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The fastest runner on artificial legs:

different limbs, similar function?

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Abstract

The recent competitive successes of a bilateral, transtibial amputee sprint runner who races with modern running prostheses has triggered an international controversy regarding the relative function provided by his artificial limbs. Here, we conducted three tests of functional similarity between this amputee sprinter and competitive male runners with intact limbs: the metabolic cost of running, sprinting endurance, and running mechanics. Metabolic and mechanical data, respectively, were acquired via indirect calorimetry and ground reaction force measurement during constant-speed, level treadmill running. First, we found that the mean gross metabolic cost of transport of our amputee sprint subject (174.9 ml O_2 kg^{-1} km^{-1}; speeds: 2.5 to 4.1 m s^{-1}) was only 3.8% lower than mean values for intact-limb elite distance runners and 6.7% lower than for sub-elite distance runners, but 17% lower than for intact-limb 400-meter specialists (210.6 [13.2; SD] ml O_2 kg^{-1} km^{-1}). Second, the speeds our amputee sprinter maintained for six all-out, constant-speed trials to failure (speeds: 6.6-10.8 m s^{-1}; durations: 2-90 s) were within 2.2 [0.6]% of those predicted for intact-limb sprinters. Third, at sprinting speeds of 8.0, 9.0 and 10.0 m s^{-1}, our amputee subject had longer foot-ground contact times (+14.7 [4.2]%), shorter aerial (-26.4 [9.9]%) and swing times (-15.2 [6.9]%), and lower stance-averaged vertical forces (-19.3 [3.1]%) than intact-limb sprinters (top speeds = 10.8 vs.10.8 [0.6] m s^{-1}). We conclude that running on modern, lower-limb sprinting prostheses appears to be physiologically similar, but mechanically different than running with intact limbs.

Introduction

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

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

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

Methods

Experimental Design

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

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

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

$$Spd_t = Spd_{aer} + (Spd_{ts} - Spd_{aer}) \cdot e^{(-k \cdot t)} \qquad \text{eq. 1}$$

where Spd_t is the speed maintained for an all-out sprint of duration t, Spd_{aer}, also known as the velocity at $\dot{V}O_2$ max (10), is the minimum running speed eliciting maximal aerobic power, Spd_{ts} is the maximum or top sprinting speed that can be attained for eight consecutive steps (~ 2 s), *e* is the base of the natural logarithm, and k is an exponential constant for running (= 0.013 s^{-1}) that describes the decrements in speed that occur with increments in the duration of all-out running.

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

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

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

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

Subject Characteristics

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

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

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

Rates of Oxygen Uptake (ml O_2 kg^{-1} min^{-1}): Rates of oxygen uptake were averaged over the last two min of each steady-state running trial to obtain the value for each trial speed. Measurements from the computerized and Douglas bag methods agreed to within an average of 1.3 [1.2]%. The values reported are those acquired from the computerized system. Both amputee and intact-limb 400 meter specialist measures were taken at speeds between 2.5 and 4.5 m s^{-1}.

Maximal Aerobic Power (ml O_2 kg^{-1} min^{-1}) *& Spd_{aer}* (m s^{-1}): The maximal rate of aerobic metabolism was the highest single minute value measured during the final all-out bout of the treadmill test. The minimum speed eliciting maximal aerobic power (Spd_{aer}) was determined from the measured aerobic maximum and the $\dot{V}O_2$-speed regression relationship for each subject. The latter was formulated using steady-state $\dot{V}O_2$ values from only those trials eliciting < 90% of the subject's maximal aerobic power.

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

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

Hypothesis Test II. Sprinting Endurance

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

Hypothesis Test III. Sprinting Mechanics

Subjects tested to evaluate our 3rd hypothesis completed progressive, discontinuous, horizontal treadmill tests to assess their running mechanics and determine their 8-step top sprint speed as previously described (35). Tests were completed on a custom, high-speed force treadmill (AMTI, Watertown, MA). The treadmill has a belt width of 0.610 m, is powered by a Baldor 23H series motor and the treadmill bed (0.686 x 2.083 m) serves as a strain gage-based force platform. Subjects were strapped into a harness secured overhead and slackened sufficiently to become taut only in the event of a fall. Each trial was initiated by the subject lowering himself from the handrails onto the treadmill belt after it had fully accelerated to the desired speed. Our amputee and control subjects were all generally able to transition quickly from standing to running without losing their balance. In the few instances in which these transitions were not made rapidly, subjects were immediately instructed to dismount the treadmill, recover, and prepare for another attempt. These treadmill tests started at speeds of 2.0 to 2.5 m s^{-1}. Speed increments ranged from 0.5 to 1.0 m s^{-1} through roughly 80% of the subject's estimated top speed after which speed increments were reduced to 0.1 to 0.4 m s^{-1}. The magnitude of each increment was selected in accordance with subject performance on the previous trial and their verbal feedback regarding difficulty. All subjects completed trials at 3.0, 4.0, 5.0, 6.0, 7.0, 8.0, 9.0 and 10.0 m s^{-1} except one of four intact-limb sprinters. Slower and intermediate speed trials lasted from 10 to 30 s, while faster speed trials lasted from 2 to 10 s. Subjects were encouraged to take as much rest as needed for full recovery between trials.

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

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

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

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

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

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

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

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

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

Results

Hypothesis Test I. Metabolic Energy Expenditure during Running

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

The gross metabolic cost of transport for our amputee subject averaged 174.9 [2.2] ml O_2 kg^{-1} km^{-1} (Fig. 2B) and was virtually constant across the five speeds measured. Our amputee sprint subject's gross metabolic cost of transport was 3.8% lower than the mean for elite male distance runners (181.9 [9.1] ml O_2 kg^{-1} km^{-1}, (22)), 6.7% lower than the mean for sub-elite distance runners (187.5 [9.7] ml O_2 kg^{-1} km^{-1}, (22)) and 17.0% lower than our 400-meter specialists (210.6 [13.2] ml O_2 kg^{-1} km^{-1}). Expressed in terms of the between-subject standard deviations of the respective groups, the mean transport cost of our amputee sprint subject was, respectively, -0.8, -1.3 and -2.7 X SD lower.

The maximal rate of aerobic metabolism of our amputee subject was 7.6% lower than that of our intact-limb 400 meter subjects (52.7 vs. 57.0 [3.4] ml O_2 kg^{-1} min^{-1}; n=3). However, he attained essentially the same running speed at VO_{2max} (Spd_{aer}) as our intact-limb 400 meter specialists (5.0 vs. 4.9 [0.02] m s^{-1}) because his metabolic cost of running was relatively lower.

Hypothesis Test II. Sprinting Endurance

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

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

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

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

Hypothesis Test III. Sprinting Mechanics

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

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

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

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

Discussion

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

A significant concern prior to testing was the potential difficulty our amputee subject might have performing on the treadmill. A number of factors assured us that this testing apparatus did not hinder his performances in relation to overground running. First, our amputee subject reported being well-habituated to treadmill running from the regular use of his home treadmill. Second, he was able to execute trials of all speeds on our high-speed treadmill in the same manner as our intact-limb subjects did. Third, his sprinting performance during all-out treadmill running at 400-meter race speed matched that reported for overground efforts earlier in the off-season. Fourth, the metabolic and mechanical data acquired during treadmill running tests on our amputee subject were identical or very similar to those we obtained during overground running tests. Because virtually all of the intact-limb metabolic and mechanical data available for the three tests undertaken were acquired on the treadmill, we have presented only the treadmill data here.

Hypothesis Test 1: The Metabolic Cost of Running

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

The results of our 1st hypothesis test evaluating the metabolic cost of running were mixed. Our amputee subject's costs were lower than the means for intact-limb runners, but only slightly so; being 3.8 and 6.7%, and 0.8 and 1.3 SD, respectively, lower than those of elite and sub-elite distance runners (22). However, his values were 17% and 2.7 standard deviations lower than those of the intact-limb 400-meter specialists tested here, and two or more SDs below the means reported for four other groups of sub-elite male sprinters (24, 25, 31, 34) and 1.67 SDs below those of a fifth group (30). We therefore conclude that our amputee's metabolic cost of running is similar to that of intact-limb elite and sub-elite distance runners and lower than that of intact-limb, male sprinters. However, the differences in the respective metabolic costs incurred by our amputee and intact-limb sprint subjects were largely offset by parallel differences in the aerobic power available to them. As a result, the respective values for the aerobic variable most relevant for sprinting performance, the velocity at $\dot{V}O_2$ max, or Spd_{aer} (7, 36), were nearly identical (5.0 vs. 4.9 [0.02] m s^{-1}).

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

Hypothesis Test 2: Sprinting Endurance

The results of our 2nd hypothesis test indicated that our amputee subject's sprinting endurance is virtually identical to that of intact-limb runners. Although his atypically fast closing speeds in races and carbon fiber lower limbs led us to expect a fatigue resistance that would translate into an appreciably greater ability to maintain speed, particularly for those trials lasting as long as 200 and 400 meter track events, this was not the case. Rather, we found that our amputee subject's all-out sprinting speeds decreased in relation to trial duration in the same manner that the speeds of intact-limb runners did (eq. 1). The speeds we predicted for our amputee subject using intact-limb norms (7, 36) matched those he actually maintained to within 2.2 [0.6]% for six all-out trials between 2 and 90 s in duration.

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

Hypothesis Test 3: Running Mechanics

The results of our 3rd test indicated substantial functional dissimilarity between our amputee and intact-limb subjects in running mechanics. The degree of dissimilarity was almost completely speed-dependent; being largely absent at slow speeds, moderate at intermediate speeds, and substantial at the fastest speeds (Fig. 1 and Fig. 4). Because running performance at all three Olympic sprint distances is determined primarily by the top sprinting speed of the athlete (7, 36), the mechanics of greatest functional relevance are those we observed at the fastest speeds.

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

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

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

Conclusions

Perhaps our most striking result, given the interdependence of locomotor physiology and mechanics (18, 26, 27, 32), is that our amputee subject could be simultaneously similar to intact-limb runners physiologically, but dissimilar mechanically. Physiological similarity is most likely explained by the reliance of both transtibial amputee and intact-limb runners on the large groups of extensor muscles that act across the hip and knee joints. There was no *a priori* reason for us to expect that the lower limb prostheses of our amputee subject would alter either the metabolic cost of force production (18, 27) or fatigability (7, 8, 38) at the tissue or fiber level in these skeletal muscles. However, running with lower-limb prostheses might have substantially altered the nature of their activity. Our finding that the whole-body manifestations of these respective skeletal muscle properties: running economy and sprinting endurance, were largely similar suggests that the prostheses, to some extent, approximate the spring-like mechanical function that characterizes intact lower limbs. Although the provision of spring-like behavior from limb segments that lack skeletal muscle is not the norm for human limbs, this phenomenon has biological precedent. Through evolution, the distal limb segments of horses, antelope and ostriches have lost skeletal muscle and come to rely solely on passive-elastic tendons and ligaments to provide spring-like function.

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

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References

1. **Bangsbo J.** Is the O2 deficit an accurate quantitative measure of the anaerobic energy production during intense exercise? *J Appl Physiol* 73: 1207-1209, 1992.

2. **Bangsbo J.** Quantification of anaerobic energy production during intense exercise. *Med Sci Sports Exerc* 30: 47-52, 1998.

3. **Brown MB, Millard-Stafford ML, Allison AR.** Running-specific prostheses permit energy costs similar to non-amputees. *Med Sci Sports Exerc* 41:1080-1087, 2009.

4. **Bruggeman GP, Arampatzis A, Emrich F, Potthast W.** Biomechanics of double transtibial amputee sprinting using dedicated sprint prostheses. *Sports Technol* 4-5: 220-227, 2009.

5. **Buckley JG.** Sprint kinematics of athletes with lower-limb amputations. *Arch Phys Med Rehab* 80: 501-508, 1999.

6. **Buckley JG.** Biomechanical adaptations of transtibial amputee sprinting in athletes using dedicated prostheses. *Clin Biomech* 15: 352-358, 2000.

7. **Bundle MW, Hoyt RW, Weyand PG.** High speed running performance: a new approach to assessment and prediction. *J Appl Physiol* 95: 1955-1962, 2003.

8. **Bundle MW, Ernst CL, Bellizzi MJ, Wright S, Weyand PG.** A metabolic basis for impaired muscle force production and neuromuscular compensation during sprint cycling. *Am J Physiol Regul Integr Comp Physiol* 291: R1457-1464, 2006.

9. **Czerniecki JM, Gitter A, Munro C.** Joint moment and muscle power output characteristics of below knee amputees during running: the influence of energy storing prosthestic feet. *J Biomech* 24: 63-75, 1991.

10. **Daniels J, Daniels N.** Running economy of elite male and female runners. *Med Sci Sports Exerc* 24: 483-489, 1992.

11. **Engsberg JR, Lee AG, Tedford KG, Harder JA.** Normative ground reaction force data for able-bodied and trans-tibial amputee children during running. *Prosth Orthot Int* 17: 83-89, 1993.

12. **Farley CT and Ferris DP.** Biomechanics of walking and running: from center of mass movement to muscle action. *Exerc Sport Sci Rev*, 26:253-285, 1998.

13. **Gray J.** *How animals move.* Edinburgh: Pelican Books, 1959.

14. **Hermansen L, Medbo JI.** The relative significance of aerobic and anaerobic processes during maximal exercise of short duration. In: *Physiological Chemistry of Training and Detraining Medical Sports Science*, edited by Marconnet P, Portmans J, Hermansen L. Basel: Krager, 1984, vol. 17, pp. 56-67.

15. **Hildebrand M.** How animals run. *Sci Am* 5: 148-157, 1960.

16. **Howell AB.** *Speed in animals.* Chicago, Chicago University Press, 1944.

17. **Jacobs R, Bobbert MF, van Ingen Schenau GJ.** Mechanical output from individual muscles during explosive leg extensions: the role of biarticular muscles. *J Biomech* 29: 513-23, 1996.

18. **Kram R, Taylor CR.** Energetics of running: a new perspective. *Nature* 346: 2265-2267, 1990.

19. **Lucia A, Oliván J, Bravo J, Gonzalez-Freire M, Foster C.** The key to top-level endurance running performance: a unique example. *Br J Sports Med* 42:172-174, 2008.

20. **Margaria R, Cerretelli P, Mangili F.** Balance and kinetics of anaerobic energy release during strenuous exercise in man. *J Appl Physiol* 19: 623-628, 1964.

21. **Medbø JI, Mohn AC, Tabata I, Bahr R, Vaage O, Sejersted OM.** Anaerobic capacity determined by maximal accumulated O2 deficit. *J Appl Physiol* 64: 50-60, 1988.

22. **Morgan DW, Bransford DR, Costill DL, Daniels JT, Howley ET, Krahenbuhl GS.** Variation in the aerobic demand of running among trained and untrained subjects. *Med Sci Sports Exerc* 27: 404-409, 1995.

23. **Nummela A, Rusko H, Mero A.** EMG activities and ground reaction forces during fatigued and nonfatigued sprinting. *Med Sci Sports Exerc* 26:605-609, 1994.

24. **Olesen HL.** Accumulated oxygen deficit increases with inclination of uphill running. *J Appl Physiol* 73: 1130-1134, 1992.

25. **Olesen HL, Raabo E, Bangsbo J, Secher NH.** Maximal oxygen deficit of sprint and middle distance runners. *Eur J Appl Physiol Occup Physiol* 69: 140-146, 1994.

26. **Roberts TJ, R. Kram R, Weyand PG, Taylor CR.** Energetics of bipedal running. I. Metabolic cost of generating force. *J Exp Biol* 201: 2745-2751, 1998.

27. **Roberts TJ, Chen MS, Taylor CR.** Energetics of bipedal running. II. Limb design and running mechanics. *J Exp Biol* 201: 2753-2762, 1998.

28. **Saltin B.** Anaerobic capacity. Past, Present, Prospective. In: *Procedings of the 7th International Biochemistry of Exercise Symposium*, edited by: Taylor AW, Champaign IL, Human Kinetics, 1990, pp. 387-412.

29. **Saltin B, Larsen H, Terrados N, Bangsbo J, Bak T, Kim CK, Svedenhag J, Rolf CJ.** Aerobic exercise capacity at sea level and at altitude in Kenyan boys, junior and senior runners compared with Scandinavian runners. *Scand J Med Sci Sports*. 5: 209-21, 1995.

30. **Spencer MR, Gastin PB.** Energy system contribution during 200- to 1500-m running in highly trained athletes. *Med Sci Sports Exerc* 33: 157-162, 2001.

31. **Svedenhag J, Sjödin B.** Maximal and submaximal oxygen uptakes and blood lactate levels in elite middle- and long-distance runners. *Int J Sports Med* 5:255-61, 1984.

32. **Taylor CR.** Relating mechanics and energetics during exercise. In: *Adv Vet Sci Comp Med* edited by: Jones JH, 38A: 181-215, 1994.

33. **van Ingen Schenau, GJ, Cavanagh PR.** Power equations in endurance sports. *J Biomech* 23: 865-881, 1990.

34. **Weyand PG, Cureton KJ, Conley DS, Sloniger MA, Liu YL.** Peak oxygen deficit predicts sprint and middle-distance track performance. *Med Sci Sports Exerc* 26: 1174-80, 1994.

35. **Weyand PG, Sternlight DB, Bellizzi MJ, Wright S.** Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J Appl Physiol* 81: 1991-1999, 2000.

36. **Weyand PG, Bundle MW.** Energetics of high-speed running: integrating classical theory and contemporary observations. *Am J Physiol Regul Integr Comp Physiol* 288: R956-R965, 2005.

37. **Weyand PG, Davis JA.** Running performance has a structural basis. *J Exp Biol* 208, 2625-2631, 2005.

38. **Weyand PG, Lin JE, Bundle MW.** Sprint performance duration relationships are set by the fractional duration of external force application. *Am J Physiol Regul Integr Comp Physiol* 290:R758-R765, 2006.

39. **Williams KR, Cavanagh PR.** A model for the calculation of mechanical power during distance running. *J Biomech* 16:115-128, 1983.

Figure Captions

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

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

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

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

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

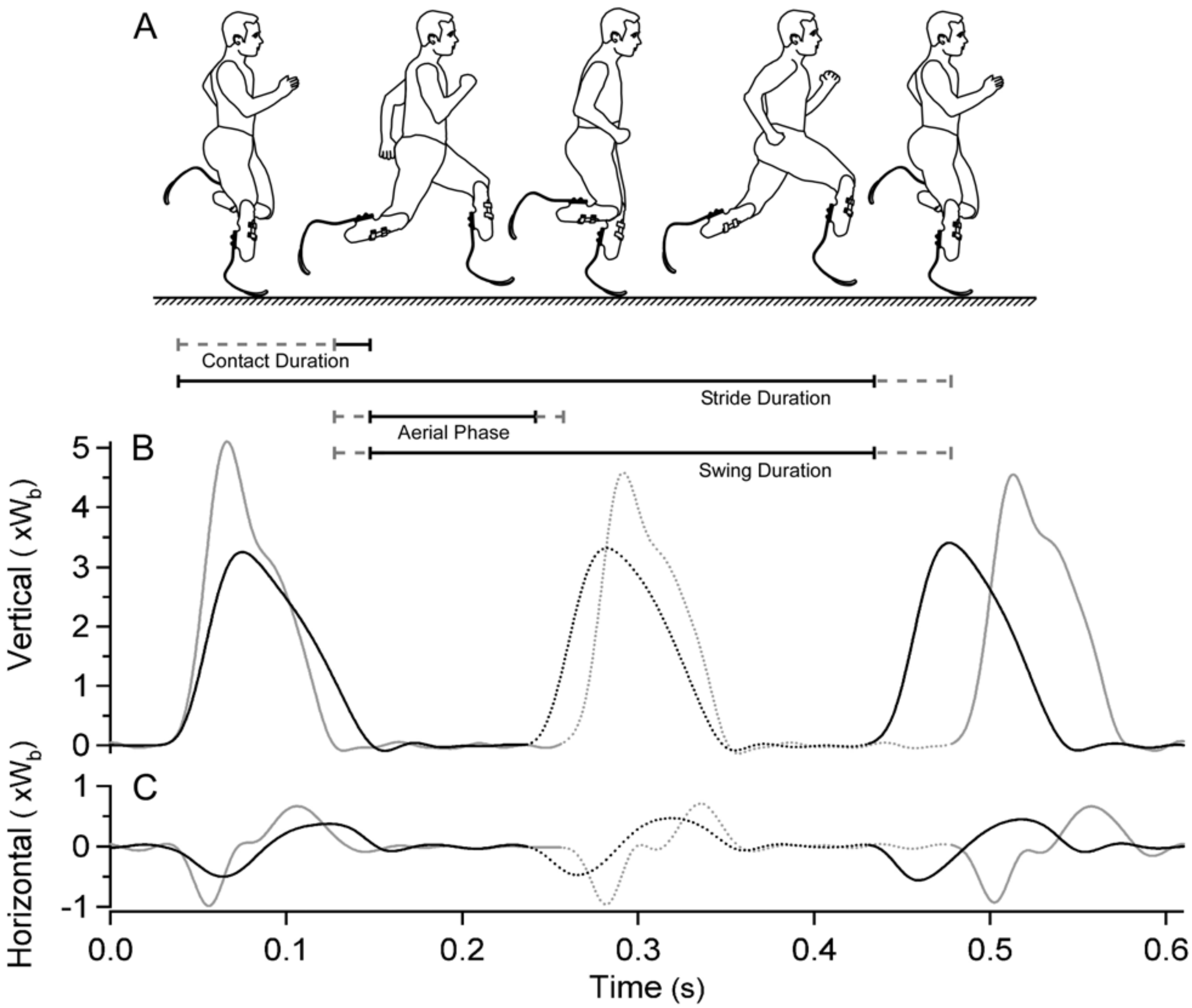
Tables

Table 1. Sprinting mechanics

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



A
Contact Duration
Stride Duration
Aerial Phase
Swing Duration
B
C
Vertical (xW_b)
Horizontal (xW_b)
Time (s)

Figure 2

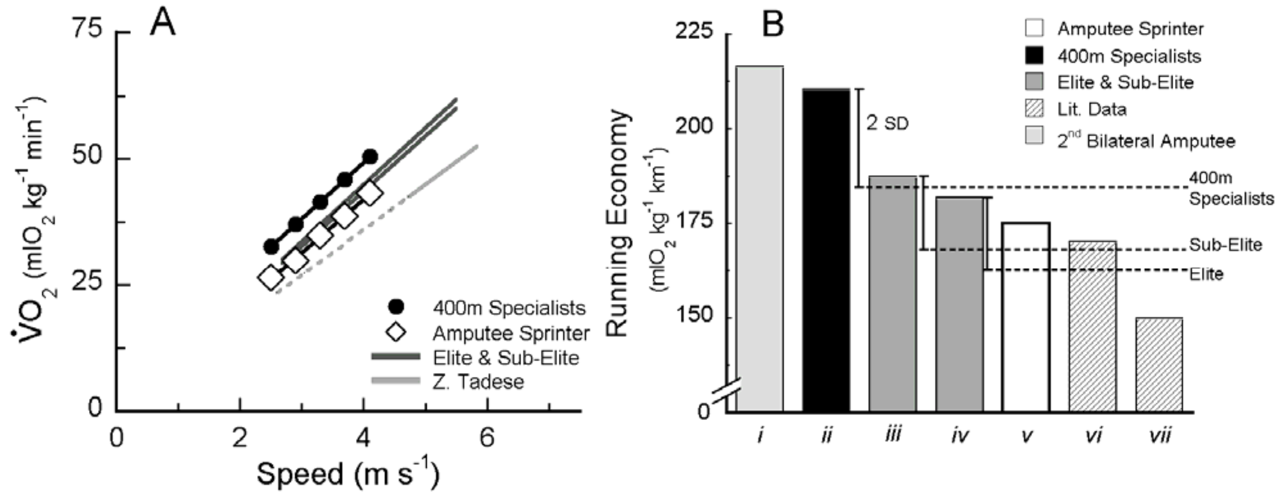
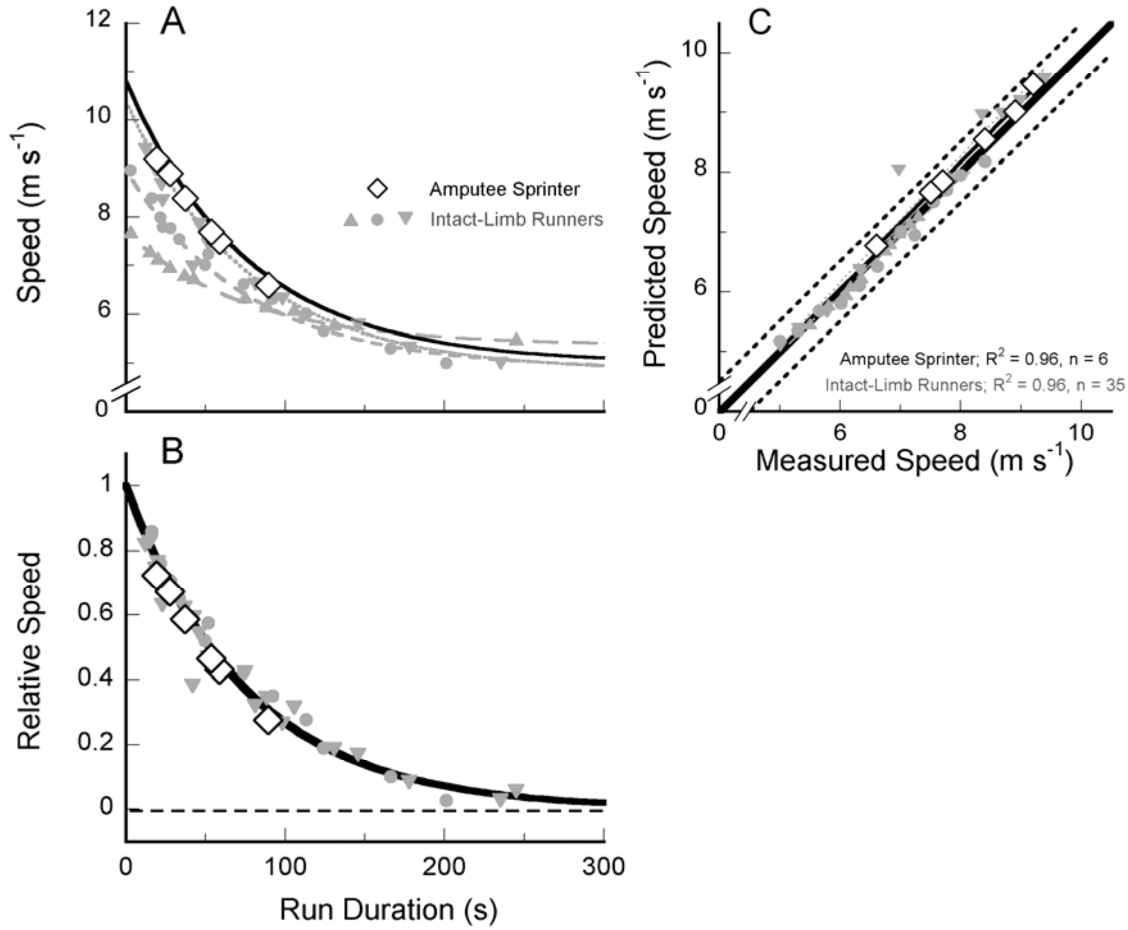
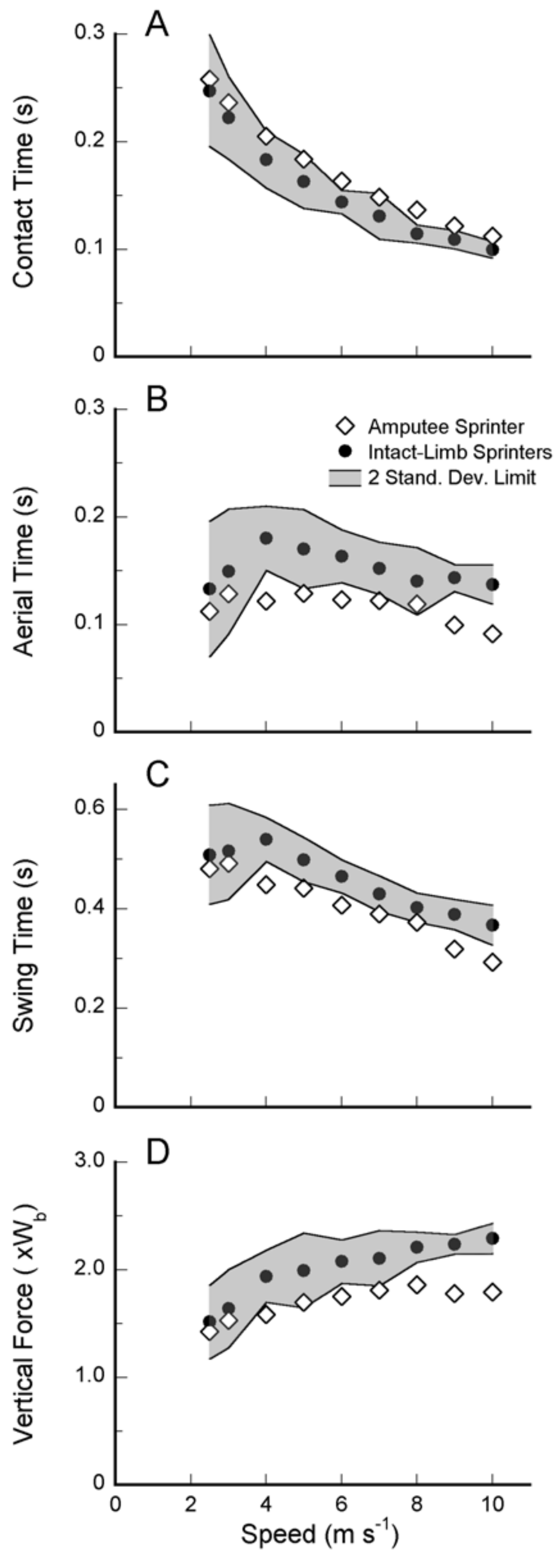

A
75
50
25
0
0
2
4
6
$\dot{V}O_2$ (mlO$_2$ kg^{-1} min^{-1})
Speed (m s^{-1})
400m Specialists
Amputee Sprinter
Elite & Sub-Elite
Z. Tadese
B
225
200
175
150
0
Running Economy
(mlO$_2$ kg^{-1} km^{-1})
Amputee Sprinter
400m Specialists
Elite & Sub-Elite
Lit. Data
2nd Bilateral Amputee
2 SD
400m
Specialists
Sub-Elite
Elite
i
ii
iii
iv
v
vi
vii

Figure 3



A
B
C
Amputee Sprinter
Intact-Limb Runners
Speed (m s-1)
Relative Speed
Run Duration (s)
Predicted Speed (m s-1)
Measured Speed (m s-1)
Amputee Sprinter; R2 = 0.96, n = 6
Intact-Limb Runners; R2 = 0.96, n = 35

Figure 4



A
B
C
D
Contact Time (s)
Aerial Time (s)
Swing Time (s)
Vertical Force (xW$_b$)
Amputee Sprinter
Intact-Limb Sprinters
2 Stand. Dev. Limit
Speed (m s^{-1})