

1 **Title:** Shorter Muscle Fascicle Operating Lengths Increase
2 the Metabolic Cost of Cyclic Force Production
3

4 **Running Title:** Shorter Muscles Increase Metabolic Cost
5

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19 **Abstract**

20 During locomotion, force-producing limb muscles are predominantly responsible for an animal's
21 whole-body metabolic energy expenditure. Animals can change the length of their force-
22 producing muscle fascicles by altering body posture (*e.g.*, joint angles), the structural properties
23 of their biological tissues over time (*e.g.*, tendon stiffness), or the body's kinetics (*e.g.*, body
24 weight). Currently, it is uncertain whether relative muscle fascicle operating lengths have a
25 measurable effect on the metabolic energy expended during cyclic locomotion-like contractions.
26 To address this uncertainty, we quantified the metabolic energy expenditure of human
27 participants as they cyclically produced two distinct ankle moments at three ankle angles (90°,
28 105°, 120°) on a fixed-position dynamometer using their soleus. Overall, increasing participant
29 ankle angle from 90° to 120° (more plantar flexion) reduced minimum soleus fascicle length by
30 17% (both moment levels, $p < 0.001$) and increased metabolic energy expenditure by an average
31 of 208% across both moment levels (both $p < 0.001$). For both moment levels, the increased
32 metabolic energy expenditure was not related to greater fascicle positive mechanical work
33 (higher moment level, $p = 0.591$), fascicle force rate (both $p \geq 0.235$), or model-estimated active
34 muscle volume (both $p \geq 0.122$). Alternatively, metabolic energy expenditure correlated with
35 average relative soleus fascicle length ($r = -0.72$, $p = 0.002$) and activation ($r = 0.51$, $p < 0.001$).
36 Therefore, increasing active muscle fascicle operating lengths may reduce metabolic energy
37 expended during locomotion.

38

39 **New & Noteworthy**

40 During locomotion, active muscles undergo cyclic length-changing contractions. In this study,
41 we isolated confounding variables and revealed that cyclically producing force at relatively
42 shorter fascicle lengths increases metabolic energy expenditure. Therefore, muscle fascicle
43 operating lengths likely have a measurable effect on the metabolic energy expenditure during
44 locomotion.

45 **Key Words:** Energetic, Economy, Efficiency, Dynamometer, Locomotion, Length

46 **Introduction**

47 During locomotion, many limb extensor muscles operate at shorter lengths than optimal for
48 active force production (1-6). For instance, during the stance phase of human walking and
49 running, soleus fascicles operate between ~0.65 to 1.01 of their optimal length (1, 2). A shorter
50 than optimal fascicle operating range is functionally relevant because muscles produce less force
51 per unit activation (7-9) and per adenosine triphosphate (ATP) utilization (10-13) further down
52 the ascending limb of their force-length relationship (Fig. 1). That is because at shorter than
53 optimal lengths, sarcomere geometry yields fewer overlapping actin myosin filaments (7), less
54 force per cross bridge cycle (14), and greater passive force that places tension the muscle fascicle
55 (10, 15). Thus, to produce the requisite force and sustain locomotion with shorter muscle
56 operating lengths (16, 17), animals must activate additional ATP-consuming cross bridges and
57 ion pumps than they otherwise would at optimal lengths (18-20).

58

59 Despite the aforementioned rationale, muscle operating lengths are not often considered to have
60 a notable effect on whole-body metabolic energy expenditure during locomotion (2, 17, 21-24).
61 This omission may be because the metabolic influence of producing force at different muscle
62 lengths is conventionally studied during isolated isometric contractions at a given activation (10,
63 11, 13). This is different than integrated cyclic length changing contractions at a given average
64 force, which emulates important aspects of locomotion mechanics. It is also difficult to separate
65 the metabolic effect of muscle operating length *per se*, from other biomechanical parameters
66 during locomotor-like contractions (9). For example, during concentric contractions, force-
67 producing muscles expend more metabolic energy the further that they shorten (25). As such,
68 scientists commonly attribute increased metabolic energy expenditure to greater muscle
69 shortening (25) and/or mechanical work production (24-27). However, in some cases, the
70 measured metabolic increase may be attributed to muscles producing force at less economical
71 lengths. Experimentally disentangling the metabolic effect of muscle operating lengths from
72 other metabolically relevant biomechanical parameters during locomotion (*e.g.*, force, work, and
73 velocity) is challenging, particularly during walking and running. Fortunately, a well-controlled
74 experiment using isolated contractions to emulate aspects of locomotion may be revealing.

75

76 Thus, to help reveal the link between locomotion mechanics and metabolic energy
77 expenditure, our goal was to determine the metabolic influence of cyclically producing a fixed
78 submaximal force at different muscle fascicle lengths. To accomplish this goal, we quantified the
79 mechanics and metabolic energy expenditure of human soleus muscles as they cyclically
80 produced force and changed length within different regions of the force-length relationship. We
81 hypothesized that cyclically producing the same submaximal force with relatively shorter muscle
82 fascicles would increase metabolic energy expenditure.

83

84 **Methods**

85 *Participants.* Nine volunteers completed the protocol (average \pm SD; 8 male and 1 female; age:
86 26.3 ± 2.6 years; standing height: 1.77 ± 0.07 m; mass: 74.9 ± 11.4 kg; resting metabolic power
87 87 ± 12 W; optimal soleus fascicle length: 41 ± 6 mm; maximum soleus fascicle shortening
88 velocity: 182 ± 25 mm/s (2)). We estimated maximum soleus fascicle shortening velocity to
89 equal 4.4 resting lengths per second (2) based on the assumption that only slow oxidative soleus
90 fibers are active during sustained submaximal metabolic trials (28). Prior to the study, each
91 participant gave informed written consent in accordance with the Georgia Institute of
92 Technology Central Institutional Review Board.

93

94 *Protocol.* Participants arrived at the laboratory in the morning following an overnight fast. Upon
95 arrival, participants laid supine on a dynamometer with custom attachments that supported their
96 legs in the testing position: right knee and ankle supported at 50° and 90° , respectively (Fig. 2).
97 90° indicates perpendicular segments and more acute angles indicates joint (dorsi)flexion. In this
98 position, participants rested for 10 minutes while breathing into a mouthpiece that channeled
99 expired air to a metabolic cart (TrueOne 2400, ParvoMedic, Sandy, UT). Next, we shaved
100 participant leg hair and used electrode preparation gel to lightly abrade the skin superficial to
101 their right soleus, lateral gastrocnemius, and tibialis anterior (NuPrep, Weaver and Co., Aurora,
102 CO). We placed bipolar surface electrodes over the skin superficial to each respective muscle
103 belly and in approximately the same orientation as the muscle fascicles (Delsys Inc., Natick,
104 MA). We secured a linear-array B-mode ultrasound probe to the skin superficial of each

105 participant's right medial soleus (Telemed, Vilnius, Lithuania). We placed reflective markers on
106 the dynamometer at its axis of rotation, 10 cm above the axis of rotation, as well as on the
107 participant's skin/clothes superficial to their right leg's medial knee-joint center, medial
108 malleolus, and first metatarsal head (Fig. 2). We measured each participant's Achilles tendon
109 moment arm during barefoot standing (ankle angle: 90°). Then, we estimated each participant's
110 triceps surae muscle-tendon unit length as well as the Achilles tendon moment arms at 105° and
111 120° using equation 13 from Bobbert et al. (29). Average \pm SD participant Achilles tendon
112 moment arm distance at 90°, 105°, and 120° equaled 49 ± 4 mm, 54 ± 4 mm, and 59 ± 5 mm,
113 respectively.

114

115 In a random order, participants performed four maximum voluntary contractions (MVCs) with
116 their ankle joint at 90° in-line with the dynamometer's axis of rotation (Biodex Medical Systems
117 Inc., NY) and their knee at 70°, 60°, and 50°: three plantar flexion MVCs and one dorsiflexion
118 MVC. At least two minutes of rest preceded each MVC to mitigate fatigue (30). Because MVC
119 ankle moment did not increase with more extended knee angles, we deemed the contribution of
120 the bi-articular gastrocnemius on ankle moment to be negligible (1). Additionally, soleus' force
121 producing capacity is $\sim 2x$ that of all uni-articular plantar flexor muscles combined (31), thus we
122 simply attributed ankle moment generation to soleus force production.

123

124 Subsequently, participants performed six, five-minute trials with their knee at 50° separated by at
125 least five minutes of rest. Participants performed trials at each of the two dynamometer torque
126 levels (10 Nm and 15 Nm) at the following ankle angles: 90°, 105°, and 120°. These trials
127 consisted of each participant repeatedly producing plantar flexor moments on a fixed-position
128 dynamometer foot-pedal following the sound of an audible metronome (metronome frequency
129 0.75 Hz and duty cycle 0.5) (Fig. 2). To guide ankle plantar flexor moments throughout each
130 trial, participants watched a computer screen that displayed the trial's target peak dynamometer
131 torque and the recorded dynamometer torque profile over the previous 5-10 s. We randomized
132 the trial order and collected metabolic data, dynamometer torque data (100 Hz), motion capture
133 data (200 Hz) (Vicon Motion Systems, UK), soleus fascicle length and orientation data (100 Hz),

134 as well as the surface electromyography signals from the soleus, tibialis anterior, and lateral
135 gastrocnemius (1000 Hz) (Fig. 2).

136

137 *Soleus fascicle mechanics.* To determine soleus fascicle kinematics, we recorded B-mode
138 ultrasound images containing the posterior-medial soleus compartment. We recorded soleus
139 fascicle images during 20 seconds in the last two minutes of the metabolic trials. Within these 20
140 seconds, we post-processed soleus fascicle lengths and pennation angles throughout six
141 consecutive moment generation cycles using a semi-automated tracking software (32). We
142 filtered soleus fascicle pennation angle and length using a fourth-order low-pass Butterworth
143 filter (6 Hz) and took the derivative of fascicle length with respect to time to determine fascicle
144 velocity.

145

146 To quantify soleus kinetics, we used a custom MATLAB script (Mathworks Inc., Natick, MA)
147 that filtered motion capture data using a fourth-order low-pass Butterworth filter (6 Hz) and
148 subtracted the gravitational dynamometer torque from the corresponding trial. We computed net
149 dynamometer torque from 12 consecutive moment generation cycles that encompassed the
150 analyzed fascicle kinematic data. Due to small fluctuations in dynamometer torque, we
151 implemented a 1 Nm dynamometer torque threshold to determine the duration of active force
152 production. Using filtered data, we calculated net ankle moment using dynamometer torque and
153 the position of the ankle's axis of rotation relative to the dynamometer's axis of rotation. Using
154 the estimated change in soleus muscle-tendon moment arm distance at each ankle angle (29), we
155 divided net ankle moment (m_{ank}) by the respective Achilles tendon moment arm distance (r_{AT}) to
156 calculate muscle-tendon force. In turn, we divided muscle-tendon force by the cosine of fascicle
157 pennation angle (θ_p) to calculate active soleus fascicle force (F_{sol}).

158
$$F_{sol} = \frac{m_{ank}}{r_{AT} \cos(\theta_p)} \quad \text{Eqn. 1}$$

159 We assumed passive muscle fascicle forces are negligible. We also omitted data from one five-
160 minute metabolic trial because the participant achieved an average maximum ankle moment that

161 was >5 Nm more than targeted. Further, we assumed that optimal soleus fascicle length was
162 consistent across muscle activation magnitudes (33) and that it was the value that we measured
163 during resting at a 90° ankle angle (28, 34).

164

165 *Relating Biomechanics to Metabolism.* Recently, two studies performed similar experimental
166 protocols and linked the mechanics of muscle fascicles cyclically producing force to metabolic
167 energy expenditure. One study (24) indicated that the overall rate of metabolic energy
168 expenditure (\dot{E}_{met}) scaled with metabolic rate associated with 1) the rate of peak force
169 production and force production cycle frequency ($\dot{E}_{FR} \propto \dot{F}_{peak} \cdot f$), the rate of mechanical work
170 ($\dot{E}_W \propto \dot{W}$), and the force-time integral ($\dot{E}_{FT} \propto \int F dt$) (Eqn. 2). The other study (28) suggested
171 that metabolic energy expenditure (\dot{E}_{met}) is well-explained by active muscle volume, which was
172 calculated using active muscle fascicle force production (F_{act}), optimal fascicle length (l_0), stress
173 (σ), and the fascicle's force-length and force-velocity force potential as per a Hill-type muscle
174 model (FL and FV , respectively) (Eqn. 3) (35). Due to the similarities between these previous
175 studies (24, 28) and the current study, our secondary objective was to test whether these
176 published biomechanical equations could explain the present study's metabolic data (Eqn. 2 and
177 3).

178
$$\dot{E}_{met} = \dot{E}_{FR} + \dot{E}_W + \dot{E}_{FT} \quad \text{Eqn. 2}$$

179
$$\dot{E}_{met} \propto V_{act} = \frac{F_{act} \cdot l_0}{\sigma \cdot FL \cdot FV} \quad \text{Eqn. 3}$$

180 *Muscle activation.* We band-pass filtered raw soleus, lateral gastrocnemius, and tibialis anterior,
181 electromyography signals between 20 and 450 Hz from the same 12 consecutive torque
182 generation cycles that we used to assess net ankle moment. We full wave rectified the filtered
183 electromyography signals and calculated the root mean square of the rectified signals using a 40
184 ms moving window. Due to technical issues, we were unable to collect one participant's tibialis
185 anterior activation during the metabolic trials.

186

187 *Metabolic energy expenditure.* During the resting trial and each cyclic force-production trial, we
188 used open-circuit expired gas analysis to record the participant's rates of oxygen uptake ($\dot{V}O_2$)

189 and carbon dioxide production (\dot{V}_{CO_2}). We averaged \dot{V}_{O_2} and \dot{V}_{CO_2} over the last minute of each
190 trial and used a standard equation to calculate metabolic power (W) (36). Next, we subtracted
191 each participant's resting metabolic power from their experimental values to yield net metabolic
192 power. We removed three metabolic values (of 54) from our analyses because the corresponding
193 respiratory exchange ratio did not reflect a respiratory quotient value that was indicative of fat
194 and/or carbohydrate oxidation (36).

195
196 *Statistical analyses.* Unless otherwise specified, we performed all statistical tests within the
197 targeted lower and higher ankle moment trials independently. We performed a t-test to determine
198 whether the targeted lower and higher cycle-average torque trials elicited different average ankle
199 moments. We performed linear mixed models to determine the influence of ankle angle on
200 kinetics, kinematics, muscle activity, and net metabolic power. We also performed linear mixed
201 models with two independent variables (average muscle fascicle length and positive mechanical
202 work) and one dependent variable (net metabolic power). Across both moment levels, we
203 performed independent linear regressions to determine the correlation between average relative
204 muscle fascicle length, positive muscle fascicle mechanical work, and average soleus muscle
205 activation on net metabolic power. We set the significance level ($\alpha = 0.05$) and performed
206 statistical analyses using RSTUDIO software (RSTUDIO, Inc., Boston, MA, USA).

207

208 **Results**

209 *Biomechanics.* Consistent with the study design, participants produced two distinct cycle average
210 \pm SD ankle moment levels: 4.85 ± 0.72 Nm and 6.58 ± 0.94 Nm ($p < 0.001$) (Fig. 3). Within each
211 moment level, the duration of active force production (both $p \geq 0.158$), force production cycle
212 frequency (both $p \geq 0.375$), and cycle average ankle moment (both $p \geq 0.678$) remained constant
213 across ankle angles. However, not all metrics remained constant across ankle angles. Plantar
214 flexing the ankle angle 30° increased the distance of participant Achilles tendon moment arms by
215 ~ 0.9 cm (29), thereby decreasing average soleus muscle-tendon force (both $p \leq 0.002$) (Fig. 3).
216 Greater ankle angles also increased average and maximum soleus fascicle pennation angles (both
217 $p \leq 0.001$) (Fig. 3), which yielded statistically similar cycle average soleus fascicle force

218 production across ankle angles for the low moment level ($p=0.063$) but not the higher moment
219 level ($p=0.003$) (Fig. 3). Similarly, at the lower moment level, soleus fascicle force-time integral
220 was independent of ankle angle ($p=0.070$), but it decreased by 19% due to increasing ankle angle
221 from 90° to 120° within the higher moment level ($p=0.003$) (Fig. 4).

222
223 Increasing ankle angle systematically shortened soleus fascicle lengths but it did not alter many
224 biomechanical parameters that previous dynamometer studies linked to net metabolic power.
225 Regarding Eqn. 2 (24), as aforementioned, soleus fascicle force-time integral remained constant
226 or slightly decreased at greater ankle angles (Fig. 4). Soleus fascicle force-rate was independent
227 of ankle angle (both $p \geq 0.235$) (Fig. 4) while positive soleus fascicle work increased across ankle
228 angles within the lower ankle moment level ($p < 0.001$), but not within the higher ankle moment
229 level ($p=0.591$) (Fig. 4). Regarding Eqn. 3 (35), both average and minimal soleus fascicle
230 operating lengths decreased with increasing ankle angle (both $p < 0.001$). These shorter fascicle
231 operating lengths reduced the average soleus fascicle force-length potential by 7-8% across ankle
232 moment levels ($p < 0.001$) (Fig. 5). Greater ankle angles yielded faster maximum soleus fascicle
233 shortening velocities within the lower ankle moment level ($p < 0.001$), but not statistically in the
234 higher ankle moment level ($p=0.099$). Combining cycle average fascicle force production and
235 force-length-velocity potential (35), ankle angle did not affect the model-estimated cycle average
236 soleus active muscle volume (both $p \geq 0.122$) (Fig. 5). Therefore, neither of the published
237 equations (Eqn. 2 & 3) would predict an increased metabolic energy expenditure at more plantar
238 flexed ankle angles due to constant and decreasing mechanical variables.

239
240 *Metabolic power.* Ankle angle dramatically affected the metabolic power of cyclic force
241 production. Changing ankle angle from 90° to 120° increased net metabolic power by 189% and
242 228% within the lower and higher ankle moment levels, respectively (both $p < 0.001$) (Fig. 6).
243 Unlike previous dynamometer studies (24, 28), neither the combined cost of muscle force-time
244 integral, positive mechanical work, and force rate (Eqn. 2); nor modeled active muscle volume
245 (Eqn. 3) could explain the metabolic data. This is especially evident within the higher moment
246 level where net metabolic power increased by 228% across ankle angles, but all the
247 biomechanical variables were either unchanged or decreased with increasing ankle angle: force-

248 time integral (Fig. 4), force rate (Fig. 4), positive mechanical work (Fig. 4), and active muscle
249 volume (Fig. 5). Within each moment level, positive mechanical work did not relate to net
250 metabolic power while controlling for average fascicle length ($p \geq 0.405$). On the contrary, while
251 controlling for positive mechanical work, decreasing average fascicle length was associated with
252 an increased net metabolic power (both $\beta = -1.4$ to -3.1 ; $p \leq 0.047$). Pooled across ankle moment
253 levels and participants, without controlling for other mechanical parameters, average relative
254 muscle fascicle operating length inversely correlated with net metabolic power ($r = -0.72$,
255 $p = 0.002$), whereas positive muscle fascicle mechanical work was not correlated to net metabolic
256 power ($p = 0.125$). Additionally, average soleus activation positively correlated with net metabolic
257 power across ankle moment levels and participants ($r = 0.51$, $p < 0.001$) (Fig. 6). Therefore,
258 cyclically producing force with 16-17% shorter muscle fascicles yielded ~200% more metabolic
259 energy expenditure.

260

261 *Muscle activation.* Cyclically producing force at different ankle angles altered plantar flexor
262 muscle activation. Both soleus and lateral gastrocnemius muscle activation increased by 146-
263 196% with increasing ankle angle within each moment level (all $p < 0.001$) (Fig. 7). Even though
264 tibialis anterior activation statistically increased at greater ankle angles (both $p \leq 0.027$), we
265 considered its influence on net metabolic power to be trivial because its cycle average activation
266 was merely 0.02 to 0.05 of its MVC value across conditions.

267

268 **Discussion**

269 During locomotion, muscle fascicle operating lengths depend on body segment geometry, the
270 structural properties of biological tissues, and the body's kinetics. In the present study, we
271 controlled for participant structural properties (within participant design), limb-joint kinetics
272 (constant ankle moment cycle), and independently altered muscle fascicle operating lengths via
273 geometric changes (changing ankle angle). Using this protocol, we revealed that shorter muscle
274 fascicle operating lengths increased metabolic energy expenditure during cyclic force production
275 – supporting our hypothesis.

276

277 Producing a constant force with shorter muscle fascicles than optimal likely elicits multiple
278 neuromechanical changes that increase metabolic energy expenditure. Consistent with the sliding
279 filament (37, 38) and cross-bridge (39, 40) theories, at relatively short muscle lengths there is
280 less overlap between actin and myosin filaments (7), reducing the number of force producing
281 cross bridges per active sarcomere. At shorter lengths, sarcomere force production decreases
282 faster than the corresponding ATP utilization within a given muscle fiber, eliciting less
283 economical force production. For example, Hilber et al. (10) demonstrated that rabbit psoas
284 muscles produced force ~27% and 88% less economically at 0.8 and 0.6 of the muscle's optimal
285 length versus at the optimal length, respectively. Additionally, to keep producing the same force,
286 the body needs to activate more force producing sarcomeres, which further increases metabolic
287 energy expenditure due to additional ATP use for ion pumping (calcium & sodium-potassium
288 pumping) (19, 41). Second, the distance between actin and myosin filaments increases at shorter
289 muscle lengths than optimal (increased lattice spacing) (14). This increased lattice spacing
290 changes cross bridge geometry and kinetics such that there is less force produced per cross
291 bridge cycle, and therefore less force per ATP utilization (14). Thus, to produce the same force at
292 shorter lengths than optimal requires the body to activate more force producing cross bridges,
293 increasing metabolic energy expenditure due to additional cross-bridge cycling and ion pumping.
294 Finally, as muscles shorten, filaments compress, various intra- and extra-cellular components
295 deform (*e.g.*, extracellular matrix and blood), and subtle volumetric changes provide force that
296 attempts to lengthen the muscle (10, 15). To counteract these lengthening forces and produce the
297 same net fascicle force, the body likely activates additional motor units; again, increasing
298 metabolic energy expenditure due to both greater cross-bridge cycling and ion pumping.
299 Altogether, producing the same net force with shorter fascicles than optimal has multiple effects:
300 reduced actin myosin overlap, increased lattice spacing, and increased lengthening forces, that
301 collectively increase the metabolic energy expended due to the greater cost of cross bridge
302 cycling and ion pumping.

303

304 In addition to testing our hypothesis, we also revealed that two published equations were unable
305 to relate our participants' soleus fascicles mechanics to the corresponding metabolic energy
306 expenditure (Eqn. 2 & 3) (24, 28). One such equation (Eqn. 2) (24) did not include muscle

307 operating length in the estimate of metabolic energy expenditure. Interestingly, the other
308 equation (Eqn. 3) (35) did include an idealized Hill-type muscle force-length potential and still
309 failed to predict our measured metabolic data. The inability of this second equation (Eqn. 3) to
310 predict our participant's metabolic energy expenditure (or muscle activity) suggests that Hill-
311 type muscle models under-predict physiological changes that occur when intact leg muscles
312 cyclically produce force at different operating lengths. While we were unable to completely rule
313 out the potential effects of other mechanical parameters (*e.g.*, differences in muscle shortening
314 velocities), our results suggest that muscle operating lengths affect metabolic energy expenditure
315 more than conventionally thought. Therefore, future attempts to link biomechanics to metabolic
316 energy expenditure during cyclic muscle contractions may benefit from directly considering the
317 influence of muscle operating lengths.

318

319 As like studies are added to the literature, we encourage researchers to compare datasets and
320 form testable hypotheses regarding how locomotor-like mechanics affect metabolic energy
321 expenditure. However, numerous methodological discrepancies limit the utility of inter-study
322 comparisons. For example, the present study's net metabolic power values are 2-6x greater than
323 those reported from a study that involved cyclic bilateral knee moments at roughly similar torque
324 magnitudes and cycle frequencies (24). While this comparison is thought provoking, there is not
325 enough information to deduce the factor(s) responsible for the metabolic differences. Simply
326 using different protocols and testing different participants introduces discrepancies that affect
327 inter-study comparisons. Further, compared to the knee extensors, soleus muscles are typically
328 more pennate and have shorter moment arms (42), thereby eliciting greater muscle force
329 production per unit joint moment. Moreover, the soleus' relatively greater force production,
330 more compliant tendon (43, 44), and optimally shorter muscle fascicles (45) likely yielded
331 greater relative muscle fascicle shortening compared to that of the knee extensors – contributing
332 to the metabolic differences between the studies (24-27). Even when muscle mechanics are
333 identical, metabolic power can vary due to dissimilar rates of enzymatic activity (*e.g.*, ATPase
334 activity) (18). Hence, due to a myriad of potential factors affecting inter-study comparisons, we
335 encourage researchers to independently test their hypotheses and thoroughly detail their
336 experimental methods and results.

337 It is unlikely that the neuromechanics of non-soleus plantar flexors affect our conclusion that
338 soleus metabolic power increased $\sim 200\%$ across ankle angles and muscle lengths. In our study,
339 for simplicity we assumed that gastrocnemius metabolic power remained constant across ankle
340 angles because, due to the prescribed knee joint angle, it was severely limited in its force and
341 mechanical work capacity (see methods). We recognize that lateral gastrocnemius activation
342 increased like that of the soleus at more plantar flexed ankle angles (Fig. 7), and thus it may have
343 also increased its metabolic power like that of the soleus. If we update our assumption to state
344 that the gastrocnemius muscles increased their metabolic power proportional to their activation,
345 our conclusions regarding soleus metabolism would remain unchanged. That is because lateral
346 gastrocnemius and soleus activation both increased by roughly the same percentage across ankle
347 angles ($\sim 200\%$) (Fig. 7). Simply stated, if the gastrocnemius (and other synergistic plantar
348 flexors) increased their metabolic energy expenditure $\sim 200\%$ across ankle angles, the absolute
349 magnitude of soleus metabolic energy expenditure would change but its relative increase across
350 ankle angles would remain the same. An unlikely scenario where the soleus would not increase
351 its metabolic power $\sim 200\%$ across ankle angles would only occur if synergistic muscles
352 collectively increased their metabolic power much more than that of the soleus across ankle
353 angle conditions. We are dubious of this scenario because the soleus is $\sim 130\%$ more massive
354 than the combination of all synergistic muscles that could produce plantar flexor moment in our
355 study (42). Therefore, even if the synergistic muscles increased their metabolic power across
356 ankle angles, it remains likely that the soleus increased its metabolic power by $\sim 200\%$ across
357 ankle angles.

358

359 We acknowledge that there are multiple assumptions that may limit the findings of this study.
360 First, we assumed that the soleus had uniform fascicle mechanics throughout the entire muscle,
361 which oversimplifies the muscle's complex architecture (46). While passively changing muscle-
362 tendon length alters soleus fascicle lengths and pennation angles in the same direction across
363 muscle compartments (46), perhaps our ultrasound imaged compartment had less fascicle
364 shortening across ankle angles compared to other compartments. If so, the greater fascicle
365 shortening throughout the other compartments would yield a lower overall muscle force potential
366 and a greater increase in activation and metabolic energy expenditure across ankle angles.
367 Second, we assumed that the soleus is primarily comprised of homogeneous muscle fibers (47)
368 and that these fibers are exclusively recruited during the present study's submaximal metabolic
369 trials (48). Hence, we deemed that all active soleus muscle fascicles have the same maximum
370 shortening velocity across experimental activation levels (2). Third, we assumed that soleus'
371 optimal fascicle length equaled the resting fascicle length at a 90° ankle angle (34). This
372 assumption straddles the conflicting reports that optimal soleus sarcomere length occurs at more
373 dorsiflexed (49) and plantar flexed (50) ankle angles. If the optimal soleus sarcomere length
374 occurred at an ankle angle <90°, we may have underestimated the decrease in force potential
375 across ankle angles due to operating along steeper regions of the force-length relationship.
376 Fourth, we assumed that each participant's optimal soleus fascicle length remained the same
377 value across the experimental conditions. This assumption does not correspond with the notion
378 that optimal muscle length decreases with greater activation (51, 52). An activation-dependent
379 decrease in optimal muscle length may have reduced the difference in the soleus' force-length
380 operating region between the 120° versus 90° ankle angle conditions. Alternatively, decreasing
381 optimal fascicle length would also elicit a narrower force-length relationship (in mm), such that

382 an absolute decrease in fascicle length would travel further down the ascending limb of the
383 force-length relationship. Thus, it is difficult to predict how an activation-dependent shift in
384 optimal fascicle length affects soleus force potential across ankle angles. Fifth, our surface
385 electromyography measurements were likely influenced by changing muscle geometry across
386 ankle angles (53, 54). Sixth, we also assumed that participants used ideal force-length and force-
387 velocity profiles (7, 8, 55). Regardless of these assumptions, our conclusion that cyclically
388 producing force with relatively shorter muscle fascicles increases metabolic energy expenditure
389 remains sound. We also find assurance when comparing our results to the most analogous
390 locomotion experiment – walking and running in footwear with different heel heights. Similar to
391 our study, increasing footwear heel height elicits postural changes that decrease relative muscle
392 fascicle operating lengths (56, 57) and increase metabolic energy expenditure during walking
393 and running compared baseline conditions (*i.e.*, barefoot or in flats) (58, 59).

394

395 *Conclusions*

396 In conclusion, increasing the operating length of muscle fascicles that produce force on the
397 ascending limb of their force-length relationship may measurably decrease metabolic energy
398 expenditure during locomotion. This finding may help resolve why locomotion economy differs
399 within and across animal species, in addition to informing biomechanical interventions that
400 reduce user metabolic energy expenditure.

401

402 *Authors' contributions.* O.N.B. contributed to the conception and design of the study, acquisition
403 of data, the analysis and interpretation of data, as well as the drafting of the article. L.H.T. &

404 J.N.S contributed to acquisition of data. J.R.F. contributed to the conception of the study,
405 interpretation of data, as well as the drafting of the article. G.S.S. contributed to the conception
406 and design of the study, the analysis and interpretation of data, as well as the drafting of the
407 article. All authors approve of the manuscript and agree to be held accountable for all aspects of
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409 appropriately investigated and resolved.

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412

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Figure Captions

561 **Figure 1.** Representation of soleus fascicles lengthening during mid-stance of walking a) in
 562 high-heeled shoes (56, 57), barefoot, and with an ankle exoskeleton (60). b) Conceptual graph
 563 showing isometric muscle fascicle force production and adenosine triphosphate (ATP) utilization
 564 relative to muscle length (10). c) Actin-myosin ATP utilization per net isometric muscle fascicle
 565 force production at a given activation versus muscle fascicle operating length (10). L and L_0
 566 indicate actual and optimal muscle fascicle length, respectively.

567 **Figure 2.** a) Experimental setup of a participant cyclically generating soleus muscle force to
 568 produce a plantar flexor moment that exerts an external torque on a fixed dynamometer pedal
 569 following the cues of an audible metronome and visual feedback. EMG, electromyography;
 570 SOL, soleus; LG, lateral gastrocnemius; TA, tibialis anterior. b) Illustrations of the two target
 571 torque levels (peak torque: 10 Nm and 15 Nm), three ankle angles (90° , 105° , and 120°) with the
 572 corresponding hypothetical minimum soleus fascicle operating lengths and their respective
 573 location on a muscle force-length relationship.

574 **Figure 3.** Top row: time-series plots of average a) ankle moment (m_{ank}), b) muscle-tendon force
 575 (F_{MT}), c) soleus fascicle pennation angle, and d) active soleus fascicle force (F_{M}). Bottom row:
 576 average \pm SE e) average ankle moment, f) average MT force, g) maximum fascicle pennation
 577 angle, and h) average soleus fascicle force versus ankle angle. Black and red symbols are offset
 578 for clarity and indicate the lower and higher ankle moment levels, respectively. Lighter to darker
 579 colors indicate more dorsiflexed to plantar flexed ankle angles per moment level. Figure details:
 580 Sample size: 9; Sex: 8 male/1 female; Statistical tests: linear mixed model. Black and red
 581 asterisks (*) indicate that there is an effect of ankle angle on the indicated moment level's
 582 dependent variable ($p < 0.05$).

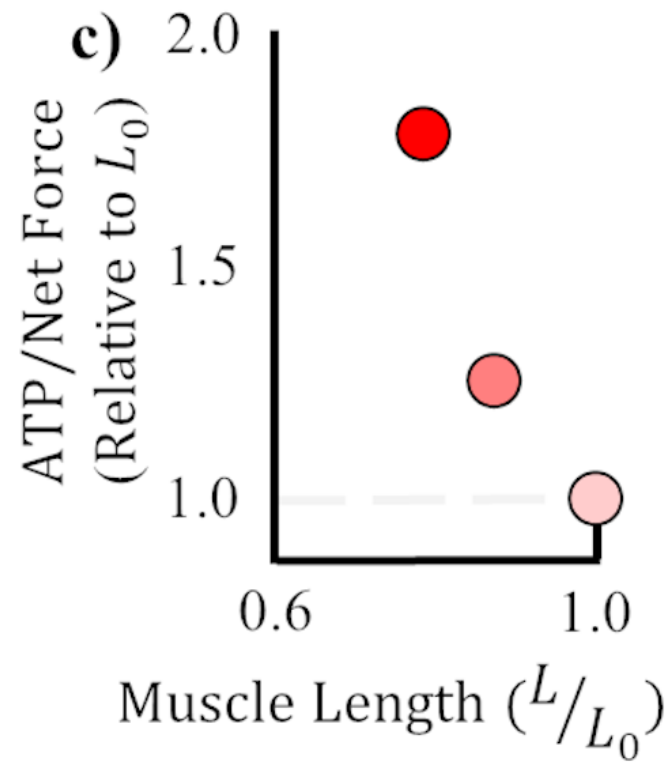
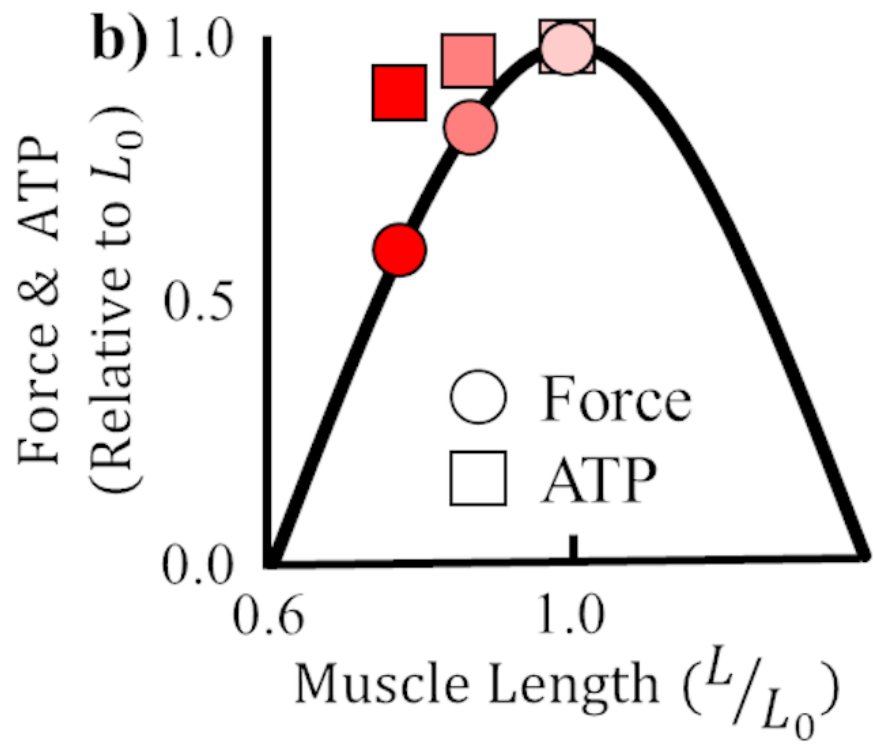
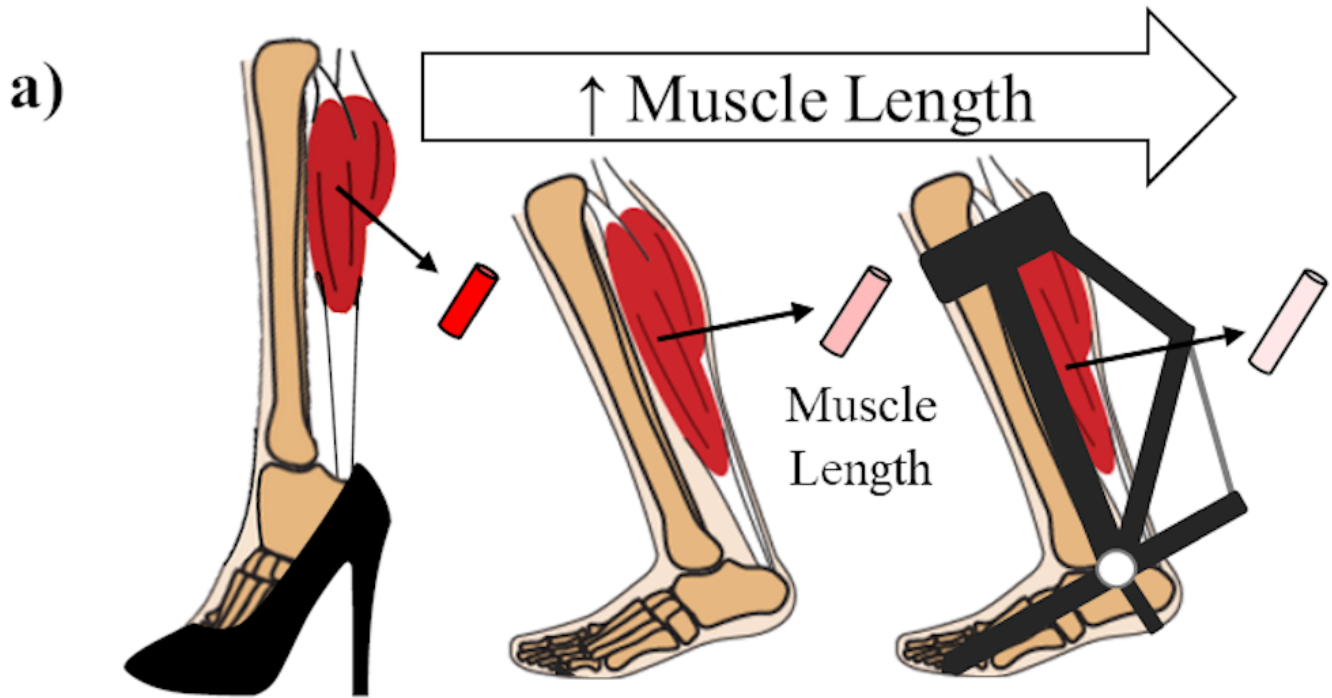
583 **Figure 4.** Time-series plots of average soleus fascicle a) force and d) power, as well as average \pm
 584 SE soleus fascicle b) total force-time integral, c) force rate, d) and positive mechanical work.
 585 Black and red symbols are offset for clarity and indicate the lower and higher ankle moment
 586 levels, respectively. Lighter to darker colors indicate more dorsiflexed to plantar flexed ankle
 587 angles per moment level. Figure details: Sample size: 9; Sex: 8 male/1 female; Statistical tests:
 588 linear mixed model. Black and red asterisks (*) indicate that there is an effect of ankle angle on
 589 the indicated moment level's dependent variable ($p < 0.05$).

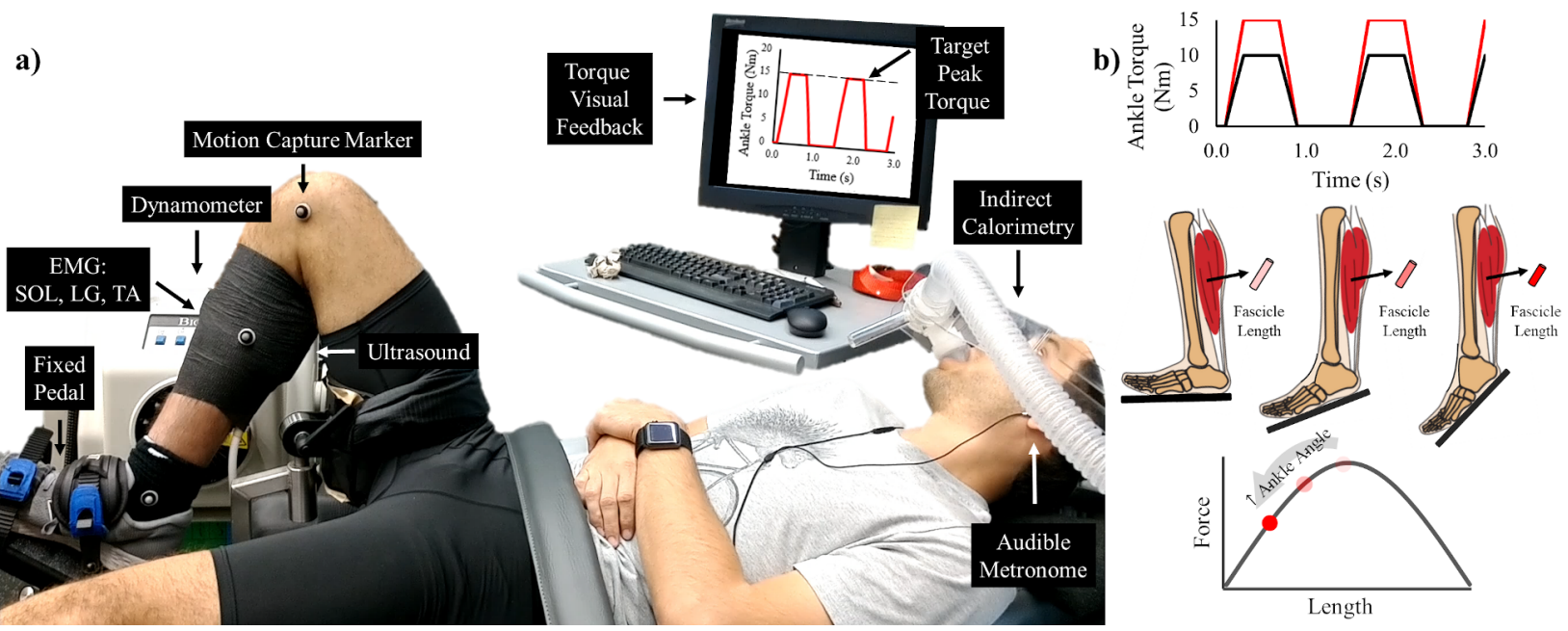
590 **Figure 5.** Top row: time-series plots of average soleus a) fascicle length, b) fascicle velocity, and
 591 c) active muscle volume. Bottom row: average \pm SE d) minimum Hill-type force-length
 592 potential, e) minimum Hill-type force-velocity potential, and average f) active muscle volume
 593 versus ankle angle. Within panels d) and e) are the respective force-potentials plotted on the
 594 force-length and force-velocity curves, respectively. Regarding fascicle velocity, shortening and
 595 lengthening equals positive and negative velocity, respectively. Black and red symbols are offset
 596 for clarity and indicate the lower and higher ankle moment levels, respectively. Lighter to darker
 597 colors indicate more dorsiflexed to plantar flexed ankle angles per moment level. Figure details:
 598 Sample size: 9; Sex: 8 male/1 female; Statistical tests: linear mixed model. Black and red
 599 asterisks (*) indicate that there is an effect of ankle angle on the indicated moment level's
 600 dependent variable ($p < 0.05$).

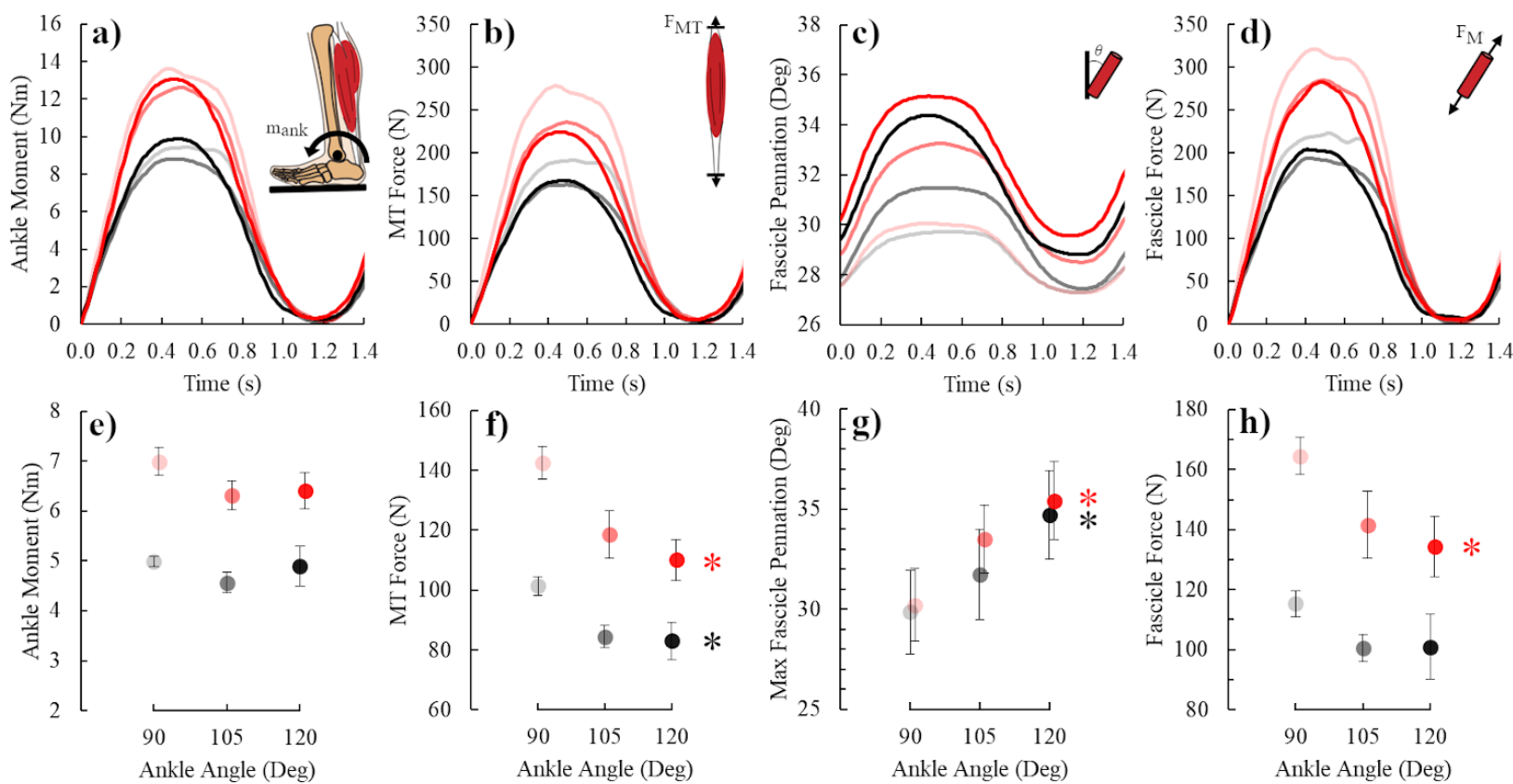
601 **Figure 6.** Average \pm SE net metabolic power versus a) ankle angle, b) minimum fascicle length,
 602 and c) average soleus activation. Black and red symbols are offset for clarity and indicate the

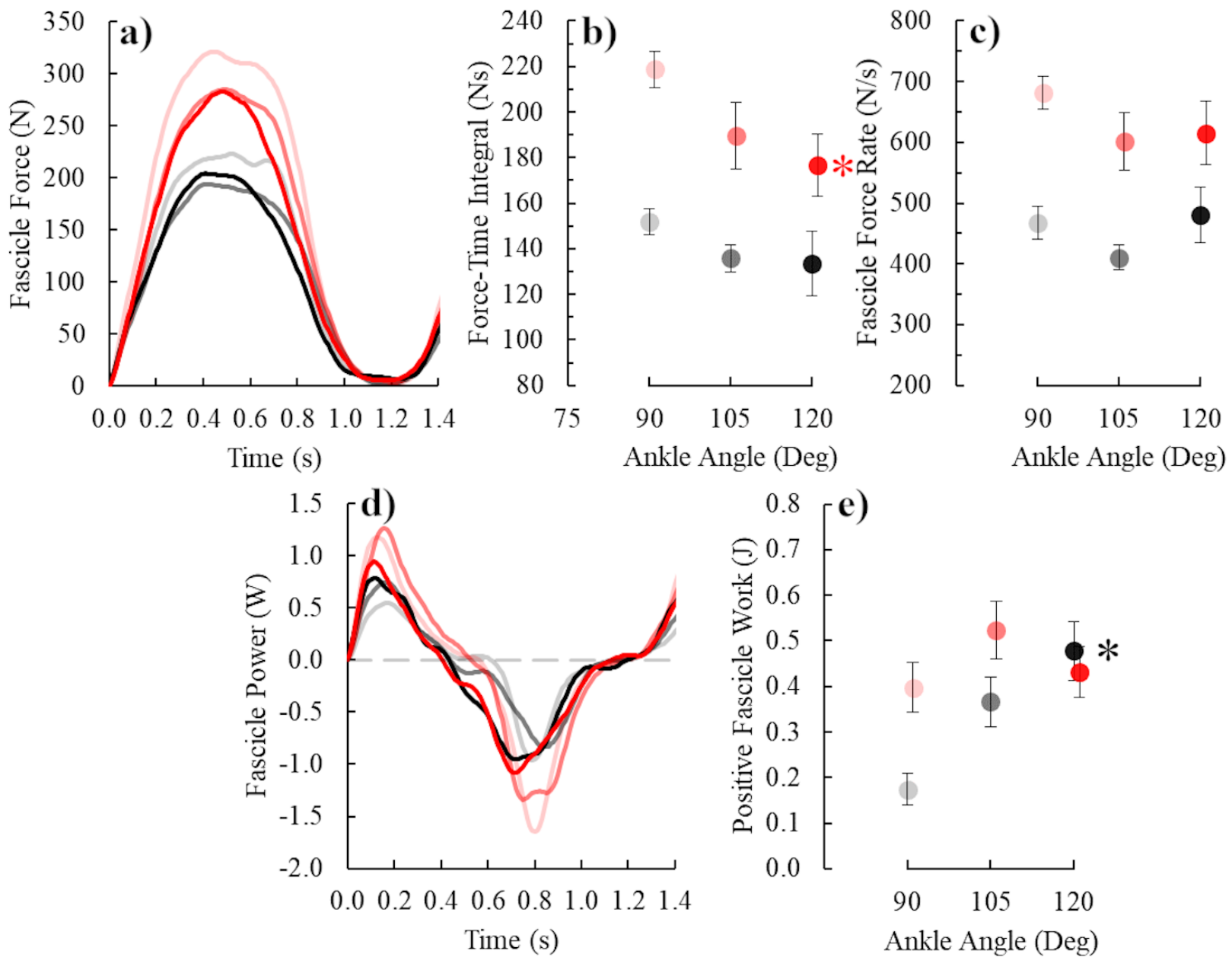
603 lower and higher ankle moment levels, respectively. Lighter to darker colors indicate more
604 dorsiflexed to plantar flexed ankle angles per moment level. Figure details: Sample size: 9; Sex:
605 8 male/1 female; Statistical tests: linear mixed model. Black and red asterisks (*) indicate that
606 there is an effect of ankle angle on the indicated moment level's dependent variable ($p < 0.05$).

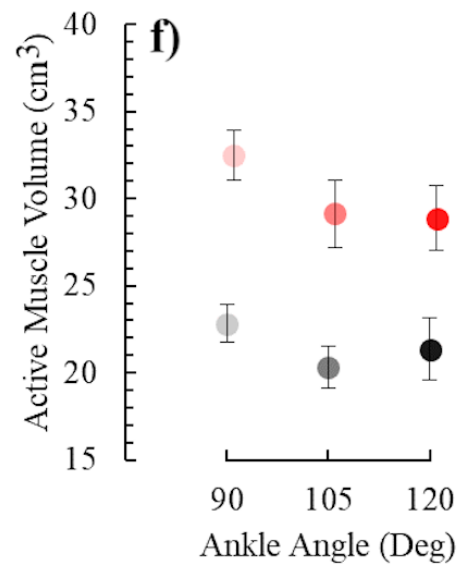
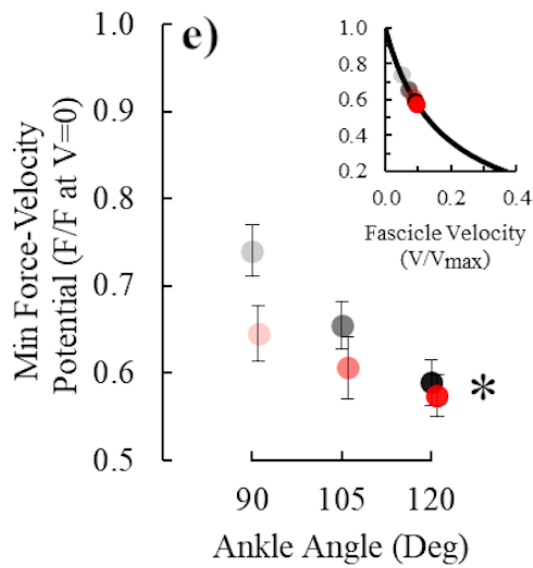
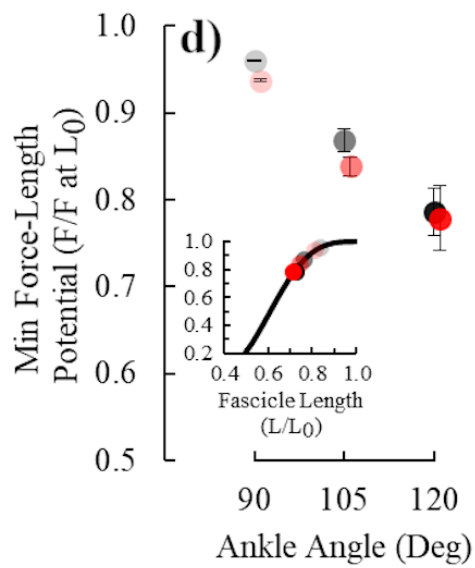
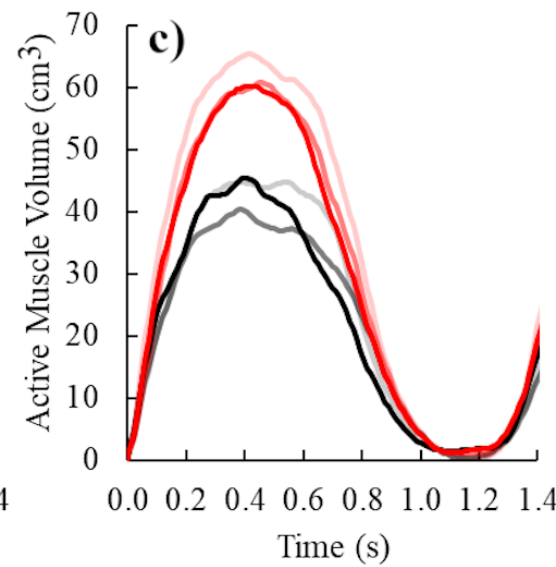
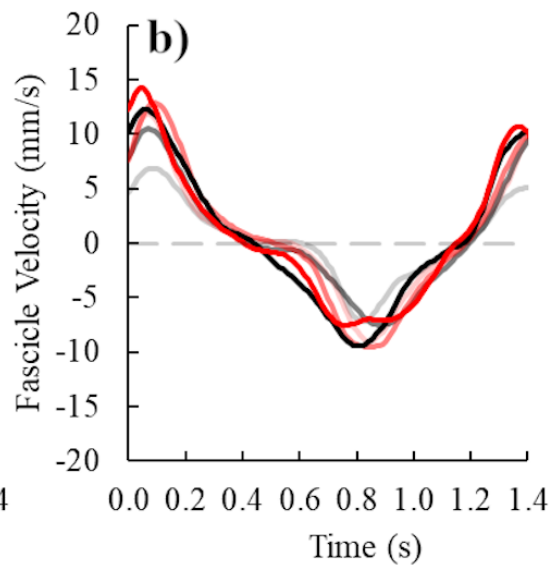
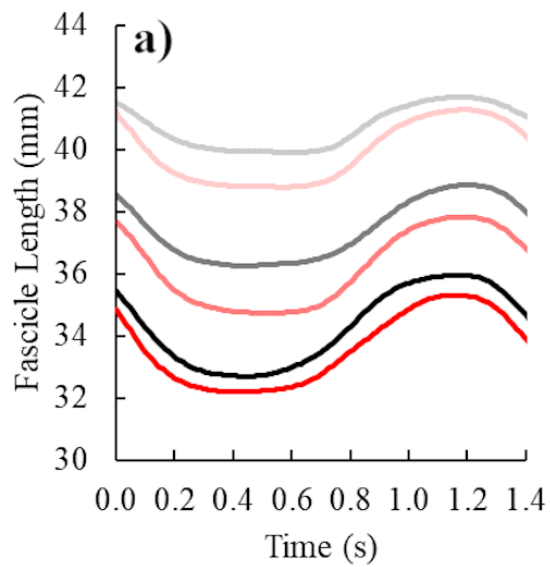
607 **Figure 7.** Top row: time-series plots of average a) soleus (SOL) activation (Act), b) lateral
608 gastrocnemius (LG) activation, and c) tibialis anterior (TA) activation. Bottom row: average \pm
609 SE d) SOL activation, e) LG activation, and f) TA activation versus ankle angle. MVC is
610 maximum voluntary contraction. Black and red symbols are offset for clarity and indicate the
611 lower and higher ankle moment levels, respectively. Lighter to darker colors indicate more
612 dorsiflexed to plantar flexed ankle angles per moment level. Figure details: Sample size: 9; Sex:
613 8 male/1 female; Statistical tests: linear mixed model. Black and red asterisks (*) indicate that
614 there is an effect of ankle angle on the indicated moment level's dependent variable ($p < 0.05$).

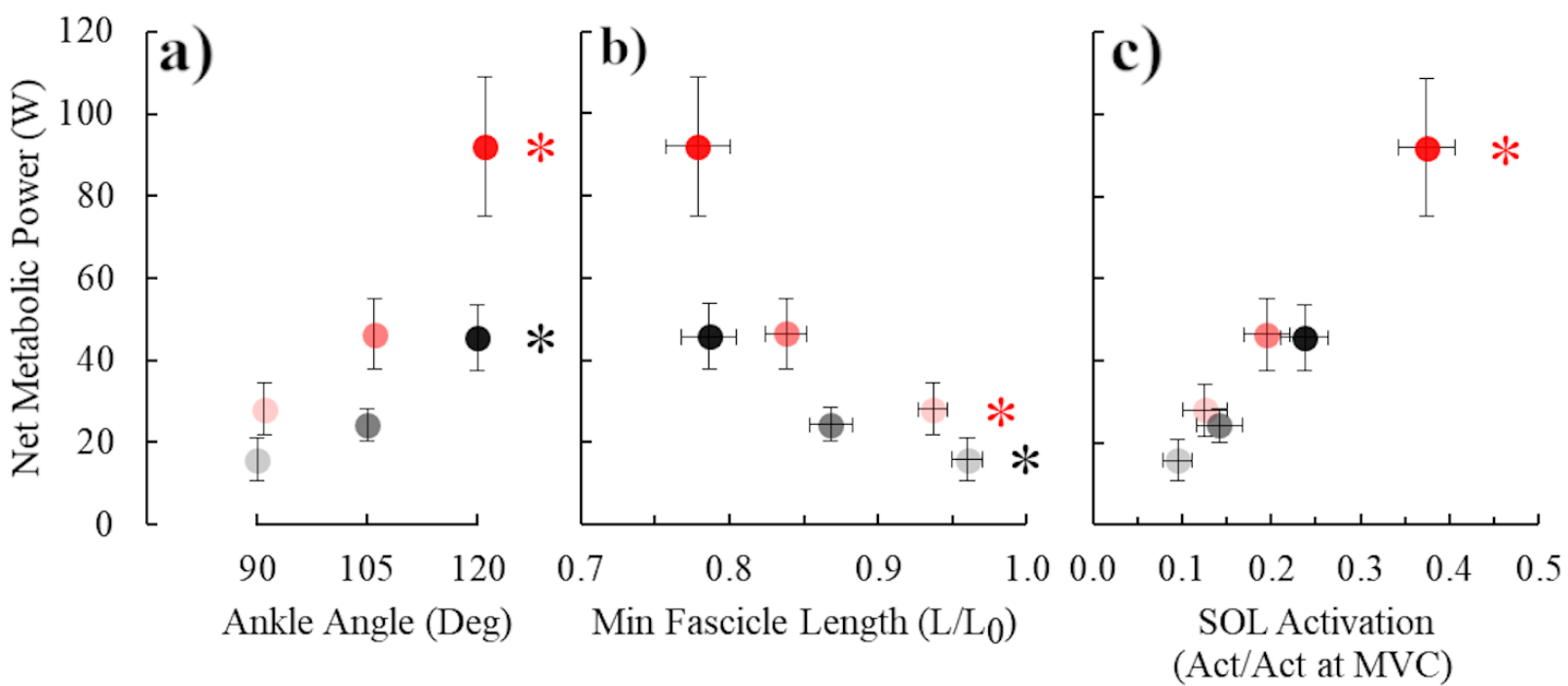








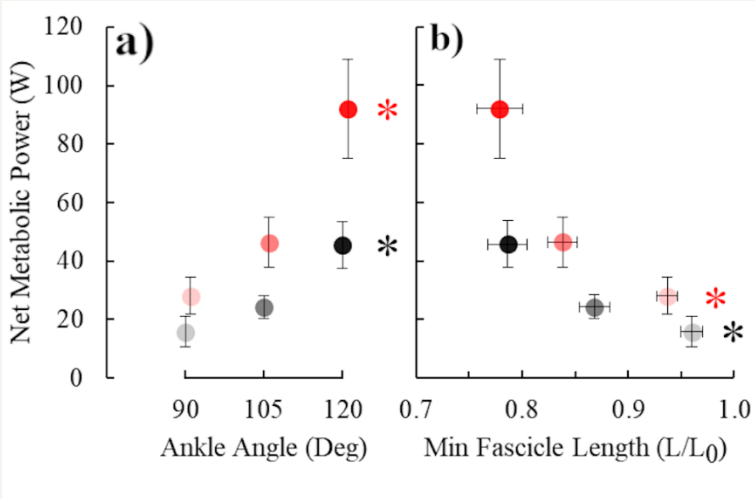
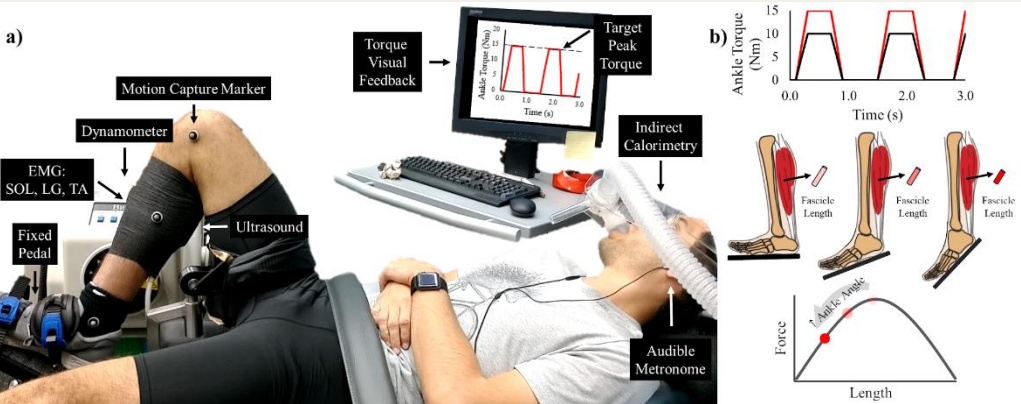




Shorter Muscle Fascicle Operating Lengths Increase the Metabolic Cost of Cyclic Force Production

Humans cyclically produced force at different soleus lengths

Producing force with shorter muscles increased metabolic power



Muscle fascicle operating lengths likely have a measurable effect on the metabolic energy expenditure during locomotion