

1 The effect of habitual foot strike pattern on the Gastrocnemius
2 medialis muscle-tendon interaction and muscle force production
3 during running.

4 Wannes Swinnen¹, Wouter Hoogkamer², Tijs Delabastita¹, Jeroen Aeles³, Friedl De Groot¹, Benedicte
5 Vanwanseele¹

6 ¹Human Movement Biomechanics Research Group, Department of Movement Sciences, KU
7 Leuven, Leuven, Belgium

8 ²Locomotion Laboratory, Department of Integrative Physiology, University of Colorado
9 Boulder, Boulder, USA

10 ³Centre for Sensorimotor Performance, School of Human Movement and Nutrition Sciences,
11 The University of Queensland, Brisbane, Australia

12 **Address for correspondence:** Wannes Swinnen - Human Movement Biomechanics Research Group,
13 Tervuursevest 101 - box 1501, 3001 Leuven, Belgium. E-mail: wannes.swinnen@kuleuven.be Phone:
14 +32 16 37 38 63

15 **Running head:** Effect foot strike pattern on muscle and tendon

16 **Authors contribution**

17 Wannes Swinnen: Conception and design of the study, conducted experiments, processed
18 and analysed the data, interpreted the results, wrote, edited and approved the manuscript.

19 Wouter Hoogkamer: Conception and design of the study, interpreted the results, edited and
20 approved the manuscript.

21 Tijs Delabastita: Conducted experiments, interpreted the results, edited and approved the
22 manuscript.

23 Jeroen Aeles: Conducted experiments, interpreted the results, edited and approved the
24 manuscript.

25 Friedl De Groot: Interpreted the results, edited and approved the manuscript.

26 Benedicte Vanwanseele: Conception and design of the study, interpreted the results, wrote,
27 edited and approved the manuscript.

28
29 **New & Noteworthy**

30 Kinetic and kinematic differences between foot strike patterns during running imply (not previously
31 reported) altered muscle tendon interaction. Here, we studied muscle tendon interaction using
32 ultrasonography. We found greater fascicle contraction velocities and lower muscle forces in rearfoot
33 compared to mid-/forefoot strikers. Our results suggest that the higher metabolic energy demand
34 due to greater fascicle contraction velocities might offset the lower metabolic energy demand due to
35 lower muscle forces in rearfoot compared to mid-/forefoot strikers.

36

Keywords

37 Forefoot, Locomotion, Rearfoot, Triceps Surae, Ultrasonography

38

Abstract

39

40 The interaction between Gastrocnemius medialis (GM) muscle and Achilles tendon, i.e. muscle-
41 tendon unit (MTU) interaction, plays an important role in minimizing the metabolic cost of running.
42 Foot strike pattern (FSP) has been suggested to alter MTU interaction and subsequently the
43 metabolic cost of running. However, metabolic data from experimental studies on FSP is inconsistent
44 and a comparison of MTU interaction between FSP is still lacking. We therefore investigated the
45 effect of habitual rearfoot and mid-/forefoot striking on MTU interaction, ankle joint work and
46 plantar flexor muscle force production while running at 10 and 14 km/h. GM muscle fascicles of 9
47 rearfoot and 10 mid-/forefoot strikers were tracked using dynamic ultrasonography during treadmill
48 running. We collected kinetic and kinematic data, and used musculoskeletal models to determine
49 joint angles and calculate MTU lengths. In addition, we used dynamic optimization to assess plantar
50 flexor muscle forces. During ground contact, GM fascicle shortening ($p = 0.02$) and average
51 contraction velocity ($p = 0.01$) were 40 to 45% greater in rearfoot strikers than mid-/forefoot strikers.
52 Differences in contraction velocity were especially prominent during early ground contact. Moreover,
53 GM ($p = 0.02$) muscle force was greater during early ground contact in mid-/forefoot strikers than
54 rearfoot strikers. Interestingly, we did not find differences in stretch or recoil of the series elastic
55 element between FSP. Our results suggest that, for the GM, the reduced muscle energy cost
56 associated with lower fascicle contraction velocity in mid-/forefoot strikers may be counteracted by
57 greater muscle forces during early ground contact.

58

Introduction

59

60 Over the last decade, foot strike pattern (FSP) has become one of the most discussed topics in
61 running research (9, 10, 13, 19, 32, 33, 56, 58, 61, 66), primarily since it has been suggested to alter
62 running injury risk and performance (13, 56, 61). Typically FSP are classified in three groups based on
63 the location of the center of pressure at initial contact with the ground. Cavanagh and LaFortune (10)
64 originally defined these three groups as rearfoot strike where initial contact with the ground occurs
65 with the posterior 1/3 of the foot, midfoot strike where initial contact occurs with middle 1/3 of the
66 foot and forefoot strike in which initial contact occurs with anterior 1/3 of the foot.

67 Many studies have investigated the kinetic and kinematic differences between rearfoot and mid-
68 /forefoot striking (9, 10, 19, 32–34, 58, 66, 67). Primary differences are the absence of a ground
69 reaction force impact peak (10) and shorter ground contact times (19, 58) during mid-/forefoot

70 striking. Furthermore, mid-/forefoot strikers demonstrate greater negative ankle power and work
71 during the ground contact phase of running (34, 67). This greater negative ankle power and work is
72 largely absorbed by the muscle-tendon unit (MTU) containing the Triceps Surae muscles and Achilles
73 tendon. During running, this MTU plays a significant role, especially in minimizing the metabolic cost
74 (26, 28, 39, 44, 63). The ankle plantar flexors, Gastrocnemius medialis (GM), Gastrocnemius lateralis
75 (GL) and Soleus (SOL), produce force to support body weight and contribute to forward propulsion
76 during running. All three muscles are connected to the foot through their respective aponeuroses
77 and merge into a common tendon, the Achilles tendon. During running, the elastic tissues in this
78 MTU act in a spring-like manner storing mechanical energy during the first part of the ground contact
79 phase and returning mechanical energy during the second part (51, 52, 63). Moreover, the series
80 elastic element (SEE, i.e. tendinous tissue) also interacts with the connected plantar flexor muscles to
81 adapt to different gait speeds and minimizes the metabolic cost of muscle contraction (28, 49, 54,
82 55).

83 Since it has been observed that top finishers in middle and long distance races more often run with a
84 mid- or forefoot strike (14, 37), several researchers have suggested that mid-/forefoot striking may
85 be more economical compared to rearfoot striking and have speculated on a more effective energy
86 storage and return in the SEE (20, 37, 38, 61). However, Gruber et al. (31) showed that the running
87 economy, i.e. the amount of metabolic energy consumed to run at certain submaximal speed, of
88 mid-/forefoot striking runners is not lower compared to their rearfoot striking competitors.
89 Moreover, Ogueta-Alday and colleagues (59) reported the running economy of rearfoot strike
90 runners to be better than forefoot strike runners when running at 11 and 13 km/h, whereas no
91 significant difference was observed at 15 km/h.

92 Although differences in kinetics and kinematics between FSP suggest altered MTU interaction, i.e.
93 altered influence of tendon on the muscle and *vice versa* (34, 67), this has not yet been investigated.
94 The larger ankle dorsiflexion rotation due to the greater internal plantar flexor moment during early
95 stance – causing increased negative work - in mid-/forefoot strikers will likely result in immediate
96 lengthening of the MTU. In contrast, during rearfoot striking the foot undergoes a fast plantar flexion
97 directly after foot-ground contact and thus the MTU can be expected to lengthen less during early
98 stance. It can be hypothesized that the greater lengthening of the MTU in mid-/forefoot strikers may
99 induce more stretching of, and hence more elastic energy stored in, the SEE. Due to the initial
100 internal dorsiflexion moment during rearfoot striking, stretching of the SEE may be supposed to
101 either take place later in stance phase or by actively shortening the muscle. This mechanism seems
102 likely as forefoot strikers demonstrate higher average Achilles tendon loading rates, strain, strain
103 rates, stress and impulses compared to rearfoot strikers (6, 57, 62). Besides greater stretch of the

104 SEE, the greater internal plantar flexor moment in mid-/forefoot strikers presumably also induces
105 increased plantar flexor muscle forces to produce the greater moment. This surmised greater muscle
106 force production is further supported by muscle activity studies demonstrating an earlier, higher and
107 longer muscle activation of the plantar flexor muscle in mid-/forefoot strike running compared to
108 rearfoot strike running (4, 20).

109 Here, we investigated the effect of habitual rearfoot and mid-/forefoot striking on MTU interaction,
110 ankle joint work and plantar flexor muscle force production while running at 10 and 14 km/h. First,
111 based on the greater dorsiflexion angle at initial ground contact in rearfoot strikers, we hypothesized
112 1) that greater length changes and contraction velocities of the GM muscle fascicles would occur in
113 rearfoot strikers compared to mid-/forefoot strikers. Second, we hypothesized that during mid-
114 /forefoot striking greater internal plantar flexor moments would occur accompanied by 2) higher
115 forces produced by the muscles and 3) greater stretch and recoil of the SEE.

116 In addition to FSP, we also investigated the effect of running speed on MTU interaction. Based on the
117 “cost of generating force” hypothesis from Kram and Taylor who argued that muscle force rather
118 than muscle work determines the metabolic cost of running (45, 46), no difference in muscle fascicle
119 length changes across running speeds would be expected. Nevertheless, there is ample evidence that
120 GM muscle fascicles shorten throughout the ground contact phase of running (12, 24, 40, 41, 51, 52,
121 54). Therefore, we hypothesized that 4) GM muscle fascicle length changes during ground contact
122 would not be altered by running speed. However, the shorter ground contact times associated with
123 faster running would coincide with a higher average contraction velocity of the muscle fascicles and
124 higher maximal force produced by the muscles during ground contact. Lastly, as higher running
125 speed also induces greater ground reaction forces and thus greater internal plantar flexion moments,
126 we hypothesized that 5) SEE stretch and recoil would increase when running faster.

127 [Methods](#)

128

129 **Participants.** Nineteen runners participated in the study, ten habitual forefoot or midfoot strikers (6
130 males, 4 females; body mass: 65.2 ± 7.7 kg; body height: 1.78 ± 0.07 m) and nine habitual rearfoot
131 strikers (6 males, 3 females; body mass: 72.7 ± 12.5 kg; body height: 1.81 ± 0.08 m). All the
132 participants were trained runners who ran 30 km or more a week. Furthermore, participants did not
133 have or any Achilles tendon or calf injury in the last 6 months prior to the study and were injury free
134 at the time of testing. None of the participants have had Achilles tendon surgery. All participants
135 gave written informed consent, approved by the local ethical committee (Medical Ethical Committee
136 of UZ Leuven).

137 **Experimental protocol.** Prior to the experimental testing, participants had a 10-minute warm-up on a
138 motorized force measuring treadmill (Motekforce Link, Amsterdam, The Netherlands), involving 2-4
139 minutes walking and 6-8 minutes running at a self-selected speed. Next, participants performed one
140 five-minute running trial during which they ran 2.5 minutes at 10 and 14 km/h in randomized order.
141 All participants wore standardized running shoes (Li Ning Marathon, Luhta sportswear company,
142 Lahti, Finland). We collected kinetic, kinematic, muscle activation and ultrasound data during the last
143 minute of running at each speed, as to have data for at least four strides.

144 **Kinetics and kinematics.** We attached forty-seven spherical reflective markers, including four cluster
145 markers, to the participant's body to track the positions of anatomical body landmarks. Thirteen
146 infrared motion capturing cameras (Vicon, Oxford Metrics, UK) captured trajectories of these
147 markers at a sampling rate of 150 Hz. The static trial (Nexus 2.4, Vicon Metrics, UK) was used to scale
148 a musculoskeletal model in OpenSim 3.3 (18, 35). After scaling, we used inverse kinematic
149 calculations, based on a Kalman Smoothing algorithm, to acquire joint angles (15). These joint angles
150 were then used as input for a muscle analysis procedure, also conducted in OpenSim, to calculate the
151 muscle tendon unit lengths taking into account both the joint angles and the muscle moment arms as
152 a function of the joint angles. Ground reaction force during running was measured using the force
153 plate embedded in the treadmill with a sampling frequency of 900 Hz. Force plate data was first low-
154 pass filtered in MatLab (Mathworks, Natick, US) using a recursive fourth order Butterworth filter with
155 a cut-off frequency of 20 Hz and then used to determine the ground contact phase during running
156 using a threshold of 30 N.

157 We combined the force data and joint angles in an inverse dynamics analysis to calculate internal
158 joint moments, i.e. Newton-Euler inverse dynamics approach. Joint moments were low pass filtered
159 using a recursive fourth order Butterworth filter with cut-off frequency of 20 Hz. Next, ankle power
160 was calculated as the product of the joint moment and the joint angular velocity, calculated as the
161 time derivative of the joint angles. We computed joint work (positive, negative and net) as the time
162 integral of the ankle joint power curve. Joint moments, power and work were all normalized to body
163 mass and stride.

164 **Foot strike angle.** We determined FSP using the first metatarsal-phalangeal joint marker and heel
165 marker of the left foot when the vertical ground reaction force exceeded 30N, i.e. initial ground
166 contact (7). Using the angle between the line through these markers and the ground, the foot strike
167 angle (FSA) was calculated. According to Altman and Davis (7), rearfoot strike was considered when
168 the FSA was greater than 8°, runners with a FSA between -1.6 and 8° were defined as midfoot strikers
169 and a FSA lower than -1.6° was considered forefoot strike. In this study we did not make any

170 differentiation between midfoot or forefoot strike, hence a FSA under 8° was defined as mid-
171 /forefoot strike. Although we acknowledge that FSP is rather a continuum than three different foot
172 strike types, we assumed that the average differences of more than 15° between both groups (Table
173 1) would be enough for a clear distinction. We averaged the FSA over the strides used for ultrasound
174 analysis (at least 4). Foot strike type (rearfoot or mid-/forefoot) was consistent within subjects across
175 running speeds.

176 **Electromyography.** EMG signals of the GM muscle of the right leg was collected using a wireless EMG
177 acquisition system (ZeroWire EMG Aurion, Milano, Italy), with a sampling frequency of 900 Hz. EMG
178 signals were synchronized with the 3D motion analysis system and force plate using a central
179 computer. EMG signals were first band-pass filtered (20-400 Hz), rectified and then low-pass filtered
180 at a cut-off frequency of 20 Hz with a recursive fourth order Butterworth filter. We defined the
181 maximal activation of each muscle for each subject using a moving average over 10 data points. Next,
182 we normalized the EMG waveforms towards this maximal activation.

183 To determine GM muscle activation, we first calculated the individual mean activation and standard
184 deviation for the series of recorded steps during every moment in the stride. We used this subject-
185 specific minimum, appearing between 45 and 75% of stride where GM EMG signal was very low
186 (Figure 1), plus three times the standard deviation at that instant, as the threshold to define when
187 the muscle was active. From this activation data, we determined the start of the muscle activation
188 (pre-activation timing) and deactivation timing. Since we did not measure, and hence normalize to,
189 maximal voluntary muscle contraction, it should be noted that the magnitude of the EMG signals
190 during ground contact cannot be compared between FSP groups.

191 **Dynamic ultrasound imaging.** GM muscle fascicles of the left leg were visualized with a B-mode
192 ultrasound system (Telemed Echoblaster 128 CEXT system) with a sampling frequency of 86 Hz. At
193 least four strides were collected each time. A linear transducer (UAB Telemed, Vilnius, Lithuania, LV
194 7.5/60/128Z-2) operating at 8 MHz was placed on the mid-belly of the muscle and aligned along the
195 muscle fascicles. The transducer was securely attached to the calf with tape and elastic bandages.
196 We used a trigger pulse at the start of the ultrasound imaging to synchronize the ultrasound images
197 with the Vicon motion capturing system, force plates and EMG system. Afterwards, all the data were
198 splined to the ultrasound frequency when GM muscle fascicle or SEE length changes were calculated
199 using a custom made MatLab script. The tracking of the muscle fascicles was conducted in MatLab,
200 using a semi-automatic tracking algorithm (22). To calculate fascicle length and pennation angle (i.e.
201 the angle between the muscle fascicle and deep aponeurosis) we drew three tracking lines on each
202 image. A first line was drawn on the inner border of the superficial aponeurosis, another on the inner

203 border of the deep aponeurosis and the third tracking line is drawn parallel to the muscle fascicles
204 (3). If needed, we manually adjusted the tracking lines to match the aforementioned locations. As the
205 complete muscle fascicle from deep to superficial aponeurosis was not always visible due to the
206 limited field of view of the ultrasound transducer, we linearly extrapolated the aponeurosis and
207 muscle fascicle (3). Muscle fascicle length was then calculated as the distance between the
208 intersection of the fascicle with the superficial and deep aponeurosis. Fascicle lengths and pennation
209 angles were low-pass filtered using a recursive fourth-order Butterworth filter with cut-off frequency
210 of 12 Hz (MatLab R2018a) (3). We analyzed at least four strides for every participant.

211 According to the Hill-type muscle model, the estimated length of the SEE can be derived after
212 combining the muscle fascicle lengths and pennation angles from the ultrasound images with the
213 calculated MTU lengths. Fukunaga et al. (29) previously described this method and SEE length (L_{SEE})
214 was calculated as:

$$L_{SEE} = L_{MTU} - L_{Fascicle} * \cos(\alpha)$$

215 Where L_{MTU} describes the muscle-tendon unit length, $L_{Fascicle}$ the fascicle length and α the pennation
216 angle.

217 We calculated length changes of the fascicle, SEE and MTU relative to their respective lengths at toe-
218 off. We calculated fascicle shortening during stance as the difference between maximal and minimal
219 muscle fascicle length. Maximal SEE and MTU stretch during stance was calculated as the difference
220 between maximal SEE/MTU length and minimal SEE/MTU length during the first part of the stance
221 phase whereas SEE and MTU recoil was calculated as the difference between maximal SEE/MTU
222 length and SEE/MTU length at toe off. Fascicle contraction velocities are calculated as the time
223 derivative of the length changes during stance. All data were splined to 100 data points per stride
224 (starting at initial ground contact) to allow comparison between subjects and running speeds.

225 **Muscle force.** Non-invasive direct measurement of muscle force is not possible. Therefore, we
226 estimated muscle forces during ground contact using an optimization approach to solve the muscle
227 redundancy problem. We used a dynamic optimization algorithm that takes into account muscle-
228 tendon dynamics of the 43 lower limb muscles in our model. We used the Hamner OpenSim model
229 (35) that was scaled to the subject's dimensions to obtain individual muscle moment arms, MTU
230 lengths and properties (optimal muscle fiber length, optimal pennation angle and tendon slack
231 length). Maximal isometric muscle force was scaled based on the subject's body mass and height
232 (36). Gerus et al. (30) reported that the Achilles tendon is more compliant than the generic tendon
233 described by Zajac (70). Hence, to more closely follow the tracked muscle fascicle length changes, the
234 scaling factor (normalized tendon stiffness) to calculate GM, GL and SOL tendon stiffness from the

235 ratio between maximal isometric force and tendon slack length was set at 5 for all individuals. All
236 other muscles had the default normalized stiffness value of 35. Inverse dynamic joint moments along
237 with MTU lengths and moment arms were used as inputs to solve the muscle redundancy problem
238 by minimizing muscle activations squared. In contrast to commonly used static optimization
239 approaches that simplify muscle-tendon dynamics by neglecting activation dynamics and assuming
240 rigid tendons, muscle activation and contraction dynamics were taken into account (16, 17). The
241 resulting dynamic optimization problem was solved through direct collocation using GPOPS-II
242 software (16, 60). The resulting nonlinear program was solved using ipopt (69). Simulated GM muscle
243 fascicle length changes predicted the ultrasound measured fascicle length changes well (≤ 1 mm
244 differences in mean GM muscle fascicle shortening during ground contact for all groups). Next, to
245 calculate the actual instantaneous muscle forces along the line of the fascicle, forces were divided by
246 the cosine of the simulated pennation angle of the muscle. In a couple cases the optimization
247 algorithm failed to find an optimal solution and hence these strides were excluded. Yet, for each
248 subject we still used at least 3 ground contact phases. GM muscle force was normalized to body mass
249 and ground contact phase.

250 **Statistics.** We present all the data in the text as mean \pm standard deviation. The data were
251 categorized in four groups: mid-/forefoot strike 10 km/h (FFS 10), mid-/forefoot strike 14 km/h (FFS
252 14), rearfoot strike 10 km/h (RFS 10) and rearfoot strike 14 km/h (RFS 14). We used Shapiro-Wilk test
253 to test for normality for all groups. However, not all data were normally distributed. If the data from
254 all the groups were normally distributed, we performed a mixed analysis of variance (ANOVA) to
255 determine the differences in main effects (FSP and running speed) and interaction between both,
256 using SPSS v.24 (IBM SPSS, Armonk, New York, USA). When an interaction effect between FSP and
257 running speed was found, we determined the difference separately for each FSP and each running
258 speed using an unpaired t-test (FSP) and paired t-test (running speed). If not all the data in the
259 groups were normally distributed, a non-parametric test was performed. We used a Mann-Whitney
260 U test to compare the mean differences between FSP at 10 and 14 km/h. To determine the effect of
261 running speed for these datasets, the data was first grouped according to running speed and again
262 checked upon normality. If both datasets followed a normal distribution, we performed a paired t-
263 test, if not we performed a Wilcoxon signed-rank test. Furthermore, when we found a significant
264 difference, partial eta squared (η_p^2) was calculated as a measure of the effect size for the mixed
265 ANOVA results where $\eta_p^2 < 0.13$ was considered as a small effect size, $0.13 \leq \eta_p^2 < 0.26$ a medium
266 effect and $\eta_p^2 \geq 0.26$ a large effect. If mixed ANOVA could not be performed due to violations against
267 normality, eta squared (η^2) was calculated with $\eta^2 < 0.06$ considered as a small effect size, $0.06 \leq \eta^2 <$
268 0.14 a medium effect and $\eta^2 \geq 0.14$ a large effect. Differences in muscle fascicle contraction velocity

269 and GM muscle force production during ground contact time were tested with statistical parametric
270 mapping (SPM) (64). Our probability criterion for statistical significance was set at $p < 0.05$.

271 Results

272
273 FSA, the criterion to separate mid-/forefoot strikers from rearfoot strikers, was significantly different
274 between the groups (Table 1; $p < 0.01$; $\eta_p^2 = 0.80$). Although previous research revealed significant
275 shorter ground contact during mid-/forefoot striking than rearfoot striking, we did not find a
276 significant difference ($p > 0.11$). Still, faster running was associated with shorter ground contact times
277 ($p < 0.01$; $\eta^2 = 0.38$).

278 Rearfoot strikers demonstrated 3.9mm and 3.7mm (40 to 45%) more fascicle shortening during
279 ground contact than mid-/forefoot strikers at 10 and 14 km/h respectively (Table 1; $p = 0.02$; $\eta_p^2 =$
280 0.29). Also, average fascicle contraction velocity during ground contact time was higher in rearfoot
281 strikers ($p = 0.01$; $\eta_p^2 = 0.32$). When analyzing fascicle contraction velocity during ground contact,
282 differences between FSP appeared primarily different during early ground contact (approximately 0
283 to 30% of ground contact, Figure 2), but none reached significance after the first 0.4% of ground
284 contact. The total fascicle shortening during ground contact was nearly identical between the two
285 running speeds, but the shorter ground contact time at 14 km/h induced higher average contraction
286 velocities ($p < 0.01$; $\eta_p^2 = 0.56$). Maximal muscle fascicle contraction velocities were higher when
287 running faster ($p = 0.02$; $\eta^2 = 0.14$), but not significantly different between FSP ($p > 0.15$).
288 Furthermore, GM fascicle length at initial ground contact was not different between FSP ($p = 0.32$) or
289 running speeds ($p = 0.10$).

290 As expected, mid-/forefoot strikers demonstrated greater negative ankle work compared to rearfoot
291 strikers ($p < 0.01$; $\eta_p^2 = 0.53$). However, this greater negative ankle work did not result in an increased
292 stretch of the SEE in mid-/forefoot strikers during ground contact (Figure 1; $p = 0.20$). In contrast,
293 greater lengthening of the entire MTU in mid-/forefoot strikers was observed ($p < 0.01$; $\eta_p^2 = 0.66$).
294 No significant differences in MTU or SEE recoil during ground contact were detected between FSP or
295 running speeds ($p \geq 0.10$). Despite the GM being bi-articular, also spanning the knee joint, differences
296 in MTU length changes during ground contact were not accompanied with differences in knee
297 kinematics or work across FSP or running speeds ($p \geq 0.10$).

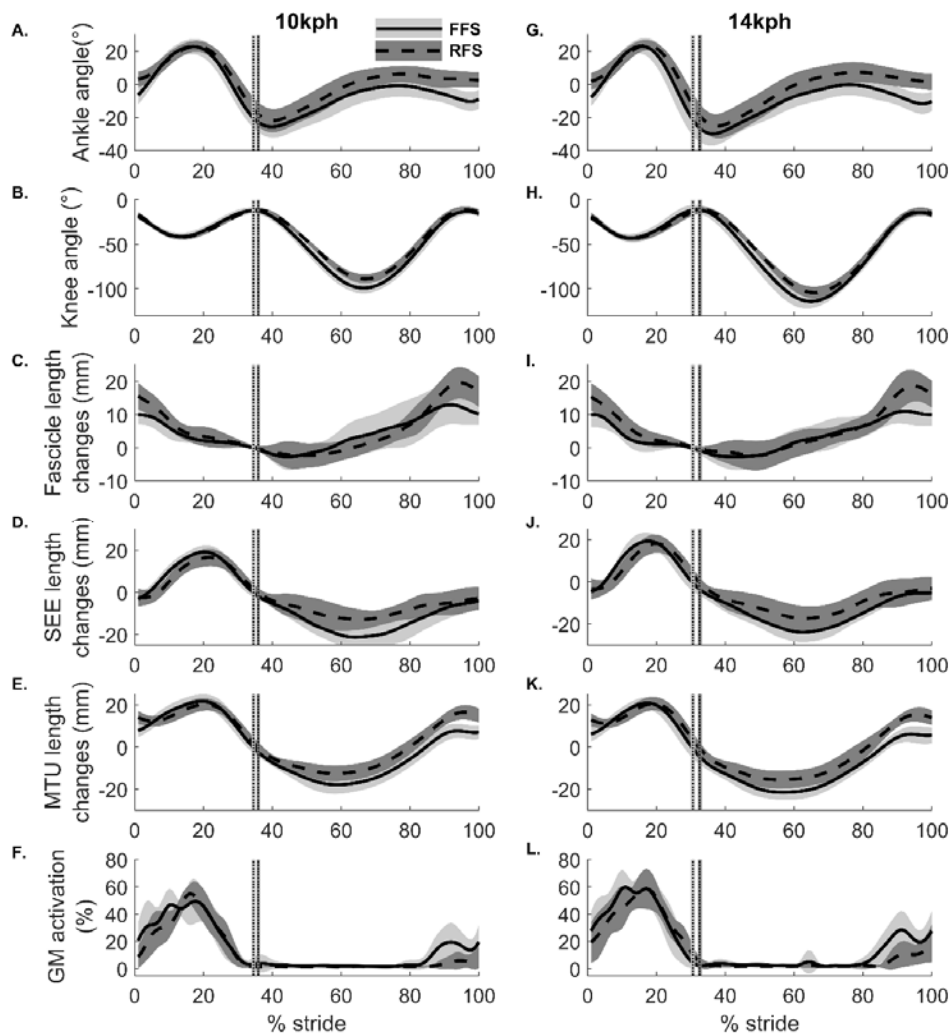
298 Mid-/forefoot strikers demonstrated greater GM muscle force production during early ground
299 contact (Figure 2; $p = 0.02$; 6 – 13% ground contact). Irrespective of FSP, GM muscle force during
300 ground contact, as well as peak muscle forces, were higher at 14 km/h than at 10 km/h ($p < 0.01$; η_p^2
301 = 0.83). The greater GM muscle force production during early ground contact was accompanied by

302 an earlier GM muscle activation in mid-/forefoot strikers compared to rearfoot strikers (Figure 1;
 303 Table 1; $p < 0.01$; $\eta_p^2 = 0.41$). Faster running also yielded an earlier pre-activation of the GM muscle
 304 ($p < 0.01$; $\eta_p^2 = 0.40$).

305 *Table 1. Comparison between mid-/forefoot and rearfoot strikers and between 10 and 14 km/h. All data are expressed as*
 306 *mean \pm SD. * significant main foot strike effect. † significant main running speed effect. ‡ significant difference between foot*
 307 *strike patterns only at 14 km/h. § significant interaction effect.*

		speed	Forefoot strike	Rearfoot strike
Foot strike angle (FSA)	(°)*	10 km/h	-0.4 \pm 4.4	14.8 \pm 3.7
		14 km/h	0.3 \pm 5.3	17.2 \pm 5.4
Ground contact time	(ms)†	10 km/h	250.6 \pm 16.3	259.9 \pm 12.6
		14 km/h	209.2 \pm 13.7	218.2 \pm 16.6
GM muscle fascicle	Length at ground contact	10 km/h	51.4 \pm 10.2	56.3 \pm 6.9
	(mm)	14 km/h	51.1 \pm 11.0	54.7 \pm 7.9
	Shortening during ground contact (mm)*	10 km/h	11.2 \pm 3.9	16.1 \pm 3.6
		14 km/h	11.3 \pm 4.3	16.0 \pm 4.1
	Average velocity ground contact (mm/s)*†	10 km/h	-42.6 \pm 12.7	-62.1 \pm 14.6
		14 km/h	-50.3 \pm 18.4	-72.3 \pm 20.3
	Maximal velocity ground contact (mm/s)†	10 km/h	-157 \pm 52	-186 \pm 27
		14 km/h	-185 \pm 91	-218 \pm 70
SEE	Stretch (mm)†	10 km/h	22.7 \pm 2.7	20.3 \pm 3.0
		14 km/h	24.7 \pm 4.5	22.9 \pm 4.0
	Recoil (mm)	10 km/h	19.5 \pm 3.2	17.0 \pm 4.1
		14 km/h	20.0 \pm 4.4	18.3 \pm 4.3
MTU	Stretch (mm)*†	10 km/h	14.1 \pm 3.0	8.3 \pm 1.0
		14 km/h	15.2 \pm 2.4	10.0 \pm 1.6
	Recoil (mm)	10 km/h	21.8 \pm 3.4	20.3 \pm 3.0
		14 km/h	21.2 \pm 3.2	20.7 \pm 3.2
Ankle work	Negative (J/kg)*†§	10 km/h	-0.74 \pm 0.12	-0.55 \pm 0.09
		14 km/h	-1.01 \pm 0.16	-0.71 \pm 0.11
	Positive (J/kg)†	10 km/h	1.02 \pm 0.12	0.94 \pm 0.16
		14 km/h	1.29 \pm 0.11	1.17 \pm 0.21
	Net (J/kg)	10 km/h	0.29 \pm 0.17	0.39 \pm 0.10
		14 km/h	0.28 \pm 0.21	0.46 \pm 0.21

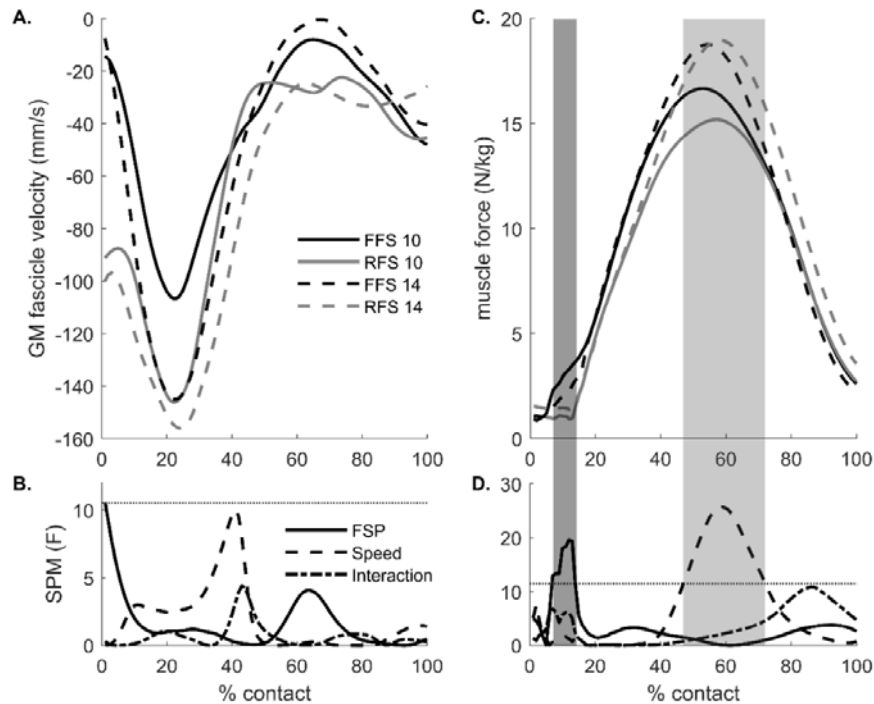
Knee work	Negative (J/kg)	10 km/h	-0.22 ± 0.08	-0.26 ± 0.07
		14 km/h	-0.22 ± 0.10	-0.27 ± 0.07
	Positive (J/kg)	10 km/h	0.25 ± 0.10	0.24 ± 0.06
		14 km/h	0.27 ± 0.12	0.26 ± 0.09
	Net (J/kg)	10 km/h	0.03 ± 0.08	-0.02 ± 0.06
		14 km/h	0.05 ± 0.11	-0.01 ± 0.11
GM muscle activation	Pre-activation timing (% stride)*†	10 km/h	84.6 ± 4.6	92.6 ± 5.7
		14 km/h	82.0 ± 3.6	86.3 ± 5.1
	Deactivation timing (% stride)	10 km/h	33.8 ± 6.0	31.2 ± 2.6
		14 km/h	35.3 ± 10.9	33.4 ± 2.5
GM muscle force	Peak (N/kg)†	10 km/h	16.9 ± 1.3	16.5 ± 1.6
		14 km/h	19.4 ± 2.1	20.1 ± 2.1



309

310 Figure 1. Mean ankle (A, G) and knee angles (B, H), mean Gastrocnemius medialis muscle fascicle length changes (C, I),
 311 Series elastic element length changes (SEE; D, J), muscle tendon unit length changes (MTU; E, K), Gastrocnemius medialis
 312 (GM) activation (F, L) during stride compared between mid-/forefoot strikers (FFS; solid; N = 10) and rearfoot strikers (RFS;
 313 dashed; N = 9) at 10 km/h (A-E) and 14 km/h (F-J). Fascicle, SEE and MTU length changes are normalized to the length at
 314 toe-off. Grey area represents standard deviation. Mean timing of toe-off \pm SEM is indicated with vertical dashed lines and
 315 grey area for FFS (light grey) and RFS (dark grey).

316



317

318 *Figure 2. Mean Gastrocnemius medialis muscle fascicle velocity (A) and mean muscle force (C) during the ground contact*
 319 *phase of running for mid-/forefoot strikers (FFS; grey; N = 10) and rearfoot strikers (RFS; black; N = 9) at 10 km/h (solid lines)*
 320 *and 14 km/h (dashed lines). For clarity SD was left out. Negative velocities indicate fascicle shortening (A). The results of the*
 321 *statistical parametric mapping (SPM) are shown in B and D with foot strike pattern effect (solid), speed effect (dashed),*
 322 *interaction effect (dashed dotted) and significance threshold (dotted). Dark grey background visualizes significant difference*
 323 *in forces between foot strike patterns ($p = 0.02$). Light grey background visualizes significant differences in speed ($p < 0.01$).*
 324 *No interaction effect was found for both fascicle velocity and muscle force. No significant differences in fascicle velocity*
 325 *between foot strike pattern after the first 0.4% of ground contact. No significant speed effect was found for fascicle velocity.*

326 Discussion

327

328 Our primary focus in this study was to investigate the effect of FSP on GM MTU dynamics. We
 329 confirmed our first hypothesis that GM muscle fascicle shortening and average contraction velocity
 330 during ground contact was greater in rearfoot strikers compared to mid-/forefoot strikers. While GM
 331 muscle fascicle contraction velocities were primarily different during early ground contact (Figure
 332 2A), GM muscle force production was significantly lower in rearfoot strikers compared to mid-
 333 /forefoot strikers (Figure 2C) confirming our second hypothesis. However, since SEE stretch and
 334 recoil was not significantly different between FSP, we cannot accept our third hypothesis.

335 Our next hypotheses concerned the effect of running speed on GM MTU behavior. We confirmed our
 336 fourth hypothesis that GM muscle fascicle shortening during ground contact was not different
 337 between running speeds of 10 and 14km/h for either FSP. As expected, the shorter ground contact
 338 times, associated with faster running, resulted in greater GM muscle fascicle contraction velocities
 339 and higher (peak) muscle force. We could not confirm our fifth hypothesis that greater running speed
 340 would enhance the stretch and recoil of the SEE. Surprisingly, only SEE stretch during the first part of

341 ground contact was greater at 14 km/h compared to 10 km/h, whereas SEE recoil was not different
342 between speeds.

343 The observed absence of differences in SEE stretch and recoil between FSP suggest that FSP does not
344 influence mechanical energy storage and release in the SEE. The Triceps Surae MTU plays a key role
345 in optimizing human locomotion (28) and hence SEE stretch and recoil is important for whole body
346 metabolic energy consumption. Since Kubo and colleagues demonstrated that the Achilles tendon
347 stiffness is not different between FSP, this would indicate that SEE stretch and recoil are directly
348 related to mechanical energy storage and return in the SEE (47). However, we did not measure
349 Achilles tendon stiffness for the runners in our samples.

350 We observed differences in both GM muscle fascicle contraction velocity and force which can be
351 expected to have opposing effects on metabolic energy consumption between FSP. The metabolic
352 energy consumption of skeletal muscle contraction is higher with higher force, higher contraction
353 velocity (force-velocity relationship) and when the muscle fascicles are operating further away from
354 their optimal length (force-length relationship) (27, 70). We found no difference in the GM muscle
355 fascicle length at initial ground contact and, although we did not measure fascicle resting length,
356 there is no direct reason to assume that the GM is working at a different part of its force-length
357 relationship across FSP. We found higher GM muscle fascicle contraction velocities in rearfoot
358 strikers than in mid-/forefoot strikers. Yet, GM muscle forces (Figure 2C) during early ground contact
359 were estimated to be higher in mid-/forefoot strikers. These greater muscle force estimations are
360 also supported by our muscle activation data (Figure 1). The GM pre-activated earlier in mid-
361 /forefoot strikers compared to rearfoot strikers. In addition, previous research already demonstrated
362 that mid-/forefoot strikers activated their plantar flexor muscles earlier, higher and longer compared
363 to rearfoot strikers (4, 20). Hence, from our data it seems reasonable to predict that the metabolic
364 energy consumption of the GM muscle may not be different between FSP as the greater muscle
365 contraction velocity observed in rearfoot strikers may be counterbalanced by the lower muscle force
366 production during early ground contact. Moreover, since no differences in SEE stretch and recoil
367 were revealed, we have no indications that differences in running economy between FSP may exist.
368 Recent studies also demonstrate that gait retraining from rearfoot to forefoot strike running did not
369 change running economy when sufficient intervention trainings (≥ 8) were provided (21, 65). As such,
370 our study seems to further support recent studies showing no difference in running economy
371 between habitual rearfoot strikers and habitual mid-/forefoot strikers (31, 59).

372 While the comparison of GM MTU interaction between FSP is new, more is known about the effect of
373 running speed on GM MTU interaction. In line with previous studies, we demonstrated that the GM

374 muscle fascicles shorten throughout the ground contact phase of running (12, 24, 40, 41, 51, 52, 54).
375 In addition, as initial fascicle length and fascicle length changes were not different between running
376 speeds, our data seems to indicate that GM muscle is working in the same region of its force-length
377 relationship across the running speeds we measured (10 and 14 km/h). Despite nearly identical
378 length changes during ground contact, the reduced ground contact time at higher running speeds
379 induces higher muscle contraction velocities. Higher contraction velocity as well as greater muscle
380 force production on a shorter time interval impose more muscle fascicle activation (Figure 1D. and
381 I.). Hence, from a muscular perspective we further support the hypothesis of Kram and Taylor (46)
382 that the metabolic cost of running is inversely related to the time course of force production, i.e.
383 ground contact time.

384 While there is evidence that muscle fascicle contraction velocity increases with faster running, more
385 discussion appears about whether or not the muscle operates within the same region of its force-
386 length relationship across running speeds. Farris and Sawicki (24) investigated running speeds
387 ranging from 7.2 to 11.7 km/h, Lai and colleagues (51) collected data up to 18 km/h, while Ishikawa
388 and Komi (40) went up to 23.4 km/h. Similar to our findings, muscle fascicle contraction velocity
389 during ground contact phase seemed to increase across running speeds. In agreement with Farris
390 and Sawicki (24) and Ishikawa and Komi (40), we found no difference in initial fascicle length at the
391 relatively low speeds analyzed in this study. However, Ishikawa and Komi (40) found that fascicle
392 length at initial ground contact was shorter when running faster (18 and 23.4 km/h). This might
393 indicate that the GM muscle is only working in a similar region of its force-length relationship within
394 a range of (submaximal) running speeds. Another hypothesis would be that there is a gradual
395 decrease in initial fascicle length with increasing running speed. The latter hypothesis would suggest
396 that these differences are rather small and that all studies to date lack statistical power to
397 demonstrate this gradual decrease.

398 In addition, it is interesting to note that in our study the SEE stretch during the first part of ground
399 contact was always greater than the recoil during the second part. We assumed that SEE stretch and
400 recoil during ground contact would be well tuned and thus more or less equal. One can postulate
401 that the SEE will be in slack at initial ground contact, especially in mid-/forefoot strikers where the
402 ankle is more plantar flexed at initial ground contact. But, in accordance with Ahn et al. (4), we found
403 that the GM activates earlier in mid-/forefoot strikers (Table 1; Figure 1F and L.). This pre-activation
404 can be assumed to bring the SEE in tension, so energy can immediately be stored once the foot hits
405 the ground. Furthermore, Figure 1 clearly demonstrates that the SEE recoils further after toe-off (i.e.
406 around 30 to 35% of stride depending on FSP and running speed), indicating that part of the energy
407 stored during the first part of the ground contact is released too late, i.e. when the foot has already

408 left the ground. While we did not determine the SEE slack length of each participant, and therefore
409 cannot exclude that the SEE is in slack at initial ground contact, we presume it to be unlikely.
410 Nevertheless, animal studies in turkeys (63) and horses (8) have demonstrated that the released
411 elastic strain energy in tendons increased with increased speed. Moreover, a simulation study by Lai
412 and colleagues (50) estimated that the relative contribution of elastic strain energy provided by the
413 SEE to the total positive work done by the Triceps Surae MTU increased across running speeds
414 (ranging from jogging to sprinting), especially for the SOL. Although, we did not detect a significant
415 increase in SEE recoil between the two running speeds, on average there was an increase in SEE
416 recoil at 14 km/h ($p = 0.10$), which may become a significant increase at higher speeds.

417 Our study has some limitations. First, we did not measure GM muscle fascicle resting length or SEE
418 slack length. Knowing GM muscle fascicle resting length and SEE slack length would have helped to
419 better interpret and normalize the results, especially between subject groups. Secondly, we did not
420 measure Achilles tendon stiffness and relied on previous research (47) demonstrating that Achilles
421 tendon stiffness is not different between runners with different FSP. Hence, while our conclusions
422 partly rely on these results we do not know if the same characteristics apply to our study. Moreover,
423 the lack of difference in GM SEE stretch and recoil between FSP but the greater GM force production
424 during early ground contact may suggest a contradiction if Achilles tendon stiffness is assumed to be
425 constant. In addition, although the normalized Triceps Surae tendon stiffness value of 5 used during
426 the simulations allows for a close match between simulated and measured GM fascicle length
427 changes, it is lower than most in vivo mechanical property studies have measured (5, 25, 53).
428 Furthermore, we focused on muscle fascicle length changes in one specific muscle of the Triceps
429 Surae, the GM, yet the SOL may be an interesting muscle to add, considering the importance of the
430 muscle during running (49, 51). In this study, we tried to link GM muscle fascicle behavior to whole
431 body metabolic energy consumption, however this is only one muscle with a relatively small
432 physiological cross-sectional area and we did not measure metabolic energy consumption.
433 Nevertheless, Fletcher and MacIntosh (26) calculated that 25 to 40% of the total metabolic energy
434 during running is consumed by the plantar flexor muscles. Moreover, in combination with the great
435 amount of positive ankle work produced during ground contact and the ability of ankle exoskeletons
436 to reduce whole metabolic energy consumption during walking (11) and hopping (23), we believe
437 that investigating the interaction between Triceps Surae muscles and SEE can therefore be
438 significantly linked to running economy. In addition, we did not evaluate the effect of greater fascicle
439 contraction velocity versus lower force production on the muscle metabolic energy consumption.
440 Future research, using a simulation based approach, can further address this question. This study
441 involves ultrasound imaging to visualize and track muscle fascicles. Ultrasound imaging is a 2D

442 measurement, albeit we are measuring in a 3D environment. Hence, this method only holds true
443 when the muscle fascicles act in the same 2D plane as our ultrasound image. However, good
444 reliability and accuracy has been proven previously (1, 2, 48).

445 Lastly, we only considered energy storage and return in the SEE. While this elastic structure is the
446 primary source of energy recovery during locomotion, it is not the only one. For example, the arch of
447 the foot also stores and return mechanical energy during each stride (42–44, 68). Although we did
448 not find any difference in energy storage and return in the SEE, difference in energy storage and
449 return in the arch of the foot may exist.

450 Acknowledgements

451 The authors would like to thank Li-Ning for providing the running shoes.

452 References

453

- 454 1. **Aeles J, Lenchant S, Vanlommel L, Vanwanseele B.** Bilateral differences in muscle fascicle
455 architecture are not related to the preferred leg in jumping athletes. *Eur J Appl Physiol* 117:
456 1453–1461, 2017.
- 457 2. **Aeles J, Lichtwark GA, Lenchant S, Vanlommel L, Delabastita T, Vanwanseele B.** Information
458 from dynamic length changes improves reliability of static ultrasound fascicle length
459 measurements. *PeerJ* 5: e4164, 2017.
- 460 3. **Aeles J, Lichtwark GA, Peeters D, Delecluse C, Jonkers I, Vanwanseele B.** The effect of a pre-
461 hop on the muscle-tendon interaction during vertical jumps. *J Appl Physiol* 124: 1203–1211,
462 2017.
- 463 4. **Ahn AN, Brayton C, Bhatia T, Martin P.** Muscle activity and kinematics of forefoot and
464 rearfoot strike runners. *J Sport Heal Sci* 3: 102–112, 2014.
- 465 5. **Albracht K, Arampatzis A.** Exercise-induced changes in triceps surae tendon stiffness and
466 muscle strength affect running economy in humans. *Eur J Appl Physiol* 113: 1605–1615, 2013.
- 467 6. **Almonroeder T, Willson JD, Kernozek TW.** The effect of foot strike pattern on achilles tendon
468 load during running. *Ann Biomed Eng* 41: 1758–1766, 2013.
- 469 7. **Altman AR, Davis IS.** A kinematic method for footstrike pattern detection in barefoot and
470 shod runners. *Gait Posture* 35: 298–300, 2012.
- 471 8. **Biewener AA.** Muscle-tendon stresses and elastic energy storage during locomotion in the
472 horse. *Comp Biochem Physiol - B Biochem Mol Biol* 120: 73–87, 1998.
- 473 9. **Breine B, Malcolm P, Van Caekenberghe I, Fiers P, Frederick EC, De Clercq D.** Initial foot
474 contact and related kinematics affect impact loading rate in running. *J Sports Sci* 35: 1556–
475 1564, 2017.
- 476 10. **Cavanagh PR, Lafortune MA.** Ground reaction forces in distance running. *J Biomech* 13: 397–
477 406, 1980.
- 478 11. **Collins SH, Wiggin MB, Sawicki GS.** Reducing the energy cost of human walking using an
479 unpowered exoskeleton. *Nature* 522: 212–215, 2015.

- 480 12. **Cronin NJ, Finni T.** Treadmill versus overground and barefoot versus shod comparisons of
481 triceps surae fascicle behaviour in human walking and running. *Gait Posture* 38: 528–533,
482 2013.
- 483 13. **Daoud AI, Geissler GJ, Wang F, Saretsky J, Daoud YA, Lieberman DE.** Foot strike and injury
484 rates in endurance runners: A retrospective study. *Med Sci Sports Exerc* 44: 1325–1334, 2012.
- 485 14. **de Almeida MO, Saragiotto BT, Yamato TP, Lopes AD.** Is the rearfoot pattern the most
486 frequently foot strike pattern among recreational shod distance runners? *Phys Ther Sport* 16:
487 29–33, 2015.
- 488 15. **De Groot F, De Laet T, Jonkers I, De Schutter J.** Kalman smoothing improves the estimation
489 of joint kinematics and kinetics in marker-based human gait analysis. *J Biomech* 41: 3390–
490 3398, 2008.
- 491 16. **De Groot F, Kinney AL, Rao A V., Fregly BJ.** Evaluation of Direct Collocation Optimal Control
492 Problem Formulations for Solving the Muscle Redundancy Problem. *Ann Biomed Eng* 44:
493 2922–2936, 2016.
- 494 17. **De Groot F, Pipeleers G, Jonkers I, Demeulenaere B, Patten C, Swevers J, De Schutter J.** A
495 physiology based inverse dynamic analysis of human gait: Potential and perspectives. *Comput*
496 *Methods Biomech Biomed Engin* 12: 563–574, 2009.
- 497 18. **Delp SL, Anderson FC, Arnold AS, Loan P, Habib A, John CT, Guendelman E, Thelen DG.**
498 OpenSim: Open source to create and analyze dynamic simulations of movement. *IEEE Trans*
499 *Biomed Eng* 54: 1940–1950, 2007.
- 500 19. **Di Michele R, Merni F.** The concurrent effects of strike pattern and ground-contact time on
501 running economy. *J Sci Med Sport* 17: 414–418, 2014.
- 502 20. **Divert C, Mornieux G, Baur H, Mayer F, Belli A.** Mechanical comparison of barefoot and shod
503 running. *Int J Sports Med* 26: 593–598, 2005.
- 504 21. **Ekizos A, Santuz A, Arampatzis A.** Short- and long-term effects of altered point of ground
505 reaction force application on human running energetics. *J. Exp. Biol.* (2018). doi:
506 10.1242/jeb.176719.
- 507 22. **Farris DJ, Lichtwark GA.** UltraTrack: Software for semi-automated tracking of muscle fascicles
508 in sequences of B-mode ultrasound images. *Comput Methods Programs Biomed* 128: 111–
509 118, 2016.
- 510 23. **Farris DJ, Robertson BD, Sawicki GS.** Elastic ankle exoskeletons reduce soleus muscle force
511 but not work in human hopping. *J Appl Physiol* 115: 579–585, 2013.
- 512 24. **Farris DJ, Sawicki GS.** Human medial gastrocnemius force-velocity behavior shifts with
513 locomotion speed and gait. *Proc Natl Acad Sci* 109: 977–982, 2012.
- 514 25. **Fletcher JR, Esau SP, MacIntosh BR.** Changes in tendon stiffness and running economy in
515 highly trained distance runners. *Eur J Appl Physiol* 110: 1037–1046, 2010.
- 516 26. **Fletcher JR, MacIntosh BR.** Achilles tendon strain energy in distance running: consider the
517 muscle energy cost. *J Appl Physiol* 118: 193–199, 2015.
- 518 27. **Fletcher JR, MacIntosh BR.** Running economy from a muscle energetics perspective. *Front.*
519 *Physiol.* (2017). doi: 10.3389/fphys.2017.00433.
- 520 28. **Fukunaga T, Kawakami Y, Kubo K, Kanehisa H.** Muscle and Tendon Interaction During Human
521 Movements. *Exerc Sport Sci Rev* 30: 106–110, 2002.

- 522 29. **Fukunaga T, Kubo K, Kawakami Y, Fukashiro S, Kanehisa H, Maganaris CN.** In vivo behaviour
523 of human muscle tendon during walking. *Proc R Soc B Biol Sci* 268: 229–233, 2001.
- 524 30. **Gerus P, Rao G, Berton E.** Ultrasound-based subject-specific parameters improve fascicle
525 behaviour estimation in Hill-type muscle model. *Comput Methods Biomech Biomed Engin* 18:
526 116–123, 2015.
- 527 31. **Gruber AH, Umberger BR, Braun B, Hamill J.** Economy and rate of carbohydrate oxidation
528 during running with rearfoot and forefoot strike patterns. *J Appl Physiol* 115: 194–201, 2013.
- 529 32. **Hall JPL, Barton C, Jones PR, Morrissey D.** The biomechanical differences between barefoot
530 and shod distance running: A systematic review and preliminary meta-analysis. *Sport Med* 43:
531 1335–1353, 2013.
- 532 33. **Hamill J, Gruber AH.** Is changing footstrike pattern beneficial to runners? *J Sport Heal Sci* 6:
533 146–153, 2017.
- 534 34. **Hamill J, Gruber AH, Derrick TR.** Lower extremity joint stiffness characteristics during running
535 with different footfall patterns. *Eur J Sport Sci* 14: 130–136, 2014.
- 536 35. **Hamner SR, Seth A, Delp SL.** Muscle contributions to propulsion and support during running. *J*
537 *Biomech* 43: 2709–2716, 2010.
- 538 36. **Handsfield GG, Meyer CH, Hart JM, Abel MF, Blemker SS.** Relationships of 35 lower limb
539 muscles to height and body mass quantified using MRI. *J Biomech* 47: 631–638, 2014.
- 540 37. **Hasegawa H, Yamauchi T, Kraemer WJ.** Foot strike patterns of runners at the 15-km point
541 during an elite-level half marathon [Online]. *J Strength Cond Res* 21: 888–893, 2007.
- 542 38. **Hayes P, Caplan N.** Foot strike patterns and ground contact times during high-calibre middle-
543 distance races. *J Sports Sci* 30: 1275–1283, 2012.
- 544 39. **Hill A V.** The maximum work and mechanical efficiency of human muscles, and their most
545 economical speed. *J Physiol* 56: 19–41, 1922.
- 546 40. **Ishikawa M, Komi P V.** The role of the stretch reflex in the gastrocnemius muscle during
547 human locomotion at various speeds. *J Appl Physiol* 103: 1030–1036, 2007.
- 548 41. **Ishikawa M, Pakaslahti J, Komi P V.** Medial gastrocnemius muscle behavior during human
549 running and walking. *Gait Posture* 25: 380–384, 2007.
- 550 42. **Kelly LA, Cresswell AG, Farris DJ.** The energetic behaviour of the human foot across a range of
551 running speeds. *Sci. Rep.* (2018). doi: 10.1038/s41598-018-28946-1.
- 552 43. **Kelly LA, Farris DJ, Lichtwark GA, Cresswell AG.** The Influence of Foot-Strike Technique on the
553 Neuromechanical Function of the Foot. *Med. Sci. Sports Exerc.* (2018). doi:
554 10.1249/MSS.0000000000001420.
- 555 44. **Ker RF, Bennett MB, Bibby SR, Kester RC, Alexander RM.** The spring in the arch of the human
556 foot. *Nature* 325: 147–149, 1987.
- 557 45. **Kram R.** Muscular force or work: what determines the metabolic energy cost of running?
558 *Exerc Sport Sci Rev* 28: 138–144, 2000.
- 559 46. **Kram R, Taylor RC.** Energetics of running: a new perspective. *Nature* 346: 265–267, 1990.
- 560 47. **Kubo K, Miyazaki D, Tanaka S, Shimoju S, Tsunoda N.** Relationship between Achilles tendon
561 properties and foot strike patterns in long-distance runners. *J Sports Sci* 33: 665–669, 2015.

- 562 48. **Kwah LK, Pinto RZ, Diong J, Herbert RD.** Reliability and validity of ultrasound measurements
563 of muscle fascicle length and pennation in humans: a systematic review. *J Appl Physiol* 114:
564 761–769, 2013.
- 565 49. **Lai A, Lichtwark GA, Schache AG, Lin Y-C, Brown NAT, Pandy MG.** In vivo behavior of the
566 human soleus muscle with increasing walking and running speeds. *J Appl Physiol* 118: 1266–
567 1275, 2015.
- 568 50. **Lai A, Schache AG, Lin Y-C, Pandy MG.** Tendon elastic strain energy in the human ankle
569 plantar-flexors and its role with increased running speed. *J Exp Biol* 217: 3159–3168, 2014.
- 570 51. **Lai AKM, Lichtwark GA, Schache AG, Pandy MG.** Differences in in vivo muscle fascicle and
571 tendinous tissue behavior between the ankle plantarflexors during running. *Scand J Med Sci*
572 *Sport* : 1828–1836, 2018.
- 573 52. **Lichtwark GA, Bougoulis K, Wilson AM.** Muscle fascicle and series elastic element length
574 changes along the length of the human gastrocnemius during walking and running. *J Biomech*
575 40: 157–164, 2007.
- 576 53. **Lichtwark GA, Wilson AM.** In vivo mechanical properties of the human Achilles tendon during
577 one-legged hopping. *J Exp Biol* 208: 4715–4725, 2005.
- 578 54. **Lichtwark GA, Wilson AM.** Interactions between the human gastrocnemius muscle and the
579 Achilles tendon during incline, level and decline locomotion. *J Exp Biol* 209: 4379–4388, 2006.
- 580 55. **Lichtwark GA, Wilson AM.** Optimal muscle fascicle length and tendon stiffness for maximising
581 gastrocnemius efficiency during human walking and running. *J Theor Biol* 252: 662–673, 2008.
- 582 56. **Lieberman DE, Venkadesan M, Werbel WA, Daoud AI, D’Andrea S, Davis IS, Ojiambo**
583 **Mang’Eni R, Pitsiladis Y.** Foot strike patterns and collision forces in habitually barefoot versus
584 shod runners. *Nature* 463: 531–535, 2010.
- 585 57. **Lyght M, Nockerts M, Kernozek TW, Ragan R.** Effects of foot strike and step frequency on
586 Achilles tendon stress during running. *J Appl Biomech* 32: 365–372, 2016.
- 587 58. **Mercer JA, Horsch S.** Heel-toe running: A new look at the influence of foot strike pattern on
588 impact force. *J Exerc Sci Fit* 13: 29–34, 2015.
- 589 59. **Ogueta-Alday A, Rodríguez-Marroyo JA, García-López J.** Rearfoot striking runners are more
590 economical than midfoot strikers. *Med Sci Sports Exerc* 46: 580–585, 2014.
- 591 60. **Patterson MA, Rao A V.** GPOPS-II: A MATLAB software for solving multiple-phase optimal
592 control problems using hp-adaptive Gaussian quadrature collocation methods and sparse
593 nonlinear programming. *ACM Trans. Math. Softw.* (2014). doi: 10.1145/2558904.
- 594 61. **Perl DP, Daoud AI, Lieberman DE.** Effects of footwear and strike type on running economy.
595 *Med Sci Sports Exerc* 44: 1335–1343, 2012.
- 596 62. **Rice H, Patel M.** Manipulation of Foot Strike and Footwear Increases Achilles Tendon Loading
597 during Running. *Am J Sports Med* 45: 2411–2417, 2017.
- 598 63. **Roberts, T. J.; Marsh, R. L.; Weyand, P. G.; Taylor CR.** Muscular Force in Running Turkeys: The
599 Economy of Minimizing Work. *Science* 275: 1113–1115, 1997.
- 600 64. **Robinson MA, Vanrenterghem J, Pataky TC.** Statistical Parametric Mapping (SPM) for alpha-
601 based statistical analyses of multi-muscle EMG time-series. *J Electromyogr Kinesiol* 25: 14–19,
602 2015.
- 603 65. **Roper JL, Doerfler D, Kravitz L, Dufek JS, Mermier C.** Gait Retraining from Rearfoot Strike to

- 604 Forefoot Strike does not change Running Economy. *Int J Sports Med* 38: 1076–1082, 2017.
- 605 66. **Shih Y, Lin KL, Shiang TY.** Is the foot striking pattern more important than barefoot or shod
606 conditions in running? *Gait Posture* 38: 490–494, 2013.
- 607 67. **Stearne SM, Alderson JA, Green BA, Donnelly CJ, Rubenson J.** Joint kinetics in rearfoot versus
608 forefoot running: Implications of switching technique. *Med Sci Sports Exerc* 46: 1578–1587,
609 2014.
- 610 68. **Stearne SM, McDonald KA, Alderson JA, North I, Oxnard CE, Rubenson J.** The Foot ' s Arch
611 and the Energetics of Human Locomotion. *Sci. Rep.* (2016). doi: 10.1038/srep19403.
- 612 69. **Wächter A, Biegler LT.** On the implementation of an interior-point filter line-search algorithm
613 for large-scale nonlinear programming. *Math. Program.* (2006). doi: 10.1007/s10107-004-
614 0559-y.
- 615 70. **Zajac FE.** Muscle and tendon: properties, models, scaling, and application to biomechanics
616 and motor control. *Crit Rev Biomed Eng* 17: 359–410, 1989.

617

618 [Figure captions](#)

619

620 Figure 1. Mean ankle (A, G) and knee angles (B, H), mean Gastrocnemius medialis muscle fascicle
621 length changes (C, I), Series elastic element length changes (SEE; D, J), muscle tendon unit length
622 changes (MTU; E, K), Gastrocnemius medialis (GM) activation (F, L) during stride compared between
623 mid-/forefoot strikers (FFS; solid; N = 10) and rearfoot strikers (RFS; dashed; N = 9) at 10 km/h (A-E)
624 and 14 km/h (F-J). Fascicle, SEE and MTU length changes are normalized to the length at toe-off. Grey
625 area represents standard deviation. Mean toe-off \pm SEM timing is indicated with vertical dashed lines
626 and grey area for FFS (light grey) and RFS (dark grey).

627 Figure 2. Mean Gastrocnemius medialis muscle fascicle velocity (A) and mean muscle force (C) during
628 the ground contact phase of running for mid-/forefoot strikers (FFS; grey; N = 10) and rearfoot
629 strikers (RFS; black; N = 9) at 10 km/h (solid lines) and 14 km/h (dashed lines). For clarity SD was left
630 out. Negative velocities indicate fascicle shortening (A). The results of the statistical parametric
631 mapping (SPM) are shown in B and D with foot strike pattern effect (solid), speed effect (dashed),
632 interaction effect (dashed dotted) and significance threshold (dotted). Dark grey background
633 visualizes significant difference in forces between foot strike patterns ($p = 0.02$). Light grey
634 background visualizes significant differences in speed ($p < 0.01$). No interaction effect was found for
635 both fascicle velocity and muscle force. No significant differences in fascicle velocity between foot
636 strike pattern after the first 0.4% of ground contact. No significant speed effect was found for fascicle
637 velocity.

Table 1. Comparison between mid-/forefoot and rearfoot strikers and between 10 and 14 km/h. All data are expressed as mean \pm SD. * significant main foot strike effect. † significant main running speed effect. ‡ significant difference between foot strike patterns only at 14 km/h. § significant interaction effect.

		speed	Forefoot strike	Rearfoot strike
Foot strike angle (FSA)	(°)*	10 km/h	-0.4 \pm 4.4	14.8 \pm 3.7
		14 km/h	0.3 \pm 5.3	17.2 \pm 5.4
Ground contact time	(ms)†	10 km/h	250.6 \pm 16.3	259.9 \pm 12.6
		14 km/h	209.2 \pm 13.7	218.2 \pm 16.6
GM muscle fascicle	Length at ground contact (mm)	10 km/h	51.4 \pm 10.2	56.3 \pm 6.9
		14 km/h	51.1 \pm 11.0	54.7 \pm 7.9
	Shortening during ground contact (mm)*	10 km/h	11.2 \pm 3.9	16.1 \pm 3.6
		14 km/h	11.3 \pm 4.3	16.0 \pm 4.1
	Average velocity ground contact (mm/s)*†	10 km/h	-42.6 \pm 12.7	-62.1 \pm 14.6
		14 km/h	-50.3 \pm 18.4	-72.3 \pm 20.3
	Maximal velocity ground contact (mm/s)†	10 km/h	-157 \pm 52	-186 \pm 27
		14 km/h	-185 \pm 91	-218 \pm 70
SEE	Stretch (mm)†	10 km/h	22.7 \pm 2.7	20.3 \pm 3.0
		14 km/h	24.7 \pm 4.5	22.9 \pm 4.0
	Recoil (mm)	10 km/h	19.5 \pm 3.2	17.0 \pm 4.1
		14 km/h	20.0 \pm 4.4	18.3 \pm 4.3
MTU	Stretch (mm)*†	10 km/h	14.1 \pm 3.0	8.3 \pm 1.0
		14 km/h	15.2 \pm 2.4	10.0 \pm 1.6
	Recoil (mm)	10 km/h	21.8 \pm 3.4	20.3 \pm 3.0
		14 km/h	21.2 \pm 3.2	20.7 \pm 3.2
Ankle work	Negative (J/kg)*†§	10 km/h	-0.74 \pm 0.12	-0.55 \pm 0.09
		14 km/h	-1.01 \pm 0.16	-0.71 \pm 0.11
	Positive (J/kg)†	10 km/h	1.02 \pm 0.12	0.94 \pm 0.16
		14 km/h	1.29 \pm 0.11	1.17 \pm 0.21
	Net (J/kg)	10 km/h	0.29 \pm 0.17	0.39 \pm 0.10
		14 km/h	0.28 \pm 0.21	0.46 \pm 0.21
Knee work	Negative (J/kg)	10 km/h	-0.22 \pm 0.08	-0.26 \pm 0.07
		14 km/h	-0.22 \pm 0.10	-0.27 \pm 0.07
	Positive (J/kg)	10 km/h	0.25 \pm 0.10	0.24 \pm 0.06
		14 km/h	0.27 \pm 0.12	0.26 \pm 0.09

	Net (J/kg)	10 km/h	0.03 ± 0.08	-0.02 ± 0.06
		14 km/h	0.05 ± 0.11	-0.01 ± 0.11
GM muscle activation	Pre-activation timing	10 km/h	84.6 ± 4.6	92.6 ± 5.7
	(% stride)*†	14 km/h	82.0 ± 3.6	86.3 ± 5.1
	Deactivation timing	10 km/h	33.8 ± 6.0	31.2 ± 2.6
	(% stride)	14 km/h	35.3 ± 10.9	33.4 ± 2.5
GM muscle force	Peak (N/kg)†	10 km/h	16.9 ± 1.3	16.5 ± 1.6
		14 km/h	19.4 ± 2.1	20.1 ± 2.1

