

The biological limits to running speed are imposed from the ground up

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2 **Abstract**

3 Running speed is limited by a mechanical interaction between the stance and swing phases of the
4 stride. Here, we tested whether stance phase limitations are imposed by ground force maximums
5 or foot-ground contact time minimums. We selected one-legged hopping and backward running
6 as experimental contrasts to forward running, and had seven athletic subjects complete
7 progressive discontinuous treadmill tests to failure to determine their top speeds in each of the
8 three gaits. Vertical ground reaction forces (in body weights, W_b) and periods of ground force
9 application (T_c , s) were measured using a custom, high-speed force treadmill. At top speed, we
10 found that both the stance-averaged (F_{avg}) and peak (F_{peak}) vertical forces applied to the treadmill
11 surface during one-legged hopping exceeded those applied during forward running by more than
12 one-half of the body's weight [$F_{avg} = 2.71 \pm 0.15$ vs. $2.08 \pm 0.07 W_b$; $F_{peak} = 4.20 \pm 0.24$ vs. 3.62
13 $\pm 0.24 W_b \pm sem$] and that hopping periods of force application were significantly longer [$T_c =$
14 0.160 ± 0.006 vs. 0.108 ± 0.004 s]. Next, we found that the periods of ground force application
15 at top backward and forward running speeds were nearly identical, agreeing to within an average
16 of 0.006 s [$T_c = 0.116 \pm 0.004$ s vs. 0.110 ± 0.005 s]. We conclude that the stance phase limit to
17 running speed is imposed, not by the maximum forces that the limbs can apply to the ground, but
18 rather by the minimum time needed to apply the large, mass-specific forces necessary.

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20

21

22 **Introduction**

23 The prospect of humans running at speeds in excess of 50 to 65 kilometers per hour seems
24 science fictional, but why? Racing horses, dogs, and even hopping kangaroos can readily travel
25 at these speeds. Moreover, these animals do so with biological tissues and limb mechanics that
26 are similar to those of human runners. Their muscles, tendons and bones are made of the same
27 materials and work in much the same way as those of humans (5, 14, 24, 32, 36). Their high-
28 speed gaits, whether galloping, hopping or bipedal running, involve using the limbs in a spring-
29 like manner to allow the body to ‘bounce’ along the ground much like a rubber ball (9, 11).
30 These fundamental tissue and gait similarities beg a basic question: what factors prevent humans
31 from running at much faster speeds than they actually do? The explanation undoubtedly
32 involves both the stride mechanics selected in bouncing gaits and the functional limits of the
33 biological tissues used to execute them. However, how these factors combine to impose the
34 speed limits of terrestrial animals is not well understood.

35 Our previous work identified the interaction between the stance and swing phases of the
36 stride that determines the mechanical limit to running speed (44). This limit follows from the
37 mechanics used by individual runners to modulate their speeds: increases from intermediate to
38 top speed are achieved by applying greater ground support forces, using shorter periods of foot-
39 ground force application, repositioning the swing limbs more rapidly and thereby taking less
40 time in the air between steps. The limit to speed is reached when foot-ground contact times and
41 effective vertical impulses (i.e. the product of foot-ground contact time and the vertical force
42 exceeding the body’s weight) decrease to the minimums that provide just enough aerial time to
43 reposition the swing limb for the next step. Because the swing period consists of two aerial
44 periods separated by the contact period of the opposite limb (Fig. 1A), human runners typically

45 require aerial times of 0.12 s or more to attain the minimum swing time of ≈ 0.350 s generally
46 observed at top speed.

47 One consequence of the manner in which gait mechanics limit running speed is a
48 mechanical interdependence between the stance and swing phases of the stride (43, 44).
49 Specifically, the vertical forces and impulses required to attain any speed are largely dependent
50 on how rapidly the limbs can be repositioned (43). Relatively longer swing times lengthen the
51 aerial times necessary for limb repositioning, thereby increasing the ground support forces and
52 impulses required to elevate the body. Conversely, relatively shorter swing times have the
53 opposite effect. We recently noted (43) that minimum swing times 20% shorter than typical
54 values substantially reduce the vertical forces and impulses required to attain the same sprint
55 running speeds.

56 Previous observations suggest the active muscles likely operate at their functional limits
57 during the stance, but not the swing phase of the stride (27, 31, 33, 35, 44). Although faster
58 individuals have predominantly fast-twitch muscle fibers that contract and generate force more
59 rapidly (15), these individuals do not swing their limbs more rapidly at their much faster top
60 running speeds. For example, runners with top speeds varying by 1.8-fold ($6.2 - 11.1 \text{ m s}^{-1}$) differ
61 negligibly in their minimum swing times (44). This result is consistent with the possibility that
62 much of the mechanical energy to reposition the limbs is provided by passive mechanisms of
63 energy transfer rather than via active muscular power. In contrast, stance-phase mechanics differ
64 between faster and slower runners in a manner consistent with established differences in muscle
65 fiber composition and contractile properties (14, 15). At top speed, faster runners apply
66 appreciably greater mass-specific ground forces and do so during shorter periods of foot-ground
67 contact (44).

68 We undertook this study to identify the stance phase mechanics of human running that
69 limit speed. The relative force and rate requirements for increasing running speed, and the force
70 and rate properties of the extensor muscles of the human limb (1, 3, 21, 22, 25, 38), led us to
71 hypothesize that a limit is imposed, not by the maximum forces the limbs can apply to the
72 ground, but rather by how rapidly they can do so. We selected two gaits for comparison to
73 forward running to test these possibilities: one-legged hopping and backward running. These
74 gaits are similar to forward running in requiring the application of sufficiently large ground
75 support forces during the stance phase to elevate the body for the next step, and in involving only
76 the relatively small horizontal forces necessary to maintain a constant speed. However, each
77 comparison gait differs from forward running during the stance phase in an experimentally
78 desirable way. The first comparison gait, one-legged hopping was selected to alter the amount of
79 force applied to the ground, while the second, backward running was selected to alter the rates of
80 ground force application. In the first case, in keeping with the expected absence of a limitation
81 on maximal ground force, we predicted that the ground support forces applied at top speed would
82 be greater for one-legged hopping than for forward running. In the second case, in keeping with
83 the expected rate limitation, we predicted that the periods of foot-ground contact during which
84 force is applied would fall to the same minimum values at the different top speeds attained
85 during backward and forward running.
86

87 **Methods**

88 *Theoretical Framework*

89 For theoretical and conceptual purposes we developed a quantitative framework that expresses
90 speed in terms of the force and time variables we wished to test as potential limits. We
91 recognized that we could accomplish this in a manner applicable to all three gaits by expressing
92 the lengths of the step taken in terms of the ground forces applied, and the frequencies of these
93 steps in terms of the durations of foot-ground force application. Hence, our first step was simply
94 to express speed as the product of the length and frequency of the steps taken:

95

96
$$\text{Speed} = L_{\text{step}} \bullet \text{Freq}_{\text{step}} \qquad \text{Eq. 1}$$

97

98 where L_{step} is the horizontal distance traveled-during a step, here defined as the time between
99 consecutive footfalls and therefore consisting of the stance and the subsequent aerial phases, and
100 $\text{Freq}_{\text{step}}$ is the number of steps taken per unit time. Under conditions in which speed is constant
101 and the center of mass has the same height at the first and last instants of the foot-ground contact
102 period, the average vertical force applied during the contact period, when expressed in relation to
103 the body's weight (F_{avg}/W_b), equals the ratio of the total step time (T_{step}) to contact time (T_c) and
104 the ratio of the step length (L_{step}) to contact length (L_c):

105

106
$$F_{\text{avg}}/W_b = T_{\text{step}}/T_c = L_{\text{step}}/L_c \qquad \text{Eq. 2}$$

107

108 By rearranging the terms in Eq. 2 to isolate L_{step} , the distance traveled between consecutive
109 footfalls can be expressed as the product of the average vertical force applied to the surface in

110 relation to the body's weight and the forward distance through which the body travels, (contact
111 length, L_c), respectively, during the time of foot-ground contact:

112

$$113 \quad L_{\text{step}} = F_{\text{avg}}/W_b \bullet L_c \quad \text{Eq. 3}$$

114

115 Next, we expanded the $\text{Freq}_{\text{step}}$ term in Eq. 1 to express step frequencies in terms of the durations
116 of foot-ground contact. We did so by expressing step times as the sum of the contact (T_c) and
117 aerial (T_{aer}) portions of each step:

118

$$119 \quad T_{\text{step}} = T_c + T_{\text{aer}} \quad \text{Eq. 4}$$

120

121 and step frequencies as the inverse of the period required to complete each step:

122

$$123 \quad \text{Freq}_{\text{step}} = 1/(T_c + T_{\text{aer}}) \quad \text{Eq. 5}$$

124

125 We then rearranged Eq. 1 by substituting Eq. 3 for L_{step} and Eq. 5 for $\text{Freq}_{\text{step}}$ to obtain:

126

$$127 \quad \text{Speed} = [F_{\text{avg}}/W_b \bullet L_c] \bullet [1/(T_c + T_{\text{aer}})] \quad \text{Eq. 6}$$

128

129 Equation 6 allows the influence of each of these stride variables on forward speed to be
130 evaluated quantitatively. However, for experimental purposes all of the variables above were
131 measured directly; none were calculated from the equations provided. Therefore, the validity of

132 the assumptions used to derive our conceptual framework had no effect on the hypothesis testing
133 process.

134

135 *Experimental Design*

136 To test our first hypothesis on maximum ground forces, we chose one-legged hopping as an
137 experimental tool because this gait, in contrast to forward running, requires that the same limb,
138 rather than alternating limbs, be used for consecutive footfalls. Logic and our preliminary data
139 both suggested that this requirement would elevate ground force requirements (i.e. F_{avg}/W_b) at
140 common speeds above those observed during forward running. Thus, we expected that both
141 F_{avg}/W_b and T_{aer} would be substantially greater for one-legged hopping than forward running. In
142 accordance with our first hypothesis that maximum ground force does not limit human running
143 speed, we predicted that for each subject F_{avg}/W_b would be greater for one-legged hopping than
144 forward running at the respective top speeds in these two gaits.

145 Stance limb function dictates that an upper limit on the ground forces applied in bouncing
146 gaits would ultimately be imposed by the force limits of the extensor muscles acting across the
147 ankle, knee and hip to counteract the ground reaction force. Because the logical origin of our
148 maximum ground force hypothesis is the upper biological limit on the forces produced by the
149 limb extensor muscles, we assessed both muscle and ground forces for our first hypothesis test.
150 This was necessary because the leverage of the stance limb could conceivably differ between
151 forward running and one-legged hopping. A specific concern was that subjects might use
152 straighter limbs in order to more closely align the ground reaction force vector to their joint axes
153 of rotation during one-legged hopping vs. forward running. If so, the ground reaction forces
154 measured would not be directly representative of the counteracting limb extensor muscle forces.

155 Accordingly, for this first hypothesis test, we used an inverse solution similar to that of Biewener
156 *et al.*, (4, 6) to estimate the stance limb extensor muscle forces produced at the hip, knee and
157 ankle joints during one-legged hopping and forward running. The technique relies on a balance
158 of torques approach to determine the relationship between the net extensor muscle forces (F_m)
159 needed to counteract the torque produced by the ground reaction force (F_g) acting at a distance R
160 from each joint, in accordance with:

161

$$162 \quad \text{EMA} = r/R = F_g / F_m \quad \text{Eq. 7}$$

163

164 where r is the weighted mean moment arm of the extensor muscle group active at each joint and
165 R is the perpendicular distance between the ground reaction force vector and the joint axis of
166 rotation. The magnitude and direction of R is determined by the vertical and horizontal ground
167 reaction forces and the location of the center of foot-ground pressure (4). Accordingly, this
168 technique allowed us to estimate the muscle forces required per unit force applied to the ground
169 in these two gaits.

170

171 To test our second hypothesis on maximal rates of ground force application, we chose
172 backward running as an experimental tool because we knew from prior experience at slower
173 speeds (46) that runners shorten both the contact and aerial portion of the stride at common
174 speeds during backward vs. forward running (Figure 1). Consequently, similar ground forces
175 (F_{avg}/W_b) are applied with shorter contact lengths, L_c , when running backward vs. forward.
176 Because forward speed during the contact phase is equal to L_c/T_c , and L_c was expected to be
177 relatively shorter when traveling backward, we anticipated that our subjects would have shorter
178 periods of foot-ground contact (T_c) during backward versus forward running at common speeds.

178 In accordance with our second hypothesis that running speed is limited by the minimum periods
179 during which the limbs can apply the ground force required, we predicted that for each subject T_c
180 would fall to the same minimum values at the respective top backward and forward running
181 speeds.

182 Recognizing that *Eqs. 1-7* apply equally to male and female runners and hoppers, we
183 recruited both male and female subjects thereby allowing our two hypotheses to be tested over a
184 relatively broad range of top speeds, ground support forces and foot-ground contact times.

185 Finally, we conducted our experiments on a treadmill rather than an overground runway
186 with an in-ground force plate because of the advantages the treadmill offered for our
187 experimental objectives. In contrast to a runway, the treadmill allows trial data to be collected
188 for numerous consecutive footfalls, at the precise speeds of interest, and at the constant speeds
189 dictated by the treadmill rather than the more variable speeds selected by the subject. We were
190 well-assured from previous studies that our treadmill data will generalize to overground
191 conditions because neither the mechanics of ground force application (18) being tested, nor the
192 sprint running performances (7, 19) of athletic subjects vary appreciably under the two
193 conditions.

194

195 *Subjects and Participation*

196 We undertook our first and second hypothesis tests sequentially, with our first hypothesis test
197 requiring the F_{avg}/W_b values to be obtained during top speed forward running and one-legged
198 hopping, and the evaluation of our second hypothesis requiring a comparison of the minimum T_c
199 values obtained during top speed forward and backward running. A total of ten subjects, five
200 males and five females volunteered and provided written informed consent in accordance with

201 the requirements of the local Institutional Review Board. Nine of the ten subjects had
202 competitive athletic experience and nine were regularly active at the time of the study. Six
203 subjects were competitive track athletes: two were competitive horizontal jumpers, two were
204 combination sprint/jump specialists, one was a 400 meter runner, and one was a 400 meter
205 hurdler. Three of the remaining subjects were regularly active at the time of the study, with one
206 each participating in rugby, basketball and step aerobics. The fourth subject was not active
207 outside of her treadmill sessions at the time of the study.

208
209 Hypothesis Test I: One-legged Hopping vs. Forward Running: A total of 7 subjects, 4 male
210 (mass 69.0 ± 2.0 kg; leg length (L_o) 0.93 ± 0.02 m, means \pm sem) and 3 female (mass 63.3 ± 1.2
211 kg, L_o 0.90 ± 0.05 m) volunteered and participated in the first series of experimental tests.
212 Subjects were habituated to treadmill running during one practice session and to one-legged
213 hopping during either one or two habituation sessions before any top speed trials took place. The
214 hopping habituation process was generally shorter for those subjects who were competitive
215 jumpers ($n = 3$ in this portion of the study) all of whom had extensive experience with
216 plyometric and bounding drills. Six of the seven subjects tested chose to hop on their right leg
217 while one subject preferred using her left.

218
219 Hypothesis Test II: Backward vs. Forward Running: A total of 7 subjects, 3 male (mass $67.2 \pm$
220 0.3 kg, L_o 0.97 ± 0.01 m) and 4 female (mass 61.9 ± 1.5 kg, L_o 0.97 ± 0.04 m) volunteered and
221 participated in our second series of experimental tests. Four of these subjects continued their
222 participation after completing the initial experiments, while three of the earlier subjects were no
223 longer available for testing. Therefore, the three newly recruited subjects also completed the

224 backward and forward running protocols without completing the one-legged hopping protocol.
225 All seven subjects were habituated to forward running with one practice session and backward
226 running with two or more sessions. All subjects completed a minimum of three total backward
227 running treadmill sessions.

228

229 *Measurements*

230 *Top Speed* (m s^{-1}): All testing was conducted on a custom high-speed force treadmill (AMTI,
231 Watertown, MA, USA) with the subjects strapped into a safety harness that would suspend them
232 above the treadmill in the event of a fall. Top speeds in all three gaits were determined via a
233 progressive, discontinuous test to failure as follows. After a brief warm-up, the tests for each
234 gait began at a trial speed between 2.0 and 3.0 m s^{-1} . The speed for successive trials was
235 typically increased by 0.5 to 1.0 m s^{-1} at slower speeds and 0.2 m s^{-1} at faster ones. All tests
236 continued through a trial speed at which the subject was unable to complete the prescribed
237 number of steps without drifting backward on the treadmill. Two to three attempts were
238 typically made at the failure speed before the test was terminated. In every case, the top speed
239 successfully attained was within 0.2 m s^{-1} of the failure speed. For each running and hopping
240 trial, the treadmill belt was set at the desired trial speed while the subject stood on the treadmill
241 platform straddling the moving belt. Once the belt had reached the desired speed, subjects
242 transferred their weight onto the moving belt using the handrails adjacent to the treadmill and
243 fixed at waist height. Subjects were allowed to take as many handrail-assisted steps as they
244 chose prior to release. Trials were considered successful if a minimum of eight running or four
245 hopping steps were completed without backward drift after full release of the handrails. Non-top
246 speed trials generally lasted 10 to 20 seconds. Subjects were encouraged to take as much rest as

247 necessary for full recovery between trials. They generally chose to take less than one minute
248 between trials at slow and intermediate speeds and from one to ten minutes between the fastest
249 ones.

250 To minimize the risks of injury and muscle soreness, sessions were discontinued if the
251 subjects reported muscle strain, discomfort or tightness before top speed was reached. Subjects
252 were allowed a minimum of three days to recover between top speed running trials.

253

254 *Treadmill Force Data:* All force data were collected from our custom high speed force treadmill
255 using AMTI NetForce software after signal amplification and digitization (DigiAmp, AMTI).
256 Data for each trial was collected for 10 s at 1000 Hz and post-processed using analysis software
257 that applied a Butterworth filter with a low pass cut-off frequency of 30 Hz (Igor Pro:IFDL,
258 Wavemetrics, OR, USA). The values at each speed represent means determined from a series of
259 consecutive steps. For the slow to intermediate speed trials, mean values were determined from
260 eight to 16 consecutive steps for one-legged hopping and from 12 to 16 consecutive steps for
261 both running gaits. For the trials at or near top speed, mean values were determined from a
262 minimum of four and eight consecutive steps for one-legged hopping and both running gaits,
263 respectively. Representative waveforms from the three gaits appear in Figure 1.

264

265 *Stance-averaged Forces (F_{avg}):* The average vertical ground reaction force applied during the
266 contact period was determined from the time during which the vertical force signal exceeded a
267 threshold of 40 N. Forces expressed as multiples of the body's weight (W_b) were determined by
268 dividing the force recorded during each trial by the weight of the subject recorded on a platform

269 scale immediately prior to treadmill testing (F_{avg}/F_{wb} ; see Fig. 1). Center of mass displacements
270 during the stance phase were determined in accordance with Cavagna (10).

271
272 *Peak forces* (F_{peak}): Peak forces were the highest vertical ground reaction force values recorded
273 over a 0.005 s interval during the last 80% of the foot-ground contact period. This practice
274 discounted the early impact force peaks that can, in some instances (see Fig. 1B) exceed the limb
275 force peaks that typically occur in the middle third of the contact period (28). Peak vertical force
276 values were also expressed as multiples of the body's weight (F_{peak}/F_{wb}).

277
278 *Effective Mechanical Advantage* (r/R): The relationship between the muscle moment arms and
279 the ground reaction force moments acting across the ankle, knee, and hip joints were determined
280 for one-legged hopping and forward running on a subset of three subjects in accordance with Eq.
281 7 across a broad range of speeds [forward run: 2.5 – 10.5 m/s; one-legged hop: 2.5 - 7.0 m/s].
282 The mean moment arms of the extensor muscle groups (r_m ; hip = 5.7 cm, knee = 5.5 cm, ankle =
283 3.7 cm) were the cadaver measurements reported by Biewener *et al.* (6). The measures of
284 ground reaction force were calculated from the vector sum of the horizontal and vertical
285 components of the ground reaction force measured from a minimum of four (mean = 9.4 ± 0.35)
286 consecutive foot-ground contacts of the right limb. R was calculated as the distance between the
287 two-dimensional coordinate location of each joint (Ariel Dynamics, Trabuco Canyon CA),
288 obtained from high-speed video (250 Hz; Redlake MASD, San Diego CA) and the ground
289 reaction force vector. This vector originates at the point of force application, or center of
290 pressure (CoP), which was calculated from:

291
$$CoP = \frac{M_x - (F_y \bullet h)}{F_z} \quad Eq. 8$$

292 where M_x is the measured lateral component of the moment experienced by the force treadmill,
293 F_y and F_z are respectively, the horizontal and vertical components of the ground reaction force,
294 and h is the distance below the belt surface of the M_x axis (4.5 cm for the force treadmill). Joint
295 axes of rotation were identified by palpation and marked with reflective tape to acquire position
296 data from the video record. A two-dimensional position matrix was used for calibration
297 purposes prior to each session. For this portion of the analysis the force data was smoothed with
298 a sixth order zero-lag Butterworth low-pass digital filter with a 20-Hz cutoff (Igor Pro 5.0) and
299 kinematically synchronized with the video data. The stance-averaged values of R were obtained
300 from the middle portion of the stance phase, using an *a priori* minimum of one-half of the
301 contact period. This treatment minimizes the influence of large and rapid fluctuations of the CoP
302 at the beginning and end of stance caused by an undefined value of Eq. 8 when force is not being
303 applied to the treadmill. Means were determined for each subject at each joint as well as the
304 entire limb across the speed ranges above for both gaits. Limb and joint values were taken from
305 the right limb during both running and hopping as this was the limb that each of these subjects
306 preferred for the hopping gait.

307
308 *Contact times* (T_c , s): The time of foot-ground contact was determined from the continuous
309 periods during which the vertical treadmill reaction force exceeded 40 N.

310
311 *Contact lengths* (L_c , m): Contact lengths were determined by multiplying the time of foot-ground
312 contact by the speed of the trial.

313

314 *Aerial times* (T_{aer} , s): Aerial times were determined from the time elapsing between the end of
315 one period of foot-ground contact and the beginning of the subsequent period.

316

317 *Effective Impulse* (Imp_{Eff} , $W_b \cdot \text{s}$): The effective impulse, or the product of the vertical force
318 applied in excess of the body's weight $[(F_{\text{avg}}/W_b) - 1]$, and the period of foot-ground contact
319 during which this force is applied $[(F_{\text{avg}}/W_b) - 1] \cdot T_c$.

320

321 *Step times* (T_{step} , s): Step time was determined from the time taken to complete consecutive foot-
322 ground contact and aerial periods (i.e. $T_c + T_{\text{aer}}$).

323

324 *Step Frequency* ($\text{Freq}_{\text{step}}$, s^{-1}): Step frequency, the number of steps taken per second, was
325 determined from the inverse of step time ($1/T_{\text{step}}$).

326

327 *Step length* (L_{step} , m): Step length, or the distance the belt traveled between consecutive periods
328 of foot-ground contact, was determined by dividing the treadmill speed by step frequency.

329

330 *Leg length* (L_o , m): Leg lengths were measured from the axis of rotation of the hip joint of the
331 right leg to the ground at the outside of the right heel during erect standing. Hip joint axes of
332 rotation were determined from palpation as the subject slowly swung the limb in the sagittal
333 plane.

334

335 *Statistics*

336 We evaluated the between-gait comparisons (one-legged hopping vs. forward running and

337 backward vs. forward running) for top speeds as well as F_{avg} , F_{peak} , r/R , L_c , L_{step} , T_c , T_{aer} , $\text{Freq}_{\text{step}}$

338 and estimated net extensor muscle forces at top speed using Student's paired T-tests in
339 accordance with the expectations and hypothesis explicitly stated in the Experimental Design.
340 All tests of significance were conducted with a critical alpha level of $P < 0.05$. All values
341 reported are means \pm sem.
342

343 **Results**

344 *Gait Mechanics as a Function of Speed*

345 Regardless of whether subjects ran forward, hopped on one leg or ran backward, they attained
346 faster speeds by applying greater mass-specific forces (F_{avg}) to the running surface during shorter
347 periods of foot-ground contact (T_c) as treadmill speed increased (Fig. 2). When considered from
348 the slowest to fastest speeds attained in each gait, the mean relative decreases in T_c were greater
349 than the relative increases in F_{avg} in all three cases (Fig. 2, 3, and 4).

350 In our first gait comparison, we found that the ground forces (F_{avg}) required at common
351 speeds during one-legged hopping were substantially greater than those required during forward
352 running for all subjects (Fig. 1, 2A and 3). Additionally, the increases in stance-average force
353 with increases in speed during one-legged hopping were nearly double those for forward running
354 [average slopes and intercepts for forward running: $F_{avg} = 1.26 + 0.098 \cdot \text{Speed}$; one-legged
355 hopping: $F_{avg} = 1.62 + 0.19 \cdot \text{Speed}$; $n=7$]. These between-gait differences in the ground forces
356 applied were due largely to the greater aerial times required by one-legged hopping. At common
357 speeds, one-legged hopping aerial times were typically about twice as long as those observed
358 during forward running (Fig. 1B and 2B).

359 In our second gait comparison, foot-ground contact times (T_c) were shorter, during
360 backward vs. forward running at the same speeds (Fig. 2A and 4), because subjects used shorter
361 contact lengths (L_c) while running backward (eq. 6).

362 The net vertical displacements of the center of mass during the stance phase were slightly
363 less than zero at top speed in each gait (forward run: -0.004 ± 0.008 m; one-legged hop: $-0.040 \pm$
364 0.012 m; backward run: -0.014 ± 0.004 m). Across all three gaits, the measured values of F_{avg}

365 used in our analysis agreed with the values obtained from the ratios of T_{step}/T_c and L_{step}/L_c (eq. 3)
366 to within less than 2% (Table 1).

367

368 *Gait Mechanics at Top Speed*

369 *Top Speeds* (m s^{-1}): Top speeds and mean values for all of the mechanical variables in equation
370 6 are presented in Table 1 for the two experimental gaits with their corresponding forward
371 running comparisons. For reliability purposes, four and six subjects, respectively, completed
372 second one-legged hopping and backward running top speed treadmill tests on different days.
373 For one-legged hopping, all duplicate top speed trials agreed to within 0.2 m s^{-1} or less with two
374 subjects each being faster and slower, respectively, on their second trial. For backward running,
375 all tests agreed to within 0.1 m s^{-1} with four subjects attaining identical top speeds on both trial
376 days, and the remaining two running 0.1 m/s faster on the day of the second trial.

377

378 *Forces* (F_{avg} , F_{peak}): Both the stance-averaged and peak vertical forces applied to the treadmill
379 surface at the respective top speeds (Fig. 5) in our first gait comparison were, on average, more
380 than $0.5 W_b$ greater during one-legged hopping than forward running (2.71 ± 0.15 vs. 2.08 ± 0.07
381 W_b and 4.20 ± 0.24 vs. 3.62 ± 0.24 , W_b , respectively). Stance-averaged and peak vertical forces
382 were also lower during backward than forward running (1.75 ± 0.05 vs. $2.10 \pm 0.07 W_b$, and 3.05
383 ± 0.11 vs. $3.60 \pm 0.24 W_b$, respectively; Fig. 5 and 6). Between gait differences in the total
384 ground reaction force, the vector sum of F_z and F_y , were nearly identical to the above differences
385 in the vertical forces only (presented as F_{avg}) because the relative contributions of the horizontal
386 forces were similarly small across all three gaits, accounting for only 2 to 3% of the F_z and F_y
387 sum.

388 *Limb Effective Mechanical Advantage* (EMA, r/R): The ratio of muscle moment arms (r) to the
389 ground reaction force moments at the ankle, knee and hip joint axes of rotation (R) during the
390 stance phase appear in Table 2. The mechanical advantage of the extensor muscles acting across
391 both the hip and ankle joints were significantly greater during forward running than one-legged
392 hopping, while values at the knee were similar in the two gaits. The average net extensor muscle
393 forces required for the entire limb were 70.3% greater for one-legged hopping than for forward
394 running at top speed. The magnitude of this between-gait difference resulted from both the
395 greater ground reaction forces required and the poorer mechanical advantage of the limb during
396 one-legged hopping vs. forward running (Table 2, Fig. 7).

397

398 *Contact lengths* (L_c , m): The forward distance the body traveled during the period of foot-ground
399 contact was not significantly different during top speed one-legged hopping and forward running
400 (0.89 ± 0.05 vs. 0.98 ± 0.04 m, respectively). In contrast, top speed backward running contact
401 lengths were significantly shorter than those used during forward running (0.74 ± 0.05 vs. $0.99 \pm$
402 0.03 m, respectively).

403

404 *Step Lengths* (L_{step} , m): The belt distance traveled between consecutive footfalls, or the length of
405 the steps taken was longer during one-legged hopping than forward running (2.51 ± 0.26 vs. 2.05
406 ± 0.14 m, respectively), but this difference was not significant. Step lengths were significantly
407 shorter at top speed during backward vs. forward running (1.29 ± 0.14 vs. 2.06 ± 0.11 m,
408 respectively).

409

410 *Contact times* (T_c , s): Although foot-ground contact times were generally similar when subjects
411 hopped on one leg and ran at the same speeds (Fig. 5), at the respective top speeds one-legged
412 hopping contact times were considerably longer than those measured during forward running
413 (0.160 ± 0.006 vs. 0.108 ± 0.004 s, respectively, Fig. 2A and 5). In contrast, foot-ground
414 contact times were shorter at the same backward and forward running speeds, but virtually the
415 same at the respective top speeds attained in the two gaits (0.116 ± 0.004 s vs. 0.110 ± 0.005 ,
416 respectively, Fig. 4 and 5).

417
418 *Aerial times* (T_{aer} , s): Aerial times were 2.3 times longer during one-legged hopping vs. forward
419 running at top speed (0.274 ± 0.019 vs. 0.119 ± 0.004 s, respectively) and significantly shorter at
420 backward vs. forward top speeds (0.109 ± 0.007 vs. 0.121 ± 0.003 s, respectively, Fig. 6).

421
422 *Impulse_{eff}* ($W_b \cdot s$): The effective impulses were also 2.3 times greater at one-legged hopping vs.
423 forward running top speeds (0.270 ± 0.02 vs. 0.115 ± 0.004 $W_b \cdot s$, respectively) and moderately
424 less for backward vs. forward top speed running (0.086 ± 0.006 vs. 0.119 ± 0.004 $W_b \cdot s$,
425 respectively, Fig. 2B).

426
427 *Step Frequencies* ($Freq_{step}$, s^{-1}): Steps were roughly half as frequent at one-legged hopping vs.
428 forward running top speeds (2.36 ± 0.13 vs. 4.51 ± 0.08 Hz, respectively) and slightly more
429 frequent during top speed backward vs. forward running (5.05 ± 0.19 vs. 4.42 ± 0.19 Hz,
430 respectively).

431

432 **Discussion**

433 We set out to determine whether the stance phase limit to running speed might be imposed by
434 either of two functional limits on limb mechanics: the maximum force the limbs can apply to the
435 running surface, or the minimum period of time needed for force application. The one-legged
436 hopping and backward running tests we employed as experimental contrasts to forward running
437 provided complimentary and consistent results. In comparison to forward running at top speed,
438 we first found that our subjects were able to apply ground forces that were greater on average by
439 more than one-half of their own body weight ($0.63 \pm 0.11 W_b$) while hopping on one leg vs.
440 running forward on two. Second, we found that the periods of foot-ground force application at
441 top backward and forward running speeds agreed with one another to within an average of 6 ± 4
442 ms out of a total 110 ± 5 ms. These comparisons to forward running under top speed conditions
443 demonstrated first, that when periods of ground force application were relatively longer, subjects
444 were able to apply greater ground forces, and second, that when the ground forces required were
445 similar or slightly reduced, subjects were not able to apply force any more rapidly. Accordingly,
446 we conclude that a limit to sprint running speed is imposed, not by the maximum forces that can
447 be applied to the ground, but rather by the maximum rates at which the limbs can apply the
448 forces required.

449

450 *Hypothesis Test 1: One-legged hopping versus forward running*

451 We selected one-legged hopping as an experimental gait to test the prevailing view that
452 maximum limb extensor forces likely limit all-out running speeds on straight and moderately
453 curved paths (13, 20, 39, 40). At common speeds, the need during one-legged hopping to
454 reposition the same leg for consecutive periods of ground force application (Fig. 1B), did elevate

455 the aerial times and vertical forces required to attain them in comparison to forward running (Fig.
456 1B and 2). This outcome was expected from the dependence of stance-limb vertical forces and
457 impulses on the duration of the swing and aerial phases (43). However, the outcome of primary
458 relevance here was whether the ground forces applied at top speed would be greater during one-
459 legged hopping than forward running. This was the case (Fig. 3, 5 and 6A): the average and
460 peak vertical forces applied to the treadmill were 30.3 and 16.0% greater, respectively, for one-
461 legged hopping vs. forward running. Although individual variability was present in the force
462 difference observed between the two gaits (i.e. the force reserve, Fig. 3), every subject applied
463 greater average and peak forces while hopping on one leg than while running forward on two.
464 Moreover, the between-gait differences in ground forces substantially under-represented the
465 differences in limb extensor muscle forces. When the poorer mechanical advantage of the limb
466 and the greater ground reaction force required during one-legged hopping vs. forward running
467 were both taken into account (Table 2), the average and peak forces generated by the extensor
468 muscles at top speed were 82 and 63% greater, respectively, in the hopping gait. Clearly, the
469 forces applied to the ground during top speed forward running are substantially less than the
470 maximums the limbs are capable of applying to the running surface.

471

472 *Biological limits on muscular force production*

473 Why would runners apply forces during all-out sprinting efforts that are substantially less than
474 maximal, particularly if doing so would limit the very performances they are attempting to
475 maximize? Our gait mechanics data, in conjunction with the established time course of force
476 production by human skeletal muscle suggest that periods of foot-ground force application at top
477 forward running speeds may be too brief to allow the limb extensor muscles to develop

478 maximum force. The profile of the ground reaction force (Fig. 5), the posture of the limb during
479 high-speed running (6) and *in vivo* muscle force data (33) indicate that the forces generated by
480 the extensor muscles peak roughly halfway through the contact period. While these muscles are
481 clearly activated well before the limb contacts the ground (31, 33), there is no appreciable
482 development of muscular force until contact occurs (33). Accordingly, a reasonable
483 approximation of the time to peak muscle tension is one-half of the measured periods of foot-
484 ground contact. For the athletic subjects tested here, this half-period was 55 ± 3 ms at their top
485 forward running speeds.

486 Several pieces of experimental evidence suggest that the periods of foot-ground force
487 application during sprint running may be too short to allow the forces produced by the limb
488 muscles to reach their contractile maximums (21, 22, 25). The time course of the development
489 and transmission of muscular force *in vivo* in response to a single electrical impulse, or twitch, in
490 human knee and ankle extensors is 81 and 120 ms, respectively, in young adult males (21).
491 Thus, the periods required for the limb muscles to generate and transmit peak isometric twitch
492 forces *in vivo* are roughly two times longer than the time available during top speed running (Fig.
493 5). Moreover, if we eliminate the electromechanical delay by assuming that the knee and ankle
494 extensor muscles develop force at their maximal tetanic contraction rates (dP_{50} : 21) throughout
495 the 55 ms first half the foot-ground contact period, these muscle groups would reach only 46 and
496 22%, respectively, of the *in vivo* isometric force maximums reported under full stimulation
497 conditions (21). Although the quantitative influence of the different contractile conditions
498 present *in vivo* during isometric vs. bouncing gait contractions is not known, the comparisons
499 offered are consistent with a temporal constraint on the ground forces that can be applied during
500 high-speed running.

501 Thus, maximizing speed in bouncing gaits involves a trade-off between the magnitude of
502 the ground forces applied and the step frequencies that can be attained as foot-ground contact
503 periods become shorter at progressively faster speeds. Here, for example, the stance-average
504 vertical forces applied to the surface were 30.2% lower while step frequencies were nearly two
505 times greater during forward running than one-legged hopping at top speed. Quantitatively, the
506 much greater running step frequencies resulted from the relative brevity of both the aerial and
507 contact phases of the step cycle. Mechanically, the brevity of the aerial phase resulted from the
508 lesser vertical impulses brought about by the relatively lower forces and shorter contact times.
509 Thus, these comparisons indicate that the ground force-step frequency combination that
510 maximizes forward speed is set largely by the minimum time needed in the air in between steps.

511

512 *Hypothesis Test II: Backward versus Forward Running*

513 Our second primary finding, that the periods of force application during top speed backward and
514 forward running did not differ, is most easily interpreted if the ground force requirements of
515 these gaits were equivalent. However, both the average and the peak forces observed in these
516 two gaits at top speed were lower during backward vs. forward running (Table 1). The different
517 patterns of ground force application in the two gaits (Fig. 5) result in part from a different
518 orientation of the limb during backward running (47) that requires the extensor muscles to
519 generate 1.14 times more force per unit ground force applied than during forward running. If we
520 adjust for this factor, the average and peak forces required of the limb extensor muscles at the
521 respective top speeds in these gaits were not different and agreed to within 5.3 ± 0.06 and $3.4 \pm$
522 0.06% , respectively. Thus, the minimum times of force application observed at the different

523 respective top speeds in these two gaits were nearly identical when the net forces required of the
524 extensor muscles during the contact period were the same.

525 A logical question raised by our finding that the brief durations of ground force
526 application limit the maximum ground forces that can be applied, is why runners do not choose
527 to take the greater contact lengths and times that would allow them to apply greater ground
528 forces? A considerable body of evidence indicates that the large ground and muscle forces
529 required to support the body's weight constrain the excursions of the stance limb to a relatively
530 narrow range of positions directly underneath the body (4, 6, 12, 27, 30). When limb excursion
531 angles and contact lengths are increased beyond those selected naturally, performance suffers
532 because both the limb's mechanical advantage and the natural spring-like rebound of the body in
533 the latter portion of the contact period are compromised (17, 30).

534

535 *Gait Mechanics and Sprinting Performance*

536 Our findings here also offer insight into which gait mechanics can and cannot be modified to
537 bring about changes in sprinting performance. Two features of bouncing gaits have emerged as
538 being mechanically constrained at similar levels across individuals: contact lengths and
539 minimum swing times. In a previous investigation, we reported that there was little to no
540 difference in the time that fast and slow runners take to reposition their limbs at top speed (44).
541 Although sprint athletes have muscle fibers with faster contractile kinetics (15), faster muscle
542 fibers do not appear to confer appreciable reductions in either aerial or swing periods at top
543 speed. Nonetheless, the minimum time for completing the swing process (343 ± 6 ms), and the
544 accompanying aerial times required for doing so largely determine the ground support forces and
545 impulses utilized to attain any given speed (Fig 2); they also directly affect the top speeds

546 attained (*Eq. 6*). As can be seen for the three gaits illustrated in Fig. 6, the greater the aerial time
547 requirement of the gait, the greater the slope of the force-speed relationship and the greater the
548 force required to attain a given top speed.

549 The third constraint that has emerged here is largely biological and more variable: the
550 lower limit to the periods of foot-ground contact during which the necessary ground forces can
551 be applied. This limit clearly varies between individuals, and likely does so in accordance with
552 the individual differences in the contractile speeds of the fibers of the limb muscles. Here,
553 within each of the three gaits examined (Fig. 6), and also previously (44), we found that faster
554 subjects were able to apply greater mass-specific ground forces during shorter periods of foot-
555 ground contact. These capabilities would be expected to be conferred by limbs with faster
556 muscle fibers, and greater rates of force development (8, 41).

557 These results identify two interventions, one physiological and one anatomical, that
558 would improve sprint running performance given the stance phase limitation imposed by the
559 minimum periods of ground force application. First, muscle fibers with more rapid contractile
560 kinetics (34) may allow greater ground forces to be applied during the progressively shorter
561 periods of foot-ground contact that sprinting at faster speeds requires. How fast might these
562 faster muscle fibers allow humans to run? The quantitative relationships introduced in the
563 Methods can be used to formulate theoretical estimates of the top speeds that would be possible
564 if faster muscle fibers were to permit the limbs to apply one-legged hopping ground force
565 maximums while running. If, for simplicity, we assume no change in contact lengths or the
566 minimum aerial times needed to reposition the swing limbs at top speed, the average and greatest
567 individual top speed hopping forces (F_{avg}) of 2.71 and 3.35 W_b would allow top running speeds
568 in $\text{m}\cdot\text{s}^{-1}$ of 14.0 and 19.3, and in $\text{km}\cdot\text{hr}^{-1}$ of 50 and 69 $\text{km}\cdot\text{hr}^{-1}$, respectively. Second, limbs

569 lengthened through evolution or perhaps prosthetically could substantially increase the top
570 running speed attained at the minimum period of foot-ground force application. For example, a
571 relatively small increase in leg length of 10 cm would increase contact lengths by nine cm and
572 the top speeds of the subjects tested here from 9.1 to 9.8 m • s⁻¹. The calculations and theoretical
573 values that would result from these two interventions while holding the other variables in eq. 6
574 constant appear in the Appendix.

575 The mechanisms by which training interventions might increase running speeds most
576 effectively have not been fully evaluated in the context of the gait mechanics considered here,
577 but such efforts would likely offer additional insight into the relationship between the functional
578 limits of musculoskeletal tissues and gait mechanics. Given the negligible extent to which
579 muscle fiber speeds are enhanced via sprint training (22) and what appears to be a fairly rigid
580 lower biological limit on minimum swing times (42, 44), the most effective training strategies
581 may be those that enhance limb extensor muscle force production without increasing the body's
582 mass or compromising rates of muscular force production.

583

584 *The biology of speed: limits, trade-offs and adaptations from the ground up*

585 Finally, while our data indicate that muscle fibers with relatively slow contractile kinetics impose
586 a biological limit to sprint running speeds, slower fibers also economize the forces produced
587 during standing and walking (3, 27, 41) and confer greater tendon and bone safety margins
588 during rapid weight-bearing movements (4, 41). These functional trade-offs may explain why
589 the fastest animal sprinters have adapted for running speed with little apparent alteration in
590 muscle fiber speeds. The muscles of cheetahs and greyhounds function at rates that differ little
591 from those of other running animals (16, 46). Rather, these animals have adapted for speed by

592 developing gait mechanics that prolong their periods of ground force application. These
593 quadrupeds gallop with pronounced backbone bending that increases their foot-ground contact
594 times and lengths (2, 23) to values (39) that approach those of humans even though their limbs
595 are only half as long (29). Relatively greater contact lengths and times allow faster running
596 speeds to be attained before foot-ground contact times fall to the minimums that muscle fiber
597 speeds permit.

598 Because humans have limbs of moderate length and cannot gallop, they lack similar
599 options for prolonging periods of foot-ground force application in order to attain faster sprinting
600 speeds at existing contact time minimums. Consequently, human running speeds in excess of 50
601 kilometers per hour are likely to be limited to the realms of science fiction, and not
602 inconceivably, gene doping.

603

604 **Appendix**

605
606 Our results and the quantitative relationships provided in the Methods, permit a theoretical
607 assessment of the top running speeds attained by limbs capable of applying greater forces to the
608 ground or those that have been artificially lengthened. The estimates that appear in the
609 Discussion and Appendix Table 1 were determined by substituting *Eq. 4* into *Eq. 2* to give

610
611
$$F_{\text{avg}} / W_b = \frac{T_c + T_{\text{aer}}}{T_c} \quad \text{Appendix Eq. 1}$$

612
613 which was solved with respect to T_c to yield:

614
$$T_c = \frac{T_{\text{aer}}}{\left(\frac{F_{\text{avg}}}{W_b} - 1\right)} \quad \text{Appendix Eq. 2}$$

615
616 and then substituted into *Eq. 6*

617
618
$$\text{Speed} = \left[\frac{F_{\text{avg}}}{W_b} \bullet L_c \right] \bullet \left[\frac{T_{\text{aer}}}{\left(\frac{F_{\text{avg}}}{W_b} - 1\right)} + T_{\text{aer}} \right]^{-1} \quad \text{Appendix Eq. 3}$$

619
620
621
622 to determine the theoretical top running speeds that would result from these two interventions
623 with L_c and T_{aer} fixed at the values measured during top speed forward running.

624 As noted in the Discussion, the method above predicts running speeds of 14.0 and 19.3 m
625 $\bullet s^{-1}$ with F_{avg} values of 2.71 and 3.35 W_b , respectively. If, in slight contrast to the above T_{sw} is
626 fixed at the typical biological limit of 0.350 s, rather than T_{aer} being fixed at 0.121 s (and thereby
627 allowing T_{sw} to fall to values lower than 0.350 s), slower theoretical top speeds of 12.5 and 16.1
628 m $\bullet s^{-1}$ result.

629 All of the projected speeds are based on simplifying assumptions that ignore the
630 incomplete understanding of the factors that determine and limit muscular force production in
631 bouncing gaits.
632

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634
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648

649

650 **References**

- 651
- 652 1. **Alexander RM, and Vernon A.** The dimensions of the knee and ankle muscles and the
653 forces they exert. *J Hum Mov Sci* 1: 115-123, 1975.
- 654
- 655 2. **Alexander RM.** Why mammals gallop. *Amer Zool* 28: 237-245, 1988.
- 656
- 657 3. **Barany M.** ATPase activity of myosin correlated with speed of muscle shortening. *J Gen*
658 *Phys* 50, Suppl: 197-218, 1967.
- 659
- 660 4. **Biewener AA.** Scaling body support in mammals: limb posture and muscle mechanics.
661 *Science* 245: 45-48, 1989.
- 662
- 663 5. **Biewener AA.** Safety factors in Bone Strength. *Calcif Tissue Int* 53 (Suppl 1): S68-S74,
664 1993.
- 665
- 666 6. **Biewener AA, Farley CT, Roberts TJ, and Temanar M.** Muscle mechanical advantage of
667 human walking and running: implications for energy cost. *J Appl Physiol* 97: 2266-2274, 2004.
- 668
- 669 7. **Bundle MW, Hoyt RW and Weyand PG.** High speed running performance: a new
670 approach to assessment and prediction. *J Appl Physiol* 95: 1955-1962, 2003.
- 671
- 672 8. **Burke RE, Levine DN and Zajac FE.** Mammalian motor units: physiological-histochemical
673 correlation in three types in cat gastrocnemius. *Science* 174: 709-712, 1971.
- 674
- 675 9. **Cavagna GA, Sabiene FP and Margaria R.** Mechanical work in running. *J Appl Physiol*
676 19: 249-256, 1964.
- 677
- 678 10. **Cavagna GA.** Force platforms as ergometers. *J Appl Physiol* 39: 174-179, 1975.
- 679
- 680 11. **Cavagna GA, Heglund NC and Taylor CR.** Mechanical work in terrestrial locomotion:
681 two basic mechanisms for minimizing energy expenditure. *Am J Physiol* 233: R243-R261, 1977.
- 682
- 683 12. **Chang YH, Huang HW, Hammerski CM and Kram R.** The independent effects of
684 gravity and inertia on running mechanics. *J Exp Biol* 203: 229-238, 2000.
- 685
- 686 13. **Chang, YH and Kram RK.** Limitations to maximum running speed on flat curves.
687 *J Exp Biol* 210: 971-982, 2007.
- 688
- 689 14. **Close RI.** Dynamic properties of mammalian skeletal muscles. *Physiol Rev* 52: 129-197.
690 1972.
- 691
- 692 15. **Costill DL, Daniels J, Evans W, Fink W, Krahenbuhl G and Saltin B.** Skeletal muscle
693 enzymes and fiber composition in male and female track athletes. *J Appl Physiol* 40: 149-154,
694 1976.
- 695

- 696 16. **Dobson GP, Parkhouse WS, Weber JM, Stuttard E, Harman J, Snow DH and**
697 **Hochachka PW.** Metabolic changes in skeletal muscle and blood of greyhounds during 800-m
698 track sprint *Am J Physiol Reg Int Comp* 255: R513-R519, 1988.
699
- 700 17. **Farley CT and Gonzalez O.** Leg stiffness and stride frequency in human running. *J*
701 *Biomech* 29: 181-186, 1996.
702
- 703 18. **Ferris DP, Louie M and Farley CT.** Running in the real world: adjusting leg stiffness for
704 different surfaces. *Proc R Soc Lond B Biol Sci* 265: 989-994, 1998.
705
- 706 19. **Frishberg BA.** An analysis of overground and treadmill sprinting. *Med Sci Sports Exerc.*
707 15: 478-485.
708
- 709 20. **Greene PR.** Running on flat turns: experiments, theory and applications. *J Biomech Eng*
710 107: 96-103, 1985.
711
- 712 21. **Harridge SDR, Bottinelli R, Canepari M, Pellegrino MA, Reggiani C, Esbjörnsson M**
713 **and Saltin B.** Whole-muscle and single fibre contractile properties and myosin heavy chain
714 isoforms in humans *Pflugers Arch* 432: 913-920, 1996.
715
- 716 22. **Harridge SDR, Bottinelli R, Canepari M, Pellegrino C, Reggiani C, Esbjörnsson M,**
717 **Balsom PD and Saltin B.** Sprint training, in vitro and in vivo muscle function and myosin heavy
718 chain expression. *J Appl Physiol* 84: 442-449, 1998.
719
- 720 23. **Hildebrand M.** How animals run. *Sci Am* 5: 148-157, 1960.
721
- 722 24. **Hill AV.** The dimensions of animals and their muscular dynamics. *Sci Prog* 38: 209-230,
723 1950.
724
- 725 25. **Korhonen MT, Cristea A, Markku A, Hakkinen K, Sipila S, Mero A, Viitasalo JT,**
726 **Larsson L and Suominen H.** Aging, muscle fiber type and contractile function in sprint-trained
727 athletes *J Appl Physiol* 101: 906-917, 2006.
728
- 729 26. **Kram R and Powell AJ.** A treadmill mounted force platform. *J Appl Physiol* 67: 1692-
730 1698, 1989.
731
- 732 27. **Kram R and Taylor CR.** Energetics of running: a new perspective. *Nature* 346: 2265-
733 2267, 1990.
734
- 735 28. **Kuitunen S, Komi PV and Kyrolainen H.** Knee and ankle joint stiffness in sprint running.
736 *Med Sci Sports Exerc* 34: 166-173, 2002.
737
- 738 29. **Lee DV, Bertram JEA and Todhunter RJ.** Acceleration and balance in trotting dogs. *J*
739 *Exp Biol* 202: 3565-3573, 1999.

- 740
741 30. **McMahon, TA, Valiant G and Frederick EC.** Groucho running. *J Appl Physiol* 62: 2326-
742 2337, 1987.
743
744 31. **Mero A, Komi PV and Gregor RJ.** Biomechanics of sprint running *Sports Med* 13: 376-
745 392, 1992.
746
747 32. **Pollock CM and Shadwick RE.** Relationship between body mass and biomechanical
748 properties of limb tendons in adult mammals. *Am J Physiol* 266: R1016-R1021, 1994.
749
750 33. **Roberts TJ, Marsh RL, Weyand PG and Taylor CR.** Muscular force in running turkeys:
751 the economy of minimizing work. *Science* 275: 1113-1115, 1997.
752
753 34. **Rome LC and Lindstedt SL.** The quest for speed: muscles built for high-frequency
754 contractions. *News Physiol Sci* 13: 261-268, 1998.
755
756 35. **Taylor CR.** Force development during sustained locomotion: a determinant of gait, speed
757 and metabolic power. *J Exp Biol* 115: 253-262, 1980.
758
759 36. **Taylor CR.** Relating mechanics and energetics during exercise. *Adv Vet Sci Comp Med*
760 38A: 181-215, 1994.
761
762 37. **Taylor CR, Heglund NC, McMahon TA and Looney TR.** Energetic cost of generating
763 muscular force during running: a comparison of large and small animals. *J Exp Biol* 63: 775-779,
764 1980.
765
766 38. **Thorpe SK, Li Y, Crompton RH and Alexander RM.** Stresses in human leg muscles in
767 running and jumping determined by force plate analysis and from published magnetic resonance
768 images. *J Exp Biol* 201: 63-70, 1998.
769
770 39. **Usherwood JR and Wilson AM.** No force limit on greyhound sprint speed. *Nature* 438:
771 753-754, 2005.
772
773 40. **Usherwood JR and Wilson AM.** Accounting for elite indoor 200 m sprint results *Biol Lett*
774 2: 47-50, 2006.
775
776 41. **Walmsley B, Hodgson JA and Burke RE.** Forces produced by medial gastrocnemius
777 during locomotion in freely moving cats. *J Neurophys* 41: 1203-1216, 1978.
778
779 42. **Weyand PG, Bundle MW.** Artificial limbs do make artificially fast running speeds
780 possible, *J. Appl. Physiol*, epub ahead of print, doi:10.1152/jappphysiol.01238.2009, Nov, 2009.
781
782 43. **Weyand PG, Bundle MW, McGowan CP, Grabowski A, Brown MB, Kram R, and**
783 **Herr H.** The fastest runner on artificial legs: different limbs, similar function? *J. Appl. Physiol*,
784 epub ahead of print, June, 2009.
785

- 786 44. **Weyand PG, Sternlight DB, Bellizzi MJ and Wright S.** Faster top running speeds are
787 achieved with greater ground forces not more rapid leg movements. *J Appl Physiol* 81: 1991-
788 1999, 2000.
- 789
790 45. **Weyand PG and Davis JA.** Running performance has a structural basis. *J Exp Biol* 208:
791 2625-2631, 2005.
- 792
793 46. **Williams TM, Dobson GP, Mathieu-Costello O, Morsbach D, Worley MB and Phillips**
794 **JA.** Skeletal muscle histology and biochemistry of an elite sprinter, the African cheetah. *J Comp*
795 *Physiol B* 167: 527-535, 1997.
- 796
797 47. **Wright S and Weyand PG.** The application of ground force explains the energetic cost of
798 running backward and forward. *J Exp Biol* 204: 1805-15, 2001.
- 799
800

801 **Figure Captions**

802 Fig. 1. Vertical ground reaction forces, contact and aerial periods of the step cycle vs. time for
803 forward running (A), one-legged hopping (B), and backward running (C) for a representative
804 subject at the same speed for all three gaits (5.0 m s^{-1}). The ground reaction forces for forward
805 running from panel A are reproduced in panels B and C (dashed curves) to allow comparisons of
806 the ground reaction forces, contact and aerial phase durations of these gaits with forward
807 running. [Note: the durations of the contact, aerial and swing phases are appreciably shorter at
808 top forward running speed]

809
810 Fig. 2. Gait mechanics as a function of speed for a representative subject in all three gaits: stance
811 average vertical force (A), effective impulses (B), step lengths (C), foot-ground contact times
812 (D), aerial times (E), and step frequencies (F), each illustrated as a function of treadmill speed.
813 In each gait, foot-ground contact times (T_c) decreased by a factor of roughly two or more while
814 the average vertical force (F_{avg}) applied during the contact period increased moderately. The
815 effective vertical impulses (Imp_{Eff}) and the aerial times (T_{aer}) were considerably greater for one-
816 legged hopping than for either forward or backward running. Error bars are obscured by most of
817 the symbols.

818
819 Fig. 3. The average vertical force applied during the foot-ground contact period as a function of
820 speed for six individual subjects during forward running and one-legged hopping. Data are
821 presented through the top speed of each subject in both gaits. For each subject, the average
822 vertical force applied at the top running speed was appreciably less than that applied at the top

823 one-legged hopping speed (i.e. the force reserve). These same data for subject 1 appear in Figure
824 2.

825
826 Fig. 4. Foot-ground contact times as a function of speed during forward and backward running
827 for six individual subjects. Data are presented through the top speed of each subject in the
828 respective gaits. Foot-ground contact times decreased by a factor of two or more for all subjects,
829 and reached similar individual minimums (dashed lines) in the two gaits. These same data for
830 subject 1 appear in Figure 2.

831
832 Fig. 5. Vertical ground reaction forces in units of the body's weight (W_b) vs. time for a single
833 footfall from subject 1 at top speed in each of the three gaits. Foot-ground contact times are
834 longer and both peak and stance-average forces are greater for one-legged hopping than for
835 either forward or backward running. [Note: top forward running speed and contact time for
836 Subject 1 were 8.0 m s^{-1} and 0.106 s , respectively].

837
838 Fig. 6. The average vertical force applied (A), the durations of the foot-ground contact (B), and
839 aerial periods (C) for different subjects at top speed in each of the three gaits. Within each gait,
840 faster subjects applied greater mass-specific forces, had shorter contact times, longer aerial times
841 and at top speed.

842
843 Fig. 7. Ground reaction moment arms during one-legged hopping (red bars & white limb), and
844 forward running (blue bars & grey limb), were measured as the perpendicular distance
(illustrated as horizontal) between the joint axis of rotation and the ground reaction force vector
(black and grey arrows one-legged hopping and forward running respectively). The product of

the ground reaction force and the ratio of the ground reaction moment to the extensor muscle moment (4, 6), provides an estimate of the required net extensor muscle force. Using the measured mid-stance ground reaction forces shown here, and the ratios reported in Table 2, the limb-averaged muscle force estimates were significantly greater for hopping vs forward running.

Table 1. Top Speed Gait Mechanics

Gait	F _{avg} (W _b)	L _c (m)	L _{step} (m)	T _c (s)	T _{aer} (s)	Freq _{step} (s ⁻¹)	Top Speed (m s ⁻¹)
Fwd Run (I)	2.08 ± 0.07	0.98 ± 0.04	2.05 ± 0.14	0.108 ± 0.004	0.119 ± 0.004	4.51 ± 0.08	9.20 ± 0.59
1-Leg Hop	2.71 ± 0.15*	0.89 ± 0.05	2.51 ± 0.26	0.160 ± 0.006*	0.274 ± 0.019*	2.36 ± 0.13*	5.75 ± 0.39*
Fwd Run (II)	2.10 ± 0.07	0.99 ± 0.03	2.06 ± 0.11	0.110 ± 0.005	0.121 ± 0.003	4.42 ± 0.19	9.10 ± 0.52
Bwd Run	1.75 ± 0.05*	0.74 ± 0.05*	1.29 ± 0.14*	0.116 ± 0.004	0.091 ± 0.007*	5.05 ± 0.19*	6.42 ± 0.57*

* Significantly different than forward running ($P < 0.05$). Values were obtained from a minimum of four hopping and eight running steps for each subject.

844 **Table 2: The effective mechanical advantage (EMA) and net extensor muscle force during forward running**
 845 **and one-legged hopping**
 846

Limb Joint	Effective Mechanical Advantage (r/R)		Extensor Muscle Force ($\times W_b$)	
	Fwd Run	1-Leg Hop	Fwd Run	1-Leg Hop
Hip	2.42 ± 0.83	1.58 ± 0.51 *	1.33 ± 0.14	2.95 ± 0.46 *
Knee	0.67 ± 0.17	0.63 ± 0.20	4.18 ± 0.20	6.20 ± 0.58 *
Ankle	0.56 ± 0.18	0.39 ± 0.07 *	5.50 ± 0.52	9.66 ± 0.84 *
Limb Average	1.22 ± 0.32	0.87 ± 0.21 *	3.67 ± 0.25	6.25 ± 0.52 *

847 Ratio of measured ground reaction force moments to the anatomical muscle moments, or effective
 848 mechanical advantage (4, 6), and the estimated net extensor muscle forces, during Fwd Run (Speed range:
 849 2.5-10.5 m s⁻¹; n = 23 trials, stances analyzed = 209) and 1-Leg Hop (2.5-7.5 m s⁻¹; n = 18 trials, stances
 850 analyzed = 170); presented as means for the entire speed range.

* Significantly different than forward running ($P < 0.05$)

Appendix Table 1. Theoretical Top Running Speeds Achieved *via* Increased Force Application and Leg Length

Measured/ Theoretical	F_{avg} (W_b)	L_c (m)	L_{step} (m)	T_c (s)	T_{aer} (s)	$Freq_{step}$ (s^{-1})	Top Speed ($m\ s^{-1}$)
Fwd Run (II) (measured)	2.10 ± 0.07	0.99 ± 0.03	2.06 ± 0.11	0.110 ± 0.005	0.121 ± 0.003	4.42 ± 0.19	9.10 ± 0.52
ΔF_{avg}^* (theoretical)	2.71	0.99	2.68	0.071	0.121	5.22	14.0
ΔL_o^* (theoretical)	2.10	1.08	2.27	0.110	0.121	4.32	9.80

*The theoretical ΔF_{avg} and ΔL_o (+0.10 m) top speeds were estimated in accordance with the algebraic procedure described in the Appendix and by assuming that the L_c and T_{aer} values measured during top speed forward running would not be altered by either condition. Shaded entries identify the values not changed from those measured during top speed forward running.

Fig. 1

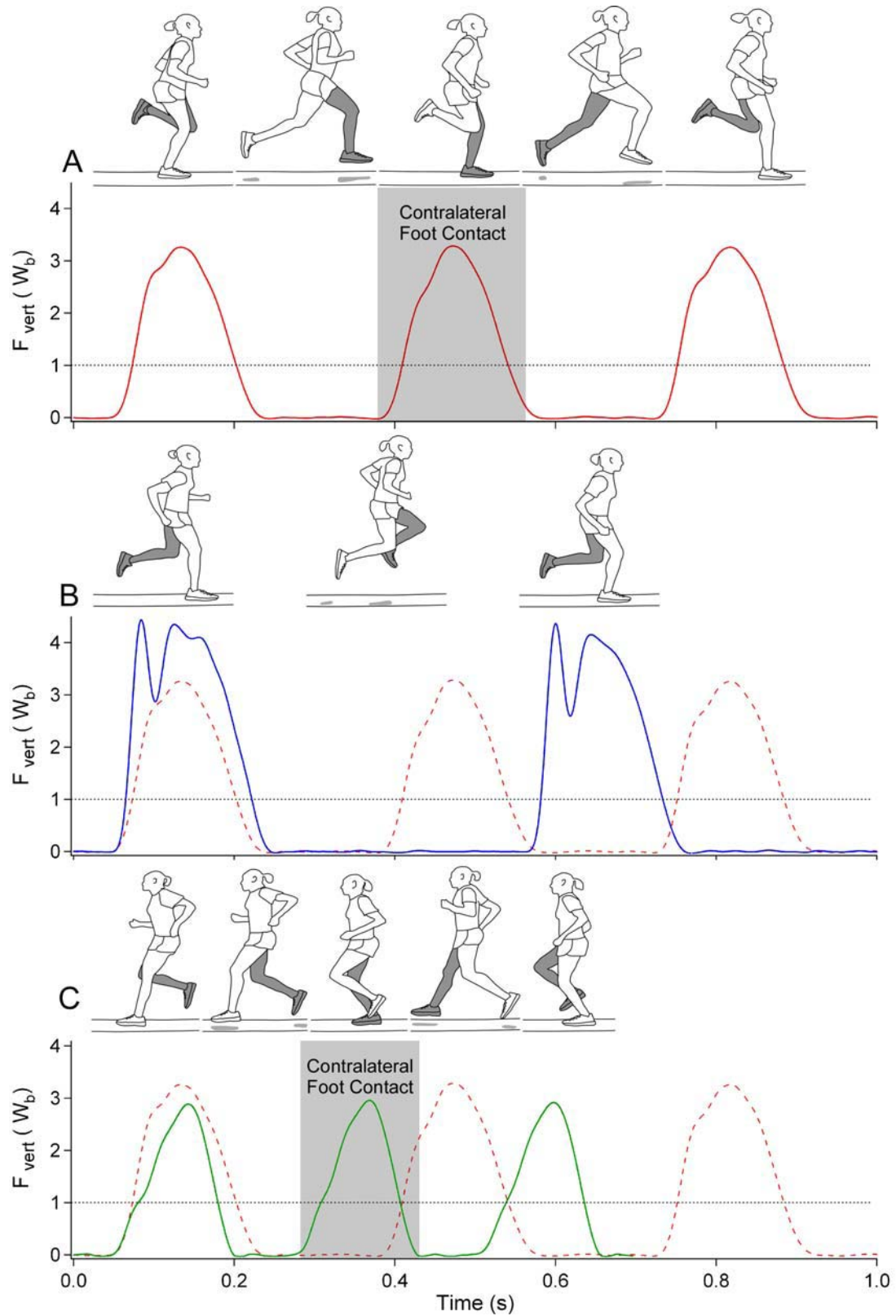


Fig. 2

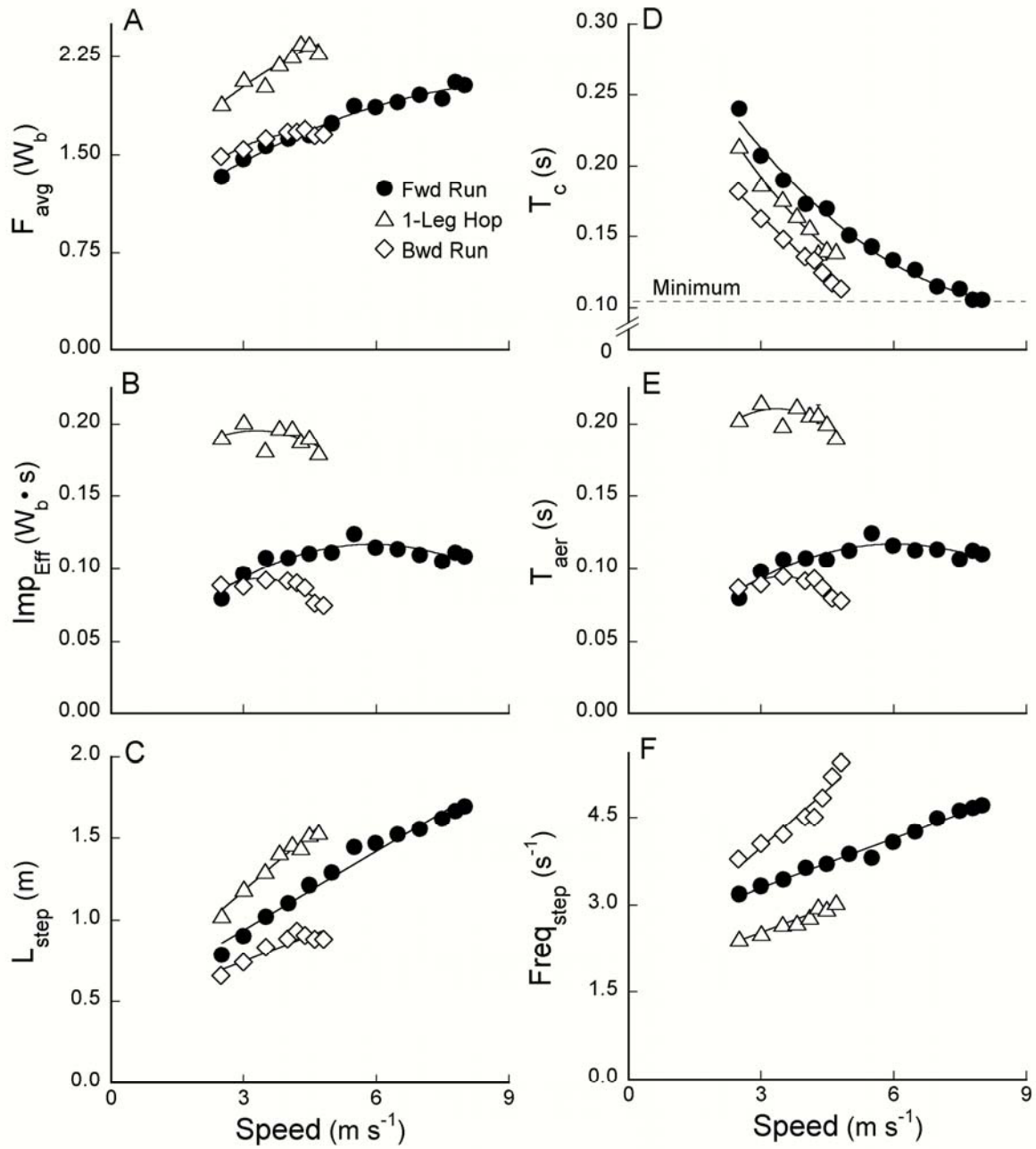


Fig. 3

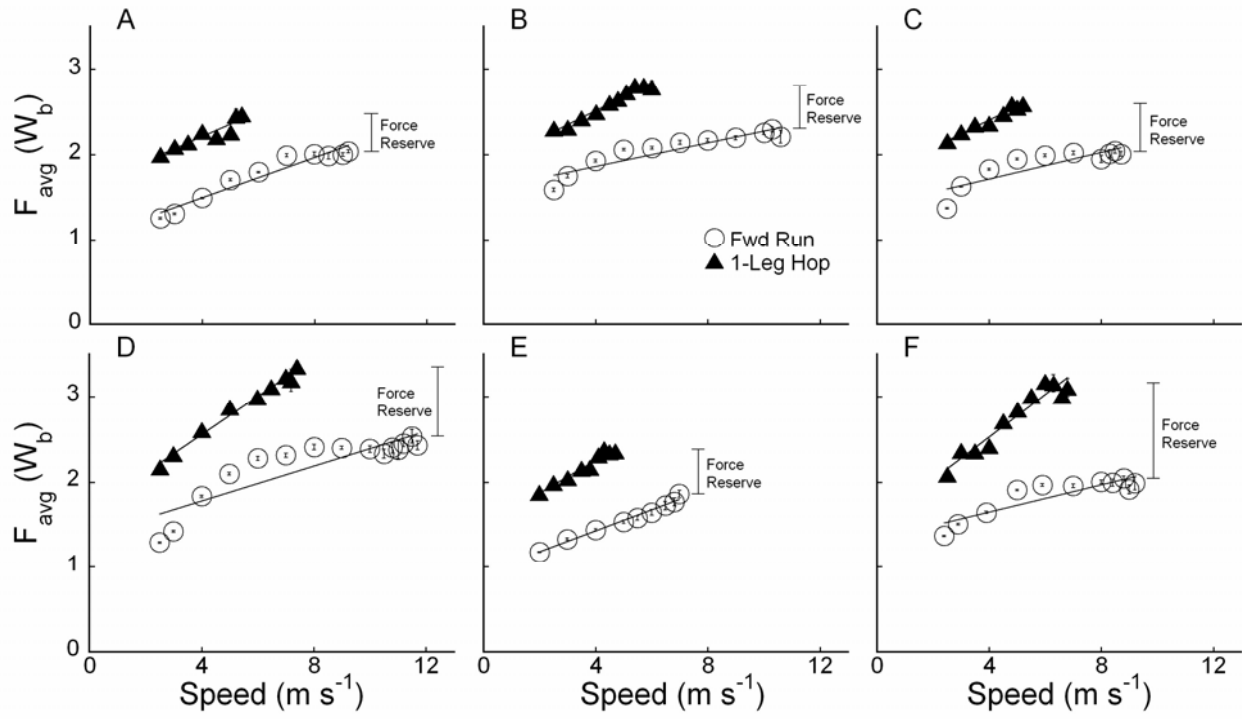


Fig. 4

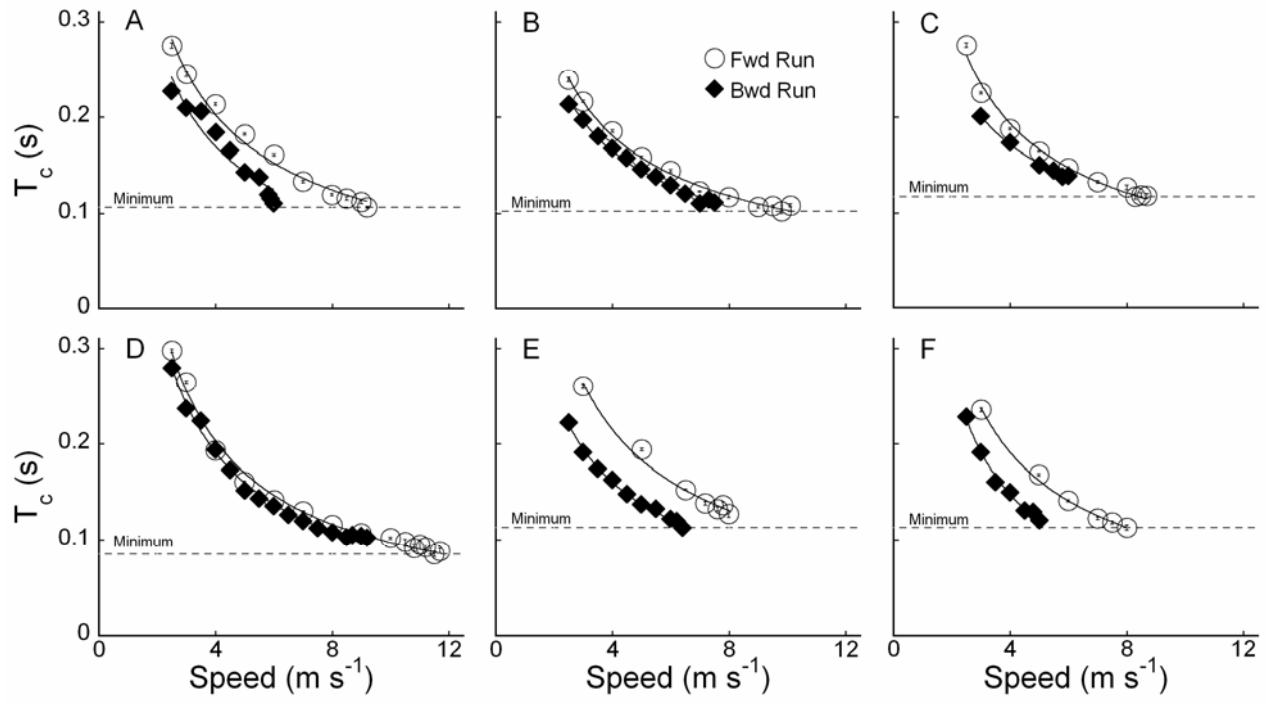


Fig. 5

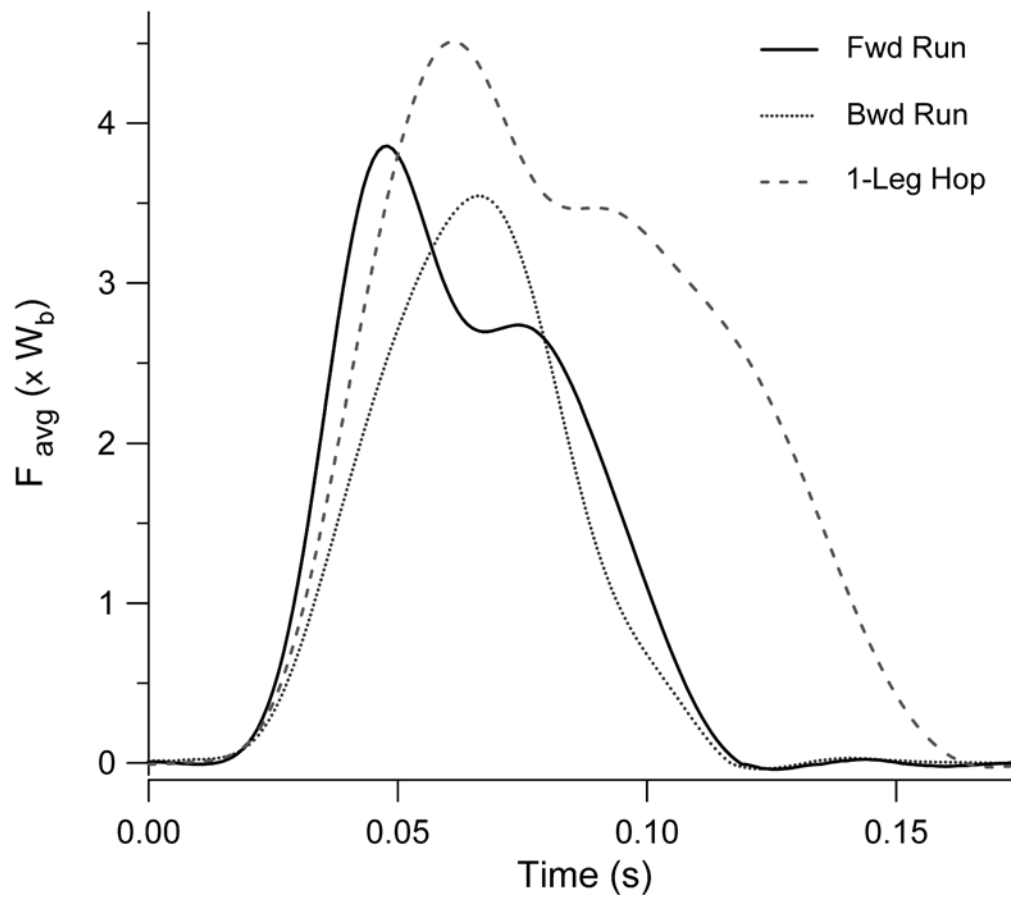


Fig. 6

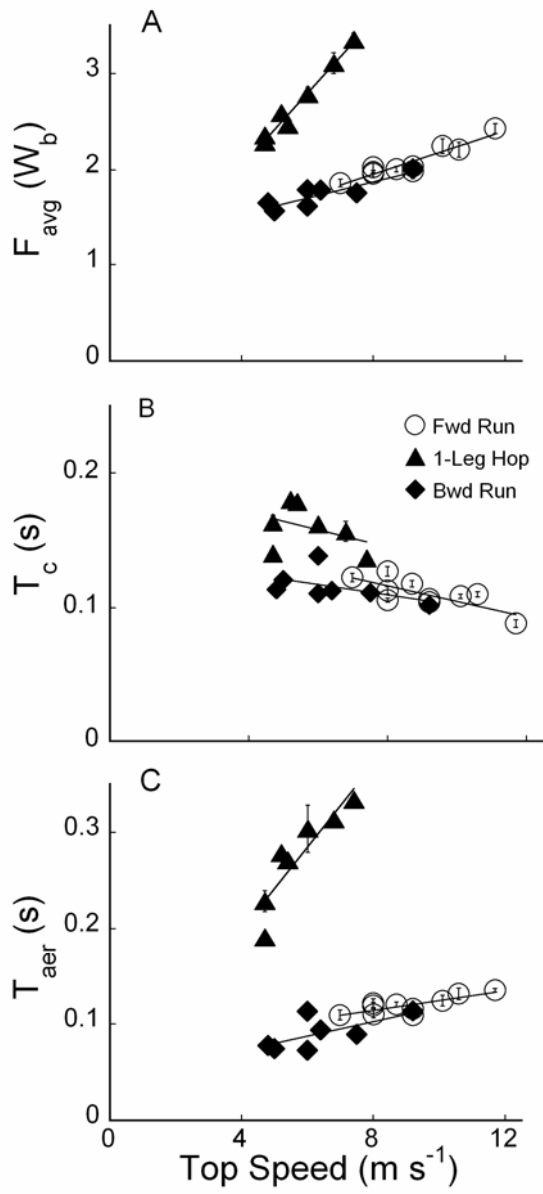


Fig. 7

