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**The fastest runner on artificial legs:
different limbs, similar function?**

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Running head: The fastest runner on artificial legs

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44 **Abstract**

45 The recent competitive successes of a bilateral, transtibial amputee sprint runner who
46 races with modern running prostheses has triggered an international controversy
47 regarding the relative function provided by his artificial limbs. Here, we conducted three
48 tests of functional similarity between this amputee sprinter and competitive male runners
49 with intact limbs: the metabolic cost of running, sprinting endurance, and running
50 mechanics. Metabolic and mechanical data, respectively, were acquired via indirect
51 calorimetry and ground reaction force measurement during constant-speed, level
52 treadmill running. First, we found that the mean gross metabolic cost of transport of our
53 amputee sprint subject ($174.9 \text{ ml O}_2 \text{ kg}^{-1} \text{ km}^{-1}$; speeds: 2.5 to 4.1 m s^{-1}) was only 3.8%
54 lower than mean values for intact-limb elite distance runners and 6.7% lower than for
55 sub-elite distance runners, but 17% lower than for intact-limb 400-meter specialists
56 ($210.6 [13.2; \text{SD}] \text{ ml O}_2 \text{ kg}^{-1} \text{ km}^{-1}$). Second, the speeds our amputee sprinter maintained
57 for six all-out, constant-speed trials to failure (speeds: 6.6 - 10.8 m s^{-1} ; durations: 2-90 s)
58 were within 2.2 [0.6]% of those predicted for intact-limb sprinters. Third, at sprinting
59 speeds of 8.0 , 9.0 and 10.0 m s^{-1} , our amputee subject had longer foot-ground contact
60 times (+14.7 [4.2]%), shorter aerial (-26.4 [9.9]%) and swing times (-15.2 [6.9]%), and
61 lower stance-averaged vertical forces (-19.3 [3.1]%) than intact-limb sprinters (top speeds
62 = 10.8 vs. $10.8 [0.6] \text{ m s}^{-1}$). We conclude that running on modern, lower-limb sprinting
63 prostheses appears to be physiologically similar, but mechanically different than running
64 with intact limbs.

65

66 **Introduction**

67 Prosthetic legs have existed for millennia, but even today's most advanced models
68 generally do not provide full biological function. The recent athletic performances of a
69 bilateral, transtibial amputee sprinter indicate that the long-standing assumption of
70 functional inferiority may no longer be valid. This amputee athlete has had extraordinary
71 success while racing with prosthetic limbs over the last several years. He narrowly
72 missed the automatic qualifying standard for the 400-meter dash at the able-bodied 2008
73 Olympic Games. He also finished second in the able-bodied National Championships of
74 South Africa in 2007. These unprecedented achievements for an amputee athlete have
75 raised a provocative question about relative limb function: are modern running prostheses
76 now equal or perhaps superior to biological limbs?

77 An international scientific and athletic controversy has arisen over this intriguing
78 question. The controversy is rooted at least in part in the limited understanding of the
79 mechanical and physiological consequences of running with prosthetic vs. biological
80 limbs. Here, we present three experimental comparisons between this amputee athlete
81 and competitive runners with intact limbs. Our general objective was to evaluate whether
82 running with lower-limb prostheses vs. intact, biological limbs is functionally similar or
83 not. For this purpose, we tested three hypotheses at the whole-body level that would
84 provide relevant, straightforward comparisons: the metabolic cost of running, sprinting
85 endurance and sprinting mechanics. Conversely, we avoided estimations of whole-body
86 and joint mechanical power and energy transfers because their interpretation is
87 ambiguous (32, 33, 39) and their relationship to sprint running performance is not well
88 understood.

89 While there are many informative running studies on unilateral amputee runners
90 (5, 6, 9), the scientific literature contains little information on bilateral amputees (4). The
91 extremely limited, directly applicable information on bilateral, transtibial prosthetic
92 running led us to rely largely on established mechanistic relationships and reasoning to
93 formulate our three hypotheses. First, we assumed that the absence of lower-limb
94 musculature would result in smaller muscle volumes being active during prosthetic
95 running. Accordingly, we hypothesized that the metabolic cost of running with bilateral,
96 transtibial prostheses would be lower than for running with intact limbs. Second, given
97 that mechanical running prostheses do not fatigue, we hypothesized that bilateral,
98 transtibial prostheses would allow a greater proportion of the athlete's top sprinting speed
99 (i.e. anaerobic speed reserve; (7)) to be maintained during sprint efforts of longer
100 durations. Third, given that passive, elastic prostheses are designed to provide the spring-
101 like function that human lower limbs do during the stance phase of each stride (12), we
102 hypothesized that the mechanics of sprinting at common speeds would be similar for a
103 bilateral transtibial amputee and runners with intact limbs. Specifically, we hypothesized
104 that the magnitudes of the ground reaction forces in relation to body weight, and the
105 respective durations of the contact, aerial and swing phases of the stride would not differ.

106 **Methods**

107 *Experimental Design*

108 We conducted our evaluations of functional similarity for prosthetic vs. intact-
109 limb running as follows. First, we used existing data to establish the biological
110 variability present among intact-limb runners on each of the three whole-body measures
111 of interest. Next, we acquired the same data on our amputee sprint subject. We then
112 compared the values measured for our amputee subject to an appropriate group of intact-
113 limb runners. If the values measured during prosthetic running fell within the range of
114 values naturally present for runners with intact limbs, we reached a conclusion of
115 functional similarity; if not, we reached a conclusion of dissimilarity. Quantitatively, we
116 evaluated these comparisons by using a conventional criterion for significance (i.e. $p <$
117 0.05). We assumed normal distributions about the intact-limb means, and thus set our *a*
118 *priori* thresholds for functional dissimilarity at differences of two standard deviations
119 (SD) or greater between amputee and intact-limb values. This statistically conventional,
120 but conservative threshold was chosen to minimize the risk of a Type I error since we
121 only studied one bilateral, transtibial amputee sprinter.

122 To test our 1st hypothesis, regarding the metabolic cost of running, we used the
123 range of biological variability for runners with intact limbs from the most comprehensive
124 study in the literature for competitive male distance runners at the elite and sub-elite
125 levels (22). Additionally, we acquired metabolic data on subjects who were competitive
126 400 meter runners with best performances similar to our amputee subject. Our 1st
127 hypothesis was that the metabolic cost of running for our amputee subject would be
128 greater than two SD below the means reported for each of these three intact-limb

129 comparison groups (i.e. elite runners, sub-elite runners, and 400-meter specialists with
 130 similar best performances).

131 To test our 2nd hypothesis, regarding sprinting endurance, we established intact-
 132 limb norms using the sizeable database present in the literature for competitive runners
 133 (7, 36). These studies indicate that the all-out speeds of intact-limb runners during any
 134 trial lasting from a few seconds to a few minutes can be accurately predicted from two
 135 variables: the top sprint speed and the minimum speed eliciting maximal aerobic power.
 136 If both of these speeds are known, the speed for any all-out trial from 3 to 300 s is
 137 provided by:

138

$$139 \quad \text{Spd}_t = \text{Spd}_{\text{aer}} + (\text{Spd}_{\text{ts}} - \text{Spd}_{\text{aer}}) \cdot e^{(-k \cdot t)} \quad \text{eq. 1}$$

140

141 where Spd_t is the speed maintained for an all-out sprint of duration t , Spd_{aer} , also known
 142 as the velocity at $\dot{V} \text{O}_2 \text{ max}$ (10), is the minimum running speed eliciting maximal
 143 aerobic power, Spd_{ts} is the maximum or top sprinting speed that can be attained for eight
 144 consecutive steps (~ 2 s), e is the base of the natural logarithm, and k is an exponential
 145 constant for running ($= 0.013 \text{ s}^{-1}$) that describes the decrements in speed that occur with
 146 increments in the duration of all-out running.

147 For our sprinting endurance comparisons, we evaluated whether the measured
 148 speeds obtained from all-out sprints of different durations conformed to those predicted
 149 by eq. 1. This relationship has previously been shown to predict all-out sprint
 150 performances to within an average of $\pm 3\%$ (7, 36). To evaluate functional similarity for
 151 this comparison, we used a criterion of twice the standard error of estimate (SEE). The

152 SEE is the most commonly used statistic for comparing actual vs. predicted values, and is
153 the statistical and formulaic analogue of the standard deviation. The SEE value utilized
154 here was determined from 84 all-out treadmill trials previously completed by seven
155 competitive runners (7).

156 Our 2nd hypothesis was that our amputee subject would have appreciably
157 enhanced sprinting endurance because carbon fiber prostheses do not fatigue during
158 sprinting as skeletal muscle does (7, 8, 23, 38). This possibility was suggested by his
159 superior relative performances in longer vs. shorter sprint races and his atypically fast
160 closing velocities while racing. We tested this possibility during constant-speed treadmill
161 trials to eliminate the potentially confounding influence of the start and acceleration
162 portions of overground sprint races. The race velocities of our amputee subject vs. intact-
163 limb competitors in the second half of his 400 meter races on the track led us to expect
164 all-out speeds approximately 10% faster than those of intact-limb controls for any all-out
165 efforts lasting longer than 20 s.

166 To test our 3rd hypothesis, regarding running mechanics, we compared our
167 amputee subject's sprinting mechanics to the mechanics of a group of track athletes with
168 similar top treadmill sprinting speeds. Here also, we set a functional dissimilarity
169 threshold of greater than two standard deviations from intact limb control means at the
170 same running speeds for each of the following variables: foot-ground contact times, aerial
171 times, swing times, stance-average and peak vertical ground reaction forces. Our 3rd
172 hypothesis was that the running mechanics of our amputee subject would be functionally
173 similar to those of intact-limb runners.

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176

177 *Subject Characteristics*

178 Our amputee subject's average mass while wearing his prostheses (combined prostheses
179 mass: 2.50 kg) was 80.0 kg. His height while standing on his running prostheses (Össur
180 Cheetah, category 5) was 1.86 meters; his leg length under the same conditions was 1.01
181 meters. The intact-limb subjects tested to evaluate our 1st hypothesis were competitive
182 male 400-meter specialists with personal best times that were within ± 2.0 seconds of our
183 amputee subject ($n = 4$, mass = 75.3 [3.8; SD] kg). The intact-limb runners used to
184 evaluate our 2nd hypothesis were competitive runners whose data led to the formulation
185 of eq. 1 and the anaerobic speed reserve model (7, 36). The intact-limb subjects used to
186 evaluate our 3rd hypothesis were competitive track athletes with top treadmill sprinting
187 speeds similar to that measured for our amputee sprint subject ($n = 4$; mass = 72.7 [3.7]
188 kg; leg length = 0.97 [0.04] meters). The leg lengths of intact limb subjects tested for our
189 3rd hypothesis matched that of our amputee subject to within 4.0 cm. The body masses of
190 these subjects and our amputee subject conformed to the mean ± 2 SD reported ($76.2 \pm$
191 14.0 kg) of elite male 400 meter runners (37). Testing took place in the Locomotion
192 Laboratory of Rice University during February and March of 2008. Subjects provided
193 written informed consent in accordance with the Institutional Review Board of Rice
194 University.

195

196 *Hypothesis Test I. Metabolic Energy Expenditure during Running:* Steady-state rates of
197 oxygen uptake were measured using two methods: a computerized metabolic system

198 (Parvo Medics TrueMax 2400, Sandy Utah) and the Douglas bag method using the
199 specific protocol described by Weyand & Bundle (36). Subjects completed a
200 progressive, discontinuous, horizontal treadmill test that consisted of 5 to 7 min bouts of
201 running interspersed with 3-5 min rest periods. The test was initiated at 2.5 m s^{-1} and
202 terminated when the subject could not complete the prescribed bout duration of 5 to 7
203 min while putting forth an all-out effort. Throughout the test, expired air was directed via
204 a one-way breathing valve and tubing through a pneumotach into a mixing chamber.
205 During the last two min of each bout, expired air was also collected in meteorological
206 balloons via the exhaust port of the mixing chamber. Bag volumes were determined
207 using a Parkinson-Cowan dry gas meter with simultaneous temperature determination.
208 Aliquots were drawn from both the mixing chamber and the balloons for analysis of O_2
209 and CO_2 fractions using paramagnetic and infrared analyzers, respectively. All values
210 were corrected to STPD conditions.

211

212 *Rates of Oxygen Uptake* ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$): Rates of oxygen uptake were averaged over
213 the last two min of each steady-state running trial to obtain the value for each trial speed.
214 Measurements from the computerized and Douglas bag methods agreed to within an
215 average of 1.3 [1.2]%. The values reported are those acquired from the computerized
216 system. Both amputee and intact-limb 400 meter specialist measures were taken at
217 speeds between 2.5 and 4.5 m s^{-1} .

218

219 *Maximal Aerobic Power* ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) & Spd_{aer} (m s^{-1}): The maximal rate of aerobic
220 metabolism was the highest single minute value measured during the final all-out bout of

221 the treadmill test. The minimum speed eliciting maximal aerobic power (Spd_{aer}) was
222 determined from the measured aerobic maximum and the $\dot{V}O_2$ -speed regression
223 relationship for each subject. The latter was formulated using steady-state $\dot{V}O_2$ values
224 from only those trials eliciting < 90% of the subject's maximal aerobic power.

225

226 *Metabolic Cost of Transport* ($ml O_2 kg^{-1} km^{-1}$): The oxygen or metabolic energy cost per
227 unit distance traveled was determined by dividing the rate of oxygen uptake by the speed
228 of the trial. To maintain consistency with literature values, no baseline subtractions of
229 resting oxygen uptake were performed. Thus, all oxygen uptake rate and transport cost
230 data are gross rather than net values. Throughout the manuscript, we have reported
231 metabolic energy expenditure in units of oxygen uptake, rather than in true units of
232 energy. This practice conforms to physiological convention and facilitates comparisons
233 to the large majority of data previously reported for competitive runners.

234 Functional similarity for the metabolic cost of running was evaluated using
235 metabolic transport costs rather than rates of oxygen uptake for two reasons. First, our
236 original rates of oxygen uptake were acquired at different specific speeds for our amputee
237 subject vs. intact-limb 400 meter runners, and over different speed ranges vs. the elite and
238 sub-elite distance runners (22), as well as many of the other literature values. Direct
239 comparisons of the rates of oxygen uptake acquired at different speeds are not valid.
240 Second, because individual metabolic transport costs vary little across speed (10), the
241 most robust and representative single value for the metabolic cost of running for an
242 individual is provided by the average of the transport costs obtained across a series of
243 steady-state running speeds.

244

245

246 *Hypothesis Test II. Sprinting Endurance*

247 In addition to the previously described test to determine the minimum running speed that
248 elicits maximal aerobic power (Spd_{aer}), each subject completed a progressive
249 discontinuous treadmill test to determine their top sprinting speed (Spd_{ts}). Subjects also
250 completed a total of six to 15 constant-speed, all-out treadmill trials at speeds selected to
251 elicit failure at durations ranging from three seconds to five min. During individual test
252 sessions, the number of all-out trials completed ranged from two to five in accordance
253 with previous descriptions (7, 36). Each all-out trial was initiated by the subject lowering
254 himself from the handrails onto the treadmill belt after it had fully accelerated to the
255 desired speed. Subjects were instructed to terminate the run when they were physically
256 unable to match the speed of the tread by grabbing the handrails and straddling the belt
257 until it was stopped.

258

259 *Hypothesis Test III. Sprinting Mechanics*

260 Subjects tested to evaluate our 3rd hypothesis completed progressive, discontinuous,
261 horizontal treadmill tests to assess their running mechanics and determine their 8-step top
262 sprint speed as previously described (35). Tests were completed on a custom, high-speed
263 force treadmill (AMTI, Watertown, MA). The treadmill has a belt width of 0.610 m, is
264 powered by a Baldor 23H series motor and the treadmill bed (0.686 x 2.083 m) serves as
265 a strain gage-based force platform. Subjects were strapped into a harness secured
266 overhead and slackened sufficiently to become taut only in the event of a fall. Each trial

267 was initiated by the subject lowering himself from the handrails onto the treadmill belt
268 after it had fully accelerated to the desired speed. Our amputee and control subjects were
269 all generally able to transition quickly from standing to running without losing their
270 balance. In the few instances in which these transitions were not made rapidly, subjects
271 were immediately instructed to dismount the treadmill, recover, and prepare for another
272 attempt. These treadmill tests started at speeds of 2.0 to 2.5 m s⁻¹. Speed increments
273 ranged from 0.5 to 1.0 m s⁻¹ through roughly 80% of the subject's estimated top speed
274 after which speed increments were reduced to 0.1 to 0.4 m s⁻¹. The magnitude of each
275 increment was selected in accordance with subject performance on the previous trial and
276 their verbal feedback regarding difficulty. All subjects completed trials at 3.0, 4.0, 5.0,
277 6.0, 7.0, 8.0, 9.0 and 10.0 m s⁻¹ except one of four intact-limb sprinters. Slower and
278 intermediate speed trials lasted from 10 to 30 s, while faster speed trials lasted from 2 to
279 10 s. Subjects were encouraged to take as much rest as needed for full recovery between
280 trials.

281

282 *Top Speed (Spd_{ts})(m s⁻¹):* Top speed was defined as the fastest speed at which the
283 subject was able to complete eight consecutive steps without backward drift on the
284 treadmill. This was determined by administering trials at progressively faster speeds
285 until a speed was reached at which the subject was unable to match the belt speed for the
286 requisite number of steps while putting forth a maximal effort. Each subject failed on a
287 minimum of two all-out attempts before the test was terminated. In all cases, the top
288 speed successfully completed was within 0.2 m s⁻¹ or less of the subject's failure speed.

289

290 *Treadmill Force Data:* Force data for each trial were acquired using AMTI NetForce
291 software after signal amplification and digitization (DigiAmp, AMTI). Data at each trial
292 speed were acquired at 1000 Hz and subsequently processed with custom software that
293 applied a Butterworth filter with a low pass cut-off frequency of 30 Hz (Igor Pro:IFDL,
294 Wavemetrics, OR, USA). The values reported for each speed represent means
295 determined from a minimum of eight consecutive steps. Values at three speeds for one of
296 the four intact-limb subjects were interpolated; in each case from measures taken within
297 0.3 m s^{-1} of the interpolated speed. Representative traces from our amputee and one
298 intact-limb subject appear in Figure 1.

299
300 F_{avg} (F_{avg}/F_{wb}): The average vertical ground reaction force applied during the contact or
301 stance phase was determined from the time during which the vertical force signal
302 continuously exceeded a threshold of 40 N. Forces were expressed as multiples of body
303 weight by dividing the force recorded during each trial by the weight of the subject
304 recorded on a platform scale prior to treadmill testing.

305
306 *Contact time* (T_c , s): The time of foot-ground contact was determined from the periods
307 during which the vertical treadmill reaction force continuously exceeded 40 N.

308
309 *Aerial time* (T_{aer} , s): Aerial times were determined from the time interval between the end
310 of foot-ground contact with one limb and the beginning of foot-ground contact with the
311 other limb.

312

313 *Swing time* (T_{sw} , s): Swing time, or the time taken to reposition a single limb, was
314 determined from the time elapsing between the end, and subsequent beginning of foot-
315 ground contact periods by the same limb. The swing period includes two aerial periods
316 as well as the contact period of the contra-lateral limb (Fig. 1).

317

318 *Stride time* (T_{str} , s^{-1}): Stride time was determined from the time elapsing between the first
319 instants of contact for consecutive foot-strikes by the same limb.

320

321 *Leg length* (L_o , m): Leg length was measured from the axis of rotation of the right hip
322 joint to the ground at the outside of the right heel or prosthesis blade during erect
323 standing. Hip joint axis of rotation was determined by palpation as the subject slowly
324 swung the limb in the sagittal plane.

325

326 *Statistics*: Differences in mean values obtained from our amputee sprinter (AS) and
327 intact limb (IL) subjects are reported as percentages $[(AS-IL)/IL \cdot 100]$ and as multiples
328 of the intact-limb SD or SEE.

329

330 **Results**

331 *Hypothesis Test I. Metabolic Energy Expenditure during Running*

332 Rates of oxygen uptake for our amputee sprint subject increased from steady-state values
333 of 26.5 ml O₂ kg⁻¹ min⁻¹ at a treadmill speed of 2.5 m s⁻¹ to 43.3 ml O₂ kg⁻¹ min⁻¹ at the
334 fastest steady-state speed of 4.1 m s⁻¹ and were well-described by a linear fit ($\dot{V}O_2 =$
335 $10.6 \cdot \text{Spd} - 0.45$; $R^2 > 0.99$; Fig. 2A). Over the same range of speeds, rates of oxygen
336 uptake for intact-limb 400 meter specialists increased from 32.7 [1.5] at 2.5 m s⁻¹ to 50.4
337 [3.9] ml O₂ kg⁻¹ min⁻¹ at 4.1 m/s, a relationship also well described by a linear fit ($\dot{V}O_2 =$
338 $11.1 \cdot \text{Spd} + 4.9$; $R^2 > 0.99$).

339 The gross metabolic cost of transport for our amputee subject averaged 174.9
340 [2.2] ml O₂ kg⁻¹ km⁻¹ (Fig. 2B) and was virtually constant across the five speeds
341 measured. Our amputee sprint subject's gross metabolic cost of transport was 3.8%
342 lower than the mean for elite male distance runners (181.9 [9.1] ml O₂ kg⁻¹ km⁻¹, (22)),
343 6.7% lower than the mean for sub-elite distance runners (187.5 [9.7] ml O₂ kg⁻¹ km⁻¹,
344 (22)) and 17.0% lower than our 400-meter specialists (210.6 [13.2] ml O₂ kg⁻¹ km⁻¹).
345 Expressed in terms of the between-subject standard deviations of the respective groups,
346 the mean transport cost of our amputee sprint subject was, respectively, -0.8, -1.3 and -
347 2.7 x SD lower.

348 The maximal rate of aerobic metabolism of our amputee subject was 7.6% lower
349 than that of our intact-limb 400 meter subjects (52.7 vs. 57.0 [3.4] ml O₂ kg⁻¹ min⁻¹; n=3).
350 However, he attained essentially the same running speed at VO_{2max} (Spd_{aer}) as our intact-
351 limb 400 meter specialists (5.0 vs. 4.9 [0.02] m s⁻¹) because his metabolic cost of running
352 was relatively lower.

353 *Hypothesis Test II. Sprinting Endurance*

354 The all-out treadmill running speeds in relation to run duration for our amputee sprint
355 subject ($\text{Spd}_{\text{ts}} = 10.8 \text{ m s}^{-1}$; $\text{Spd}_{\text{aer}} = 5.0 \text{ m s}^{-1}$) appear in Figure 3A. In absolute terms,
356 these all-out speeds ranged from an eight-step top treadmill speed of 10.8 m s^{-1} achieved
357 during a $< 2.0 \text{ s}$ effort, to a speed of 6.6 m s^{-1} for an 89.5 s effort.

358 For comparative purposes, the data for three intact-limb subjects, one sprinter and
359 two distance runners, also appear in Figure 3. The all-out running performances of these
360 three intact-limb runners were essentially fully normalized when their trial speeds were
361 expressed as a percentage of their anaerobic speed reserves ($\text{Spd}_{\text{ts}} - \text{Spd}_{\text{aer}}$; Figure 3B).
362 The average agreement between the actual speeds they maintained ($n=35$) and those
363 predicted by eq. 1 was $\pm 2.1 [2.8] \%$ (Fig. 3C).

364 When the same anaerobic speed reserve normalization was applied to the all-out
365 performances of our amputee sprint subject, the result was similar (Fig. 3B). The all-out
366 speeds measured matched those predicted from eq. 1 (using the measured values for top
367 speed and the minimum speed eliciting maximal aerobic power) to within an average of
368 $2.2 [0.6] \%$ (Fig. 3C).

369 Thus, agreement with the established relationship was essentially the same for our
370 amputee and intact-limb subjects. The all-out speed values for our amputee sprint subject
371 fell within the two SEE (0.50 m s^{-1}) prescribed range of functional similarity.

372

373 *Hypothesis Test III. Sprinting Mechanics*

374 The mechanical means by which our amputee subject increased his running speed
375 from a jog to a fast sprint largely paralleled the patterns observed for intact-limb subjects.

376 The directional changes observed in foot-ground contact times, aerial times, swing times
377 and stance-averaged vertical force with increasing speed were all similar for our amputee
378 and intact-limb subjects. As treadmill speed was increased from $< 2.0 \text{ m s}^{-1}$ to a sprint of
379 10.0 m s^{-1} , foot-ground contact times (Fig. 4A) became progressively shorter. Both aerial
380 (Fig. 4 B) and swing times (Fig. 4C) exhibited maximum values at 4.0 m s^{-1} , and tended
381 to decrease with speed increases from 4.0 to 10.0 m s^{-1} . Stance-averaged vertical forces
382 (Fig. 4D) increased sharply from 2.5 m s^{-1} to 4.0 m s^{-1} , but relatively slowly from 4.0 to
383 10.0 m s^{-1} . Across the fastest three speeds of 8.0 , 9.0 and 10.0 m s^{-1} , F_{avg} increased
384 slightly for intact limb runners, but did not increase at all for our amputee sprint subject.

385 Although the patterns of change across speed in these four gait variables were
386 similar, magnitudes tended to be less pronounced for our amputee vs. intact limb
387 subjects. Consequently, differences between our amputee and intact limb subjects were
388 minimal at 2.5 and 3.0 m s^{-1} , modest at intermediate speeds of 4.0 and 5.0 and
389 appreciable at speeds from 6.0 to 10.0 m s^{-1} . At the fastest common speed of 10.0 m s^{-1} ,
390 our amputee subject's foot-ground contact times were 14.1% longer (0.113 vs. 0.099
391 $[0.004]$ s), aerial times were 34.3% shorter (0.092 vs. $0.140 [0.011]$ s), swing times were
392 21.0% shorter (0.293 vs. $0.371 [0.023]$ s) and stance-average vertical forces were 22.8%
393 less (1.79 vs. $2.32 [0.10]$ W_b) than those of intact-limb sprinters. When expressed in
394 intact-limb SD units for each variable, the differences observed at 10 m s^{-1} were $+3.5$, -
395 4.4 , -3.4 and -5.2 SD for T_c , T_{aer} , T_{sw} and F_{avg} , respectively. The differences observed at
396 the top sprinting speeds (10.8 vs. $10.8 [0.6]$ m s^{-1} , Table 1) were similar to those observed
397 at 10 m s^{-1} .

398 Horizontal impulses and peak forces were substantially lower for our amputee vs.
399 intact-limb subjects at every speed (Fig. 1). The vertical forces reported throughout the
400 manuscript are therefore conservative in under-representing resultant ground reaction
401 force differences between our amputee and intact-limb sprint subjects.

402 **Discussion**

403 We set out to determine whether near Olympic-level sprint running performance was
404 occurring via similar or dissimilar physiological and mechanical processes in our
405 amputee and intact-limb subjects. This experimental opportunity was novel, but also
406 limited. Sprint running at near-elite speeds with two prosthetic limbs is without
407 precedent and largely unstudied. However, circumstances limited us to testing the one
408 amputee athlete who has these performance capabilities and availed little directly
409 applicable prior information. These limitations might have led to inconclusive results, an
410 inability to distinguish between prosthetic-related and physiological variability, or
411 conceivably both. Yet, the results of all three of our tests were relatively clear. Our 1st
412 and 2nd hypotheses were primarily physiological comparisons of the metabolic cost of
413 running and sprinting endurance, respectively. Our results indicated that physiological
414 function was largely similar, and virtually identical, respectively, between our amputee
415 and intact-limb subjects. The results from tests of our 3rd hypothesis, regarding running
416 mechanics, indicated substantial dissimilarity while sprinting. Accordingly, we conclude
417 that running for our amputee subject is physiologically similar, but mechanically
418 dissimilar to running with intact limbs.

419 A significant concern prior to testing was the potential difficulty our amputee
420 subject might have performing on the treadmill. A number of factors assured us that this
421 testing apparatus did not hinder his performances in relation to overground running.
422 First, our amputee subject reported being well-habituated to treadmill running from the
423 regular use of his home treadmill. Second, he was able to execute trials of all speeds on
424 our high-speed treadmill in the same manner as our intact-limb subjects did. Third, his

425 sprinting performance during all-out treadmill running at 400-meter race speed matched
426 that reported for overground efforts earlier in the off-season. Fourth, the metabolic and
427 mechanical data acquired during treadmill running tests on our amputee subject were
428 identical or very similar to those we obtained during overground running tests. Because
429 virtually all of the intact-limb metabolic and mechanical data available for the three tests
430 undertaken were acquired on the treadmill, we have presented only the treadmill data
431 here.

432

433 *Hypothesis Test 1: The Metabolic Cost of Running*

434 Because a measurement technique that provides valid estimates for the anaerobic portion
435 and total metabolic energy released during sprinting running has not been developed
436 despite extensive efforts to do so (1, 2, 14, 20, 21, 28), we tested our first hypothesis at
437 the slower speeds required for obtaining valid metabolic data. This was probably not a
438 significant limitation due the nature of the metabolic rate-running speed relationship.
439 Because this relationship is well-described by a linear fit with a near zero-intercept (Fig
440 1A), the metabolic cost of transport, or energy expended per unit distance traveled, varies
441 little across speed for different individuals (10, 22).

442 The results of our 1st hypothesis test evaluating the metabolic cost of running
443 were mixed. Our amputee subject's costs were lower than the means for intact-limb
444 runners, but only slightly so; being 3.8 and 6.7%, and 0.8 and 1.3 SD, respectively, lower
445 than those of elite and sub-elite distance runners (22). However, his values were 17%
446 and 2.7 standard deviations lower than those of the intact-limb 400-meter specialists
447 tested here, and two or more SDs below the means reported for four other groups of sub-

448 elite male sprinters (24, 25, 31, 34) and 1.67 SDs below those of a fifth group (30). We
449 therefore conclude that our amputee's metabolic cost of running is similar to that of
450 intact-limb elite and sub-elite distance runners and lower than that of intact-limb, male
451 sprinters. However, the differences in the respective metabolic costs incurred by our
452 amputee and intact-limb sprint subjects were largely offset by parallel differences in the
453 aerobic power available to them. As a result, the respective values for the aerobic
454 variable most relevant for sprinting performance, the velocity at $\dot{V}O_2 \text{ max}$, or Spd_{aer} (7,
455 36), were nearly identical (5.0 vs. 4.9 [0.02] m s^{-1}).

456 We also note that the metabolic transport cost values that are available for several
457 notable world-class endurance runners with fully intact limbs are lower than those of our
458 amputee subject. These include two World Cross-country champions: John Ngugi (29)
459 and Zersenay Tadese (19). Finally, the only other metabolic measurements for a
460 bilateral, transtibial amputee runner (3) that we are aware of, that from a 5-hour
461 marathoner, indicated that his metabolic transport costs were 19% greater than our
462 amputee sprinter (Fig. 2B) and similar to non-athletes with intact limbs (22). Without
463 additional data from bilateral, transtibial amputees, a definitive conclusion regarding
464 whether passive-elastic, lower-limb prostheses economize their running is not possible.

465

466 *Hypothesis Test 2: Sprinting Endurance*

467 The results of our 2nd hypothesis test indicated that our amputee subject's sprinting
468 endurance is virtually identical to that of intact-limb runners. Although his atypically fast
469 closing speeds in races and carbon fiber lower limbs led us to expect a fatigue resistance
470 that would translate into an appreciably greater ability to maintain speed, particularly for

471 those trials lasting as long as 200 and 400 meter track events, this was not the case.
472 Rather, we found that our amputee subject's all-out sprinting speeds decreased in relation
473 to trial duration in the same manner that the speeds of intact-limb runners did (eq. 1).
474 The speeds we predicted for our amputee subject using intact-limb norms (7, 36) matched
475 those he actually maintained to within 2.2 [0.6]% for six all-out trials between 2 and 90 s
476 in duration.

477 These results indicate that when the start and acceleration portion of overground
478 sprint racing is removed, as it was by our constant-speed treadmill trials, the abilities of
479 our amputee and intact-limb sprinters to maintain their sprinting speeds did not differ.
480 Relatively poor starts and accelerations are not surprising for an athlete who lacks ankles,
481 ankle extensor muscles and feet to transmit muscular force and power distally during the
482 push-off phase (17) of each accelerating step. The slower starts and accelerations of our
483 amputee subject during overground sprint races are likely responsible for his superior
484 performances in longer vs. shorter sprint races relative to athletes with intact legs. Poorer
485 starts and accelerations also inevitably affect pacing by selectively compromising speed
486 in only one portion of a sprint race.

487

488 *Hypothesis Test 3: Running Mechanics*

489 The results of our 3rd test indicated substantial functional dissimilarity between our
490 amputee and intact-limb subjects in running mechanics. The degree of dissimilarity was
491 almost completely speed-dependent; being largely absent at slow speeds, moderate at
492 intermediate speeds, and substantial at the fastest speeds (Fig. 1 and Fig. 4). Because
493 running performance at all three Olympic sprint distances is determined primarily by the

494 top sprinting speed of the athlete (7, 36), the mechanics of greatest functional relevance
495 are those we observed at the fastest speeds.

496 The speed limits of our amputee and intact-limb subjects were similarly imposed
497 by their gait mechanics. All reached their absolute limit, or top speed, when their foot-
498 ground contact times and vertical impulses decreased to the minimum values necessary to
499 provide sufficient aerial time to reposition the swing leg for the next step (35). Thus, at
500 top speed, our amputee and intact-limb subjects all reached likely maximums for the
501 ground forces they could apply, and minimums for the time in which they could
502 reposition their swing legs (Fig. 4, Table 1).

503 Although the top speeds attained by our amputee and intact-limb subjects were
504 similar, their aerial times, swing times, and weight-specific ground reaction forces were
505 all markedly dissimilar. Given the extent and nature of the mechanical dissimilarities
506 observed, these differences seem largely attributable to running with carbon-fiber, lower-
507 limb prostheses vs. intact limbs. We have previously noted that minimum swing times
508 differ little at the top speeds of intact-limb runners of different sprinting abilities; for
509 example, varying by only 0.03 s between runners with top speeds of 11.1 vs. 6.2 m s⁻¹
510 (35). However, our amputee subject was able to reposition his swing limbs almost 0.10 s
511 more rapidly than the mean we previously reported (0.373 [0.03] s), and 0.075 s, 21%
512 and 4.0 SD more rapidly than the intact-limb sprinters tested here (Table 1). The
513 combined mass of our amputee subject's residual limb distal to the knee and that of the
514 Cheetah prosthesis is roughly half the mass of an intact calf and foot (4). Reducing the
515 mass of the distal segment of the limb by nearly two-fold apparently allows the swing
516 limb to be repositioned appreciably more rapidly.

517 With his relatively shorter aerial (-34.4%) and swing times, and longer contact
518 times (+14.2%), our amputee subject was able to attain the same top sprinting speeds as
519 our intact-limb subjects with stance-averaged vertical forces that were 22%, 0.46 body
520 weights and 3.6 SD units lower than those of intact-limb sprinters. These large force
521 differences at top speed also seem attributable to sprinting with lower-limb prostheses
522 rather than intact limbs. Transtibial amputees lack the uniarticular, biarticular and
523 polyarticular muscles that cross one or more of the metatarsal-phalangeal, ankle and knee
524 joints of an intact limb. The specific absence of bi- and polyarticular muscles disallows
525 the transfer of muscular force possible from the knee to the ankle and foot of an intact
526 limb (17). The lesser ground reaction forces observed in the prosthetic vs. intact-limbs of
527 unilateral, transtibial amputees (11) provide direct evidence of a force impairment.

528

529 *Conclusions*

530 Perhaps our most striking result, given the interdependence of locomotor physiology and
531 mechanics (18, 26, 27, 32), is that our amputee subject could be simultaneously similar to
532 intact-limb runners physiologically, but dissimilar mechanically. Physiological similarity
533 is most likely explained by the reliance of both transtibial amputee and intact-limb
534 runners on the large groups of extensor muscles that act across the hip and knee joints.
535 There was no *a priori* reason for us to expect that the lower limb prostheses of our
536 amputee subject would alter either the metabolic cost of force production (18, 27) or
537 fatigability (7, 8, 38) at the tissue or fiber level in these skeletal muscles. However,
538 running with lower-limb prostheses might have substantially altered the nature of their
539 activity. Our finding that the whole-body manifestations of these respective skeletal

540 muscle properties: running economy and sprinting endurance, were largely similar
541 suggests that the prostheses, to some extent, approximate the spring-like mechanical
542 function that characterizes intact lower limbs. Although the provision of spring-like
543 behavior from limb segments that lack skeletal muscle is not the norm for human limbs,
544 this phenomenon has biological precedent. Through evolution, the distal limb segments
545 of horses, antelope and ostriches have lost skeletal muscle and come to rely solely on
546 passive-elastic tendons and ligaments to provide spring-like function.

547 The mechanical dissimilarities observed highlight the functional trade-offs that
548 are perhaps inevitable for artificial vs. biological limbs. The aerial and swing time
549 reductions observed for our amputee subject support the classic, but largely untested
550 arguments of functional morphologists. For more than a half-century, these scientists
551 have postulated that light, slender limbs have evolved in cursorial animals to enhance
552 speed by reducing the time required to reposition the limbs (13, 15, 16). However, the
553 meager ground reaction forces observed during amputee running here and elsewhere (4,
554 11) identify what may be a critical limitation for speed (35). Legs must perform different
555 functions during the stance and swing of the stride, as well as during the start,
556 acceleration and relatively constant-speed phases of sprint running. Collectively, our
557 results underscore the difficulty of providing these multiple mechanical functions with a
558 single, relatively simple prosthetic design, and the formidable challenges involved in
559 engineering limbs that fully mimic those produced by nature.

560

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562

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706 **Figure Captions**

707

708 Fig. 1. Tracings from video images of our amputee subject during the contact, aerial and
709 swing phases of a stride while sprinting on a treadmill at 10.5 m s^{-1} (A). The vertical (B)
710 and horizontal ground reaction forces, normalized to body weight (C), vs. time for our
711 amputee and an intact-limb subject at a treadmill speed of 10.5 m s^{-1} . The black
712 (amputee sprinter) and gray lines (intact-limb sprinter) illustrate the ground reaction force
713 traces of the right (solid) and left limbs (dotted) of the two subjects. Differences in the
714 duration of the aerial, swing and total stride times (shorter) for our amputee vs. intact-
715 limb subject correspond to the dashed line extensions of the respective lines at the bottom
716 of panel A; differences in the duration of the contact time (longer) for our amputee vs.
717 intact-limb subject correspond to the solid line extensions.

718

719 Fig. 2. Mass-specific rates of oxygen uptake vs. treadmill running speed (A) for our
720 amputee sprint subject, and runners with intact-limbs: elite distance runners, sub-elite
721 distance runners, 400-meter specialists and World Cross-country champion, Z. Tadese.
722 The mass-specific oxygen uptake expressed per unit distance traveled (Running
723 Economy, panel B) for our amputee sprint subject (v), elite distance runners (iii), sub-
724 elite distance runners (iv), and 400-meter specialists (ii). The economy of our amputee
725 subject was within two standard deviations (dashed lines) of the means of the elite and
726 sub-elite groups, but more than two standard deviations below the mean of the 400-meter
727 specialists. For comparison, the economy of an endurance-trained bilateral, transtibial
728 amputee (i) and two World Cross-country champions, J. Ngugi (vi) and Z. Tadese (vii)
729 are also shown. Data sources: (i) Brown et al. (3), (iii and iv) Morgan et al. (22), (vi)

730 Saltin et al. (29), and (vii) Lucia et al. (19). [Note: All values reported are from treadmill
731 running at an inclination of 0% except the Lucia et al. value for ZT which was collected
732 at a 1% grade].

733

734 Fig. 3. All-out running speed decreased exponentially in relation to trial duration for our
735 amputee and three intact-limb runners of different event specializations (Panel A). When
736 the speeds of the four runners' all-out trials are expressed as a fraction of their anaerobic
737 speed reserves ($Spd_{ts} - Spd_{acr}$; Relative Speed, panel B), the fraction maintained at any
738 duration was essentially identical for our amputee and intact-limb subjects. The speeds
739 our amputee sprinter maintained for trials of all durations closely matched those predicted
740 from intact-limb norms (eq. 1; solid lines panels B and C) and fell well within twice the
741 standard error of estimate (dashed lines, panel C). One intact-limb subject was a sprinter
742 (downward pointing closed triangle).

743

744 Fig. 4. Foot-ground contact time (A), aerial time (B), swing time (C) and stance-
745 averaged vertical force (D) vs. speed during constant-speed treadmill running trials for
746 our amputee and intact-limb sprint subjects (n=4) with similar top sprinting speeds. At
747 the fastest speeds, our amputee subject had longer periods of foot-ground contact, shorter
748 aerial and swing times and lower stance averaged vertical forces. The gray shading
749 within the solid lines illustrates intact-limb means ± 2 SDs. All of the mechanical
750 variables illustrated differed between our amputee and intact-limb subjects at the fastest
751 two speeds.

Tables

Table 1. Sprinting mechanics

Measure	10.0 m s ⁻¹	Top Speed
<i>Time of Contact (s)</i>		
Intact Limb Sprinters	0.099 [0.004]	0.094 [0.008]
Amputee Sprinter	0.113	0.107
Difference (× SD)	+ 3.5	+ 1.7
Percent Difference (%)	+ 14.1	+ 14.2
<i>Swing Time (s)</i>		
Intact Limb Sprinters	0.371 [0.022]	0.359 [0.019]
Amputee Sprinter	0.293	0.284
Difference (× SD)	- 3.5	- 4.0
Percent Difference (%)	- 21.0	- 21.0
<i>Aerial Time (s)</i>		
Intact Limb Sprinters	0.140 [0.011]	0.136 [0.011]
Amputee Sprinter	0.092	0.090
Difference (× SD)	- 4.4	- 4.3
Percent Difference (%)	- 34.5	- 34.4
<i>Stance Average Vertical Force (× W_b)</i>		
Intact Limb Sprinters	2.32 [0.10]	2.30 [0.13]
Amputee Sprinter	1.79	1.84
Difference (× SD)	- 5.2	- 3.6
Percent Difference (%)	- 22.9	- 21.7
<i>Peak Vertical Force (× W_b)</i>		
Intact Limb Sprinters	3.72 [0.31]	3.93 [0.51]
Amputee Sprinter	3.24	3.38
Difference (× SD)	- 1.5	- 1.1
Percent Difference (%)	- 12.8	- 14.0

Data are means and [SD] for n = 4 intact-limb sprinters. Top speeds of our amputee and intact-limb sprinters were 10.8 and 10.8 [0.6] m s⁻¹, respectively. [Top Speed: stride length = 4.22 vs. 4.86 [0.27] m; stride frequency = 2.56 vs. 2.21 [0.08] Hz; 10.0 m s⁻¹: stride length = 4.06 vs. 4.73 [0.19] m; stride frequency = 2.46 vs. 2.11 [0.089] Hz].

Figure 1

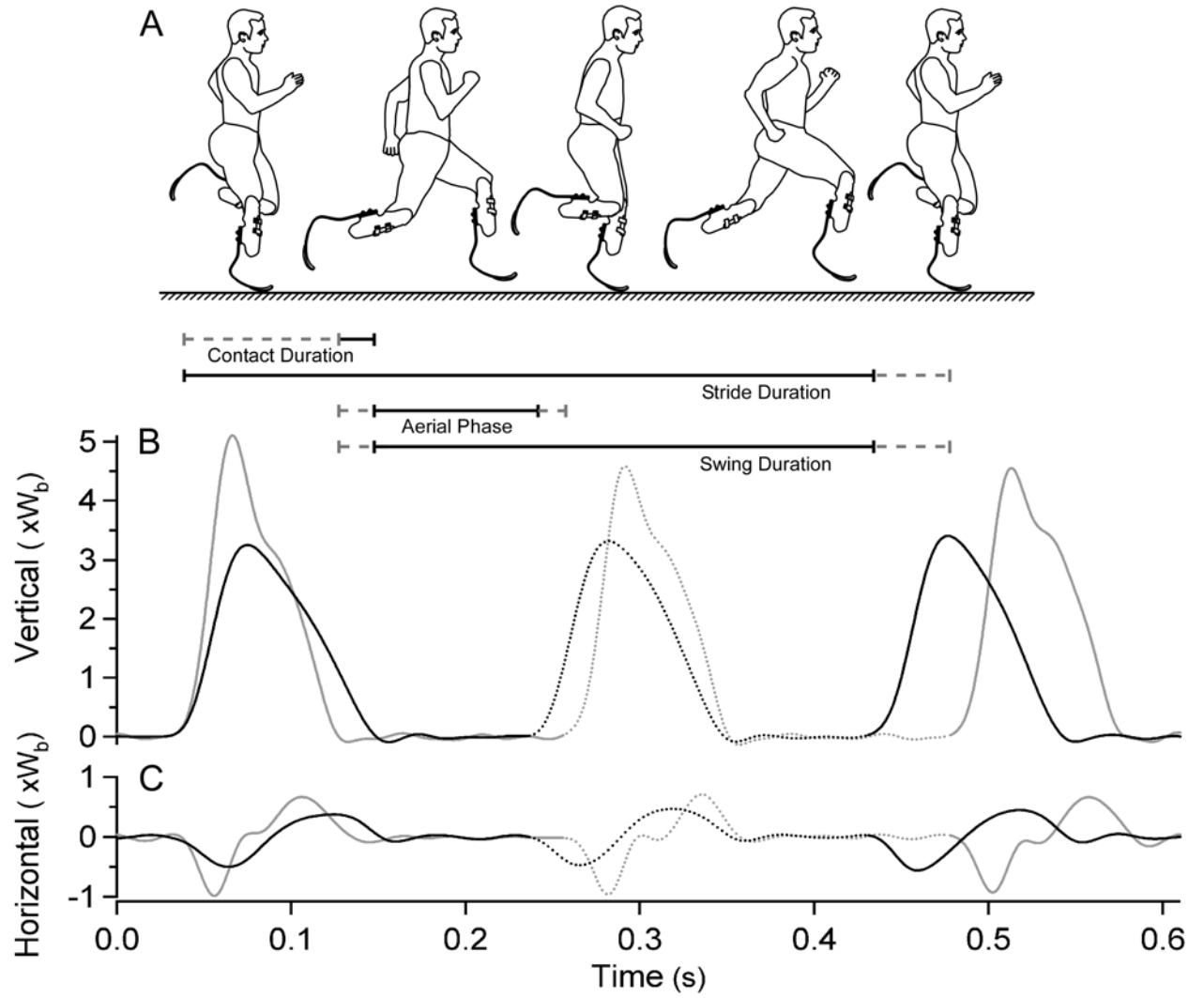


Figure 2

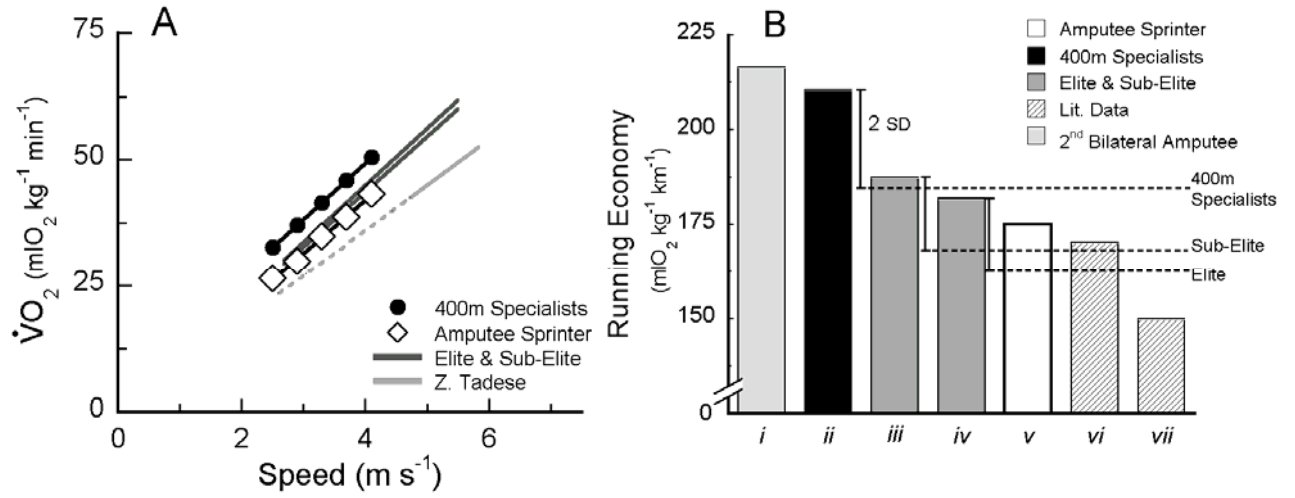


Figure 3

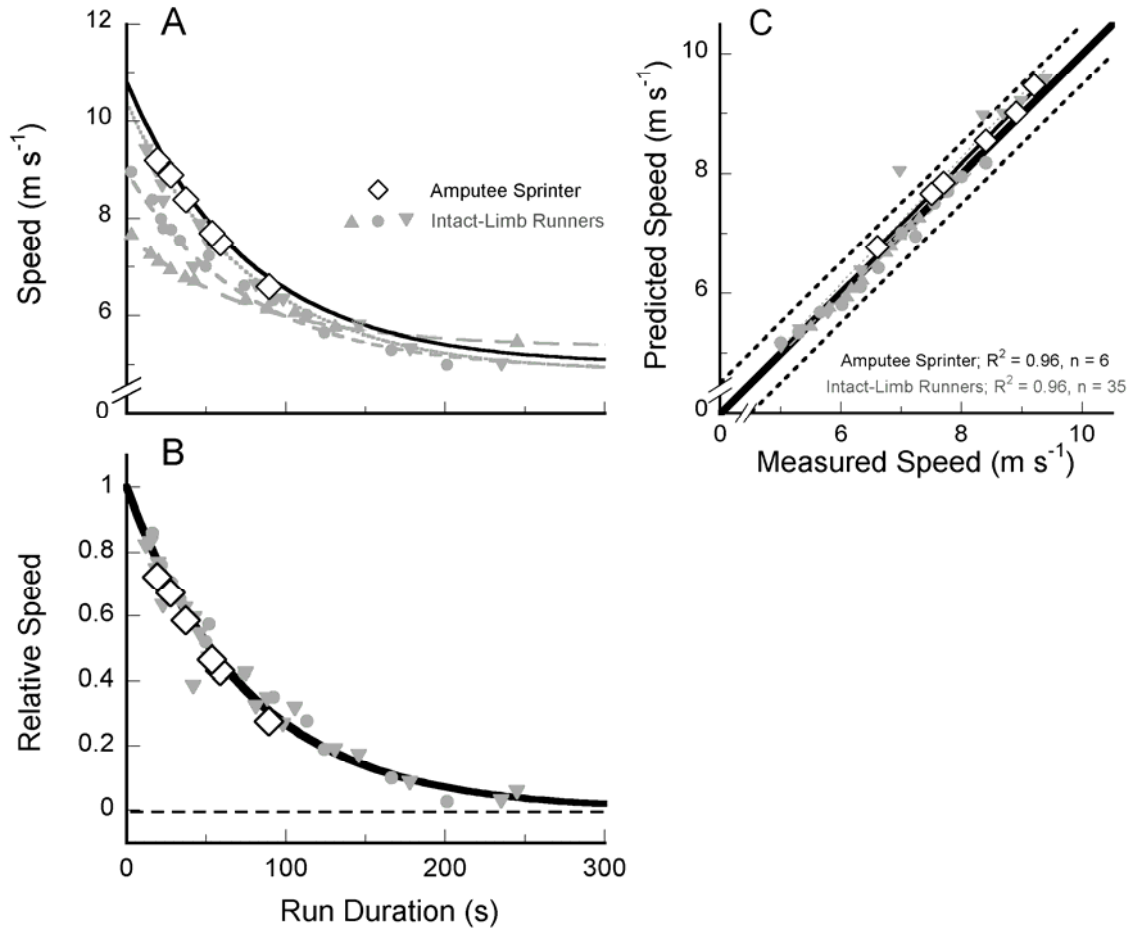


Figure 4

