

1 **Eight weeks of eccentric training at long-muscle length increases fascicle length independently**
2 **of adaptations in passive mechanical properties**

3
4 **Running title:** Skeletal muscle adaptations to eccentric exercise training

5
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34 **Availability of data**

35 The entire data set with raw data is available at

36 <https://entrepot.recherche.data.gouv.fr/dataset.xhtml?persistentId=doi:10.57745/SFBCL7>. The
37 dataset with the processed data is available from the corresponding author on reasonable request.

38
39 **Conflict of interest statement:**

40 No conflicts of interest, financial or otherwise, are declared by the authors.

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45 **ABSTRACT**

46 Eccentric exercise training is believed to induce an increase in muscle fascicle length. However, the
47 mechanisms underlying this adaptation are not fully understood. This study aimed to determine if
48 an increase in gastrocnemius medialis fascicle length following an 8-week eccentric training is
49 linked to changes in muscle tissue and joint mechanical properties. Thirty-three physically active
50 young adults were assigned to one of two training protocols targeting the plantar flexors: eccentric
51 exercise at 1) long-muscle length or 2) short-muscle length. Fascicle length and muscle shear modu-
52 lus of the gastrocnemius medialis were assessed using ultrasound imaging during passive ankle ro-
53 tations, alongside measurements of passive ankle torque. A total of 27 participants successfully
54 completed the training program and data processing stage (long-muscle length, n=15; short-muscle
55 length, n=12). Maximal voluntary isometric torque increased significantly following the training
56 programs (9.5%), with no differences between training groups. An increase in fascicle length (mean
57 8.5%) was observed in the long-muscle length group, from $39.5 \pm 0.7^\circ$ to $36.8 \pm 0.8^\circ$ in plantar flex-
58 ion; but not in the short-muscle length group. Notably, this macrostructural adaptation was detected
59 only at muscle lengths shorter than the slack length (i.e., absence of any muscle passive tension).
60 The eccentric training did not alter the muscle shear modulus or slack length. Collectively, these
61 findings suggest that fascicle length adaptations in response to eccentric training were unrelated to
62 changes in passive muscle-tendon mechanical properties. Consequently, the increase in fascicle
63 length may be attributed to an increase in sarcomere length and/or an addition of sarcomeres in se-
64 ries.

65
66 **NEW & NOTEWORTHY**

67 We demonstrate that an 8-week eccentric training program significantly increases gastrocnemius
68 medialis fascicle length in humans, independent of any adaptations in passive muscle-tendon mechan-
69 ical properties. Fascicle length adaptations were specific to the group that trained at long-muscle
70 lengths, highlighting the importance of the muscle-tendon length range during eccentric exercise
71 programs. This factor may be crucial for fine-tuning structural adaptations at the fascicle level, like-
72 ly through the addition of sarcomeres in series.

73
74 **KEYWORDS**

75 Elastography, Tissue Elasticity Imaging, Ultrasonography, Skeletal Muscle, Strength Training

76 INTRODUCTION

77 Eccentric training is well-established as an efficient modality for enhancing muscle performance (1,
78 2). Numerous studies have reported increases in ultrasound-measured fascicle length following
79 chronic eccentric training in humans (3–6). Based on animal studies demonstrating an increase in
80 the number of the sarcomeres in series (7–9), the fascicle lengthening observed in humans has been
81 interpreted as indicative of longitudinal fascicle growth (10–12). However, the training load in hu-
82 man studies is typically lower than in animals, suggesting potential differences in the underlying
83 mechanisms. Furthermore, changes in fascicle length remain a very indirect marker of sarcomere
84 number adaptation. Collectively, these factors highlight the need for a more comprehensive under-
85 standing of the adaptations resulting from strength training protocols commonly employed in sports
86 and rehabilitation programs.

87 The association between increased ultrasound-measured fascicle length and serial sarcomere num-
88 ber has only recently been studied in humans by combining a minimally invasive microendoscopy
89 method for in-situ sarcomere measurements alongside ultrasound imaging (13). This approach re-
90 vealed an increase in ultrasound-measured fascicle length following a 3-week Nordic hamstring
91 eccentric exercise training, without changes in the estimated serial sarcomere number of the biceps
92 femoris. Therefore, increased fascicle length was attributed to an increase in sarcomere length.
93 While the mechanisms underlying these findings remain unclear, it was suggested that connective
94 tissue adaptations or changes in passive mechanical properties of the muscle-tendon unit may ex-
95 plain the changes in fascicle length after such a short training period.

96 Several human studies have demonstrated that mechanical properties of the muscle-tendon unit can
97 be modified through chronic eccentric training (14, 15). However, the relationship between muscle-
98 tendon mechanical properties and changes in fascicle length has not been studied. Additionally,
99 fascicle length is often measured at a single joint angle, typically under passive muscle tension –
100 e.g., with the foot perpendicular to the leg for the gastrocnemius muscle. The observed changes in

101 fascicle length could therefore be partially attributed to adaptations in passive muscle-tendon me-
102 chanical properties (16), highlighting the importance of assessing muscle fascicle length across the
103 full range of motion – both with and without passive tension.

104 Studies involving humans (4) and animal models (8) have suggested that the range of muscle length
105 during eccentric exercise may influence muscle adaptations. Specifically, training at longer muscle
106 lengths appears to promote the adaptations in muscle fascicle length. Therefore, manipulating the
107 muscle length during the eccentric training could be relevant for better identifying the potential rela-
108 tionships between changes in muscle-tendon mechanical properties and adaptations in fascicle
109 length.

110 The primary aim of this study was to determine whether changes in muscle fascicle length in re-
111 sponse to chronic eccentric training are associated to adaptations in passive muscle mechanics. We
112 implemented an 8-week eccentric training program targeting the plantar flexor muscle group. High-
113 resolution ultrasound imaging and ultrasound shear wave elastography (SWE) methods were em-
114 ployed to simultaneously measure fascicle length and passive mechanical properties of the gas-
115 trocnemius medialis muscle across the entire ankle range of motion (ROM). Given the substantial
116 animal evidence indicating an increase in the number of sarcomeres in series (9), we hypothesized
117 that changes in fascicle length would not be related to adaptations in passive muscle mechanics.
118 Instead of a control group, we tested two distinct eccentric training groups in which exercise was
119 performed at 1) short-muscle length and 2) long-muscle length. We hypothesized that the increase
120 in fascicle length would be greater for the group performing eccentric exercise at long-muscle
121 length (4, 8). This comparison between groups could provide valuable insights into the relationship
122 between fascicle length and passive muscle-tendon mechanical properties adaptations.

123 **METHODS**

124 **Participants, Randomization, and Ethical Approval**

125 Thirty-three healthy adults participated in this single blind randomized study (10 female; age $19.8 \pm$
126 1.5 years, height 174.3 ± 11.8 cm, weight 66.3 ± 10.9 kg). All participants were sport sciences
127 students recruited from the local university. Inclusion criteria included being healthy and aged
128 between 18 and 30 years. Exclusion criteria were as follows: 1) recent (< 3 years) musculoskeletal
129 injury or disability in spine or lower limbs; 2) cardiovascular, neurological, or psychiatric disease;
130 and 3) recent enrollment in any strength training program. Based on an effect size of 0.45 for
131 fascicle length adaptations (11), a significance level of 0.05, and a power of 0.80, the required
132 sample size for a two-way repeated measures analysis (with a within-between interaction) is 12
133 participants per group (G*Power software; Kiel University, Germany). Participants were randomly
134 assigned to one of two distinct eccentric training conditions – short-muscle length or long-muscle
135 length – using a coin toss, in a 1:1 ratio. Once one group reached half of the total sample size, all
136 subsequent participants were assigned to the second group. Ethical approval was obtained from the
137 local Institutional Review Board of the University (CERNI #06012023).

138

139 **Experimental procedure**

140 *Ankle joint mechanics and range of motion.* An isokinetic dynamometer (Con-Trex MJ, CMV
141 AG, Dubendorf, Switzerland) was used to perform passive ankle rotations (Figure 1A). All meas-
142 urements were performed on the right lower leg. The lateral malleolus was considered as the rota-
143 tion center of the ankle and was aligned with the center of rotation of the dynamometer. Participants
144 were positioned with their hips flexed at 50° , the right leg parallel to the floor, and their right knee
145 fully extended. The ankle neutral position was set at 90° between the footplate and the shank. The
146 foot, the leg and the ankle were carefully attached to minimize potential heel displacement. Before
147 and during data collection, potential heel displacement was visually monitored, and adjustments to

148 the strap system were made as needed. The ankle angle and torque were both recorded at 5000Hz
149 using an analog-digital converter (LockLab, Vicon Motion Systems Ltf, Oxford, UK).

150 ***Muscle mechanics and architecture.*** B-mode and SWE clips were simultaneously acquired from
151 the gastrocnemius medialis using an ultrafast ultrasound scanner (SuperSonic Imagine, v12, Aix-en-
152 Provence, France) coupled with a linear array transducer (50mm, SuperLinear 4-15MHz, Vermon,
153 Tours, France). The muscle shear modulus, as assessed by SWE, was used as an indicator of muscle
154 stiffness (17). For all measurements, the ultrasound transducer was placed at the proximal third of
155 the lower leg length, defined as the distance between the medial malleolus and the femur's medial
156 epicondyle (18). The imaging plane was carefully aligned with the main muscle shortening direc-
157 tion and adjusted to avoid any blood vessels. The medio-lateral positioning was defined by the line
158 connecting the bony landmarks, as described earlier. For post-training assessments, pre-training
159 images were compared for each participant to guide probe placement. SWE settings, including tem-
160 poral and spatial filters were set as described elsewhere (19). A custom-made transducer holder was
161 attached to the skin with double-sided adhesive tape and secured with straps (applying minimal
162 pressure) to prevent any displacement during ankle rotations. SWE and B-mode windows were
163 simultaneously displayed and acquired on the ultrasound scanner for offline image processing (Fig-
164 ure 1A). To ensure that the region of interest was the same pre- and post-tests, B-mode images of
165 the pre-test were used to place the probe during the post-test. The sampling rate for SWE and B-
166 mode were 1.1-1.3Hz and 11Hz respectively.

167 ***Electromyography.*** Myoelectric activity was recorded for the gastrocnemius lateralis, soleus, and
168 tibialis anterior muscles using surface electromyography (EMG; MiniWave, Cometa, Bareggio,
169 Italy). The sampling rate was set at 5000 Hz, and data was recorded with an analog-digital convert-
170 er. Electrodes were placed in accordance with the SENIAM guidelines (20).

171

172 **Baseline and follow-up assessments**

173 All participants were asked to refrain from any lower limb strength training for 48 hours prior to the
174 testing sessions conducted before and after the training program. Pre-testing sessions were per-
175 formed 48 hours before the commencing of the eccentric training program, whereas post-testing
176 sessions were conducted 4 to 5 days after the last training session. Pre- and post-testing sessions
177 were performed at the same period of the day (± 4 hours). Investigators were blinded to group allo-
178 cation during the pre-testing session but not during the post-testing session.

179 The testing session comprised five steps. First, the passive maximal ankle dorsiflexion range of mo-
180 tion (ROM) was assessed. Briefly, the ankle was passively rotated at a slow and constant velocity
181 ($\sim 1^\circ/\text{s}$) from 40° of plantar flexion to the maximal dorsiflexion, defined as the onset of muscle
182 stretching pain. Two trials were conducted with a 1 min rest interval. The highest score across trials
183 was considered as the maximal dorsiflexion ROM. Second, five stretching cycles were performed at
184 $5^\circ/\text{s}$ between 40° of plantar flexion and 80% of the maximal dorsiflexion ROM for conditioning
185 purposes (21). Third, a stretching cycle was performed at $1^\circ/\text{s}$ within the same range of angular ro-
186 tation. Passive torque, ankle angle, EMG, ultrasound SWE and B-mode clips were continuously
187 recorded during the loading phase of the plantar flexion muscle group (axial) stretching. Through-
188 out the preceding steps, participants were instructed to remain as relaxed as possible. Fourth, fol-
189 lowing a preliminary warm-up, participants were asked to perform two maximal voluntary isomet-
190 ric contractions (MVIC) in plantar flexion and dorsiflexion in neutral ankle position. Only the high-
191 est MVIC was used for the statistical analysis. Peak isometric torque was registered, and EMG sig-
192 nals were further used (offline) to normalize myoelectric activity during passive ankle rotations.
193 Finally, two eccentric contractions from 40° of plantar flexion to 80% of the maximal ROM in dor-
194 siflexion were performed at $30^\circ/\text{s}$ to evaluate the peak eccentric torque. The highest peak eccentric
195 torque measured during the pre-training assessment was used for further analysis. The post-training
196 eccentric torque was then calculated at the same ankle angle at which the pre-training peak eccen-
197 tric torque was measured. All contractions were performed with a rest interval of 90-s.

198

199 **Intervention protocols**

200 All participants performed twenty-four sessions of eccentric plantar flexor exercises over the course
201 of eight weeks. The progressive nature of the training protocol was maintained by monitoring the
202 changes in the maximum concentric repetition (1-RM) every other training session for each exer-
203 cise. The eccentric workload was set at 100% of the concentric unilateral 1-RM. The training pro-
204 gram was closely monitored and supervised. Each training session started with a 10-min warm-up
205 specifically focused on the plantar flexor muscle group. The training sessions comprised: i) eccen-
206 tric heel drops performed on a Smith machine (10 sessions; Figure 2A), or ii) eccentric heel drops
207 executed on the oblique press (10 sessions; Figure 2B), or iii) eccentric plantar flexions performed
208 on an isokinetic dynamometer (4 sessions: 6th, 12th, 18th and 24th; Figure2C).

209 For the sessions involving eccentric heel drops on the Smith machine, participants stood upright
210 with the knees and hips straight, while a bar rested on their shoulders behind the neck (22). To safe-
211 ly execute the heel drops on the inclined leg press, participants were instructed to flex their hips at
212 90° and to maintain a slight flexion in their knees to prevent hyperextension during the movement.
213 Both groups executed bilateral concentric plantar flexion followed by unilateral eccentric plantar
214 flexion. The participants were carefully instructed to synchronize their movements with a 1-1-3-1
215 rhythm provided by a metronome. This rhythmic pattern consisted of 1-s for the bilateral heel rise,
216 1-s for the isometric hold, 3-s for the heel drop, (i.e. eccentric exercise) and 1-s of bilateral rest.
217 Participants performed four sets of ten repetitions on both the right and the left side, alternating left
218 and right sides, when their 1-RM was determined at the beginning of the session. Every other ses-
219 sion, when the 1-RM was not tested, they completed five sets of ten repetitions for each leg. Each
220 set was followed by a 90-s rest interval. The workload was adjusted to match the concentric 1-RM
221 of the right foot (Table 1).

222 The ankle range of motion, and consequently, the length of the plantar flexor muscles, were the
223 only parameters that differed between the two testing conditions: short-muscle vs. long-muscle
224 lengths. The short-muscle length training group performed the eccentric plantar flexions from 30°

225 plantar flexion to 0° (neutral position, with the foot on the floor). The long-muscle length training
226 group executed the eccentric plantar flexions from 0° (neutral position) to maximal dorsiflexion (~
227 30° of dorsiflexion, depending on the participants' maximal dorsiflexion range of motion). To en-
228 sure that participants respected the range of motion set for each training condition, a measuring tape
229 (in cm) was positioned on both the inclined smith squat and press machines. The tape was calibrat-
230 ed to the targeted range of motion based on joint angles previously measured in static conditions
231 using a manual goniometer. Real-time guidance was provided by one of the investigators during the
232 training session to ensure that range of motion was respected for each condition (short-muscle *ver-*
233 *sus* long-muscle lengths training group).

234

235 **Data analysis**

236 Data were processed using custom-made MATLAB (v.R2018a, MathWorks, Natick, Massachu-
237 setts, USA) scripts. All data remained coded to enable analysis to be conducted in a fully blinded
238 manner.

239 **Shear modulus.** Shear modulus data were analyzed as described elsewhere (19). The region of in-
240 terest was set to be the largest possible within the shear wave elastography map, excluding all non-
241 muscle regions and saturation (Figure 1B). Consistency in this region was ensured across both pre-
242 and post-testing. The slack angle was visually determined as the onset of increase in shear modulus
243 during the passive muscle stretching (23).

244 **Fascicle length.** Two fascicles were analyzed from the B-mode clips, exported as DICOM files,
245 using an adapted version of the 5.2 UltraTrack software (24). Fascicle length was defined as the
246 distance between the insertions of the fascicle into the superficial and deep aponeuroses. Linear
247 extrapolation was used where fascicle length exceeded the image. Manual corrections were made
248 where the tracking algorithm did not track the fascicle length well. Briefly, for each clip of muscle
249 axial loading, two fascicles were successfully linearly tracked and averaged for statistical analyses
250 purposes (Figure 1C). The slack length was considered as the fascicle length at the slack angle.

251 **Surface Electromyography.** EMG data from gastrocnemius lateralis, soleus, and tibialis anterior
252 muscles were band-pass (20-400Hz), and band-stop (50Hz) filtered with 2nd order Butterworth. The
253 root mean square of the EMG (EMG-RMS) was calculated on a 300 ms sliding window for both
254 MVIC and throughout the loading phase of the stretching cycle. Muscle activation was then ex-
255 pressed as a percentage of the maximal EMG-RMS activity reached during MVIC (25).

256 **Ankle torque and position.** The ankle torque and joint angle were filtered by a 2nd order Butter-
257 worth low-pass filter (5Hz). The torque was corrected for gravity effects of the dynamometer
258 toolkit.

259 **Synchronization.** Myoelectric activity (EMG), mechanical (torque and angle) and ultrasound-based
260 data (shear modulus, fascicle length) were synchronized using the trigger output generated by the
261 ultrasound scanner at each SWE measurement. Pre- to post-comparisons of muscle geometrical
262 (fascicle length) and mechanical (shear modulus and passive ankle torque) were conducted continu-
263 ously between 40° plantar flexion and 80% of the common greatest maximal dorsiflexion ROM
264 registered – for each participant – prior the training protocol (or following, in case where maximal
265 dorsiflexion ROM decreased). To facilitate continuous statistical analysis and data visualisation, the
266 relationships between ankle angle or fascicle length, and the muscle shear modulus and ankle pas-
267 sive torque were then interpolated every 5%, resulting in a 21-point curve (19). Muscle shear modu-
268 lus was also analysed as a function of the raw ultrasound-measured fascicle length and the fascicle
269 length normalized to the previously quantified slack length.

270

271 **Statistical analysis**

272 Two-way repeated measures analysis of variance (ANOVA) was used to investigate the effects of
273 eccentric training conditions (short-muscle length *versus* long-muscle length) and time (pre-training
274 *versus* post-training) on eccentric peak torque, gastrocnemius medialis slack angle and MVIC. Post-
275 hoc analyses were performed using Bonferroni tests for multiple comparisons. Effect sizes are
276 reported as partial *eta* squared (η_p^2). Effects of 0.01, 0.06, and 0.14 were small, medium, and large,

277 respectively. A two-way analysis of variance (ANOVA-SPM) with repeated measures on one factor
278 was performed in MATLAB (R2021a, The MathWorks Inc) using one-dimensional statistical
279 parametric mapping (SPM, Version M.0.4.10 released 2021-09-23; www.spm1d.org) (26) to
280 investigate the effects of eccentric training conditions (short-muscle length *versus* long-muscle
281 length) and time (pre-training *versus* post-training) on ankle passive torque, gastrocnemius medialis
282 fascicle length, and gastrocnemius medialis shear modulus as a function of ankle. We further
283 examined the effects of eccentric training conditions and time on the gastrocnemius medialis shear
284 modulus as a function of both fascicle length and fascicle length normalized to the slack length.
285 Pairwise comparisons with Bonferroni corrections were applied where significant main or
286 interaction effects were found. The normal distribution of the data was confirmed through the
287 Shapiro-Wilk test prior each analysis of variance. The significance level for all statistical
288 comparisons was set at $p < 0.05$. The ANOVAs and graphics were performed in GraphPad Prism
289 (version 8; GraphPad Software, Inc., CA, US). Descriptive data are presented as mean \pm standard
290 deviation.

291 RESULTS

292 Of the initial 33 participants, four withdrew from the training protocol, and one did not commence
293 participation. A total of 28 participants successfully completed the training program, with an
294 adherence rate of 24.0 ± 0.8 sessions completed. Data from 27 participants were successfully
295 analyzed (Figure 3): twelve in the short-muscle length group (5 women, age 19.2 ± 1.1 years, height
296 172.2 ± 10.9 cm, body mass 64.5 ± 10.8 kg, means \pm SD) and fifteen in the long-length group (4
297 women, age 20.3 ± 1.7 years, height 174.1 ± 11.4 cm, body mass 66.3 ± 10.8 kg). One participant
298 (short-muscle length group) was excluded from the statistical analysis because the mechanical data
299 file from the post-testing session was incomplete due to a recording issue. Prior to participating in
300 the training protocol, participants reported an average physical activity level of 2.6 ± 1.0 hours per
301 week, engaging in physical activity approximately 4.7 ± 1.7 times each week.

302 [Figure 3]

303 Functional outcomes

304 There were no significant group*time interactions for the gastrocnemius medialis slack angle,
305 plantar flexion MVIC and peak eccentric torque (Figure 4). However, a significant time effect
306 revealed an increase of 9.5% in plantarflexion MVIC ($F=7.065$; $p<0.046$; $\eta_p^2=0.371$) following
307 eccentric training. No effects of training or time were observed on the gastrocnemius medialis slack
308 angle.

309 Muscle and joint adaptations

310 The averaged continuous relationships between ankle angle and gastrocnemius medialis fascicle
311 length, shear modulus, and ankle passive torque are illustrated in Figure 5. They depict the eccentric
312 training effects for both training groups and peak eccentric torque.

313 **Fascicle length.** Two-way ANOVA-SPM analysis revealed a significant group*time interaction
314 between $39.5 \pm 0.7^\circ$ and $22.9 \pm 1.6^\circ$ of ankle plantar flexion ($p=0.045$). Post-hoc analyses indicated
315 a significant increase in gastrocnemius medialis fascicle length following the eccentric training

316 performed at long-muscle length, specifically between $-39.8 \pm 0.5^\circ$ and $-36.8 \pm 0.8^\circ$ in plantar
317 flexion (Figure 5A; $p=0.011$). In the long-muscle length group, fascicle length measured prior to the
318 training protocol were $4.23 \pm 0.67\text{cm}$ at $-39.8 \pm 0.5^\circ$ and $4.23 \pm 0.66\text{cm}$ at $-36.8 \pm 0.8^\circ$. Following
319 the training protocol, we observed an increase of $8.5 \pm 10.0\%$ ($3.4 \pm 4.2\text{ mm}$) and $8.6 \pm 10\%$ ($3.4 \pm$
320 4.2 mm) for both angles respectively. No changes were detected for the eccentric training
321 performed at short-muscle length (Figure 5B).

322 **Muscle shear modulus.** There were no effects of the eccentric training protocols on gastrocnemius
323 medialis shear modulus across the entire range of ankle motion (Figures 5C and 5D). Similarly, we
324 did not observe any effects of eccentric training when evaluating the shear modulus as a function of
325 fascicle length or fascicle length normalized to the slack length (Figures 6A and 6B). Additionally,
326 SPM analyses did not detect any differences between the training conditions (short-muscle length
327 *versus* long-muscle length).

328 **Ankle passive torque.** ANOVA-SPM analyses revealed a statistically significant time effect of
329 eccentric exercise training on passive ankle torque at angles below the muscle slack length.
330 Specifically, changes were observed from $-39.7 \pm 0.6^\circ$ to $-13.8 \pm 2.8^\circ$ in plantarflexion between
331 pre- and post-training conditions. No group*time interaction was identified (Figure 5E and 5F).

332 **EMG**

333 There were no significant effects of group or time on the EMG-RMS of the gastrocnemius lateralis,
334 soleus, and tibialis anterior muscles at any ankle angle. Activity levels across axial muscle loading
335 were low: $0.3 \pm 0.3\%$ (maximum: 1.4%) for the gastrocnemius lateralis, $0.4 \pm 0.3\%$ (maximum:
336 1.4%) for the soleus, and $0.2 \pm 0.3\%$ (maximum: 1.4%) for the tibialis anterior. Specifically, only
337 2.0% of all data points for the gastrocnemius lateralis exceeded 1.0% of muscle activation. Similar-
338 ly, 1.5% and 1.3% of all data points of the soleus and tibialis anterior exceeded 1.0% of muscle ac-
339 tivation, respectively.

340 **Discussion**

341 This study demonstrates that an 8-week eccentric training program targeting the plantar flexor mus-
342 cle group at a long-muscle length significantly increases gastrocnemius medialis fascicle length.
343 This increase in fascicle length was not associated with adaptations in passive muscle mechanical
344 properties, as evidenced by two primary findings. First, the relationships between ankle angle-
345 muscle shear modulus and fascicle length-muscle shear modulus remained unchanged across the
346 entire ankle ROM following the eccentric training. Second, the increase in fascicle length was sig-
347 nificant only at plantarflexion angles below the slack length and hence in the absence of any passive
348 muscle (axial) tension. These findings provide new insights into the mechanisms underlying the
349 long-term macrostructural adaptations of the GM muscle in response to eccentric training.

350 The effects of the eccentric training on muscle strength are in line with those reported in the
351 literature (1). In the present study, the long-term eccentric training led to overall improvements in
352 peak isometric strength of 10.74 ± 26.76 N.m (mean increase of 9.5 %), which as on average 113.56
353 ± 31.35 N.m before the protocol. These findings align with previous studies that reported an
354 average increase of 13 % in plantar flexors MVIC following eccentric training lasting 7 and 12
355 weeks (27, 28). Notably, the enhancements in muscle strength observed in this study did not differ
356 between the short-muscle length and long-muscle length training groups. This observation suggests
357 that adaptations in muscle length observed in the long-muscle length group were decoupled from
358 changes in muscle strength. This reinforces the relevance of our methodological approach,
359 comparing the effects of two different eccentric-based training stimuli on fascicle lengthening and
360 passive tissue mechanics. There was no significant time effect for peak eccentric torque ($p = 0.41$).

361 Notably, one participant in the long-muscle length group exhibited an unexpected decrease of 84.9
362 N.m in peak eccentric torque following the training protocol. Although this behavior might
363 categorize the participant as an outlier for this specific variable, the participant was not excluded
364 from the analysis because no outlier-like responses were detected in the primary outcome measures.

365 Eccentric training performed at both short- and long-muscle lengths did not alter ankle passive
366 torque between $13.8^{\circ} \pm 2.8^{\circ}$ in plantar flexion and 80% of the maximum dorsiflexion ROM. This is
367 in line with previous observations (29). Similar findings have been reported across the full passive
368 stretching cycle (14). In contrast, we found a significant decrease in ankle passive torque at plantar
369 flexion angles around or below the slack angle ($19.9 \pm 4.4^{\circ}$ in plantarflexion) following both
370 eccentric training conditions. Passive ankle torque is influenced by multiple structures, including
371 monoarticular plantarflexors (e.g., soleus), monoarticular dorsiflexors (e.g., tibialis anterior), and
372 biarticular plantarflexors (e.g., gastrocnemii). Given that the GM shear modulus remained
373 unaffected by training, and that passive torque changes occurred specifically below the GM muscle
374 slack angle, it is likely that the decrease in passive torque in plantar flexion angles was unrelated to
375 the GM muscle. Although the reasons underlying these changes remain unclear, they might be
376 related to a decrease in passive tension of the soleus and/or an increase in passive tension of
377 dorsiflexors (e.g., tibialis anterior). Considering that the maximum difference occurs at 40° of
378 plantar flexion, it is likely attributed to ankle dorsiflexors rather than the soleus. The increase in
379 passive tension of the ankle dorsiflexors may result from a decrease in slack length, an increase in
380 muscle elastic modulus, and/or hypertrophy. These changes could be associated with isometric
381 loading or the co-activation of these muscles during the eccentric exercise.

382 The increase in fascicle length in the long-muscle length group (mean increase of 8.5%) was in line
383 with previous findings. For instance, Duclay *et al.* (2009) observed a 6.8% increase in ultrasound-
384 measured fascicle length of the gastrocnemius medialis – assessed at neutral ankle position –
385 following an eccentric training of similar duration and load (27). However, the increase in fascicle
386 length observed in the present study was smaller compared to studies involving other muscles, such
387 as the quadriceps, where increases typically range from 10% to 20% (30–33). Our unique approach
388 enabled us to investigate, for the first time, the effects of eccentric training on fascicle length over a
389 large range of muscle lengthening, rather than at a single joint angle (as commonly studied).
390 Specifically, our findings indicate that fascicle length significantly increased only at plantar flexion

391 angles between $39.5 \pm 0.7^\circ$ and $36.8 \pm 0.8^\circ$. An important finding from the present study is that
392 fascicle lengthening did not occur in the short-muscle length training group. This demonstrates that
393 the range of muscle-tendon length at which eccentric training is performed is crucial for eliciting
394 structural adaptations, potentially resulting from sarcomerogenesis. Additionally, in the long-muscle
395 length training group, fascicle length increased only below the gastrocnemius medialis slack angle
396 (i.e., absence of any passive axial tension). This indicates that muscle passive tension – and thus
397 connective tissue adaptations – did not contribute to the increase in muscle fascicle length. This
398 conclusion is further supported by the lack of significant changes in muscle shear modulus, which
399 was measured at the same location as the fascicle length (Figure 1) across the stretching cycle (i.e.,
400 ankle ROM). Together, these results strongly suggest that the changes in fascicle length may be
401 related to an increase in the number of sarcomeres in series or an increase in the sarcomere length,
402 independent of changes in passive muscle mechanics. Considering the study of Pincheira *et al.*
403 (2021), an increase in sarcomere length may be the preferential mechanism involved in these
404 adaptations (13). However, the differences in training duration (3 weeks *versus* 8 weeks in the
405 present study) and the muscles examined (biceps femoris *versus* gastrocnemius medialis) limit
406 direct comparisons between the studies. It is possible that 3 weeks of eccentric training were
407 insufficient to trigger an increase in the number of sarcomeres in series and that this increase may
408 occur after 8 weeks of training. Finally, while it is feasible to measure the shear modulus of
409 hamstrings during passive lengthening (34), tracking the fascicle length of these very long muscles
410 remains challenging. This is the reason why the present study was focused on the gastrocnemius
411 medialis muscle.

412 Comparing the effects of the eccentric training used in the present study with the chronic muscle-
413 directed stretching protocol used by Andrade *et al.* (2020) reveals intriguing insights into the
414 mechanical properties of the gastrocnemius medialis (19). While the 12-week stretching protocol
415 resulted in a 13% decrease in shear modulus and an 8.2% increase in fascicle length at 0° of
416 dorsiflexion, the 8-week eccentric training led to a similar magnitude of fascicle length increase but

417 in the absence of muscle mechanical adaptations. Together, these observations suggest distinct
418 mechanisms driving skeletal muscle adaptations in response to long-term loading stimuli (i.e.,
419 passive stretching *versus* eccentric contraction).

420 We acknowledge some limitations in this study. Firstly, we used a linear extrapolation method to
421 measure fascicle length, which may introduce errors due to the potential curvature of the fascicle or
422 aponeurosis (35). However, gastrocnemii fascicles typically exhibit a relatively linear arrangement,
423 and measurement errors associated with fascicle curvature have been shown to be negligible in
424 resting gastrocnemius medialis muscle (35–37). Furthermore, the typical length of the gastrocnemii
425 fascicles is approximately equal to the size of the (linear) transducer used for the assessments (i.e., 5
426 cm). In this study, the average extrapolated fascicle length was $36.5\% \pm 10.0\%$ at the highest
427 plantar flexion angle (40°) and $40.1\% \pm 10.4\%$ at 80% of the maximal dorsiflexion range of motion.
428 Second, slight variations in probe location may have occurred due to training-induced hypertrophy
429 and changes in muscle geometry. However, we ensured that images were captured in the same
430 muscle region using bone references, applying minimal pressure, and rigorously positioning
431 participants in the same manner in the isokinetic dynamometer system before and after the
432 interventions. Additionally, we did not include a control group. Third, this study focused on the
433 muscle mechanics and architectural adaptations of the gastrocnemius medialis. However, similar
434 adaptations may have occurred in other plantar flexor muscles, particularly within the triceps surae.
435 While adaptations in the gastrocnemius lateralis are likely, they may have been to a lesser extent
436 than those in the gastrocnemius medialis (11). We speculate that adaptations in the monoarticular
437 soleus were more limited, given the specific nature of the training configuration (i.e., knee
438 extended). Fourth, we experienced some technical issues with the EMG system during the post-
439 training assessments, resulting in missing EMG data for four participants. To address these issues,
440 we carefully inspected passive torque, muscle shear modulus, and B-mode images to confirm that
441 no involuntary muscle activation occurred during the stretching cycles in post-training tests.
442 Moreover, during the pre-training test session, none of these participants had an RMS-EMG

443 activity >1% on the three measured muscles. Lastly, for the remaining participants, the RMS-EMG
444 activity of the gastrocnemius medialis, soleus and tibialis anterior muscles was notably low, well
445 below the 2% threshold identified as potential factor affecting muscle and joint stiffness (25).
446 However, it is important to acknowledge that the primary muscle of interest in this study, the
447 gastrocnemius medialis, was not assessed due to the practical challenges associated with obtaining
448 EMG data concurrently with ultrasound imaging during a passive muscle stretching.

449 **CONCLUSION**

450 This study provides new insight into how the strength, macrostructure and mechanical properties of
451 the gastrocnemius medialis muscle adapt over eccentric training performed at different muscle
452 lengths. Eight weeks of eccentric training at both short-muscle or long-muscle lengths induced
453 similar increases in isometric and eccentric peak force. Interestingly, only the eccentric training
454 performed at long-muscle length led to significant increases in fascicle length, which occurred at
455 plantar flexion angles below the muscle slack length (i.e., absence of any passive axial tension).
456 This highlights the importance of the muscle-tendon length range during eccentric exercises for
457 eliciting adaptations in fascicle length. Additionally, none of eccentric training groups exhibited
458 changes in local muscle shear modulus, measured at the same site as the fascicle length. Therefore,
459 the increase in fascicle length observed in our study may be attributed to an increase in sarcomere
460 length and/or an increase in sarcomeres in series, which appears to occur independently of
461 adaptations in passive muscle-tendon mechanical properties. Further studies are required to better
462 understand the influence of training duration and the trained muscle on changes in muscle fascicle
463 properties. Finally, the design employed in the present study, investigating both short-muscle and
464 long-muscle eccentric training groups, could be particularly relevant for assessing changes in
465 muscle mechanics and fascicle adaptations independently of changes in muscle strength. Lastly, we
466 acknowledge that our findings cannot be generalized to other skeletal muscles and do not intend to
467 provide direct recommendations regarding the most effective eccentric training protocols for
468 inducing structural changes at the tissue level. For example, the eccentric load was set at 1 maximal
469 concentric repetition. Protocols done with higher loads may provide different results.

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Figure 1. **A.** Setup for the ultrafast ultrasound imaging acquisitions; **B.** Example of a shear wave elastography map, with the region of interest for shear modulus measurements outlined in yellow; **C.** Example of fascicle length analysis using UltraTrack software (Farris & Litchwark, 2016).

Figure 2. Eccentric training exercises and ankle positions for each eccentric training condition. The first column corresponds to 30° of plantar flexion (starting position for short-muscle length group). The second column indicates the neutral position (end position for short-muscle length training group and starting position for long-length training group). The third column illustrates the maximal dorsiflexion position (end position for the long-length training group); **A.** Heel drop exercise performed on the smith machine; **B.** Heel drop exercise performed on the oblique press; **C.** Isokinetic eccentric plantar flexion exercise.

584 **Figure 3.** Flow chart illustrating the study enrollment, allocation, and analysis process.

Figure 4. Pre- to post-training effects of eccentric training performed at long-muscle and short-muscle lengths on plantar flexion maximal voluntary isometric contraction (MVIC) (**A**), peak eccentric torque in plantar flexion (**B**) and gastrocnemius medialis slack angle (**C**) per training condition (short-muscle length *versus* long-muscle length). There were no significant group*time interactions for the gastrocnemius medialis slack angle, plantar flexion MVIC and peak eccentric torque. A significant time effect revealed an increase of 9.5% in plantarflexion MVIC ($p < 0.046$) following eccentric training. No effects of training or time were observed on the gastrocnemius medialis slack angle and peak eccentric torque. Individual data points are represented by red square (pre-training, \square) and blue triangles (post-training, \triangle). MVIC: maximal voluntary isometric contraction; GM: gastrocnemius medialis.

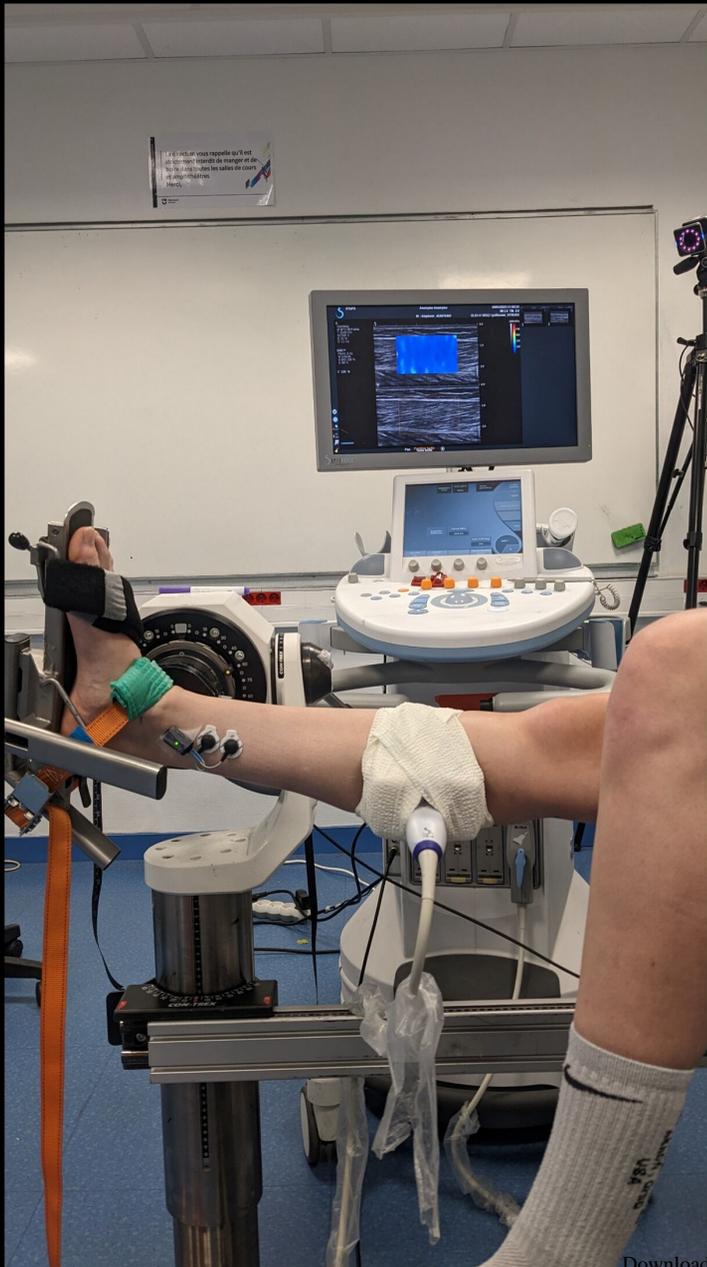
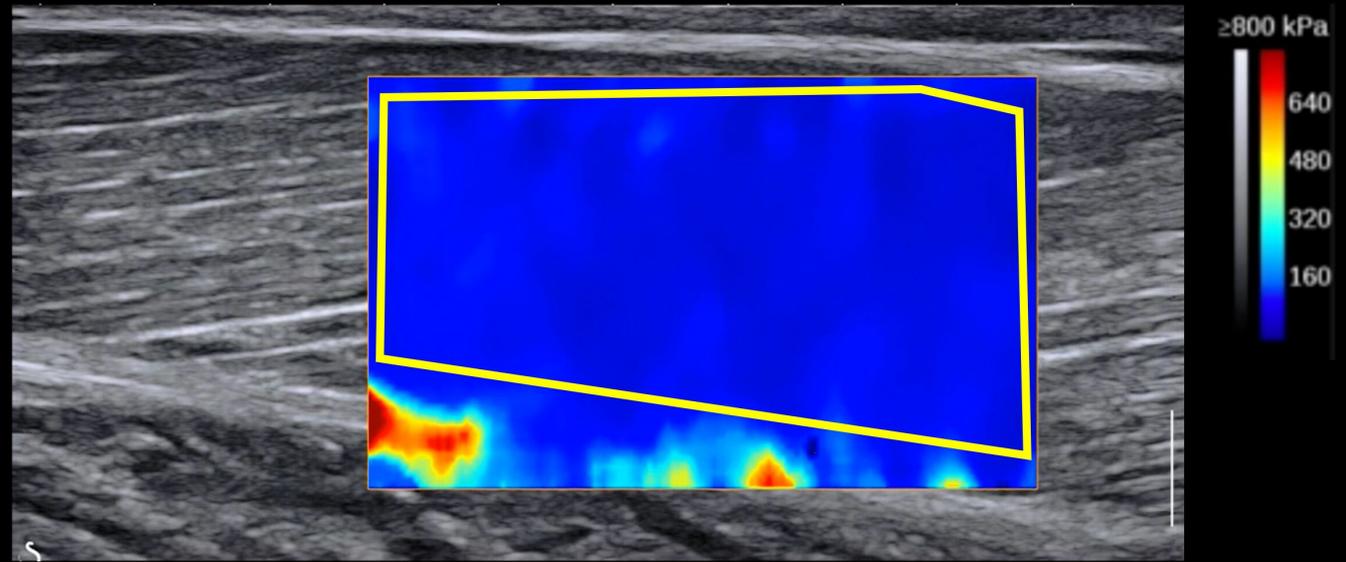
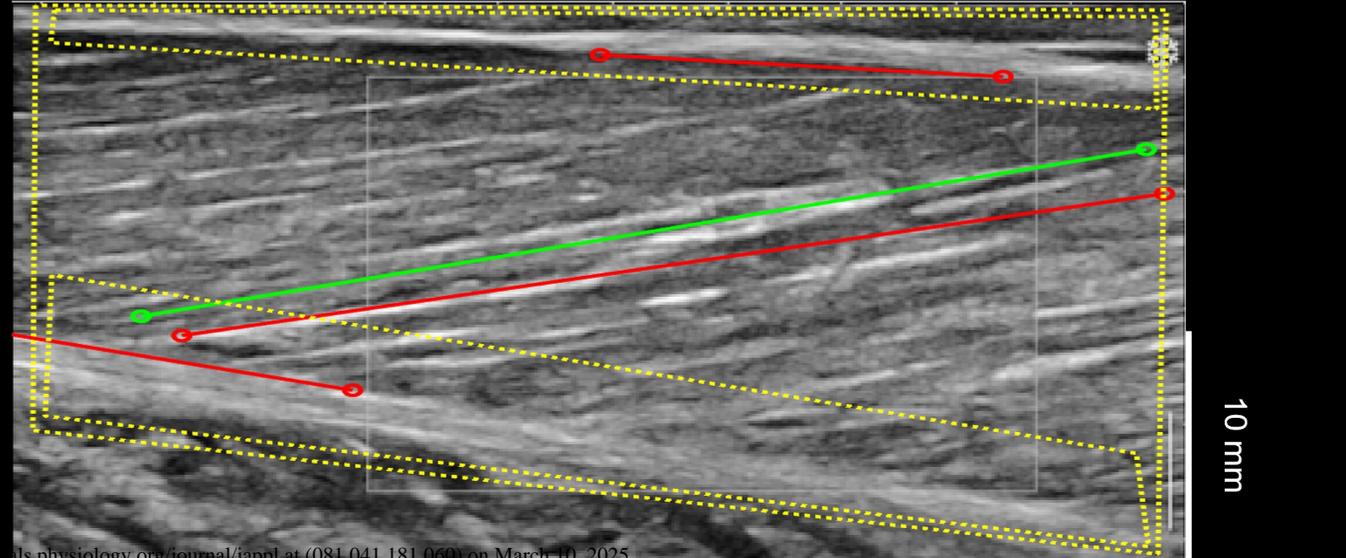
Figure 5. Effects of 8-week eccentric training at long-muscle length and short-muscle length on gastrocnemius medialis (GM) fascicle length (**A & B**), gastrocnemius medialis muscle shear modulus (**C & D**), and ankle passive torque (**E & F**) as a function of ankle angle. Panels **A**, **C**, and **E** correspond to long-muscle length training, while panels **B**, **D**, and **F** represent short-muscle length training. Individual data are illustrated as red squares (pre-training, \blacksquare) and blue triangles (post-training, \blacktriangle). GM: gastrocnemius medialis; Fl: Fascicle length; *denotes $p < 0.05$.

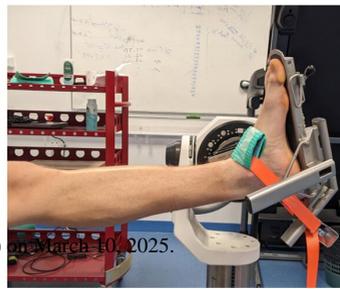
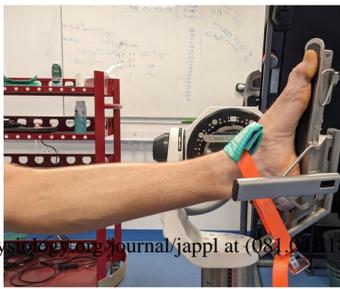
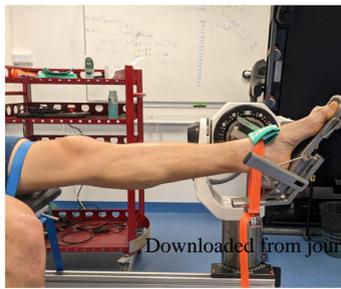
Figure 6. Gastrocnemius medialis muscle shear modulus as a function of fascicle length normalized to the slack length, pre- and post-training for the long-muscle length (**A**) and the short-muscle length (**B**) conditions. Individual data are illustrated as red squares (pre-training, \blacksquare) and blue triangles (post-training, \blacktriangle). GM: gastrocnemius medialis; Fl: fascicle length; Fl_0 : slack length; $Fl - Fl_0$: fascicle length normalized to the slack length).

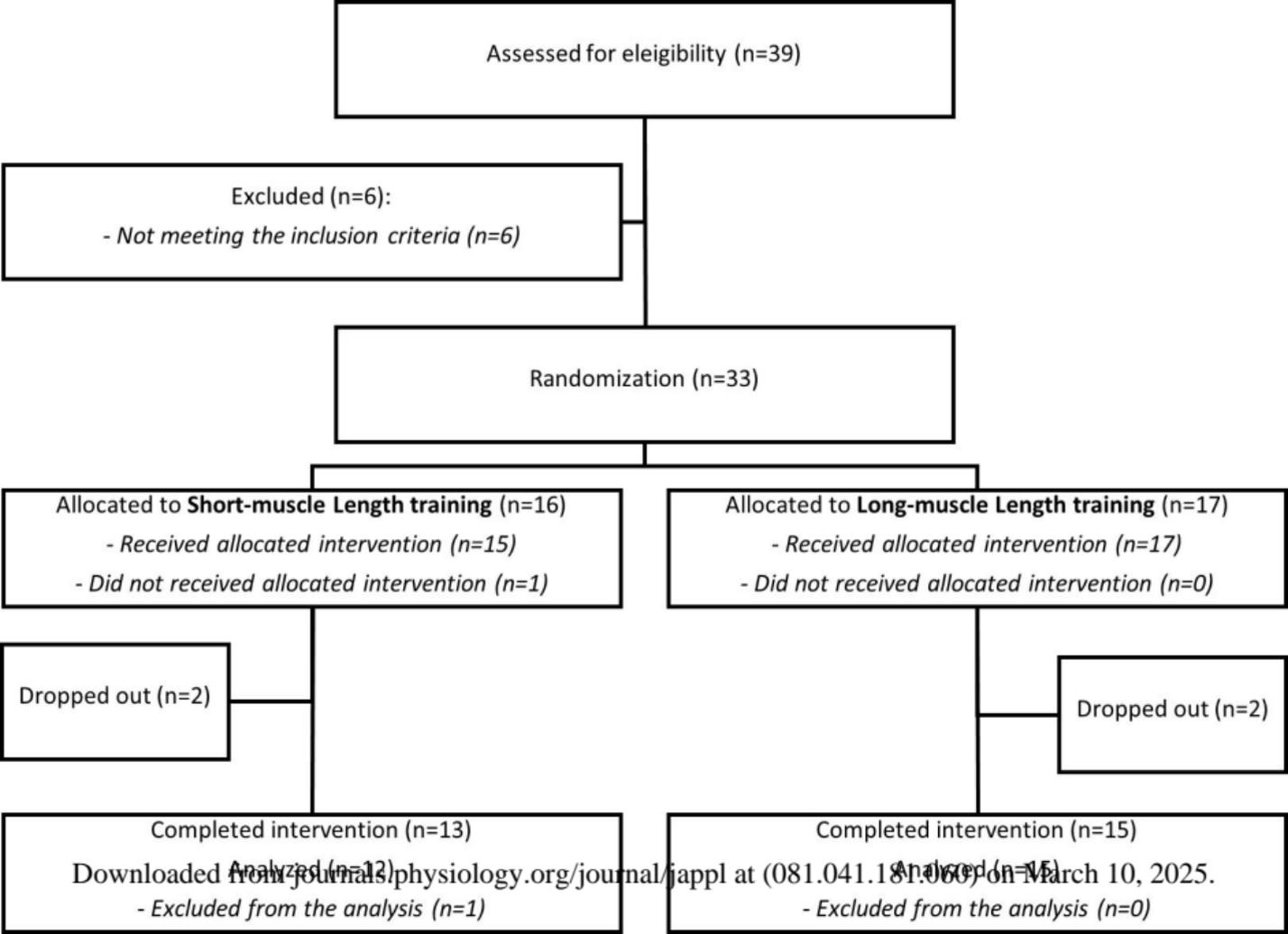
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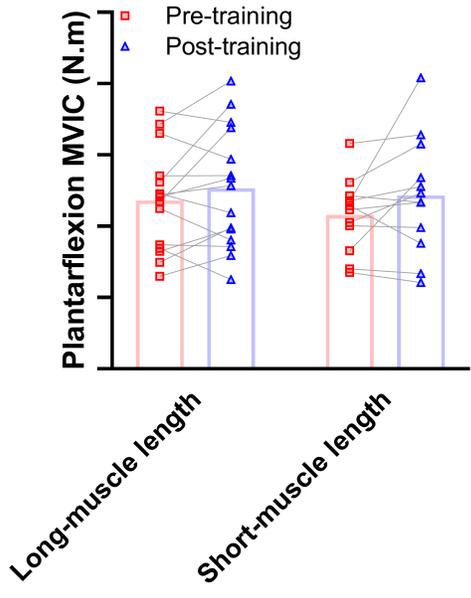
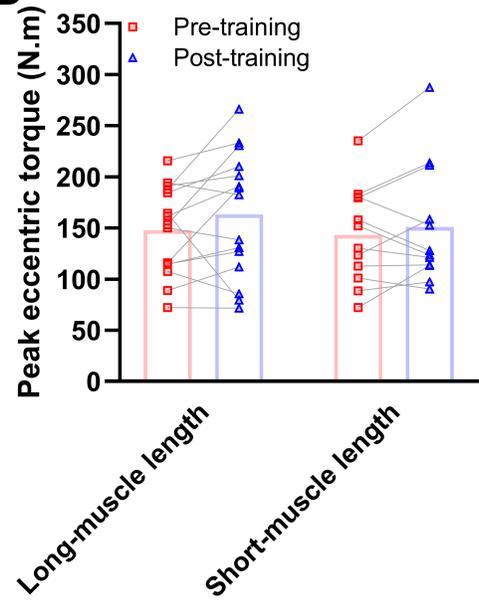
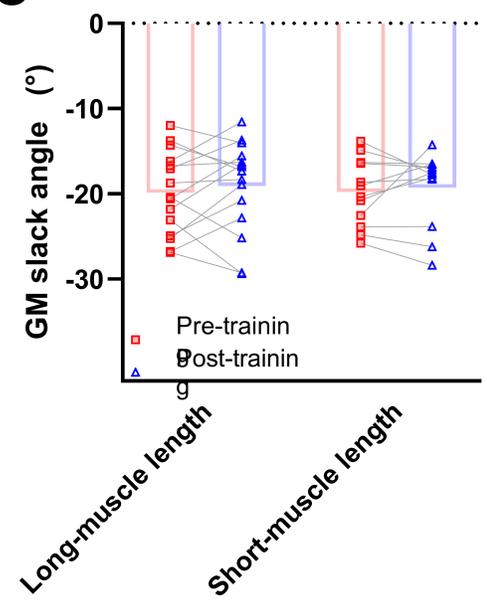
586 **TABLES LEGEND**

Table 1. Summary of the eccentric training protocol for each testing condition. 1-RM: one repetition concentric maximum; Con: concentric Ecc: eccentric; Isom: isometric. Note that the concentric part was performed bilaterally and, that for eccentric, right and left sides were involved alternatively.

A**B****C**

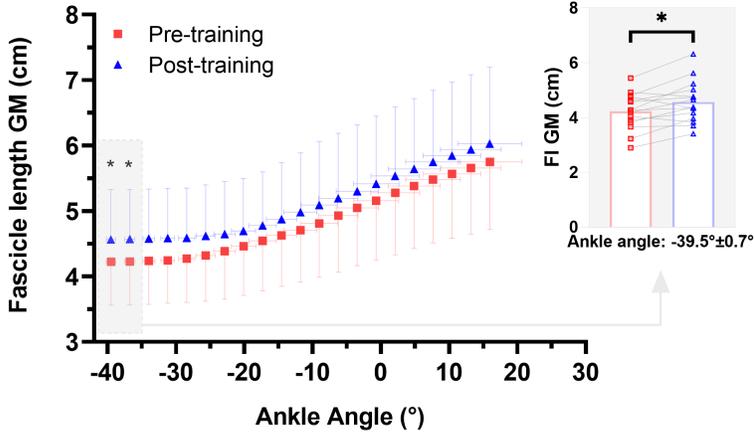
A**B****C**



A**B****C**

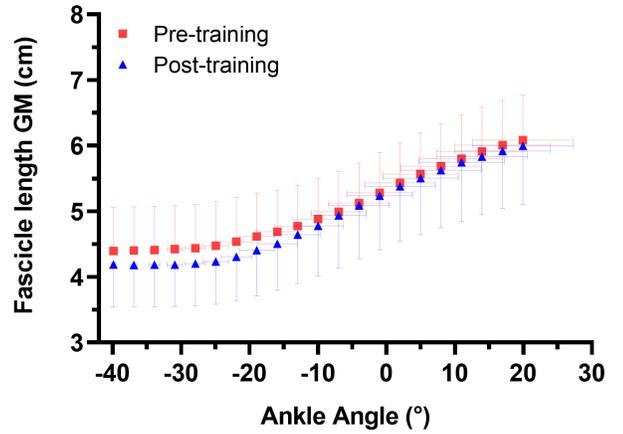
LONG-MUSCLE LENGTH

A

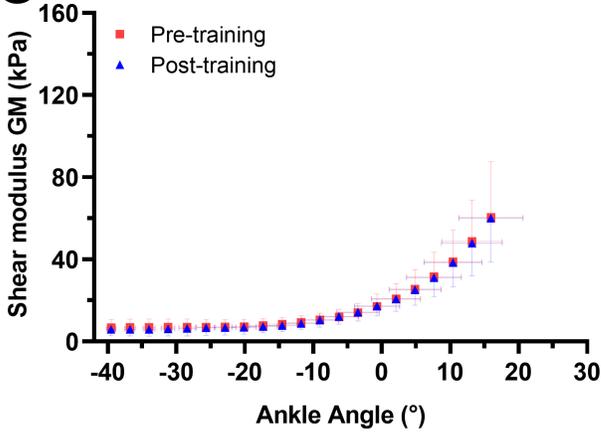


SHORT-MUSCLE LENGTH

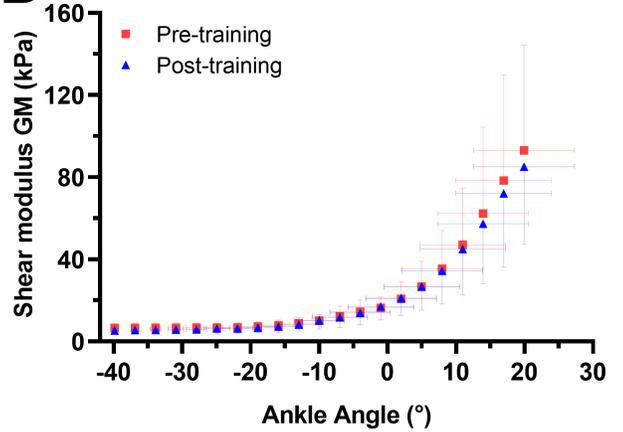
B



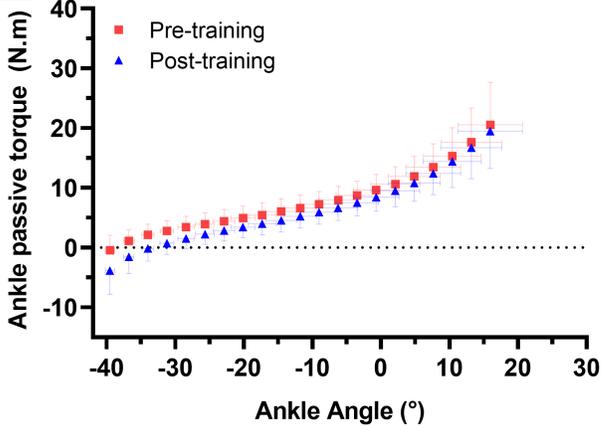
C



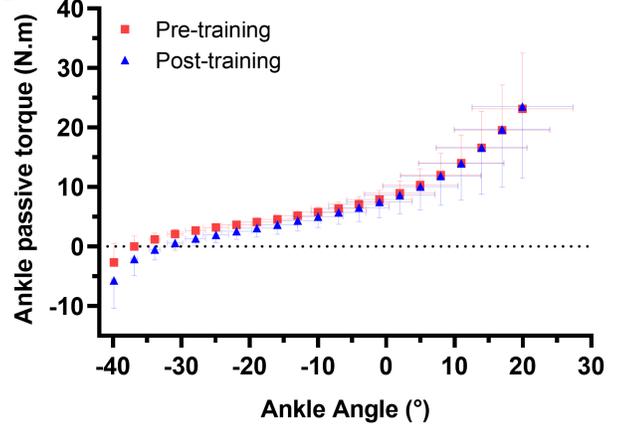
D



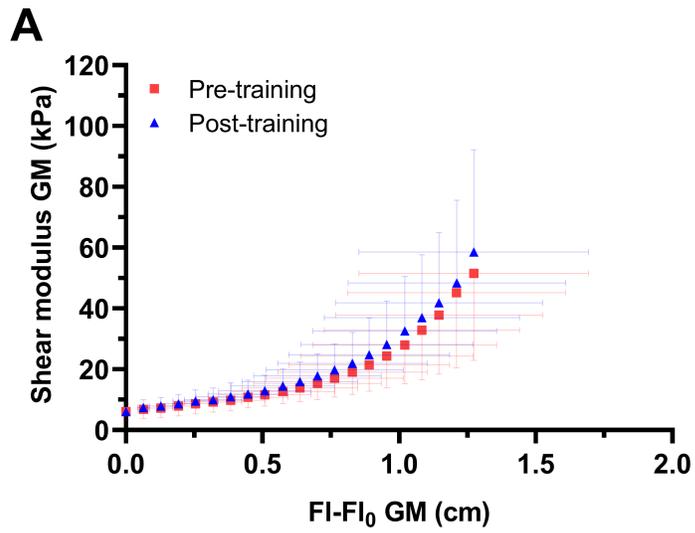
E



F



LONG-MUSCLE LENGTH



SHORT-MUSCLE LENGTH

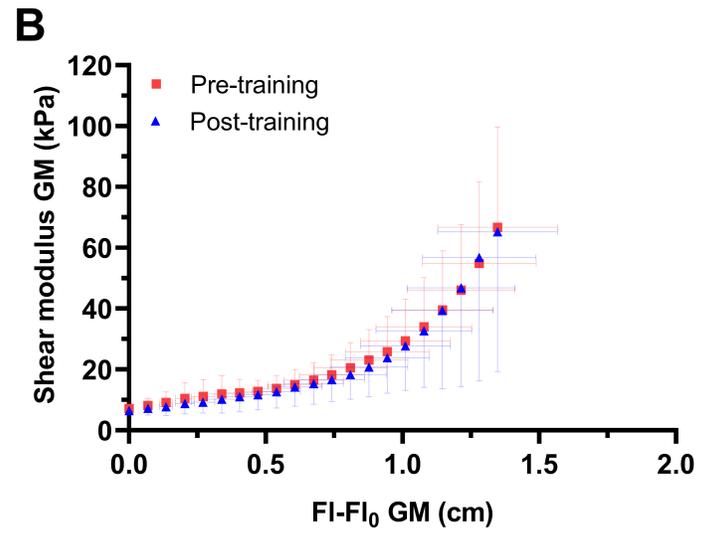


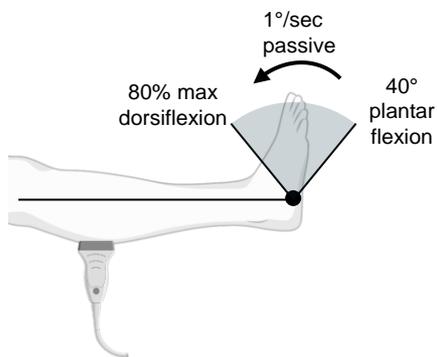
Table 1. Summary of the eccentric training protocols used in the short-muscle and long-muscle length groups. Note that the concentric phase was performed bilaterally, whereas the eccentric phase involved alternating between the right and left sides. Abbreviations: 1-RM: one repetition concentric maximum; Con: concentric; Ecc: eccentric; Isom: isometric.

Modality	Apparatus	Number of sessions	Prescription	Tempo (s) con-isom-ecc-rest	Recovery between series (s)	Loading dose
Isotonic	Heel drop on the Smith machine	5	5x10	1-1-3-1	90	100% of Concentric 1-RM
		5	1-RM assessment 4x10	1-1-3-1	90	100% of Concentric 1-RM
	Heel drop on the oblique press	5	5x10	1-1-3-1	90	100% of Concentric 1-RM
		5	1-RM assessment 4x10	1-1-3-1	90	100% of Concentric 1-RM
Isokinetic	Dynamometer	4	5x10	1-1-3-1	90	100% Eccentric

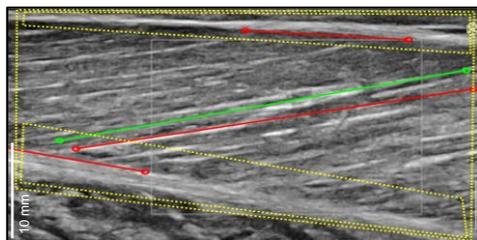
Eight weeks of eccentric training at long muscle length increase gastrocnemius medialis fascicle length without altering passive mechanics

METHODS

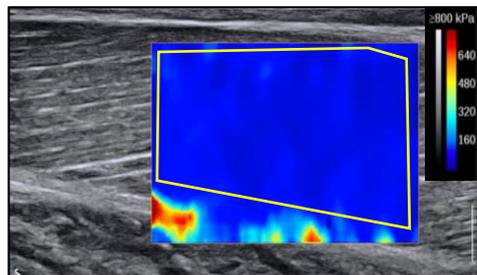
Outcomes measures:



Fascicle length

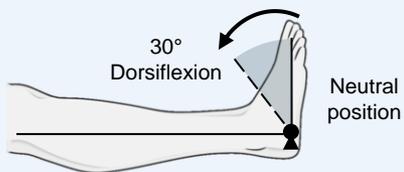


Shear modulus (stiffness)



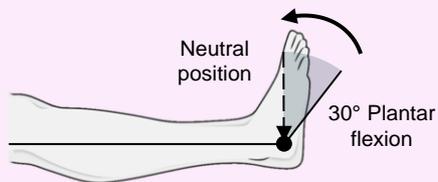
Eccentric training groups:

Long-muscle length (n=15)



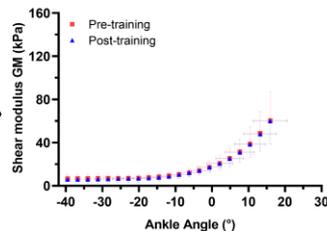
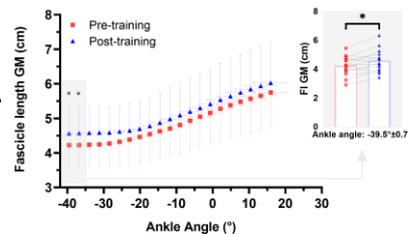
VS

Short-muscle length (n=13)

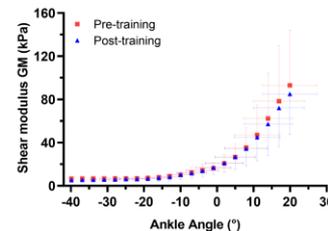
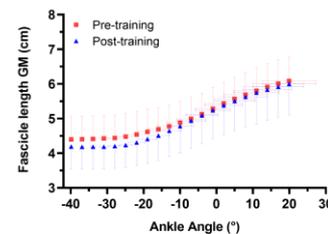


OUTCOMES

Long-muscle length



Short-muscle length



Fascicle length increased in the long-muscle length group, but only at plantar-flexed angles (i.e., without passive tension), while shear modulus remained unchanged

CONCLUSION

Fascicle length adaptations to eccentric training occurred independently of changes in passive muscle-tendon properties, likely reflecting increased sarcomere length and/or the addition of sarcomeres in series