated that this range reflects the primary functional range of the  
132 knee.

133         There were four experimental conditions for each knee angle: VL activation alone,  
134 VM activation alone, RF activation alone, and activation of all three muscles together. Nerve  
135 stimulation was performed at a frequency of 100 Hz, using rectangular 0.1 ms pulses for 500  
136 ms. The stimulation current was set at twice the level that was found to produce maximal  
137 forces to ensure recruitment of all motor units of the quadriceps muscle group. A pause of 2  
138 min was given between tests. Fatigue throughout the protocol was assessed by repeating the  
139 first torque measurement at the end of all testing. For three of the ten animals, contractions  
140 were performed for every 10° knee angle, while for the remaining animals, measurements  
141 were made every 20° and polynomial interpolation was used to estimate the data points at the  
142 intermediate knee angles.

143 The total knee extensor torque for the entire muscle group was calculated by adding  
144 the torques produced by VL, VM and RF when stimulated in isolation (SUM), and this torque  
145 was compared to that obtained when all muscles were activated simultaneously (ALL).

146 Normal distribution of the data was confirmed through Shapiro-Wilk testing. Two 2-  
147 factor (*condition* x joint angle) repeated measures ANOVA were used for analysis. The first  
148 was used to test differences between muscles (VL, VM, RF, and entire group) for the  
149 normalized joint torques across knee angles and the second was used to test for differences  
150 between the sum of the individual muscle torques (SUM) and the torques produced when all  
151 muscles were stimulated simultaneously (ALL).

## 152 **Results**

153 There was a significant interaction ( $p < 0.001$ ) between joint angle and muscle (VL,  
154 RF, VM, and ALL) for the normalized torques, indicating that the shape of the torque-angle  
155 relationship differed among muscles/group (Figure 1). VL and the agonist group  
156 (simultaneous stimulation of all muscles - ALL) worked primarily on an ascending slope and  
157 a plateau of their respective torque-angle relationships, reaching peak torque values at a knee  
158 angle of  $100^\circ$ . VM worked almost exclusively on an ascending torque-angle region (peak  
159 torque at  $110\text{-}120^\circ$ ), and RF had a substantial portion of its torque-angle relationship on a  
160 descending slope, reaching its peak torque at  $90^\circ$ .

## 161 **Figure 1**

162 The sum of the maximum torque capacity for the isolated stimulation of VL, VM and  
163 RF was approximately 20% higher than the maximum torque capacity for simultaneous  
164 stimulation of all muscles of the agonist group ( $p < 0.001$ ) and for all joint angles ( $p = 0.997$   
165 for interaction between effects) (Figure 2). Confidence intervals of the mean (95%), averaged  
166 across joint angles, indicated a minimum and maximum decrease in agonist group torque  
167 capacity of 7% and 39%, respectively, when muscles were activated simultaneously (ALL)

168 compared to when the torques were summed from the stimulation of the individual muscles  
169 (SUM).

170 **Figure 2**

171 **Discussion**

172 In this study, we analyzed the mechanics of VL, VM and RF when activated  
173 individually and simultaneously in a rabbit model. Two assumptions that are sometimes made  
174 implicitly in experimental and/or modeling studies were tested and shown to be incorrect.  
175 Specifically, we observed in a rabbit model that (i) the relative contributions of individual  
176 quadriceps muscles to the total knee joint torque are not constant across joint angles and that  
177 (ii) the torque production capacity of the quadriceps muscles as a group is substantially lower  
178 than the sum of the torque capacities of the individual muscles.

179 With the exception of VL, the individual quadriceps muscle torque-angle  
180 relationships did not represent the same shape as the torque-angle relationship of all muscles  
181 combined. This finding may suggest that torque estimates for individual muscles from the  
182 resultant knee extensor torque, as is often done in human studies (de Brito Fontana et al.,  
183 2014; Finni et al., 2003; Ichinose et al., 2000, 1997; Ishikawa et al., 2003; Kawakami et al.,  
184 1998), are likely best for VL in the rabbit. For VM and RF, the maximum torque capacity  
185 would likely be overestimated at short and long muscle lengths, respectively. The potential of  
186 VM to contribute to the total quadriceps torque increases as the knee is flexed from 60 to 120  
187 degrees, while the torque generating capacity of RF reaches its maximum at 90° and then  
188 decreases substantially more than the resultant knee extensor torque with increasing knee  
189 flexion angles. Of course, the torque-angle relationship of RF (a two joint muscle crossing the  
190 knee and hip) crucially depends on the hip angle, which was kept constant at ~140° in this  
191 study.



192           Since we did not measure muscle parameters that might help predict the force  
193   generating potential, such as fascicle/fiber length of the individual muscles for the different  
194   contractile conditions, it is not possible to explain with certainty the different responses of  
195   muscles to changes in joint angle. At the fascicle, fiber or myofibril level, a change in the  
196   active, isometric force potential is explained by the amount of overlap between actin and  
197   myosin filaments (Gordon et al., 1966). Therefore, the shape of the force-length relationship  
198   at these levels of organization depends on the number of serial sarcomeres and the sarcomere  
199   length change for a given fascicle/fiber excursion (Rassier et al., 1999; Vaz et al., 2012).

200           Lieber et al. (1989) showed that ex-vivo sarcomere lengths are similar across the  
201   individual quadriceps muscles, while the fascicle length of VL is about 70-80% longer than  
202   those found for VM and RF. This difference in fascicle length, if considered in isolation,  
203   would lead one to anticipate a wide torque-angle relationship for VL and a narrow and  
204   similarly shaped relationship for VM and RF. This prediction is indeed in conceptual  
205   agreement with our findings. However, discrepancies may occur because sarcomere length,  
206   sarcomere elongation and the ratio between fascicle and sarcomere length – an estimate of the  
207   number of sarcomeres in series – are known to vary for different regions within a muscle  
208   (Lichtwark et al., 2017; Llewellyn et al., 2008; Moo et al., 2016; Pappas et al., 2002).  
209   Furthermore, fascicle length changes are not easily related to muscle length changes during  
210   in-vivo contractions. At the muscle level, parameters such as muscle architecture (e.g.  
211   fascicle length, pennation angle), tendon compliance, and moment arm, are known to  
212   influence force and torque capacity at different joint angles (Azizi et al., 2008; de Brito  
213   Fontana and Herzog, 2016; Farris et al., 2015; Hoy et al., 1990; Lieber and Fridén, 2000).  
214   Fascicle length changes may not relate to MTU length changes in a linear manner, and  
215   fascicles are known to shorten (de Brito Fontana and Herzog, 2016; Griffiths, 1991; Ichinose  
216   et al., 1997) and moment arms to change (Tijs et al., 2014; Tsaopoulos et al., 2007) during

217 force production, even if the MTU length/joint angle is kept constant. In addition, changes in  
218 fascicle/sarcomere lengths and moment arms during isometric contractions have been shown  
219 to vary as a function of joint angle (de Brito Fontana and Herzog, 2016; Kawakami and  
220 Lieber, 2000; Tijs et al., 2014; Tsaopoulos et al., 2007; Vaz et al., 2012). All these factors  
221 make it difficult to estimate force-length or torque-angle relationships based on passive  
222 measurements of fascicle and sarcomere lengths at a given muscle length and location within  
223 the muscle.

224 To our knowledge, this is the first study to assess the torque-angle relationships of  
225 individual quadriceps muscles in-vivo through nerve stimulation. At present, there is no  
226 generally accepted method that can be used reliably to calculate or measure the force exerted  
227 by individual muscles in humans (Bey and Derwin, 2012; Fleming et al., 2000; Hicks et al.,  
228 2015). While modeling studies have long worked on muscle specific input parameters to  
229 account for the individual contributions of muscles to joint moments (Crowninshield and  
230 Brand, 1981; Erdemir et al., 2007; Herzog, 1996; Hoy et al., 1990), experimental data in  
231 animal models are necessary to both, understand the current limitations of human  
232 experimental analyses, and to validate and drive future modelling predictions.

233 In this study, we highlight another potential factor that may alter the maximum torque  
234 capacity of a muscle in vivo: the simultaneous contraction of surrounding muscles in an  
235 agonist group. We found an average decrease of 20% in torque capacity when VL, VM and  
236 RF were activated simultaneously compared to when they were activated individually (Figure  
237 2). This result challenges our current understanding of in-vivo muscle contraction, and  
238 violates assumptions that are sometimes made in human and animal movement analyses,  
239 modeling and simulation (e.g. Erdemir et al., 2007; Hardin et al., 2004; Herzog, 2017;  
240 Neptune et al., 2008; Pandy et al., 1990; van Soest and Bobbert, 1993).

241           It appears that there are at least three basic explanations for the loss of torque capacity  
242 when muscles are activated simultaneously: (i) a change in the moment arm; (ii) a change in  
243 the amount of contractile element shortening associated with series elastic element  
244 elongations between the two conditions; and (iii) a loss of longitudinal force due to the lateral  
245 compression that occurs when agonistic muscles contract simultaneously.

246           Regarding changes in moment arms between the two conditions, differences could be  
247 caused by the differences in force production. The SUM torque (Figure 2) is obtained as the  
248 algebraic sum of the torques produced by the individual muscles, thus the knee extensor  
249 forces produced for these conditions are relatively small, while for the ALL torque  
250 conditions, in which the torque is produced by the simultaneous activation of all muscles, the  
251 knee extensor force is great. A decrease in the quadriceps moment arms – resulting from  
252 increased force in the ALL compared to the SUM situation – could explain the differences we  
253 observed in torque capacity. However, we have no evidence for a change in moment arm  
254 with changing knee extensor force in rabbits, and findings from human studies suggest that  
255 quadriceps moment arms actually tend to increase (rather than decrease) with increasing force  
256 (Tsaopoulos et al., 2007).

257           Increased series elastic element elongation in the ALL condition (high forces)  
258 compared to the SUM condition (low forces) could only explain our results if the associated  
259 increase in contractile element shortening – due to differences in total force – was associated  
260 with a decrease in force generating potential. Theoretically, this situation occurs on the  
261 ascending (but not the plateau or descending) limb region of the force-length relationship.  
262 However, in our study, we found that the loss in torque capacity for the ALL compared to the  
263 SUM condition was independent of joint angle, even though this range seems to encompass  
264 the ascending, plateau and descending regions of the force-length relationship (Lieber and

265 Blevins, 1989). This finding appears to discredit the idea about different tendon elongations  
266 as the single or main explanation for the difference in torque capacity between conditions.

267 Our finding of a loss in torque capacity for the ALL compared to the SUM condition  
268 corroborates previous studies showing a reduction in muscle force capacity (5–14%) with  
269 increased transversal loading (Siebert et al., 2016, 2014a, 2014b) in isolated rat medial  
270 gastrocnemius muscles. In addition, Reinhardt et al. (2016) suggested, based on previous  
271 findings on the effect of transversal loading, that intermuscular pressure in the rabbit calf  
272 muscles during maximum contraction may reduce longitudinal muscle forces.

273 The interactions between calf muscles in-vivo have been experimentally investigated  
274 in cats (Perreault et al., 2002) and rats (Tijs et al., 2014). However, in both studies the authors  
275 report that the “non-linear summation of muscle torque”, i.e., the difference between SUM  
276 and ALL, was 3-9% in favor of the condition in which muscles were stimulated in isolation.  
277 In most studies relating individual muscle forces to forces in simultaneously activated muscle  
278 groups, force interactions were investigated with two pathways in mind: (i) force interactions  
279 through a common tendon and myotendinous connections and (ii) epimuscular myofascial  
280 connections. These interactions have been shown to lead to different forces at the origin and  
281 the insertion sites of a given muscle. In general, findings related to epimuscular myofascial  
282 force transmission have led to the understanding that the position of one muscle relative to  
283 the surrounding muscles affects isometric muscle force (Huijing et al., 2003; Maas et al.,  
284 2005, 2001; Maas and Sandercock, 2010; Tijs et al., 2014). In contrast, studies addressing the  
285 possible influence of agonistic activation, and associated intermuscular pressure on the force  
286 generating potential of a given muscle are rare (Sandercock and Maas, 2009), and  
287 measurements in this context have not been made.

288 The small magnitude of force loss during agonistic activation reported in the calf  
289 muscles for rats and cats compared to our findings in the rabbit knee extensors suggests that

290 this force loss may depend on the agonistic muscle group (Perreault et al., 2002; Sandercock  
291 and Maas, 2009; Tijs et al., 2014). However, differences in the experimental conditions may  
292 also account for some of these differences. For example, Tijs et al. (2004) used intramuscular  
293 wire electrodes to stimulate the gastrocnemius muscles, which led to a torque during  
294 contractions that was less than 20% of the maximum torque generating potential of the  
295 muscles. Furthermore, it seems that only selected compartments of the muscles were  
296 activated. This submaximal and incomplete activation may have led to transversal loads  
297 (intermuscular pressures) that were not sufficient to produce a substantial decrease in  
298 longitudinal forces (Siebert et al., 2014b). In addition, in both studies (Perreault et al., 2002;  
299 Tijs et al., 2014), no mention was made regarding the role of the plantaris muscle. Plantaris  
300 is a muscle of considerable size in these animals and is located between the soleus and  
301 gastrocnemius muscles. Since plantaris was not activated, the increase in intermuscular  
302 pressure in the ankle plantar flexor compartment may have been low, and thus, force loss  
303 with simultaneous activation of multiple ankle plantar flexor muscles may have been small.

304 Non-linearity of force summation has also been analyzed in the recruitment of motor  
305 units. Although most findings indicate that the sum of the force produced by individual motor  
306 units within muscles is higher than the force produced by simultaneous contraction of the  
307 corresponding motor units, the opposite result has also been found (Sandercock, 2000;  
308 Troiani et al., 1999). The fact that fibres belonging to different motor units are spread out  
309 within muscles, and are intimately connected to each other by a viscoelastic connective tissue  
310 matrix, is thought to be the main reason for this non-linearity of intramuscular force  
311 summation. In our study, we analyzed intermuscular interactions of individual muscles that  
312 are involved in an anatomical organization that differs substantially from that presented by  
313 individual motor units in a muscle. In addition, motor unit force summation seems to depend  
314 on muscle length (Sandercock, 2000) and fibre type (slow, fast fatigable and fast resistant)

315 (Troiani et al., 1999), factors that do not seem to play a role intermuscularly. There seems to  
316 be little evidence that the loss in torque production in the simultaneous contraction shown  
317 here is related, or shares a similar mechanism, to the non-linearity of motor unit summation  
318 described in the literature.

319         Much of our knowledge on muscle properties and function is based on research on  
320 isolated muscle preparations and experiments involving maximal force capacity. However,  
321 during normal human movement, muscles are surrounded by passive and active structures  
322 that may affect their contractile behavior and associated force capacity. Our results suggest  
323 that indeed the contractile conditions of muscles surrounding an individual muscle affect  
324 torque capacity. More specifically, simultaneous contraction of agonistic muscles seems to  
325 cause intermuscular forces that may cause a substantial reduction in the force capacity of a  
326 given muscle. This feature of agonistic muscle action, to our best knowledge, has not been  
327 considered in studies of human movement control and biomechanics, but might have  
328 important implications for human movement analysis. The expression of well-known muscle  
329 contractile properties, such as the history-dependent properties and the force-length and  
330 force-velocity relationships, may differ substantially between isolated and in-situ/in-vivo  
331 preparations due to the influence of agonist contraction on force generating potential. Force  
332 loss caused by agonistic contraction of muscles might also be relevant in cases of isolated  
333 muscle injury or peripheral nerve injury affecting single muscles, as inactivity of a single  
334 muscle in an agonistic group, and the associated reduction in intermuscular pressures, might  
335 allow for some force compensation through increased force capacity in the remaining,  
336 healthy muscles of the agonistic group.

337         Future efforts should be aimed at determining the mechanical properties of muscles  
338 when acting within the confines of the agonistic group. For example, the torque-angle curves  
339 shown here, and obtained for individual muscle activation (Figure 1), may change

340 substantially if muscles were activated simultaneously with other muscles in the agonistic  
341 group. With an average change in torque production of 20%, we do not know whether this  
342 torque/force loss is similar among the different muscles, or how this torque/force loss may  
343 modify the torque-angle relationships and contributions of individual muscles to the  
344 quadriceps group torque.

345 From the results of this study, we conclude that the torque-angle relationships of  
346 rabbit VL, VM and RF are different, and thus, the percentage contribution of these muscles to  
347 the total joint torque varies as a function of knee angle. Furthermore, the torque capacity of  
348 isolated muscles (SUM) is approximately 20% greater than the torque capacity of all muscles  
349 activated simultaneously (ALL). Future studies should focus on analyzing the generality of  
350 our results, and on determining the influence of agonist muscle contraction on longitudinal  
351 force production during submaximal contractions.

352 Even though the mechanisms underlying this reduction in torque capacity when all  
353 muscles were activated simultaneously is not known, we tentatively propose that it is related  
354 to the increase in intermuscular pressures/forces and associated differences in muscle  
355 deformations.

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#### 359 **Conflict:**

360 We have no conflict of interest to declare

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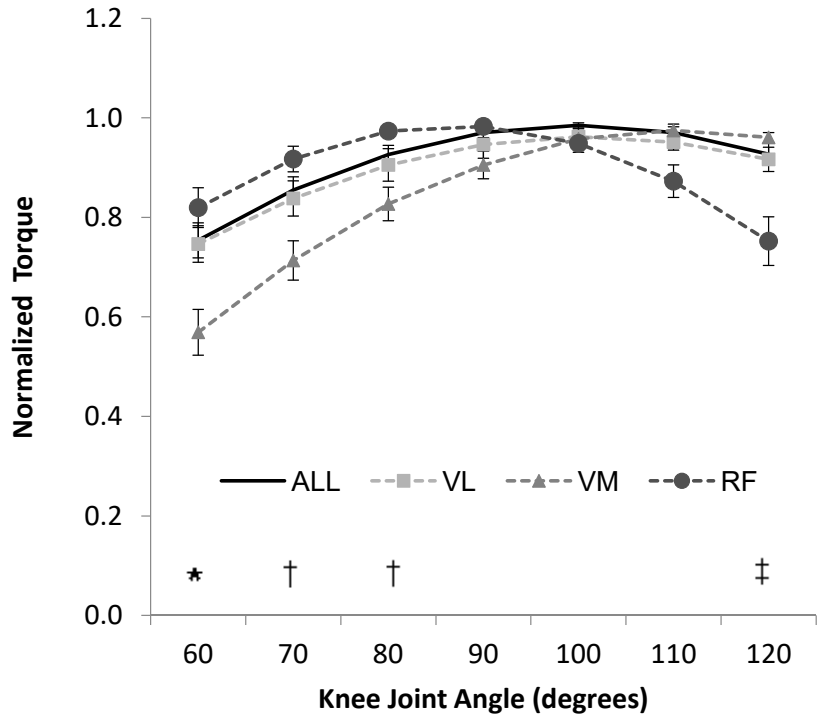
539 **Figure 1. Torque-angle relationships of the individual agonist muscles (VL - vastus**  
540 **lateralis, VM - vastus medialis and RF - rectus femoris) and of the entire agonist group**  
541 **(ALL). Muscle torque generating potential was measured by supramaximal stimulation**  
542 **of the corresponding femoral nerve branches simultaneously (ALL) and in isolation**  
543 **(VL, VM, RF). Torque values were normalized to the maximum torque for each**  
544 **condition of stimulation. Increasing knee angles indicate knee flexion and increasing**  
545 **muscle lengths (0° = full extension). Symbols: \*, indicates lower values for VM**  
546 **compared to RF, VL and ALL (0.004 < p < 0.046); †, lower values for VM compared to**  
547 **RF (p = 0.003), and ‡, lower values for RF compared to VM, VL and ALL (0.012 < p <**  
548 **0.039).**

549

550 **Figure 2. Mean ± SE of the torque-angle relationships of the agonist group obtained by**  
551 **i) simultaneous stimulation of all individual femoral nerve branches (ALL) and ii) the**  
552 **sum of the torques produced when the femoral nerve branches were stimulated**  
553 **individually (VL + VM + RF = SUM). Increasing knee angles indicate knee flexion and**  
554 **increasing muscle lengths (0° = full extension). Note that the SUM of the individual**  
555 **torque capacities is approximately 20% higher (p<0.001) than ALL, independent of the**  
556 **joint angle. Also, please note that the y axis starts at “0.4”.**

557

**Figure 1**  
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**Figure 2**

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