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Mechanical coupling between muscle-tendon units reduces peak stresses

3   Short title: Mechanism to reduce peak tissue stress

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28   **Abstract** (56 / 60 words)

29   The presence of mechanical linkages between synergistic muscles and their common tendons may

30   distribute forces among the involved structures. We review studies, using humans and other animals,

31   examining muscle and tendon interactions and discuss the hypothesis that connections between

32   muscle bellies and within tendons may serve as a mechanism to distribute forces and mitigate peak

33   stresses.

34   **Summary** (20 / 20 words)

35   We hypothesize that connective tissue linkages between muscle-tendon units serve as a mechanism to

36   distribute forces and mitigate peak stresses.

37   **Key Points** (125 / 150 words)

38   - Muscle fibers and whole muscles are embedded within a connective tissue network linking these

39   structures to surrounding structures.

40   - Mediated by these connective tissue linkages, skeletal muscles can mechanically interact with each

41   other, but the extent depends on multiple factors including muscle group, activation level and muscle

42   length. .

43   - Recent studies indicate that these linkages distribute muscle fiber forces without affecting the net

44   moments exerted at the joint level.

45   - Similarly to muscle, the connective tissue network around tendon fibers, fascicles and subtendons,

46   such as in the Achilles tendon, may serve as a mechanical linkage transmitting forces within tendon.

47   - Upon an injury the connective tissue network can provide an alternative pathway for muscular force

48   transmission and, thereby, limiting loss of muscle-tendon function.

49   **Key Words**: force transmission, skeletal muscle, connective tissue, Achilles tendon, displacement,

50   strain, injury

51

52   **INTRODUCTION**

53

54   Body or limb movements are initiated by the excitation of motor neurons in the spinal cord leading to

55   contraction of skeletal muscle fibers. The subsequent transmission of cross-bridge forces via the

56   tendons to the skeleton, creating a moment with respect to joints, is a key component in the mechanics

57   of animal movement. Within a muscle belly, many cytoskeletal proteins and collagen-reinforced

58   structures provide a medium for muscular force transmission. In other words, cross-bridge forces can

59   be distributed among many structures. Force can be transmitted to the tendon via sarcomeres in series

60   within muscle fibers and the myotendinous junction. The vast intramuscular connective tissue

61   network (i.e., endomysium, perimysium and epimysium) provides a medium through which forces

62   can also be transmitted laterally between neighboring muscle fibers. Furthermore, the connective

63   tissue network within a muscle is continuous with the connective tissue network of surrounding

64   muscles extending these effects beyond the muscle boundaries. Tendon fascicles and subtendons (i.e.,

65   tendon fascicles within a multi-muscle tendon, such as the Achilles tendon, originating from different

66   muscles) are also surrounded by a matrix, which can act to distribute forces.

67

68   In the first decade of this millennium, several studies using rats showed that, besides the origin and

69   insertion of a muscle-tendon unit, force produced by muscle fibers can be transmitted to the skeleton

70   via connective tissue linkages at their muscle belly surface (epimysium), named epimuscular

71   myofascial force transmission (1, 2). As a consequence, changes in the state (e.g., length, level of

72   activation) of one muscle can affect the force exerted at the tendon of a neighboring muscle. This

73   would imply that skeletal muscles do not act as independent functional units. Epimuscular myofascial

74   force transmission has been studied also in humans, but due to the limitations of non-invasive

75   kinematic measures and modeling approaches, this has yielded only indirect evidence. At this point,

76   the physiological significance of this phenomenon is still subject to debate. The unanswered question

77   is: Are intermuscular connections a mere by-product of the musculoskeletal organization or are they

78 functionally relevant? From a biological-evolutionary perspective, functional significance is expected

79 if this morphological feature is present within all mammalian species.

80

81 Besides the most recent findings on epimuscular myofascial force transmission, this article also

82 reviews studies investigating the role of lateral connections between tendon fascicles and subtendons

83 in transmitting force to the skeleton. While in vivo studies in humans have revealed nonuniform

84 anterior-posterior displacements within Achilles tendon, recent in vitro studies have shown that the

85 matrix between tendon fascicles has the capacity to bear substantial forces. These recent findings

86 suggest the possibility for force distribution not only between muscle bellies, but also within tendon.

87

88 Because lateral connections between different muscle-tendon units provide a medium for force and

89 stress distribution, we examine the hypothesis that connections between muscle bellies and within

90 tendons may serve as a mechanism to distribute forces and, consequently, to minimize peak stresses

91 (Fig. 1). In a case of muscle fiber or tendon injury, the connections provide an alternative pathway for

92 forces, thereby, limiting the effects of such injury on muscle-tendon function. If this mechanism is

93 active continuously, during the many motor tasks that we perform, it may also serve to prevent muscle

94 or tendon injuries. We expect that this mechanism is of greater importance in the presence of scar

95 tissue, for example after tendon transfers, because this enhances the connectivity between muscle-

96 tendon units (3, 4). In this review, we focus mainly on the triceps surae muscles and their shared

97 Achilles tendon (AT); not including the plantaris muscle. However, our analysis will apply also to

98 other muscle groups in which different muscles share a common tendon (e.g., the quadriceps).

99

100 **CONNECTIVE TISSUES PROVIDING PATHWAYS FOR FORCE DISTRIBUTION**

101

102 Several structures have been identified as pathways for epimuscular force transmission (1). At the

103 interface between muscle bellies, a layer of areolar connective tissue as well as a neurovascular tract

104 (a connective tissue structure embedding blood and lymph vessels as well as peripheral nerves) is

105   present. In addition, skeletal muscles are linked to connective tissue layers surrounding synergistic

106   muscle groups (e.g., compartmental fascia, interosseal membranes). All above mentioned structures

107   are continuous with the intramuscular connective tissue network. At the myotendinous junction, the

108   muscle fibers embedded in connective tissue are linked in an interdigitated fashion to the collagen

109   fibers eventually forming the tendon.

110

111   Tendon structural organization allows it to bear high tensile forces, but to a smaller extent also

112   transversal, rotational and shear forces as well as pressure and contusion. Hierarchy of tendon from

113   tropocollagen molecules to fascicles as well as the ground substance wherein the collagens are

114   embedded is well established. Tendon fascicles are surrounded by a matrix (the interfascicular matrix)

115   that allows these fascicles to move relative to each other for some range, but that can also bear

116   substantial forces beyond the initial stretching range. Interestingly, properties of the interfascicular

117   matrix can be different between tendons having different functions related to their capacity to store

118   energy and transmit forces (5).

119

120   **MECHANICAL INTERACTIONS BETWEEN MUSCLES – HUMAN STUDIES**

121   Human imaging studies have discussed the potential effects of epimuscular myofascial force

122   transmission based on observations of muscle motion during 1) passive joint movements, 2) selective

123   muscle stimulation or 3) voluntary contractions. One of the first human studies trying to elucidate

124   force transmission between adjacent muscles examined the relative displacement of medial

125   gastrocnemius (MG), soleus (SOL) and flexor hallucis longus muscle movements in all of the three

126   abovementioned conditions (6). During 80° passive knee extension, the authors demonstrated that the

127   neighboring distal aponeuroses of MG and SOL moved to a similar extent. This result showed that

128   also the one-joint SOL muscle deformed by knee movement, possibly involving epimuscular

129   myofascial force transmission.

130

131   When Tian et al. (7) studied the effects of 60° passive knee flexion on MG and SOL fascicle lengths,

132   they found that MG fascicles shortened while the length of proximally and distally located SOL

133   fascicles increased slightly. Using a similar experimental approach imposing 90° knee flexion, Finni

134   et al. (8) reported lengthening of only the distal SOL fascicles while the length of proximally located

135   muscle fascicles remained rather constant. These studies provide support to our hypothesis by

136   suggesting that knee movement causes deformations of SOL muscle due to force transmission from

137   the two-joint gastrocnemius muscles (GAS) via connective tissue linkages. However, the effects may

138   be location specific due to the more abundant presence of the connective tissue linkages distally. Note

139   that there are earlier reports showing no effects of passive knee joint flexion on proximally located

140   SOL fascicle lengths in humans (e.g., 9).

141

142   While effects of knee movement on SOL muscle have been repeatedly observed, estimates of the

143   magnitude of such force transmission indicated very small effects on ankle joint moment (7).

144   Assuming that SOL slack angle (i.e. angle at which the passive muscle bears no tension) occurs at 30°

145   plantarflexion, Tian et al. (7) calculated that the contribution of SOL to the ankle joint moment could

146   be as high as »12% of that of GAS force. However, they also reported that the force estimate was

147   sensitive to the selected slack length. As recently SOL slack length was reported to occur at 2°

148   dorsiflexed ankle position (10), the magnitude of intermuscular force transmission in passive

149   condition is probably even smaller than estimated by Tian et al. (7). This suggests that for the

150   substantial deformations within SOL only small forces were needed. Note, however, that in this study

151   the muscles were not activated. Interestingly, both MG and lateral gastrocnemius (LG) muscles start

152   to bear tension at a more plantar flexed ankle position than SOL (10) with possible proximal-distal

153   differences in muscle fascicle slack lengths along a single muscle (11). Overall, the observations of

154   heterogeneous slack lengths may be relevant when estimating the mechanical effects of relative tissue

155   displacements of synergist muscles at different joint angles.

156

157 Regarding the effects of knee joint angle on SOL muscle deformations, it should also be noted that

158 based on rat studies the nerve tract that also crosses the knee joint may contribute to force

159 transmission (1, 2). In humans, knee extension has been reported to result in proximal displacement of

160 the sciatic nerve (12). Such movement may then cause a load on SOL muscle and deform it. In a

161 recent rat study involving only passive muscle conditions, it was found that changes in knee angle did

162 not affect fiber length of tibialis anterior muscle (crossing only the ankle joint) but did result in

163 changes in the distribution of lengths of sarcomeres in series within muscle fibers (13). Because the

164 direction of sarcomere length changes could not be explained by effects of length changes of the

165 synergistic extensor digitorum longus muscle, the results were explained by changes in loads exerted

166 on tibialis anterior via the nerve tract. Note, however, that no effects of knee movement on

167 distribution of sarcomere lengths were found for SOL muscle (13). Considering that sarcomere

168 lengths can be affected without changes in fiber length, measurements of sarcomere lengths in

169 humans using recently developed microendoscopy techniques (14) seem warranted when

170 investigating force producing capacity and its distribution.

171

172 While the magnitude of force transmission may be small between passive muscles less is known about

173 activity dependent stiffening of connective tissues and whether it may increase the magnitude of

174 intermuscular force transmission. It was recently proposed that passive conditions are more likely to

175 involve large deformations of muscle tissues, because of the low stiffness with respect to the

176 intermuscular connections, while active conditions will involve less deformations of muscle tissues,

177 but more lengthening of myofascial connections (4). Accordingly, greater intermuscular force

178 transmission can be expected during active muscle conditions. Previous studies have reported that

179 connective tissues, the aponeurosis in particular, are stiffer during muscle contraction than in passive

180 conditions (e.g., 15). Also the extent of mechanical interaction between rat triceps surae muscles was

181 found to increase from fully passive state to all muscles being maximally activated (16).

182

183 A recent human study examined the effects of activation on relative displacement between SOL and

184 LG muscles (8). During knee extension (i.e., GAS muscle stretch) with LG selectively stimulated,

185 relative displacement between LG and SOL muscles was smaller in active as compared to passive

186 condition, indicating that muscle activation reduced movement independency of the muscles. It

187 should be acknowledged that in this experiment only low activation levels were used to ensure

188 selectivity of the stimulation and the phenomenon was statistically significant only for the shortest

189 muscle-tendon unit length of GAS (8). It may be that the short muscle length (near slack length)

190 provided a condition where even a small level of activation could induce effects while at longer

191 lengths greater forces would be required to show the effect. The above results indicate a likely effect

192 of muscle length and activation level on epimuscular myofascial force transmission.

193

194 In active conditions, the level and type of activation may affect the tissue deformations. For example,

195 supramaximal electrical stimulation of the tibial nerve induced similar length and velocity effects in

196 both SOL and MG fascicles (17), whereas under voluntary control SOL and MG may be activated

197 differently (18) and move differently (19). The observations of relative muscle motions may also be

198 task dependent (i.e., isometric vs. dynamic) or vary between individuals as shown for relative

199 movement between SOL and MG (19) and vastus lateralis and rectus femoris muscles (20).

200

201 It is important to note that the above described concurrent muscle deformations between adjacent

202 muscles do not necessarily refer to mechanical interaction. To confirm intermuscular force

203 transmission in humans, future studies need to complement the kinematic measures with modeling or

204 advanced methods such as ultrasound shear wave elastography that may provide information about

205 the forces involved. Another noteworthy issue is that some human studies report fascicle lengths (7-9,

206 17) while others present results on relative tissue displacements (6, 8). These two measures may

207 reflect slightly different phenomena: the latter on a more global and functional level and the former on

208 a local level. Note that, due to effects of muscle architecture, changes in muscle belly length are more

209 directly related to changes in tendon length and, hence, tendon forces than changes in muscle fiber

210 length. Therefore, measurements at different levels of the musculoskeletal system are needed in future

211 studies for a complete understanding of the mechanical implications of local muscle deformations.

212

213 In the next section, we will describe in situ studies using rats and cats in which the mechanical

214 consequences have been measured at the single muscle or joint level.

215

216 **MECHANICAL INTERACTIONS BETWEEN MUSCLES – STUDIES ON OTHER**

217 **ANIMALS**

218

219 As described above, there is ample evidence for connective tissue linkages between adjacent muscle

220 bellies that are sufficiently strong to transmit force. According to our hypothesis, this epimuscular

221 myofascial pathway may also be involved in the distribution of forces among synergists. However,

222 earlier studies involved muscle conditions that were beyond physiological, e.g. maximal excitation of

223 all synergistic (and sometimes also antagonistic) muscles and higher changes in muscle-tendon unit

224 length and relative position than possible in vivo (reviewed in 1, 2). In some cases, the myofascial

225 effects of the physiological conditions within those experiments were tested separately and found to

226 be significant but small (2). More recently, mechanical interactions between synergistic muscles for

227 conditions found during normal movement have been studied using two experimental approaches: (i)

228 sever the tendon of origin and/or insertion to connect them to force transducers, and imposing muscle

229 lengths mimicking those found in vivo – note that all other structures crossing the joints (e.g., other

230 muscles, neurovascular tracts, ligaments) are not manipulated (Fig. 2, left); (ii) testing muscles in a

231 nearly intact limb, leaving the tendons attached to the skeleton and changing muscle-tendon unit

232 length by joint movements (Fig. 2, right).

233

234 Using the first approach, mechanical interactions between passive and active ankle plantar flexors of

235 the rat were found (3, 16). Intermuscular interaction was assessed by measuring effects of lengthening

236 the two-joint muscles (i.e. stretching LG and plantaris proximally by 6 mm, simulating knee extension

237   from 45° to 130°) on force exerted at the distal SOL tendon which was kept at a constant length, and

238   on the force difference between the proximal and distal tendons of the two-joint muscles. These two

239   measures were shown to correlate positively (3), indicating that forces are transmitted between these

240   muscles. The extent of interaction was affected substantially by the level of muscle activation. The

241   increase of SOL force varied between 0.005 N for the condition in which all muscles were passive to

242   0.15 N for the condition in which all muscles were maximally activated. For reference, the optimal

243   force of SOL in these rats equals approximately 1.5 N. In conclusion, force transmission between

244   SOL and two-joint synergists may occur during normal joint movements, but only to a limited extent.

245   These findings support our hypothesis that some distribution of force among the ankle plantar flexors

246   can occur.

247

248   The second experimental approach exploits the presence of both one-joint and two- or multiple-joint

249   muscles within synergistic muscle groups. During isolated movements of the joint that is not spanned

250   by the one-joint muscle, only the length and relative position of neighboring two-joint muscle(s) will

251   be affected. As forces exerted at the tendons cannot be measured directly without causing tissue

252   damage, the joint moment the muscle exerts on contraction is assessed using a six degrees-of-freedom

253   load cell (see Fig. 2). Applying this approach in rat and cat studies revealed no effects of knee angle

254   and, hence, length changes of passive two-joint ankle plantar flexors, on plantar flexion moment and

255   rate of moment relaxation (the latter being a measure affected by muscle fiber length) of contracting

256   SOL muscle (21). Because MG, LG and SOL merge into the AT they have similar lines of action and

257   directions of 3D moment vectors (22), any effects of epimuscular myofascial force transmission will

258   be difficult to detect. In other words, the lack changes in SOL moment in response to changes in knee

259   angle cannot confirm the absence of epimuscular myofascial force transmission. These results indicate

260   that any connections between SOL and GAS have no mechanical effects at the joint level, but this

261   does not exclude the distribution of SOL forces to surrounding muscles or subtendons.

262

263   The same experimental approach was applied also to study mechanical interaction between one-joint

264   tibialis anterior (TA) and extensor hallucis longus (EHL) muscles and the multiple-joint extensor

265   digitorum longus (EDL) muscle (23). These muscles do not share a distal tendon and, hence, exert

266   moments in different directions (i.e., TA – ankle inversion, EDL – ankle eversion, both muscles –

267   ankle dorsiflexion). Thus for this muscle pair, intermuscular mechanical interaction should lead to

268   changes in the direction of the 3D moment vector. Instead, no effects of knee extension (decreasing

269   EDL length) on the moment exerted by TA muscle were observed (23). Therefore, these results must

270   be considered as evidence against the hypothesis of the present paper. This could be related to the

271   different functions of the ankle plantar and dorsal flexors, requiring more mechanical independence

272   within the latter muscle group.

273

274   **INTERACTIONS BETWEEN MUSCLES VIA A COMMON TENDON**

275

276   As described above, intermuscular interactions can be brought about by epimuscular myofascial

277   linkages at the interface between muscle bellies. If the tendons of several muscles merge into a single

278   tendon (e.g. the triceps surae with the Achilles tendon) and this tendon acts as a common spring, this

279   may provide another pathway for such interactions. An experimental approach to investigate if a

280   tendon acts as a common spring for two or more muscles is to assess muscle moment summation (24).

281   The active isometric joint moment (i.e., the total moment minus the passive moment) exerted by two

282   muscles simultaneously is compared to the sum of active moments exerted by each muscle

283   individually. The difference is then referred to as nonlinear moment summation, which is expected to

284   be negative. If the tendon acts as a common spring, its length change will be higher during

285   simultaneous activation than during individual activation due to greater force imposed on it. As the

286   muscle-tendon unit length is kept constant during an isometric contraction, this means a lower muscle

287   fiber length. Consequently, each muscle that is operating below its optimum length will produce

288   lower forces during simultaneous muscle activation. Hence, the sum of moments exerted by each

289   muscle individually will be higher than the moment exerted during simultaneous activation of the two

290   muscles. Experiments on cat vastus medialis and rectus femoris revealed nonlinear summation of -1%

291   (24). Similar results were found for cat and rat triceps surae (21, 22, 24). These results indicate that

292   nonlinearities are rather small, suggesting that for tested conditions the patellar and Achilles tendons

293   do not appear to act as common springs and thus the subtendons are rather independent of each other..

294   However, these findings do fully not exclude the possibility that the forces are distributed within the

295   AT. Future studies are needed to confirm the level of independence between subtendons of shared

296   tendons.

297

298   Another approach to study if a shared tendon can cause interactions between muscles is to manipulate

299   the length of only one muscle and, thereby, affect the part of the tendon that acts as a common spring.

300   For the triceps surae in humans, it has been found that passive knee extension (i.e. lengthening GAS

301   muscle) causes shortening of SOL muscle fascicles (7, 8). This may be the result of mechanical

302   interactions at the muscle belly interface, but could very well be mediated by the Achilles tendon

303   acting as a common spring. Knee extension will increase the muscle-tendon unit length of GAS

304   muscle, including its distal tendon. This may release tension on the SOL muscle fascicles, which may

305   then shorten. While knee extension in rats was shown to affect the length of the AT only when all

306   muscles were passive (21), in humans passive knee extension was accompanied with very minimal

307   distal tendon movement (1 mm as measured from distal SOL fascicle attachment, 6). Overall, more

308   studies on AT displacements are needed to understand if method and location of measurement (i.e.,

309   tracking the tendon itself vs. displacement of SOL, MG or LG fascicle insertion) provide

310   complementary observations especially in human studies.

311

312   In rats, during SOL activation or during SOL and GAS activation AT length was independent of knee

313   angle for most of the knee angles tested (i.e., between 60° and 130°)(22), which indicates a higher

314   stiffness of the AT in active muscle conditions. In agreement with this, no effects of knee angle on

315   active muscle moment summation were found (21). In a human study, low level MG stimulation in

316   flexed and extended knee positions caused smaller movements in distal SOL than those found during

317   passive knee movements (6). In particular, the movement of the distal SOL fascicle attachment to AT

318   was minimal (<1 mm), suggesting very small if any effects via the common tendon in passive and low

319   level active conditions.

320

321   Based on the above described studies, we conclude that, despite existing connections between

322   neighboring muscles and within common tendons, their effects on muscle moments exerted at the

323   joint are minimal. While passive and active muscle conditions during normal physiological conditions

324   may slightly differ from those applied experimentally, the significance of the force transmission

325   pathways may have an alternative function: that of distributing forces to reduce peak stresses. This

326   may occur not only at the muscle belly level but also within the tendon, which is discussed in the next

327   section.

328

329   **FORCE TRANSMISSION WITHIN TENDON**

330

331   In agreement with our hypothesis, we expect that there is potential for lateral force transmission

332   within tendons. This phenomenon may occur at different organizational levels of tendon and vary

333   between tendons. At a microscopic level, tendon matrix (5), cross-linking and/or fiber cross-sectional

334   area (25) can contribute to differences within (and between) tendons, while at a macroscopic level,

335   various anatomical designs can contribute to tendon specificity. For example, the patellar tendon has

336   straight fascicles of different lengths, while the AT has a twisted structure that is shared by three

337   muscles (26). Similarly to the triceps surae muscles, the quadriceps femoris and triceps brachii

338   muscles share the tendon of insertion, while the semitendinous muscle and the long head of biceps

339   femoris muscle share the tendon of origin. In such common tendons or in tendons with uneven

340   fascicle lengths, nonuniform displacements and/or strains seem very likely.

341

342   In addition to the macroscopic design of tendons, regional differences in tendon material may

343   contribute to the nonuniform behavior within tendons. In case of the patellar tendon, anterior and

344   posterior fascicles have different material properties, cross-link concentrations and fibril density (25).

345   Nonuniform behavior may also be facilitated by relative sliding between tendon fascicles that is

346   enabled by lubricin in the interfascicular matrix. This matrix is also rich in elastin that may act to store

347   energy and/or to transmit forces between the fascicles. Mechanical tests examining the properties of

348   the interfascicular matrix in equine tendons have shown that it is elastic and can bear substantial

349   forces; it has a stiffness of about half of that of tendon fascicles (5, 27). Preliminary data from a more

350   macroscopic level indicate that the matrix between the Achilles subtendons in rat has similar

351   mechanical properties as those described for the intrafascicular matrix (unpublished observations,

352   Maas & Screen) and, thus, there is potential for force transmission and distribution of stresses at

353   different organizational levels of a tendon.

354

355   The structural organization and mechanical properties described above can allow nonuniform

356   deformations within tendons. In cadavers, for example, differences in strain between anterior and

357   posterior patellar tendon and between different parts of AT can be found. Using novel *in vivo* imaging

358   methods (e.g., 28, 29), differential displacements between anterior and posterior parts have been

359   reported to exist in human patellar tendon during isometric contractions and in AT during passive

360   joint rotations, isometric contractions, eccentric contractions as well as during walking. Within the AT

361   in particular, these differential displacements may be possible due to the presence of distinct

362   subtendons for SOL, LG and MG muscles (26), but with the applied imaging methods it is not

363   possible to identify the specific anatomic locations of the displacements in humans. New evidence

364   from in vivo measurements in the rat indicates differential lengthening of the distal tendons of SOL

365   and LG muscles during controlled muscle stimulations (30) and during locomotion (31). This suggests

366   relative displacements between Achilles subtendons, which could, given the material properties of the

367   intersubtendon matrix, facilitate intersubtendon force transmission. The Achilles subtendons can be

368   dissected free, but as the connections between subtendons become tighter towards the insertion onto

369   the calcaneus, this is more difficult distally. Consequently, there may be proximal-distal variation in

370   the matrix between subtendons requiring comprehensive future experiments along the length of the

371   muscle-tendon unit. Note that the proximal-distal location also at the muscle belly level can be a

372   factor when evaluating the magnitude of mechanical interaction between the synergists (1, 2).

373

374

375   In addition to nonuniform deformations, there is also evidence of nonuniform loading within the AT

376   in humans *in vivo*. In experiments where either an optic fiber force transducer (32) or a syringe needle

377   (26) was inserted in the AT, sharp bending of the optic fiber or the needle was observed during high

378   loading conditions, such as drop jumps or maximal voluntary isometric contractions. This was most

379   likely caused by nonuniform deformations and/or forces within the tendon which, in turn, can be due

380   to differential activation of the synergists (18). In such a case the mechanical linkages between

381   muscle-tendon units can help to distribute forces and mitigate uneven AT stress (Fig. 1). For further

382   insight of asymmetrical loading of AT the reader is referred to a recent review by Bojsen-Moller &

383   Magnusson (26).

384

385   The above reviewed research supports the possibility for stress distribution within AT, in agreement

386   with our hypothesis. Relative displacement between tendon fascicles or subtendons may provoke

387   lateral force transmission via interfascicular matrix. Alternatively, such relative displacements may

388   indicate that the different triceps surae muscles transmit their forces independently. However, little is

389   known about the mechanical properties of the interfascicular and intersubtendon matrices and, thus,

390   no comprehensive conclusions about the mechanical consequences of nonuniform behavior can be

391   drawn.

392

393   **STRESS DISTRIBUTION FOLLOWING MUSCLE-TENDON INJURY**

394

395   Upon injuring muscle fibers and/or tendon fascicles, the connective tissue network may provide an

396   alternative pathway (a safety net) for force transmission and, thereby, limiting the acute loss of

397   muscle-tendon function. For animals other than humans, such a mechanism may mean the difference

398   between escaping from or being caught by its predator. Evidence of such acute redistribution of

399   muscle force in response to an injury has been derived from experiments using experimental

400   approaches similar to those presented in Figure 2 (2). In one of such experiments in rats,

401   simultaneously measuring forces exerted at distal tendons of SOL and distal and proximal LG and

402   plantaris (LG+PL) muscles, LG muscle belly was unexpectedly torn. This resulted in the following

403   events: (i) substantial LG muscle belly shortening, (ii) an immediate decrease of force exerted at the

404   tendons of LG+PL, and (iii) an immediate increase of force exerted at the distal tendon of SOL (Fig.

405   3). These results indicate that some of LG muscle fibers still exerted force and, thus, its muscle fibers

406   did not shorten to their active slack length (i.e., the length at which active force approaches zero). The

407   increase in force exerted at the distal tendon of SOL can be explained by the transmission of LG

408   muscle fiber forces via connective tissue linkages to SOL. In other words, forces produced by muscle

409   fibers in the injured muscle are redistributed to surrounding muscles. If the subtendons of a common

410   AT are separated, as in the experiment yielding the data shown in Fig. 3, such redistribution can only

411   be mediated by epimuscular myofascial pathways providing evidence for our hypothesis. In case of an

412   intact common tendon, force redistribution may occur also within the tendon given that its

413   interfascicular matrix has a notable stiffness (5).

414

415   It is worth mentioning, that our hypothesis implicitly assumes that distribution of forces leads to lower

416   stresses within the muscle-tendon unit, however, it may be that greater stress concentrations could be

417   formed if forces are redistributed from thicker to thinner structures. Clearly, future research at

418   different levels of muscle-tendon is warranted to clarify the phenomenon and its mechanisms.

419

420   Early studies examining the effects of rectus femoris tendon transfer showed that although the surgery

421   was supposed to make the rectus femoris muscle a knee flexor based on its origin and insertion, a

422   knee extensor moment was found during muscle stimulation (33). Recent evidence shows increased

423   importance of epimuscular pathways in the presence of scar tissue between muscle bellies (3, 4).

424   Bases on these recent studies, it is very likely that the same mechanism was responsible for the

425 preservation of knee extension moment following rectus femoris tendon transfer to the flexor site of

426 the knee. This suggests an important role of scar tissue in stress distribution. It should be noted that

427 scar tissue is found also following muscle-tendon injuries, having the potential to modify force

428 transmission within the system. Overall, connective tissue mediated force distribution may become

429 more significant in pathological conditions of our musculoskeletal system.

430

431 When an injury causes damage to tendon fascicles their force transmission capacity is reduced, which

432 has been studied also using fatiguing situations. In tendon, the interfascicular matrix endures only one

433 third of the loading cycles (when loaded with 30% load) as compared to the fascicles (27). In the

434 course of a fatiguing trial, the stiffness of tendon fascicles and interfascicular matrix is reduced and

435 hysteresis shows a tendency to decrease until final increase before failure (27). Similarly to the

436 muscle injury described above and in Fig 3, in tendon injury the presence of epimuscular myofascial

437 linkages may provide alternative pathways for muscle forces to be effective at joint level. These

438 alternative pathways may also be important in the prevention of tendon injuries. Distributing forces

439 among a greater cross-sectional area will reduce peak stresses and, thereby, diminish the risk of tissue

440 overload. Even if the magnitude of this mechanism is limited, its role may be crucial during the many

441 physical activities that we perform in daily life.

442

443 Besides injury, future studies need to investigate the importance of force distribution in aging because

444 of changes in connective tissue properties. For example, in aged equine energy storing tendons, less

445 sliding between the fascicles has been found (34). This result corroborates to findings in human AT

446 during walking where the shearing between anterior and posterior tendon is reduced to nearly half in

447 the elderly. This reduction in the interaction within the tendon can have negative consequences to

448 SOL and GAS muscle function that are more tightly coupled to a common tendon in elderly (35).

449

450 **CONCLUSIONS**

451

452   Synergistic muscles are coordinated by the central nervous system to perform the versatile physical

453   tasks that we perform in daily life. This involves non-simultaneous activity, at various magnitudes

454   and, thus, different forces exerted by their muscle fibers to produce the required joint moments for

455   interaction of our body with the environment. As a consequence, the structures bearing these forces

456   (e.g., intramuscular connective tissues, tendon) are loaded non-uniformly, potentially leading to high

457   stresses locally. Recent evidence described in this review provides support for a mechanism that

458   redistributes muscle fiber forces and, thereby, minimizes peak stresses. This mechanism is

459   characterized by force transmission via tissues linking muscle-tendon units within a synergistic group

460   but its magnitude may vary between species, muscle groups, proximal-distal location, activity levels

461   and muscle lengths. Due to the fact that this mechanism is active continuously, we propose that it may

462   be involved in preventing muscle or tendon injuries. In case of an acute muscle-tendon injury, the

463   connective tissue network may act as a safety net, limiting the acute loss of muscle-tendon function.

464   In the long-term, enhanced use of stress distribution by means of scar tissue formation (i.e. an

465   alternative route for transmission of forces) will allow recovery of our musculoskeletal system while

466   making use of the maximal available capacity of the intact muscle tissues.

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588

589   **Figure legends**

590   **Figure 1. Schematic illustration of the hypothesis.**

591   Simplified sagittal view of soleus (SOL) and gastrocnemius (GAS) muscles with distal Achilles

592   tendon cross-sectional viewed superiorly.

593   Left: If the muscle-tendon units of the triceps surae are mechanically independent from each other, all

594   force produced by the muscle fibers will be transmitted exclusively via the respective subtendon

595   within the Achilles tendon. No stress distribution will occur, the colors indicating different stresses

596   between the muscle-tendon units.

597   Right: If the muscle-tendon units of the triceps surae are mechanically linked to each other, either at

598   their shared muscle belly interface or within the Achilles tendon, force produced by the muscle fibers

599   can be distributed among all units. Stress will be distributed leading to a reduction of peak stresses. It

600   is important to note that in normal intact conditions the variable neural input affects forces also.

601   Typically, synergistic muscles are activated in synergy but not always and not to the same extent.

602

603   **Figure 2. Experimental setups for experimental approaches to study mechanical interactions**

604   **between synergistic muscles for conditions found during normal movement in a fully**

605   **anesthetized rat.**

606   Left: Proximal and distal tendons of LG and plantaris as well as the distal tendon of SOL were

607   connected via metal rods to separate force transducers (for details see 4). A bipolar cuff electrode was

608   placed on the tibial nerve to maximally activate all muscles.

609   Right: The femur was fixed and the foot was attached to a 6 degrees-of-freedom load cell using

610   custom-made clamps (21, 23). The ankle and knee joints were aligned with the set-up's rotational

611   axes. The knee joint angle was changed while keeping the ankle angle constant (two positions of the

612   knee joint are shown).

613

614   **Figure 3. Force distribution among synergistic muscles upon muscle rupture.**

615   Force recordings from distal tendons of soleus (SOL) and distal and proximal lateral gastrocnemius

616   and plantaris (LG+PL) muscles in a setup illustrated in Figure 2 (left). During an isometric

617   contraction induced by stimulation of the tibial nerve, LG muscle belly was unexpectedly torn (just

618   before the 2200 ms time stamp). Force exerted at the distal tendons of LG+PL decreased immediately

619   upon tear (vertical dashed line). Simultaneously, force exerted at the distal tendon of SOL increased

620   (see inset with enlarged view on SOL force signal). This indicates that some of LG muscle fibers still

621   exerted force, which was (at least partly) redistributed via connective tissue linkages to the distal

622   tendon of SOL (unpublished observations Bernabei & Maas).
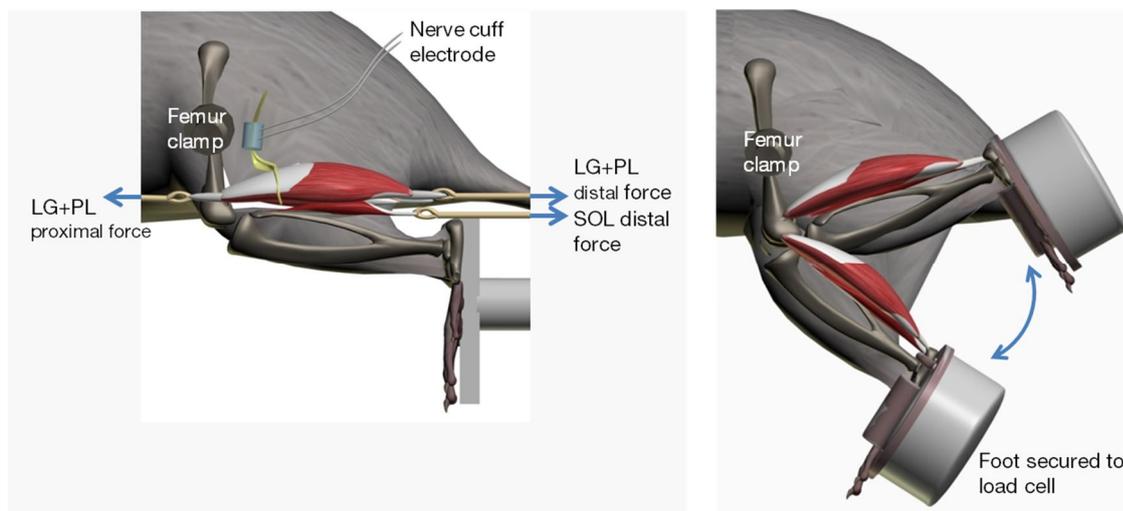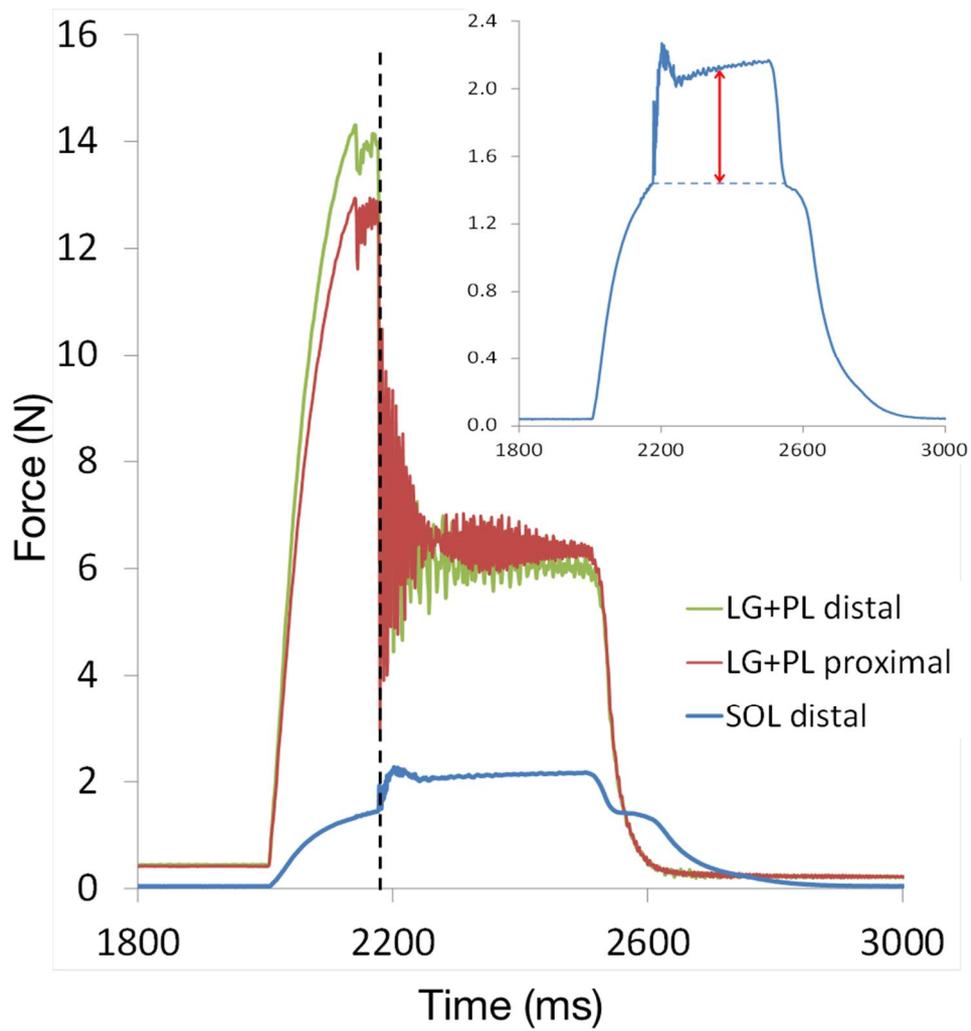
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624   **Figure 1**
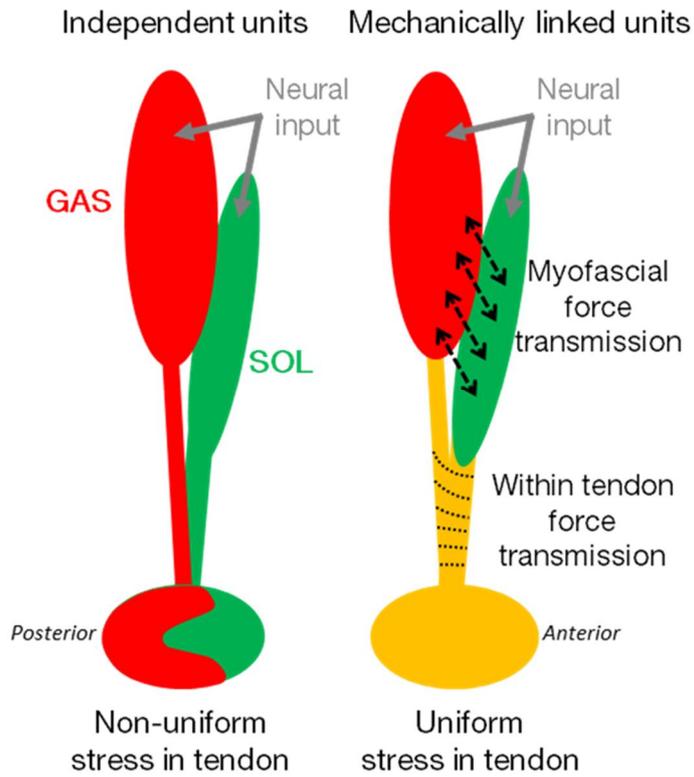
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627 **Figure 2**

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630   **Figure 3**

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