Article

Foot strike pattern during running

alters muscle-tendon dynamics of the gastrocnemius and the soleus

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1 ABSTRACT

2 Running is thought to be an efficient gait due, in part, to the behavior of the plantar flexor

3 muscles and the elastic energy storage in the Achilles tendon. Although plantar flexor muscle

4 mechanics and Achilles tendon energy storage have been explored during rearfoot striking, they

5 have not been fully characterized during forefoot striking. This study examines how plantar

6 flexor muscle-tendon mechanics during running differ between rearfoot and forefoot striking.

7 We used musculoskeletal simulations, driven by joint angles and electromyography recorded

8 from runners using both rearfoot and forefoot striking running patterns, to characterize plantar

9 flexor muscle-tendon mechanics. The simulations revealed that foot strike pattern affected the

10 soleus and gastrocnemius differently. For the soleus, forefoot striking resulted in decreased

11 tendon energy storage and decreased positive fiber work compared to rearfoot striking. For the

12 gastrocnemius, forefoot striking resulted in greater activation and increased negative fiber work

13 compared to rearfoot striking. The increased activation and negative fiber work in the

14 gastrocnemius during forefoot striking suggest that runners planning to convert to forefoot

15 striking would benefit from a progressive eccentric gastrocnemius strengthening program to

16 avoid injury.

1   INTRODUCTION

2   The efficiency of running is enhanced by elastic energy storage in muscle-tendon units. This

3   concept has supported the development of simple spring-mass models of human running[1], which

4   have been useful for understanding running mechanics[2], predicting the energy cost of running[3], and

5   examining the effects of fatigue[4,5]. The plantar flexor muscles, in conjunction with the Achilles

6   tendon, are major contributors to energy storage and return during running[6], with energy being

7   absorbed during early stance and released during late stance[7]. The elastic stretch and recoil of the

8   Achilles tendon may contribute as much as 35% of the total energy storage and return during

9   running[8]. Furthermore, the plantar flexor muscles are the largest contributors to body weight

10   support and forward propulsion during running[9].

11   The plantar flexor muscles and Achilles tendon span the ankle joint, suggesting that their

12   mechanics would be affected by foot strike pattern. Rearfoot striking, characterized by landing on

13   the heel, and forefoot striking, characterized by landing on the ball of the foot, are both naturally

14   adopted foot strike patterns. Habitual rearfoot striking runners who transition to a forefoot striking

15   pattern initially experience calf soreness[10,11], indicating that altering foot strike pattern may affect

16   the behavior of the plantar flexors and, therefore, energy storage in the Achilles tendon. Previous

17   research has focused on understanding plantar flexor mechanics during rearfoot striking[12–15], but

18   how plantar flexor mechanics are affected by converting to forefoot striking is unclear.

19   Differences between rearfoot and forefoot striking suggest how plantar flexor muscle-tendon

20   mechanics might be affected by foot strike pattern. Forefoot striking increases peak stress[16] and

21   impulse[17,18] in the Achilles tendon, suggesting an increased injury risk. Forefoot striking also results

22   in higher Achilles tendon forces[19] and strain rate[16], potentially indicating greater energy storage, but

23   no studies have estimated the change in energy storage when converting to forefoot striking. In

3

24   terms of kinematics, forefoot striking is associated with a more plantarflexed ankle[20] and flexed

25   knee[21] at initial contact compared to rearfoot striking; these changes result in shorter plantar flexor

26   muscle-tendon lengths and likely shorter muscle fiber lengths, which may affect these muscles'

27   ability to generate force. Forefoot striking runners produce greater ankle plantarflexion moments

28   during early stance[18,22], which may indicate greater forces in the plantar flexor muscles. Previous

29   studies have reported increased activity in the gastrocnemius during forefoot striking compared to

30   rearfoot striking[11,23,24] with no difference in soleus muscle activity[23,25], suggesting that the

31   gastrocnemius and the soleus may respond differently to forefoot striking. The plantar flexors are

32   crucial during the stance phase of running[9]; thus, it is critical to understand the effect of foot strike

33   pattern on tendon energy storage, the force generation ability of the plantar flexors, and the amount

34   of energy absorbed and generated by these muscles.

35   The goal of this study was to examine how plantar flexor muscle fiber and tendon mechanics

36   differ between rearfoot and forefoot striking, specifically in the gastrocnemii and soleus. We sought

37   to address four fundamental issues. First, based on the reported effects of forefoot striking on the

38   Achilles tendon[16,19], we hypothesized that energy storage in the plantar flexor tendons is greater

39   during forefoot striking compared to rearfoot striking. Second, based on differences in knee and

40   ankle kinematics at foot contact between rearfoot and forefoot striking, we anticipated changes to

41   plantar flexor fiber lengths and velocities, and examined how altering foot strike pattern affects the

42   plantar flexor muscles' ability to generate active force. Third, based on anticipated changes in

43   plantar flexor fiber kinematics and forces, we evaluated how foot strike pattern affects the positive

44   and negative work done by the plantar flexor fibers. Finally, we assessed whether the gastrocnemius

45   and the soleus were affected differently by altering foot strike pattern.

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46   We developed musculoskeletal simulations to characterize the effect of foot strike pattern on

47   plantar flexor muscle-tendon mechanics during running in unprecedented detail (Fig 1; see

48   Methods). Using electromyography (EMG) data and joint kinematics, measured in 16 habitual

49   rearfoot striking subjects running overground using both a rearfoot and forefoot striking pattern, as

50   inputs to our simulations, we simulated the mechanics of the medial gastrocnemius, lateral

51   gastrocnemius and soleus. We analyzed these simulations to evaluate how foot strike pattern affects

52   elastic energy storage in plantar flexor tendons, the force generation ability of the muscles, muscle

53   fiber lengths and velocities, and positive and negative work done by the muscle fibers. These

54   simulations were generated in OpenSim[26], an open-source simulation software. Experimental data

55   and simulation results are freely available at simtk.org/projects/rfs-ffs-pfs to allow others to

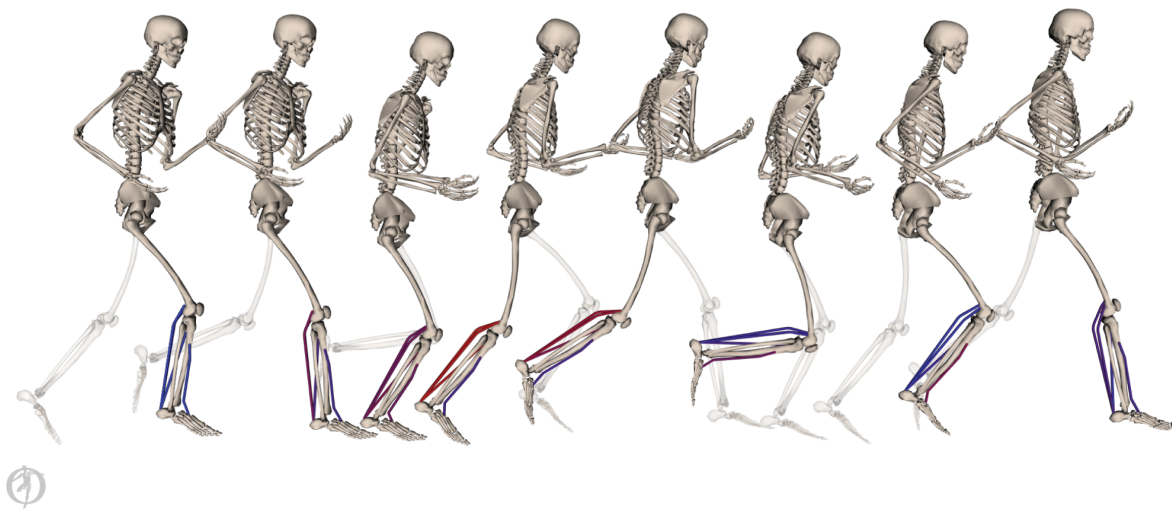56   reproduce and build upon our work.

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59 **Figure 1.** Simulations (pictured) of plantar flexor muscle-tendon mechanics were driven by
60 electromyography data and joint angles. Processed electromyography signals were applied as
61 muscle excitations. Excitations are visualized as a color gradient on the muscles from blue (low
62 excitation) to red (high excitation). Joint angles, estimated from motion capture data, were used to
63 prescribe lower body kinematics in a scaled musculoskeletal model.
64

65   RESULTS

66   Energy storage in the Achilles tendon was similar ($p = 0.703$) for rearfoot striking ($26.4 \pm$

67   4.4 J) and forefoot striking (25.7 ± 7.4 J; Fig 2A). However, foot strike pattern affected tendon

68   energy storage differently for the components of the Achilles tendon associated with the

69   gastrocnemii and the soleus. Energy storage in the gastrocnemius component of the Achilles tendon

70   increased, while energy storage in the soleus component decreased during forefoot striking

71   compared to rearfoot striking ($p = 0.002$). The timing of peak negative tendon energy storage in the

72   gastrocnemius tendon shifted significantly earlier in the gait cycle during forefoot striking (medial

73   and lateral: $p < 0.001$), with peak negative tendon power on average shifting from 20% of the gait

74   cycle during rearfoot striking to 6% of the gait cycle during forefoot striking (Fig 2B). The timing

75   for peak negative tendon energy storage in the soleus was not significantly different between

76   rearfoot and forefoot striking ($p = 0.487$). We estimated tendon energy storage using positive work

77   done by the plantar flexor tendons and assuming no energy loss. Since tendons are modeled as

78   elastic structures, the positive and negative work done by a tendon during the gait cycle should be

79   equivalent. We calculated the difference between positive and negative work done by the tendons

80   and found the average error to be within 0.3 J (2.3%) for all tendons under all conditions. Therefore,

81   we did not test for differences in negative work done by the plantar flexor tendons between foot

82   strike patterns, but expect all differences in positive work to hold for negative work as well.

83   The force generation ability (i.e. the force generated per unit of activation) at peak active

84   force was higher in the gastrocnemii (medial and lateral: $p < 0.001$) during forefoot striking

85   compared to rearfoot striking, but was not significantly different in the soleus ($p = 0.700$; Fig 3;

86   Table 1). Peak active force shifted earlier in the gait cycle for the gastrocnemii during forefoot

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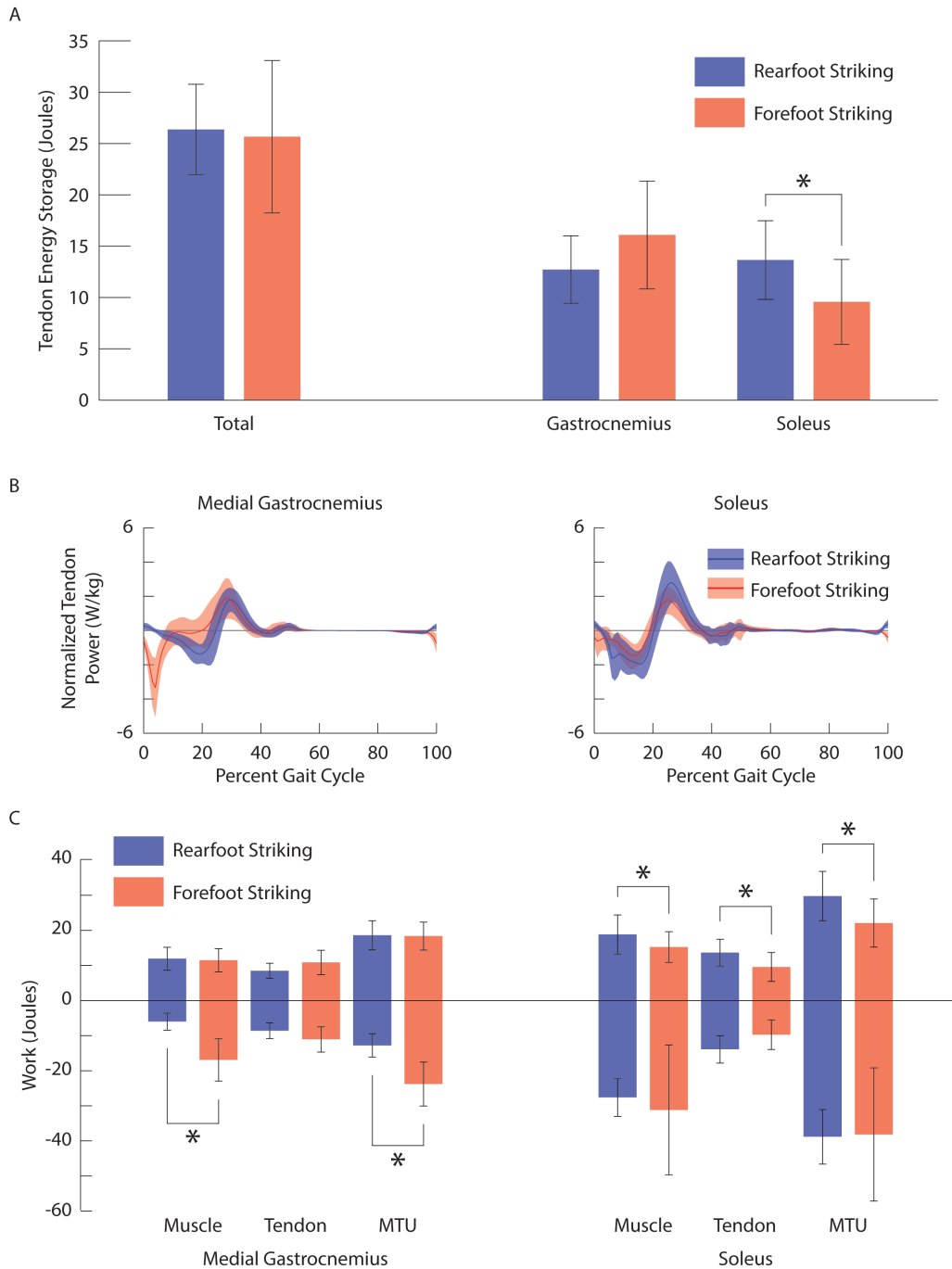
Figure 2. (A) Ensemble average ± one standard deviation tendon energy storage for all plantar flexor tendons together (left), as well as gastrocnemius and soleus components (right) during rearfoot striking (blue) and forefoot striking (red). (B) Ensemble average ± one standard deviation normalized tendon power for the medial gastrocnemius (left) and the soleus (right) during rearfoot striking (blue) and forefoot striking (red). (C) Ensemble average ± one standard deviation positive and negative work done by the muscle fibers, tendon, and muscle-tendon unit of the medial gastrocnemius (left) and the soleus (right) during rearfoot striking (blue) and forefoot striking (red). * indicates a significant difference ($p < 0.05$).

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Figure 3. Ensemble average ± one standard deviation force generation ability at peak active force for the medial gastrocnemius (left) and the soleus (right) during rearfoot striking (blue) and forefoot striking (red). * indicates a significant difference ($p < 0.05$).
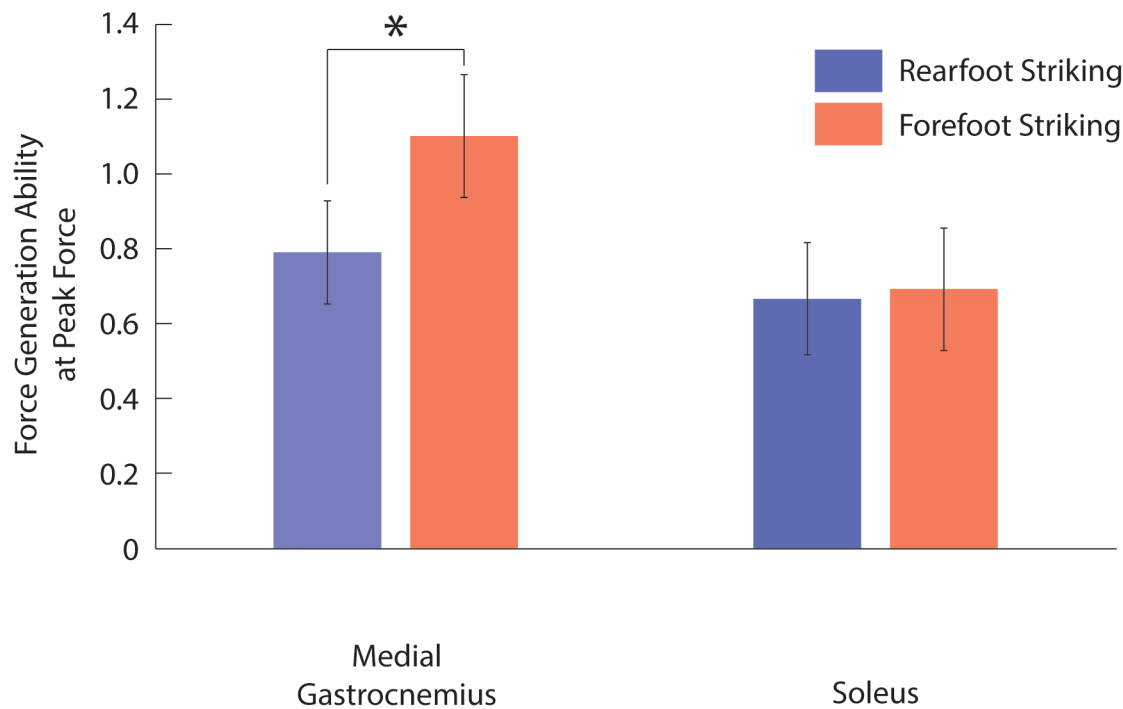
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Table 1. Force generation ability and timing of peak active force for the medial gastrocnemius, lateral gastrocnemius, and soleus during rearfoot striking (RFS) and forefoot striking (FFS). Presented are the mean (standard deviation) and associated p-values. **Bold** indicates a significant difference.

	Force Generation Ability			Timing of Peak Active Force (% Gait Cycle)		
	RFS	FFS	p-value	RFS	FFS	p-value
Medial Gastrocnemius	0.79 (0.15)	1.10 (0.16)	**< 0.001**	25.7 (2.3)	16.6 (6.7)	**< 0.001**
Lateral Gastrocnemius	0.80 (0.14)	1.09 (0.16)	**< 0.001**	25.9 (2.4)	16.4 (7.0)	**< 0.001**
Soleus	0.67 (0.12)	0.69 (0.18)	0.700	21.9 (2)	19.7 (3.7)	0.061

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8

107   striking (medial and lateral: $p < 0.001$), but the timing of peak active force did not significantly

108   change for the soleus ($p = 0.061$).

109   Forefoot striking increased activation of the gastrocnemii during $91 - 17\%$ of the gait cycle

110   compared to rearfoot striking ($p < 0.001$; the same activation was used for both the medial and

111   lateral gastrocnemii; Fig 4), but decreased activation of the soleus during $25 - 34\%$ of the gait cycle

112   ($p = 0.014$) and $81 - 89\%$ of the gait cycle ($p < 0.001$). During forefoot striking, gastrocnemii fibers

113   were shorter for the majority of the gait cycle (medial: $80 - 40\%$, $p < 0.001$; lateral: $79 - 40\%$, $p <$

114   0.001), and soleus fibers were shorter during $77 - 5\%$ of the gait cycle ($p < 0.001$) and $30 - 38\%$ of

115   the gait cycle ($p = 0.002$). Gastrocnemii and soleus fiber lengthening velocities were greater during

116   forefoot striking compared to rearfoot striking early in the stance phase of gait (medial and lateral

117   gastrocnemii: $1 - 9\%$, $p < 0.001$; soleus: $0 - 7\%$, $p < 0.001$). During $3 - 7\%$ of the gait cycle, the

118   gastrocnemii fibers were lengthening during forefoot striking, but shortening during rearfoot

119   striking. Similarly, during $1 - 4\%$ of the gait cycle, soleus fibers were lengthening during forefoot

120   striking and shortening during rearfoot striking.

121   Converting to forefoot striking resulted in greater negative work done by the gastrocnemii

122   muscle fibers (medial and lateral: $p < 0.001$) and muscle-tendon units (medial and lateral: $p <$

123   0.001), but did not affect the positive work done by the gastrocnemii muscle fibers (medial: $p =$

124   0.652; lateral: $p = 0.853$) or muscle-tendon units (medial: $p = 0.723$; lateral: $p = 0.584$; Fig 2C).

125   Conversely, converting to forefoot striking did not significantly affect the negative work done by

126   the soleus muscle fibers ($p = 0.480$) or muscle-tendon units ($p = 0.902$), but caused a reduction in

127   the positive work done by the soleus muscle fibers ($p = 0.007$) and muscle-tendon units ($p < 0.001$).

128   Our estimates for positive and negative work done by the plantar flexor muscle fibers and muscle-

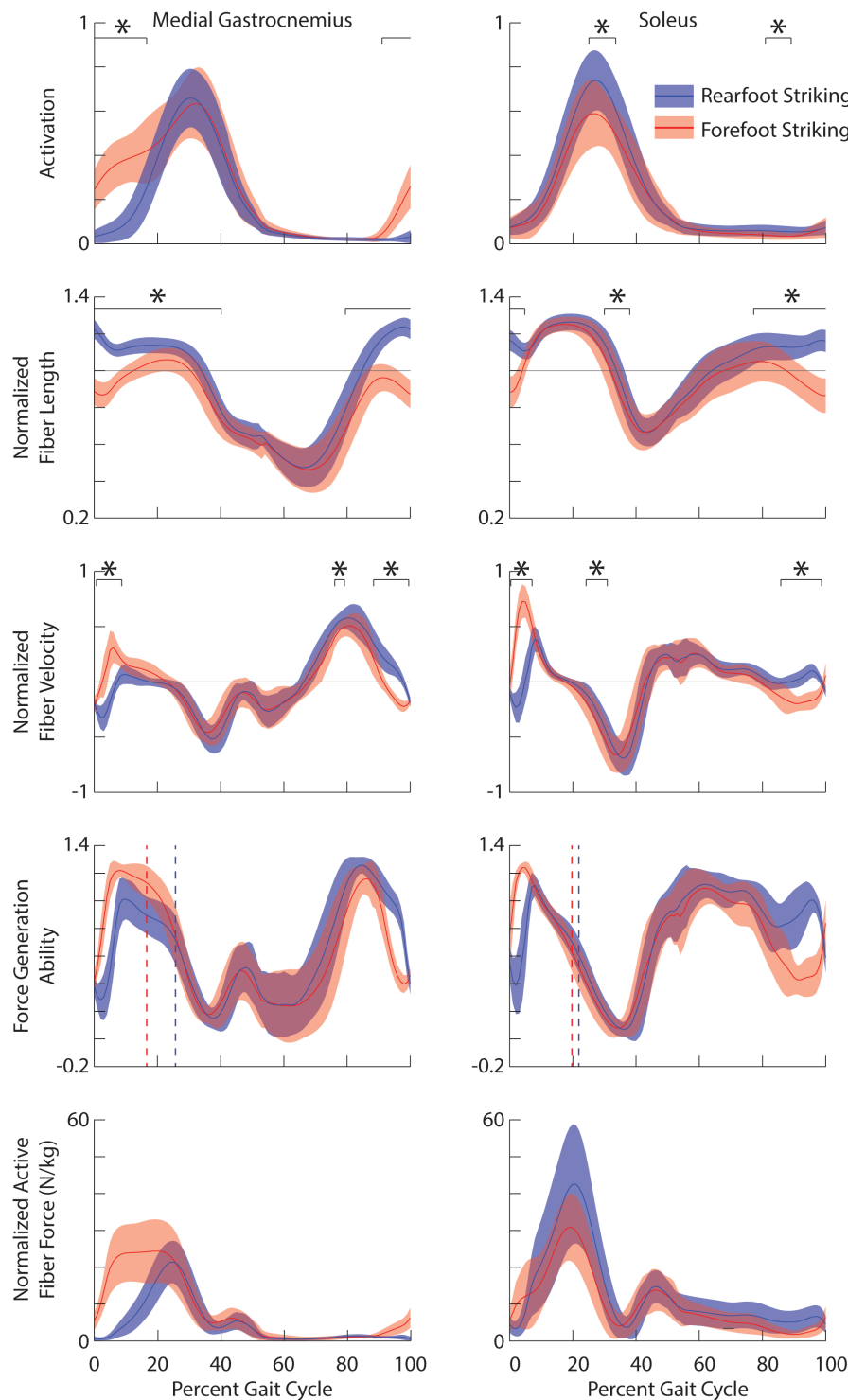129   tendon units are presented in Table 2.

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Figure 4. From top to bottom: Ensemble average ± one standard deviation activation, normalized fiber lengths, normalized fiber velocities, force generation ability and normalized active fiber force for medial gastrocnemius (left) and the soleus (right) during rearfoot striking (blue) and forefoot striking (red). Vertical dashed lines represent timing of peak active fiber force. * indicates the portions of the gait cycle when there is a significant difference ($p < 0.05$).

10

136 **Table 2.** Positive and negative work done by the muscle fibers, tendons, and muscle-tendon units
137 for the lateral gastrocnemius, medial gastrocnemius, and soleus during rearfoot striking (RFS) and
138 forefoot striking (FFS). Presented are the mean (standard deviation) and the associated p-values.
139 **Bold** indicates a significant difference.

	Muscle Fiber			Tendon			Muscle-Tendon Unit		
	RFS	FFS	p-value	RFS	FFS	p- value	RFS	FFS	p-value
Medial Gastrocnemius									
Positive Work	11.9 (3.2)	11.5 (3.3)	0.652	8.5 (2.2)	10.8 (3.5)	--	18.6 (4.2)	18.4 (4.0)	0.723
Negative Work	6.0 (2.4)	16.9 (6.0)	**< 0.001**	--	--	--	12.8 (3.3)	23.8 (6.3)	**< 0.001**
Lateral Gastrocnemius									
Positive Work	7.1 (1.8)	7.0 (1.9)	0.853	4.2 (1.1)	5.2 (1.7)	--	10.4 (2.3)	10.1 (2.1)	0.584
Negative Work	3.2 (1.3)	8.9 (3.2)	**< 0.001**	--	--	--	6.6 (1.7)	12.1 (3.3)	**< 0.001**
Soleus									
Positive Work	18.8 (5.6)	15.3 (4.4)	**0.007**	13.7 (3.8)	9.6 (4.1)	**0.002**	29.8 (7.0)	22.1 (6.9)	**< 0.001**
Negative Work	27.6 (5.4)	31.2 (18.5)	0.480	--	--	--	38.8 (7.8)	38.2 (19.0)	0.902

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142 DISCUSSION

143   The purpose of this study was to identify how plantar flexor muscle-tendon mechanics

144 differed between rearfoot and forefoot striking in habitual rearfoot striking runners. We

145 hypothesized that energy storage in the plantar flexor tendons would be greater during forefoot

146 striking yet observed no significant differences in total energy storage between rearfoot and forefoot

147 striking. This occurred because the increase in elastic energy storage in the gastrocnemius tendon

148 was offset by the decrease in elastic energy storage in the soleus tendon. As expected, altering foot

149 strike pattern affected plantar flexor muscle fiber lengths and velocities around foot contact. The

150 changes in plantar flexor fiber kinematics during forefoot striking resulted in increases in the force

151 generation ability of the gastrocnemii at the time it generates peak active force, with no significant

152 effect on the force generation ability of the soleus. When evaluating the work done by the plantar

153 flexor fibers, we found that forefoot striking increased gastrocnemius negative fiber work and

11

154 decreased positive soleus fiber work. Overall, foot strike pattern affected the gastrocnemii and the

155 soleus muscle-tendon mechanics differently.

156   Differences in tendon energy storage between the gastrocnemius and the soleus were due, in

157 part, to how forefoot striking affected these muscles' activation patterns. The activation differences

158 observed during forefoot striking affected the timing for tendon energy storage in the gastrocnemii.

159 Greater activation in the gastrocnemii prior to and immediately after foot contact resulted in greater

160 muscle and tendon forces and, consequently, greater tendon lengthening velocities during forefoot

161 striking. This combination of greater forces and greater lengthening velocities during early stance

162 with forefoot striking caused peak negative tendon power to shift earlier in the gait cycle for the

163 gastrocnemii (Fig 2B). Subjects did not increase activation of the soleus in the early stance phase

164 and experienced a smaller shift in the timing of peak negative tendon power during forefoot

165 striking.

166   Reviewing changes to force generation ability may provide insight into how increased

167 activation in the gastrocnemii may be beneficial during forefoot striking. Force generation ability

168 represents the muscle's ability to generate active force, and takes into account the effects of fiber

169 length, fiber velocity and pennation angle[13]. Our simulations show the force generation ability of

170 the soleus at peak active force was not significantly affected by foot strike pattern, while the

171 gastrocnemii had significantly higher force generation ability, as well as higher activation, at the

172 time of peak active force during forefoot striking compared to rearfoot striking (Fig 4). Thus, we

173 postulate that to generate the higher plantar flexion moments found in forefoot striking[22], runners

174 take advantage of the higher force generation ability of the gastrocnemii during forefoot striking by

175 increasing activation and force in these muscles rather than utilizing the soleus, which does not

176 benefit from improved force generation ability.

12

177   Converting to forefoot striking caused runners to increase demands on the gastrocnemii

178   without increasing demand on the soleus. In addition to greater peak muscle forces during forefoot

179   striking, activation was higher in the gastrocnemii after foot contact when the fibers were

180   lengthening. The gastrocnemii fibers were, therefore, undergoing eccentric contraction during

181   forefoot striking compared to concentric contraction during rearfoot striking. Although the soleus

182   fibers were also lengthening after foot contact in forefoot striking compared to shortening in

183   rearfoot striking, we did not find increases in activation, muscle forces or negative work, but instead

184   found a decrease in positive soleus fiber work. The differences we found in muscle-tendon

185   mechanics between the gastrocnemii and the soleus were likely due to knee kinematics and

186   differences in activation between the plantar flexors.

187   Greater activation, force, and lengthening velocity of the gastrocnemii but not the soleus in

188   forefoot striking has implications for muscle injury and fatigue. Eccentric exercise has previously

189   been shown to improve strength[27] and potentially, in the long term, prevent injury[28,29]. However, in

190   the short term, eccentric exercise has also been shown to cause muscle soreness, longer-lasting

191   fatigue, and increased risk of muscle damage compared to concentric exercise[30]. While forefoot

192   striking may be beneficial for strengthening the plantar flexors due to increased eccentric

193   contraction, the gastrocnemius may be at increased injury risk in the short-term. Additionally, given

194   that the gastrocnemius is more fatigable than the soleus[31], higher activation and force in the

195   gastrocnemius may contribute to why runners transition from forefoot striking to rearfoot striking

196   over the course of a long distance run.

197   While we analyzed habitual rearfoot strikers running with both rearfoot and forefoot striking

198   running patterns, our results may also be applicable to habitual forefoot strikers. Previous work[10]

199   has shown that acutely trained and habitual forefoot striking runners have similar kinematics. The

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200   runners in this study demonstrated increased ankle plantarflexion and knee flexion at initial contact

201   during forefoot striking compared to rearfoot striking[32], as has been found in habitual forefoot

202   striking runners[20]. Further, the trends in muscle activity are consistent with previously reported

203   differences in muscle activity between habitual rearfoot striking and habitual forefoot striking

204   runners[23]. The similarities in kinematics and muscle activity suggest that our results may also apply

205   to habitual forefoot striking runners.

206   We modeled the Achilles tendon as three distinct tendons – one for the soleus, one for the

207   medial gastrocnemius and one for the lateral gastrocnemius – as opposed to a single shared tendon.

208   In support of modeling the gastrocnemii and soleus tendons independently, Franz et al.[33] found that

209   the superficial and deep regions of the Achilles tendon undergo different deformations. Despite

210   modeling distinct tendons, our estimates of total energy storage in the Achilles tendon (rearfoot

211   striking: 26.4 J; forefoot striking: 25.7 J), found by summing the tendon energy storage in all three

212   tendons, were similar to previous estimates of energy storage in the Achilles tendon. Experimental

213   estimates[6,8,34] ranged from 17-35 J, inverse dynamics estimates[35] ranged from 10-39 J, and muscle-

214   level simulation estimates[36,37] ranged from 27-40 J. Our simulations estimated medial

215   gastrocnemius tendon contributions to positive muscle-tendon work of 46%, compared to

216   ultrasound estimates[38] of 63-70% for rearfoot striking running at similar speeds. This discrepancy

217   may result from modeling choices, particularly tendon compliance. We tested the effect of

218   increasing tendon compliance (from 4.9% to 10% tendon strain at peak force) and found increased

219   energy storage in the Achilles tendon (rearfoot striking: 28.3 J; forefoot striking: 28.4 J) and

220   increased tendon contributions to positive work done by the muscle-tendon units under all

221   conditions. Trends in the effects of foot strike pattern on tendon energy storage were unaffected by

222   a more compliant tendon in our simulations.

14

223   Although our trends in fiber kinematics are mostly consistent with the literature, our

224   reported fiber lengths are longer than previous estimates. During both rearfoot and forefoot striking,

225   estimated soleus fibers exhibited a smaller fascicle excursion than the gastrocnemii fibers,

226   consistent with previous ultrasound work [12,14]. The shorten-stretch-shorten kinematics of our

227   estimated gastrocnemius fibers during forefoot striking (Fig 4) are consistent with Ishikawa and

228   Komi[39] who studied forefoot striking running. However, our gastrocnemius fiber velocities

229   estimated during rearfoot striking, which were mostly negative with relatively small positive

230   velocities, do not agree with reported medial gastrocnemius fibers shortening throughout stance[15].

231   Our results may differ due to our subjects running at faster speeds and running overground rather

232   than on a treadmill. Previous simulations[13,36] and ultrasound imaging[39] estimated fiber lengths to be

233   less than one optimal fiber length throughout the gait cycle when running at similar speeds, but in

234   our simulations peak fiber length exceeded one optimal fiber length. Differences in normalized fiber

235   lengths likely result from using a different model, different plantar flexor tendon compliance, and

236   different estimates of optimal fiber lengths. Recent studies have shown that sarcomeres in healthy

237   individuals are longer than previously estimated using simulation[40,41], which supports our estimates

238   of longer normalized fiber lengths. Although we may overestimate normalized fiber lengths of the

239   plantar flexors, the paired nature of our data lends confidence to our results demonstrating the effect

240   of foot strike pattern on normalized fiber lengths in running.

241   This study identified differences in plantar flexor tendon energy storage, and the positive

242   and negative work done by the plantar flexor muscle fibers and muscle-tendon units between

243   rearfoot and forefoot striking. Although positive work done by the soleus fibers decreased, negative

244   work done by the gastrocnemius fibers was higher in forefoot striking compared to rearfoot striking.

245   We reported differences in plantar flexor fiber lengths and fiber velocities between foot strike

15

246   patterns, and showed that during peak active force, the gastrocnemii fibers were in a more favorable

247   state for generating forces. We postulate that converted forefoot striking runners make use of the

248   improved state of the gastrocnemius by activating this muscle rather than the soleus, a trend that we

249   believe extends to habitual forefoot strikers. Overall, this research supports the notion that runners

250   considering transitioning from rearfoot striking to forefoot striking may benefit from a progressive

251   eccentric strengthening program targeting the plantar flexors to prepare them for the increased

252   demands of forefoot striking and to help avoid injury.

253

254   METHODS

255   *Experimental Data*

256   We collected data from 16 habitual rearfoot striking subjects running overground using both

257   a rearfoot and forefoot striking pattern. The subjects were healthy recreational runners who reported

258   running at least 10 km per week (11 females, 5 males; age: 32.1 ± 9.9 years; height: 167 ± 10 cm;

259   mass: 62.5 ± 10.1 kg; mileage: 36.1 ± 19.5 km/week). The subjects ran at their self-selected speed

260   (2.94 ± 0.30 m/s) using their habitual rearfoot striking pattern and a forefoot striking pattern after

261   acute gait retraining with visual feedback as described previously[32].

262   We tracked the positions of 43 reflective markers from a full-body marker set at 200 Hz

263   using a motion capture system (Motion Analysis Corporation, Santa Rosa, CA, USA) and collected

264   ground reaction forces at 2000 Hz using in-ground force plates (Bertec Corporation, Columbus,

265   OH, USA). Simultaneously, we collected surface EMG data (Delsys Inc., Boston, MA, USA) from

266   the medial gastrocnemius, soleus and tibialis anterior at 2000 Hz. For both rearfoot and forefoot

267   striking, we analyzed data from three trials, each of which captured one stride from each subject's

16

268   dominant limb. Each subject gave informed consent prior to participation according to a protocol

269   approved by the Stanford University Institutional Review Board.

270   *Musculoskeletal Model*

271   We used a full-body musculoskeletal model with 29 degrees of freedom[42]. The model

272   included six degrees of freedom to position and orient the pelvis in space, three-degree-of-freedom

273   ball-and-socket joints to represent each hip joint, custom one-degree-of-freedom joints to represent

274   each knee joint and one-degree-of-freedom revolute joints to represent each ankle joint. The model

275   included 40 muscles per lower limb, but this study focused on analyzing only the soleus, medial

276   gastrocnemius and lateral gastrocnemius of the dominant limb. Muscle-tendon units were modeled

277   using Hill-type muscle models as described by Millard et al.[43].

278   *Simulation of Muscle-tendon Dynamics*

279   We started by scaling the generic musculoskeletal model to each subject's anthropometry. In

280   addition to scaling body segments, we scaled muscle-tendon parameters such that the ratio of

281   optimal fiber length and tendon slack length was preserved. We then used OpenSim's inverse

282   kinematics algorithm[26] to calculate joint angles that best tracked subjects' measured marker

283   positions during the running trials.

284   Muscle excitations were applied to the plantar flexors and the tibialis anterior based on

285   surface EMG data. Data from the medial gastrocnemius, soleus, and tibialis anterior were filtered

286   using a band-pass filter (50 – 500Hz), rectified and filtered again using a critically damped low-pass

287   filter with a 15 Hz cutoff. The filtered EMG signals were scaled to peak activity in the muscle over

288   all running trials. We then applied a 40 ms delay to account for electromechanical delay, consistent

289   with previous work[13]. Processed EMG signals were applied as excitations to the plantar flexors and

290   the tibialis anterior, with the medial gastrocnemius signal applied to both the medial and lateral
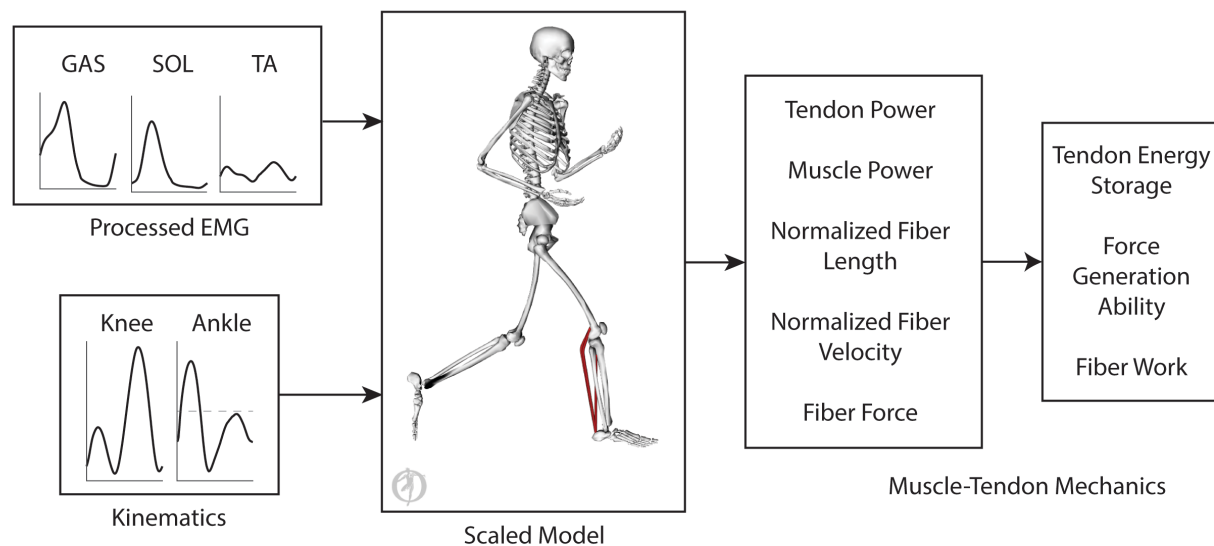
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Figure 5. Simulations of plantar flexor muscle-tendon mechanics were driven by electromyography data, applied as muscle excitations, and joint angles, which prescribed lower body kinematics. The simulations were used to estimate plantar flexor tendon power, muscle power, normalized fiber lengths, normalized fiber velocities and fiber forces. Plantar flexor tendon energy storage and positive and negative fiber work were estimated by integrating tendon power and muscle power. Force generation ability, which combines the effects of fiber length, fiber velocity and pennation angle, was also estimated.

299

300   gastrocnemii in the model. Previous studies have shown measured muscle activity to be similar

301   between the medial and lateral gastrocnemii during both rearfoot and forefoot striking[13,23,44], and

302   other simulation studies have used medial gastrocnemius activity to define excitations for both the

303   medial and lateral gastrocnemii[37]. For all other muscles, we applied an excitation of 0.01 throughout

304   the simulation.

305   Joint angles, estimated from inverse kinematics, and muscle excitations, derived from

306   processed EMG data, drove forward simulations of muscle-tendon dynamics (Fig 5). From these

307   simulations, we estimated normalized fiber lengths, normalized fiber velocities, and fiber forces,

308   along with power done by the muscle-tendon units, muscle fibers, and tendons. Using these results,

309   we estimated the force generation ability[13] of each plantar flexor muscle throughout the gait cycle.

18

310   We also estimated positive and negative work done by the plantar flexor muscle-tendon units and

311   muscle fibers. Tendon energy storage was estimated using positive work done by the plantar flexor

312   tendons and assuming no energy loss. We estimated Achilles tendon energy storage by summing the

313   positive work done by the gastrocnemii and soleus tendons. We estimated the gastrocnemius

314   component of Achilles tendon energy storage by summing the positive work done by the medial and

315   lateral gastrocnemii tendons. To estimate positive and negative work, we integrated the positive and

316   negative parts of the power curves, respectively. The library of these simulations is publicly

317   available at simtk.org/projects/rfs-ffs-pfs.

318   *Testing the simulations by comparison to experimental data*

319   To validate our simulations, we compared the sum of ankle moments and powers produced

320   by the plantar flexors and the tibialis anterior from our forward simulations with the net ankle

321   moment and power estimated from inverse dynamics during stance (Fig 6). Although our solutions

322   only included excitations from three plantar flexor muscles and the tibialis anterior, the soleus along

323   with the medial and lateral gastrocnemii can produce 93% of the model's maximum plantarflexion

324   moment, and the tibialis anterior can produce 62% of the model's maximum dorsiflexion moment.

325   When comparing peak plantarflexion moments between the forward simulation and inverse

326   dynamics results, the average timings were within 3% of the gait cycle and the average magnitudes

327   were within one standard deviation during both rearfoot and forefoot striking. When comparing the

328   average timings for peak positive and peak negative ankle power, the forward simulation and

329   inverse dynamics results were within 2% of the gait cycle during both rearfoot and forefoot striking.

330   For the rearfoot striking forward simulations, the magnitude of peak negative ankle power was

331   within one standard deviation and the magnitude of peak positive ankle power was within two

332   standard deviations of the inverse dynamics results. For the forefoot striking forward simulations,
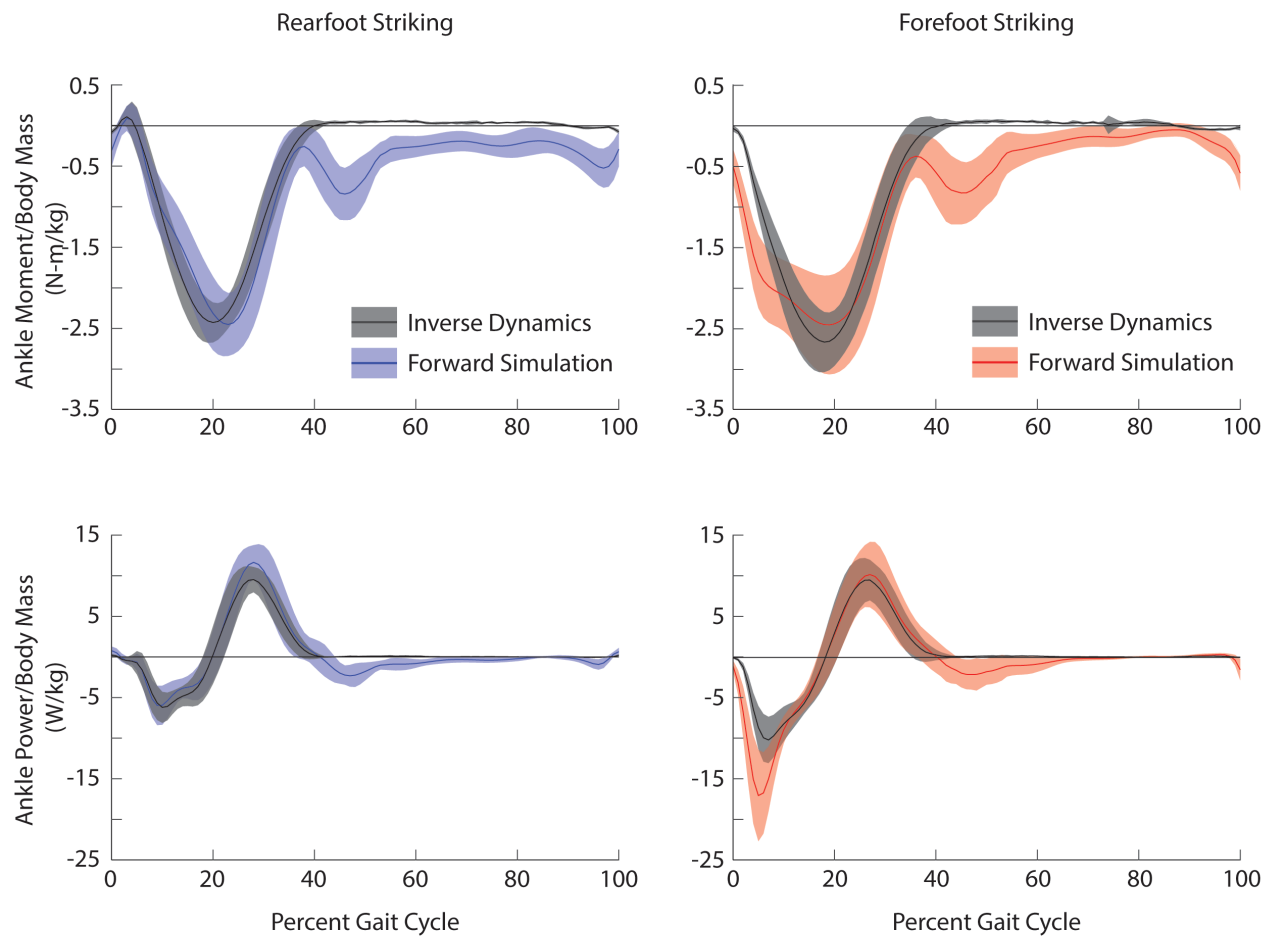
19

Figure 6. Ensemble average ± one standard deviation simulated ankle joint moments (top) and powers (bottom) estimated from forward simulations and inverse dynamics during rearfoot striking (left) and forefoot striking (right) during running. During the forward simulations, average simulated ankle joint moments were estimated based on contributions from the tibialis anterior, the medial and lateral gastrocnemii, and the soleus. Average ankle power was estimated by multiplying the summed moment with the ankle angular velocity. Forward simulation results for rearfoot and forefoot striking are shown in blue and red, respectively. Inverse dynamics results are shown in black.

the magnitude of peak negative ankle power was within three standard deviations and the

magnitude of peak positive ankle power was within one standard deviation of the inverse dynamics

results. Aside from peak negative ankle power during forefoot striking, our errors were within the

guidelines of two standard deviations, as recommended by Hicks et al.[45]. We tested the importance

20

347   of our mismatch in peak negative ankle power during forefoot striking by adjusting our model to

348   better match these peaks. We were able to best align the peak negative ankle powers during forefoot

349   striking by scaling our muscle activity such that peak excitation was 0.8 and, as has been done in

350   previous studies[13,46], increasing tendon compliance in the plantar flexors to 10% strain at maximum

351   isometric force. We ultimately chose not to use these adjustments due to obvious mismatches in

352   peak ankle moments during both rearfoot and forefoot striking, and peak negative ankle power

353   during rearfoot striking.

354   *Statistical Analysis*

355   We compared plantar flexor tendon energy storage, the timing of plantar flexor tendon

356   energy storage, the positive and negative work done by the plantar flexor muscle-tendon units and

357   muscle fibers, the force generation ability of the plantar flexors at peak active force, and the timing

358   of peak active force using paired t-tests. These analyses were done using SPSS (SPSS, IBM,

359   Armonk, NY, USA) and significance for all analyses, before corrections, was set at $p < 0.05$.

360   To identify portions of the gait cycle when fiber lengths and velocities were significantly

361   different between foot strike patterns, we compared the trajectories of plantar flexor normalized

362   fiber lengths and normalized fiber velocities using statistical parametric mapping[47]. This method

363   was also used to compare how plantar flexor activations differ between foot strike patterns.

364   Statistical parametric mapping was designed to identify time ranges when continuous curves are

365   significantly different. While testing for differences in our curves, we indicated that the data were

366   paired, included wrapping since our data are cyclical, included Bonferroni corrections when

367   necessary, and set significance, before corrections, at $p < 0.05$. These analyses were done using

368   "SPM1D" (version M.0.4.5, www.spm1d.org), a free and open source software package for

369   statistical parametric mapping in Matlab (R2015b, The Mathworks Inc., Natick, MA, USA). We

370 excluded any time ranges less than 1% of the gait cycle that were identified as significantly

371 different because our data does not have sufficient resolution to detect such changes.

372

373 CONFLICT OF INTEREST STATEMENT

374 None of the authors had any financial or personal conflict of interest with regard to this

375 study.

376

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382

383 AUTHOR CONTRIBUTIONS

384 All authors contributed to the study formation; J.Y. implemented the analysis and drafted the

385 manuscript and figures; C.D. helped develop tools for the analysis; A.S. contributed to the

386 acquisition of data; all authors reviewed and edited the manuscript and figures.

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