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PRINCIPAL INVESTIGATOR: Peter Weyand

CONTRACTING ORGANIZATION: Rice University
Houston, TX 77005-1892

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14. ABSTRACT The objective of the proposed effort is to develop a brief and accurate method for the simultaneous assessment of anaerobic and aerobic fitness that is practical for both field and laboratory use. We anticipate that a method requiring an assessment period of only a few minutes or less, and two brief, minimally fatiguing efforts is possible. Each subject will undergo established tests to assess their maximal aerobic power and anaerobic power, respectively. Subjects will also complete a series of all-out efforts to establish their performance capabilities for efforts of different durations. Our analysis will focus primarily on two questions. First, we will determine if the relationship between the metabolic power available and all-out performance capabilities is common or dependent upon the fitness level of the individual. Second, we will determine whether the relationship between metabolic power and performance varies with the type of physical activity in which soldiers are engaged. We hypothesize that a single relationship will generalize to: 1) different individuals regardless of fitness level, and 2) to different types of physical activity. The development of a simple, practical and accurate method for assessing metabolic fitness and performance capabilities will provide a number of benefits.					
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INTRODUCTION

The objective of the proposed effort has been to develop a brief and accurate method for the simultaneous assessment of anaerobic and aerobic fitness that is practical for both field and laboratory use. We also sought to understand the physiological basis of the characteristic relationship between sources of metabolic power and the performance-duration relationship. At the outset of the work, we anticipated that a method requiring an assessment period of only a few minutes or less, and two brief, minimally fatiguing efforts is possible. We had each subject undergo established tests to assess their maximal aerobic power and anaerobic power, respectively. Subjects also completed a series of all-out efforts to establish their performance capabilities for efforts of different durations. Our analysis focused primarily on two objectives. First, determining if the relationship between the metabolic power available and all-out performance capabilities is common or dependent upon the fitness level of the individual and, second, determining whether the relationship between metabolic power and performance varies with the type of physical activity in which soldiers are engaged. We hypothesized that a single relationship that will generalize to: 1) different individuals regardless of fitness level, and 2) to different types of physical activity. The development of a simple, practical and accurate method for assessing metabolic fitness and performance capabilities will provide a number of benefits.

The specific tasks identified in the approved statement of work were:

1. To determine the relationship between all-out exercise performance and anaerobic and aerobic sources of metabolic power during modes of exercise involving a significant fraction of the body's muscle mass
2. To determine the briefest testing protocol that will accurately quantify the anaerobic and aerobic fitness of soldiers or an equivalent population.
3. To determine whether the progressive recruitment of additional muscle motor units during fatiguing exercise is a factor that forces the cessation of the exercise or a decrement in performance.

BODY:

Official approval for testing of human subjects was granted by the HSRRB as of 1/13/2005. Our last report was filed on 12/4/2006. The results reported below are those that have been accomplished over the course of the entire award period, including the data on human subjects collected after the initial approval date of 1/13/2005.

BACKGROUND

The anaerobic reserve model that we have tested and extended during the award period hypothesizes that all-out performance in any mode of exercise engaging a large fraction of the boy's muscle mass could be accurately predicted by our anaerobic reserve model (1,3,4). Our model, originally developed for running (Figures 1 and 2), postulates that all-out efforts all in a common exponential manner for the maximum burst sprint performance to the maximum intensity that can be supported aerobically as the duration of the effort becomes more prolonged.

The hypothesis has the following quantitative form:

$$\text{Perf}(t) = \text{Perf}_{\text{aer}} + (\text{Perf}_{\text{mech max}} - \text{Perf}_{\text{aer}}) \cdot e^{(-k \cdot t)} \quad (1)$$

where Perf is expressed as an intensity (i.e., running speed, cycling power, etc) and thus Perf(*t*) is the power output or running speed maintained for a trial of duration *t*, Perf_{mech max} is the maximum power output for a trial of 3 seconds, Perf_{aer} is the maximum mechanical power output that can be supported by aerobic metabolism, the quantity Perf_{mech max} - Perf_{aer} is the anaerobic reserve, *e* is the base of the natural logarithm, and *k* is the exponent that describes the decrements in performance occurring with increments in the duration of all-out efforts.

For background and orientation to the running experiments, representative data from a single subject is presented above in Figure 1 and the predictive accuracy of the model for running (with *k* = 0.013) is presented in Figure 2 (5).

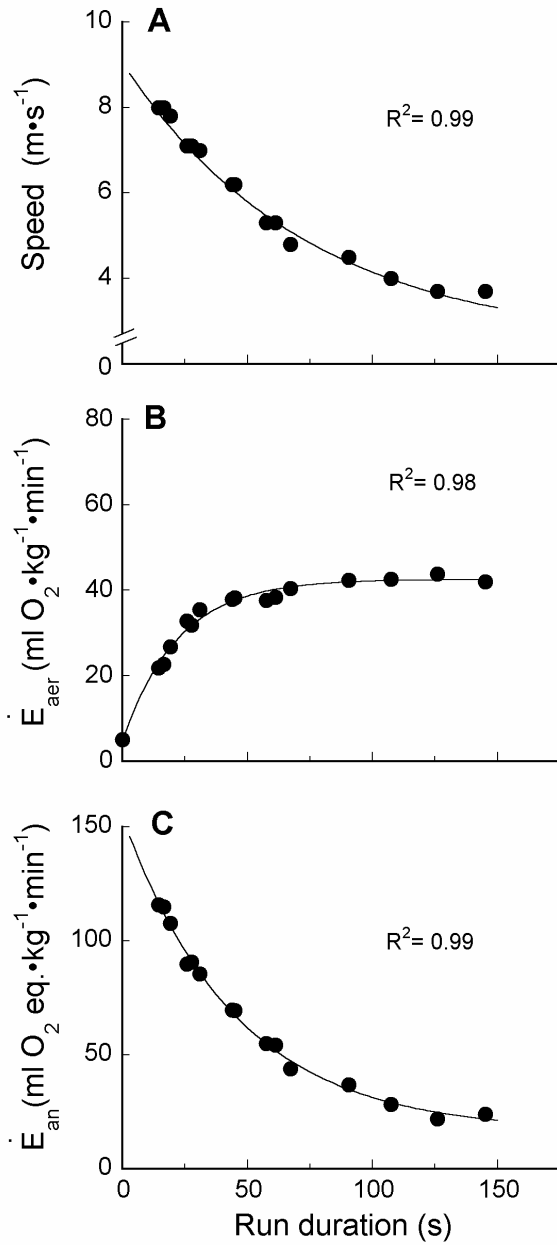


Figure 1. Speed (A) and rates of aerobic (B) and anaerobic energy release (C) during all-out running efforts of different durations for a male subject (from Weyand and Bundle, 2005).

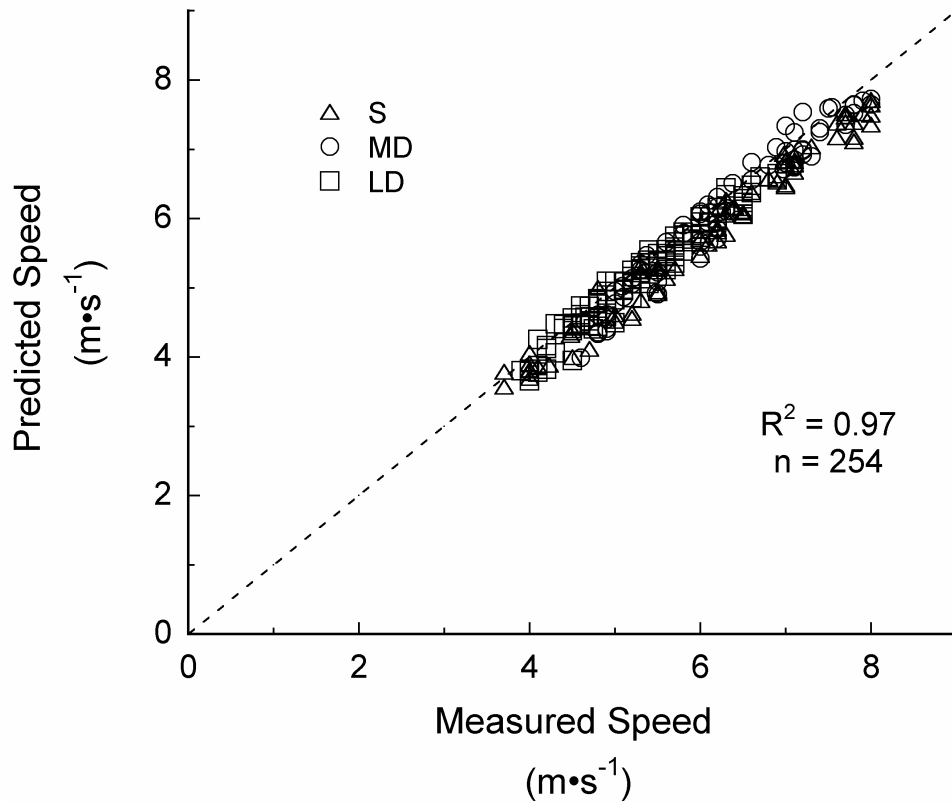


Figure 2. The speeds measured during all-out runs of different durations vs. those predicted by our anaerobic reserve model per equation one above (5). Note we have not yet performed the equivalent analysis to that above with our newly acquired running data.

As noted in our prior reports, we have also extended our model to a 2nd mode of exercise that engages a large fraction of the body's musculature, cycle ergometry. We had hypothesized that we would find that the value of the exponent k that describes duration-dependent decrements in performance would be the same for both different individuals regardless of their mechanical and aerobic maxima and for any type of exercise.

As reported, we found that the model and value of k is independent of the fitness level and therefore the absolute values of the maximum mechanical and aerobic exercise intensities of the individual as we had hypothesized. However, contrary to our expectation, we found the value of k does differ across different types of exercises. We found that the value of k for all-out cycling ($k = 0.026$) was twice that previously identified for running ($k = 0.013$) because the active muscles apply force for proportions of the total exercise time that are twice as long (i.e. the duty factor) during cycling vs. running (1)(see Figures 3 and 4).

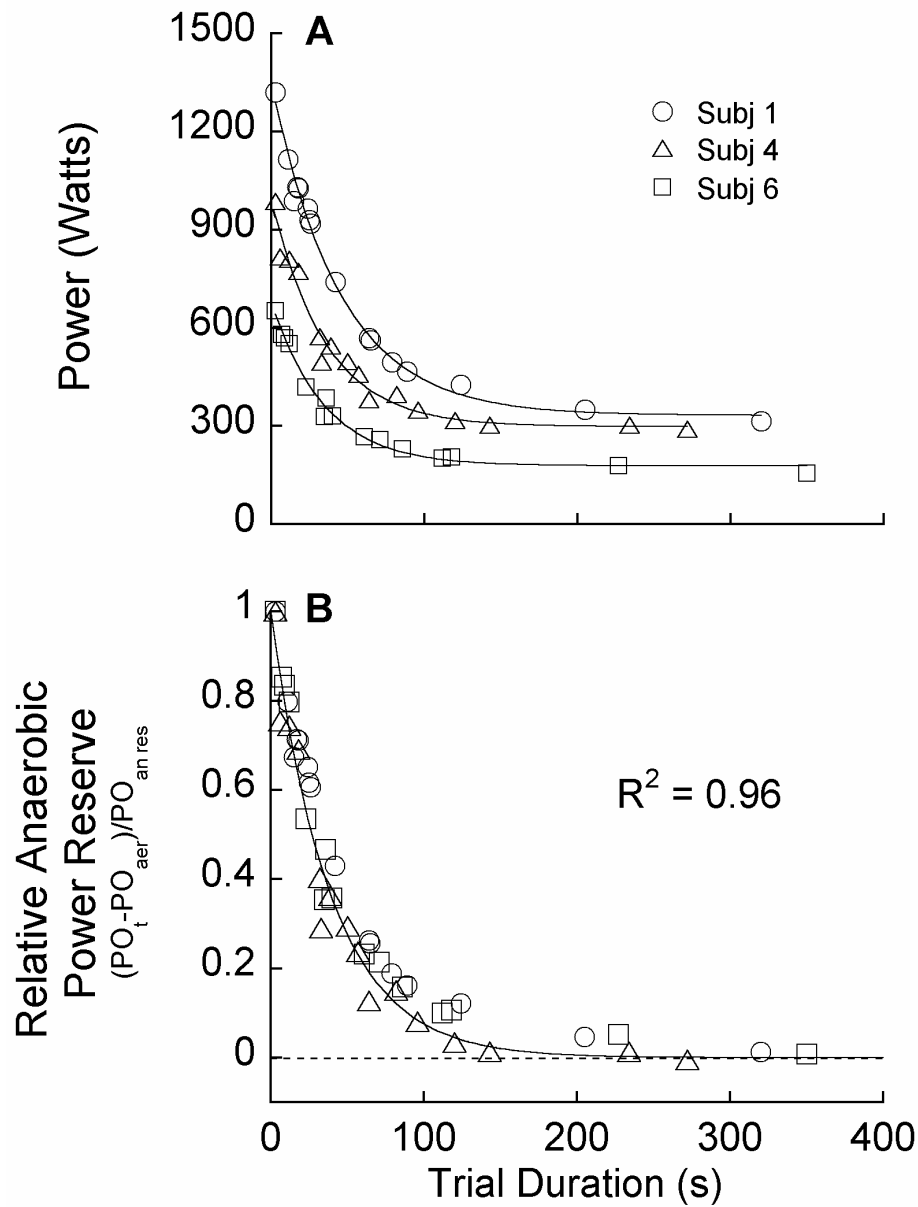


Figure 3. Mechanical power output vs. trial duration during all-out sprint cycling bouts of different durations for different three subjects who differed in their maximal mechanical power outputs and the maximum power output that they could support aerobically. When expressed in the relative terms of our model, the performance-duration relationship conforms to the same general relationship for the different subject (from Weyand et al, 2006).

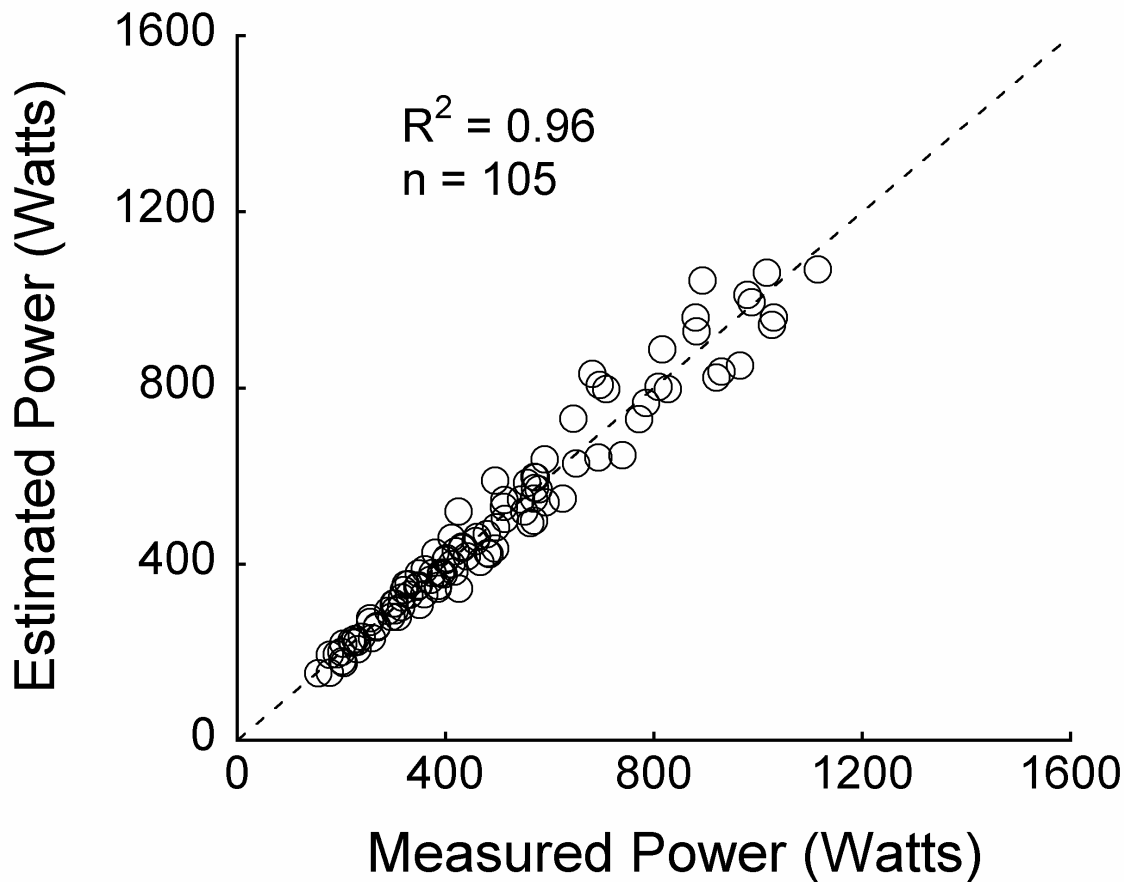


Figure 4. Actual power output vs. that predicted by our anaerobic reserve model during sprint cycle ergometry (predictions were formulated using equation 1 and a value of $k=0.026$; from Weyand et al, 2006).

In the last reporting period we focused primarily on objective three from the statement of work which hypothesizes a mechanistic basis for the general relationship provided by the model. Our model postulates that duration dependent decrements in performance result from a reliance on anaerobic metabolism that induces a progressive impairment of the forces that the active muscles can produce and that the skeleton can apply to the environment. We evaluated this possibility for both treadmill running and cycle ergometry. Cycle ergometry results from earlier work supported this postulate of the model (3). We found

muscular fatigue during sprint cycling was directly related to the relative reliance on anaerobic metabolism for force production and was similar under conditions when the aerobic power available differed (3; Figure 5).

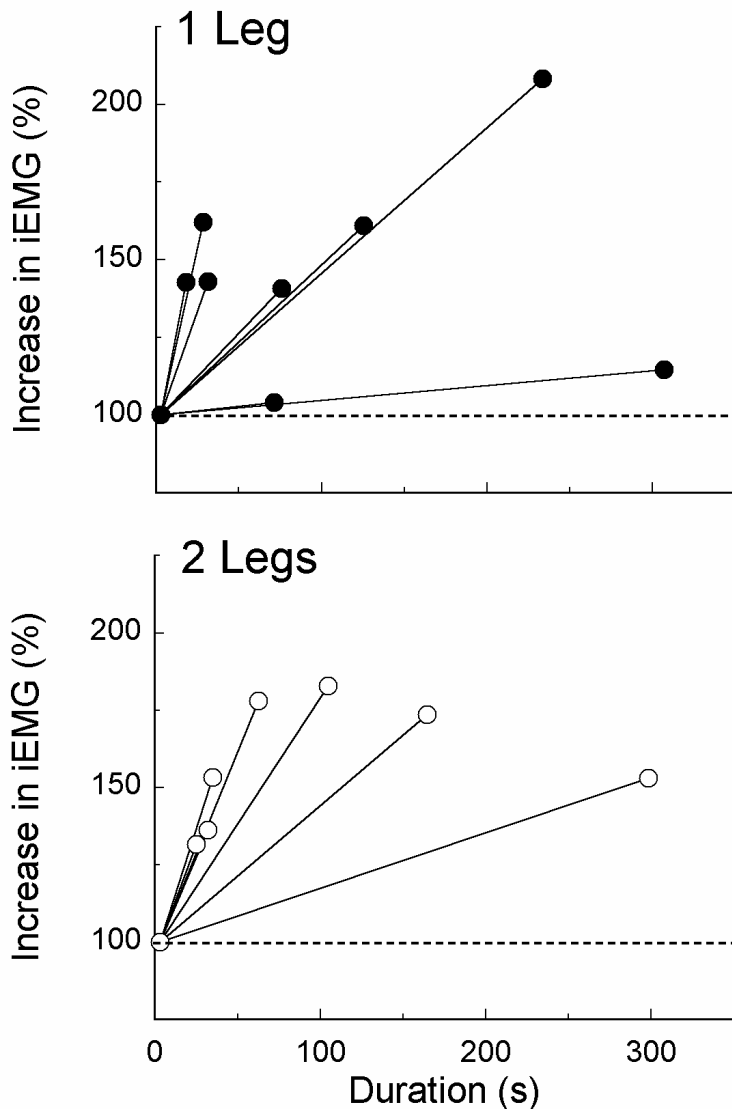


Figure 5. Rates of iEMG increase from the first five contractions to the last five contractions during the even numbered all-out trials completed by subject #1 during one- and two-legged sprint cycling. Rate of iEMG increase (slope of the line) were generally greater for shorter compared to longer trials (from Bundle et al, 2006).

We also noted previously that we can apply the model successfully to cycling ergometry under acute or instantaneous conditions. Specifically, we have found that the decline in power output over time within a single all-out effort also conforms to the common relationship postulated in our model. This is in contrast to the initial formulations and tests of the model in which we compared trials conducted at different constant intensities and therefore for different durations. In an unanticipated finding, we also found that these acute decrements in cycling power output that occur within a single bout during which the subjects perform all-out from the first instant, such as the Wingate test, can also be described accurately by our model (figure 6).

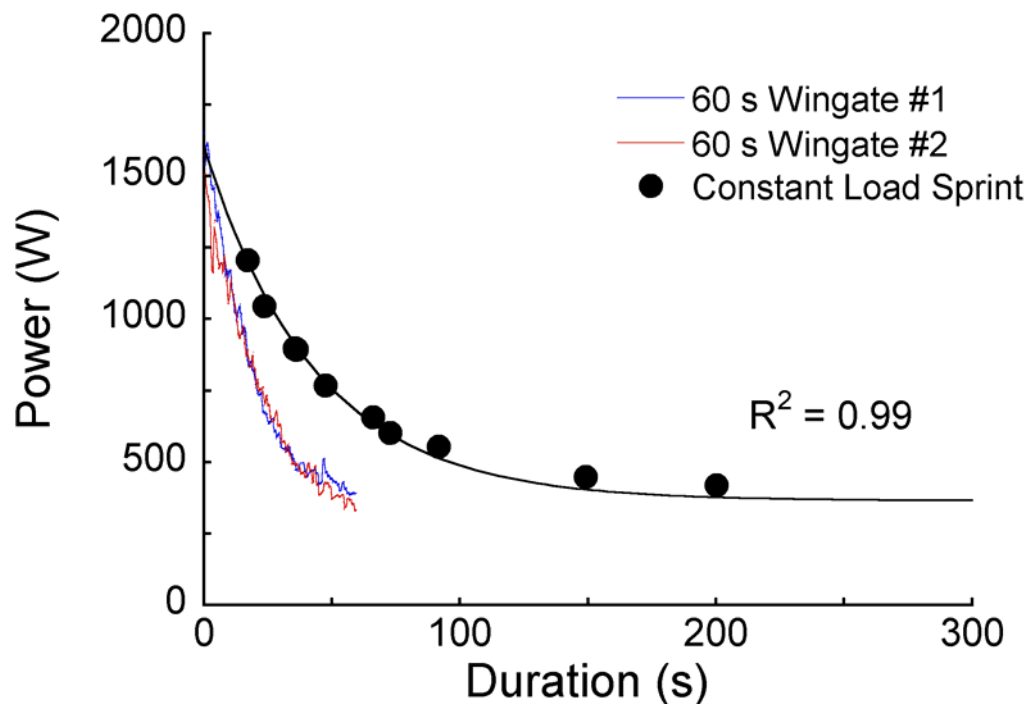


Figure 6. Decrements in power output in relation to duration for a single subject across trials of different durations (solid line, closed circles) and during two all-out per the standard all-out Wingate test of 60 s duration (blue and red colored lines, no symbols). In both cases, performance decrements are accurately described by our model. The more rapid decrements in power occurring within a single bout are described by a greater exponent or k value (0.54 vs. 0.026, respectively)

This result is significant for two reasons. First, the result provides additional support for the mechanistic biological relationships posed in the model and tested over the grant award period. Second, this raises the possibility that a single 30 to 60 second test may be sufficient to evaluate both the short (conventionally considered "anaerobic") and long-term ("aerobic") performance capabilities of different individuals. Evaluating this second outcome will require additional testing, but the possibility exists that brief, practical, accurate and mode-specific tests that provide global information on fitness and performance capabilities can be conducted using a single 30 to 60 s all-out test.

To explore the mechanistic basis of the model per our proposal, we collected simultaneous ground reaction force and electromyography (EMG) data during brief, all-out treadmill running and sprint cycle ergometry.

As noted in previous reports and our original proposal our model postulates that the mechanistic basis for the performance decrements observed as the duration of all-out exercise becomes more prolonged is metabolic. We expected that the reliance on anaerobic metabolism at exercise intensities above the maximums that could be supported aerobically would impair muscle force production. We further anticipated that impairments in muscle force production would induce the compensatory recruitment of additional muscle so that the musculoskeletal system would be able to continue to generate and apply the required force to the ground. In accordance with general practice and our application we assessed relative recruitment and force impairment indirectly using surface electromyography. In prior reports, we had presented preliminary data from treadmill running and cycle ergometry that support this essential postulate of the model.

In our last annual report, we presented preliminary EMG data collected during treadmill running and taken simultaneously with ground reaction forces from 5 different extensor muscles: vastus lateralis, vastus medialis, biceps femoris, and medial and lateral gastrocnemius muscles. As noted for the purposes of testing our model, these data were taken on 6 volunteer subjects who were tested for the maximum sprinting speeds, their maximum aerobic power, and the maximum speeds supported by their aerobic power. These subjects also completed an average of 15 all-out runs at speeds greater than their aerobic maximums. We collected simultaneous ground reaction force and EMG data for the duration of all of these trials ($n = 6 \text{ subjects} \times 15 \text{ trials each} = 90 \text{ total all-out trials}$).

As of our last report, analysis of the EMG data for these trials remained in progress. Preliminary data from one muscle, the biceps femoris (shown previously and in Figure 6 below), during the fatiguing running trials was presented. We have since finalized our custom analysis software and proceeded with the data reduction and integration of the force and EMG data acquired. We also undertaken a more rigorous examination of the patterns and rates of force application and determination of gait parameters from the force treadmill-data acquisition and reduction system we developed during the award period (see Weyand, Sandell, Prime and Bundle, in review)

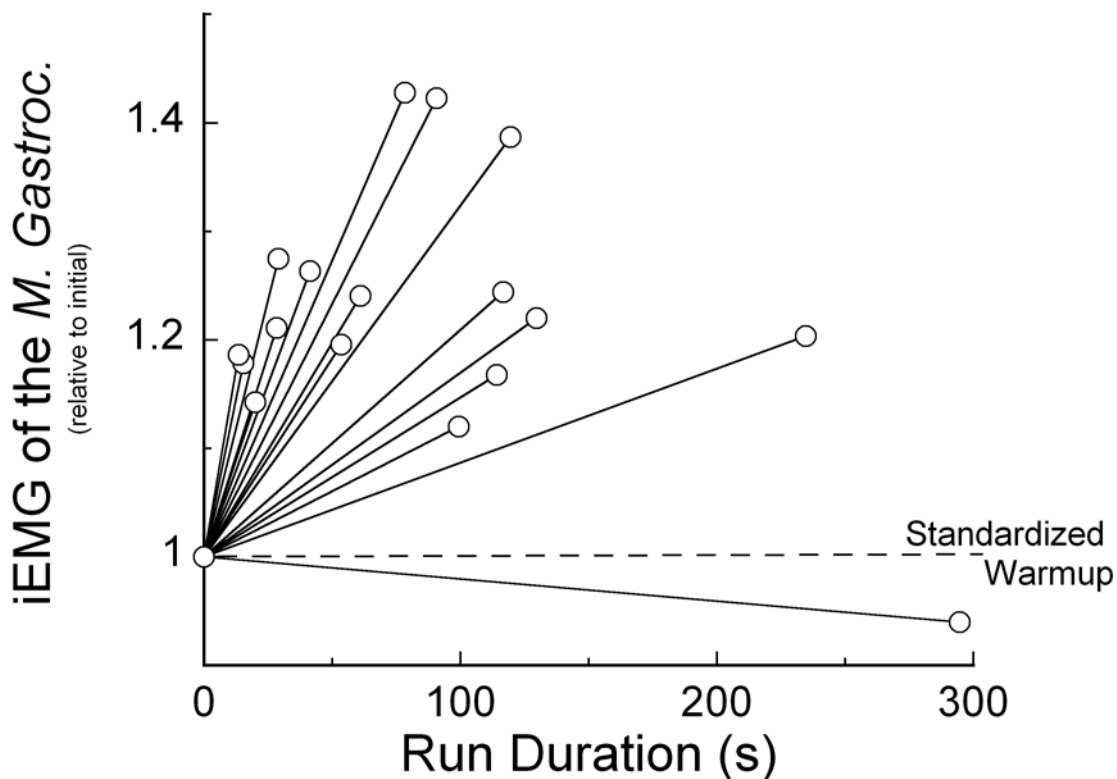


Figure 7. Surface iEMG signals from the biceps femoris of one subject during all 16 of the all-our running trials this subject completed. Increases in the iEMG signal from the beginning to the end of the trial were more rapid for those trials conducted at faster speeds. All increases are plotted relative to the average value from the initial 5 contractions (assigned a value of 1.0 for all trials). During submaximal running at a speed below the maximum that this subject could support aerobically, the iEMG signal remained constant or perhaps decreased slightly over the course of the 5 minute run.

To further assess whether a mechanistic link between a reliance on anaerobic metabolism for force production and an impairment of

muscle force production, we similarly analyzed the cycling EMG-force data taken previously and from which representative samples were presented in our last report.

We expected that the threshold at which compensatory recruitment occurred would similarly correspond to maximal pedal forces that could be supported aerobically during both cycling and running even though the absolute muscle and external (i.e. ground or pedal) forces would differ markedly.

In our previous annual reports, we provided EMG data from five different extensor muscles during all-out sprint cycling efforts encompassing a broad range of intensities and durations.

Acquiring equivalent data for weight-bearing locomotor exercise was a major objective of the grant. As we previously noted, we encountered considerable technical difficulties obtaining the ground reaction force data necessary to carry out the proposed work. This was not entirely unexpected given the potential technical issues involved in acquiring an extensive body of simultaneous force and EMG data under challenging circumstances.

Acquiring force data of sufficient fidelity required both rapid treadmill motor response for smooth and continuous belt performance and software filtering to eliminate vibration artifact from our force traces. After extensive troubleshooting of both problems, we succeeded in acquiring and reducing high quality, simultaneous ground reaction forces from our treadmill and simultaneous EMG data. In the last grant period, we finished writing and troubleshooting the custom software needed to analyze our simultaneous force-EMG files, and completed the data reduction. At present, we have completed 1st and 2nd level analyses of these treadmill data. Further analysis and manuscript preparation are in progress.

To the best of our knowledge, these are the only continuous data of this nature that exist. The novelty of this data set should allow for significant scientific advances on the specific issues identified in the grant as well as a number of physiological questions about musculoskeletal function that are still not well understood at the tissue, system and whole-body levels.

These results of the treadmill data acquisition and analysis that occurred in this last period are provided below. Simultaneous EMG, and horizontal and vertical ground reaction forces are shown in Figure 8. The reproducibility of the ground reaction force traces during "non-fatigued" and "fatigued" running can be seen in Figure 9. The relationship between the ground reactions forces and the EMG signals and the increases in EMG activity that occur as a result of metabolically-induced fatigue are shown in Figures 10 and 11, respectively.

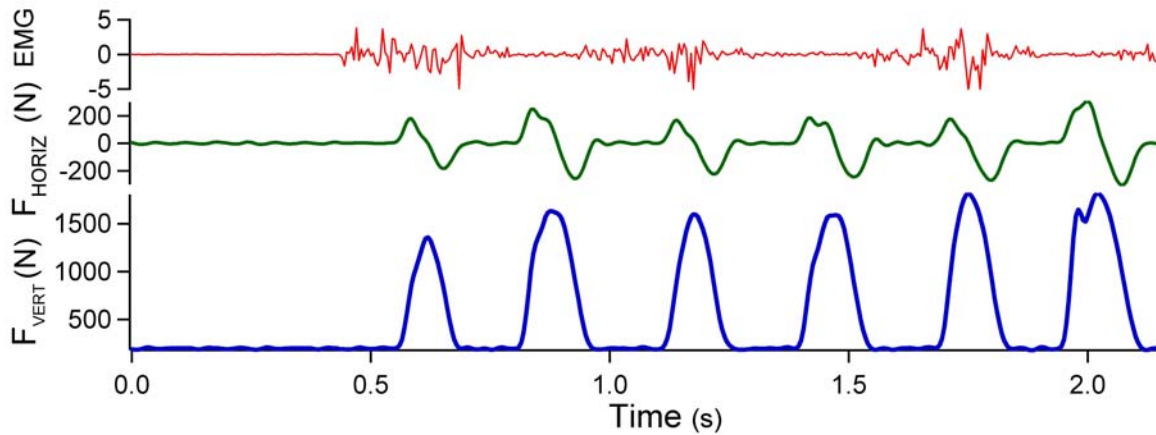


Figure 8. Simultaneous data during high-speed treadmill running from surface electrodes (from the vastus lateralis muscle, top panel) to record muscle activation, horizontal and vertical ground reaction forces (middle and bottom panels, respectively).

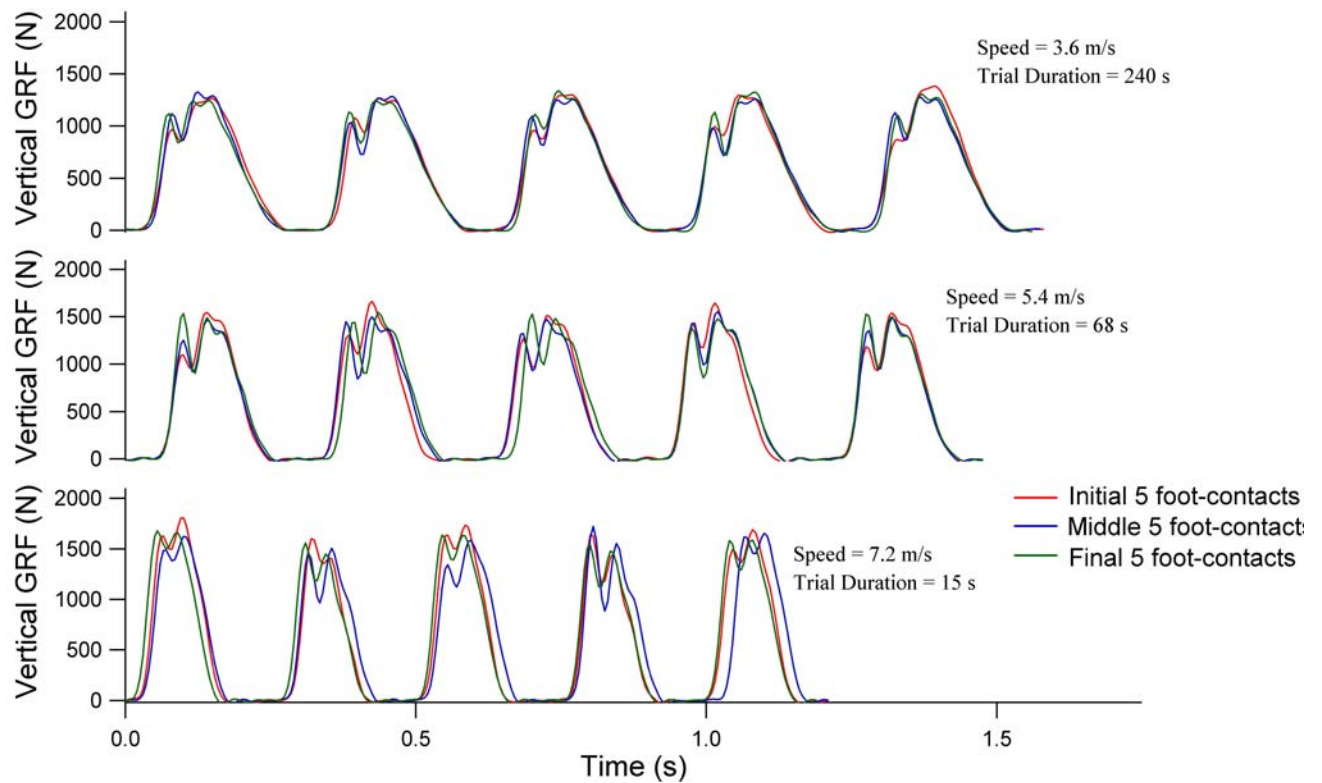


Figure 9. Vertical ground reaction force races from 5 consecutive footfalls at the beginning, middle and end of treadmill efforts under steady-state conditions (top panel) and two fatiguing efforts taking place at high speeds (5.4 m/s, middle panel, and 7.2 m/s, bottom panel). Note that the timing of the footfalls and patterns of vertical force application are essentially unchanged across the early, middle and late footfalls regardless of the speed of the trial.

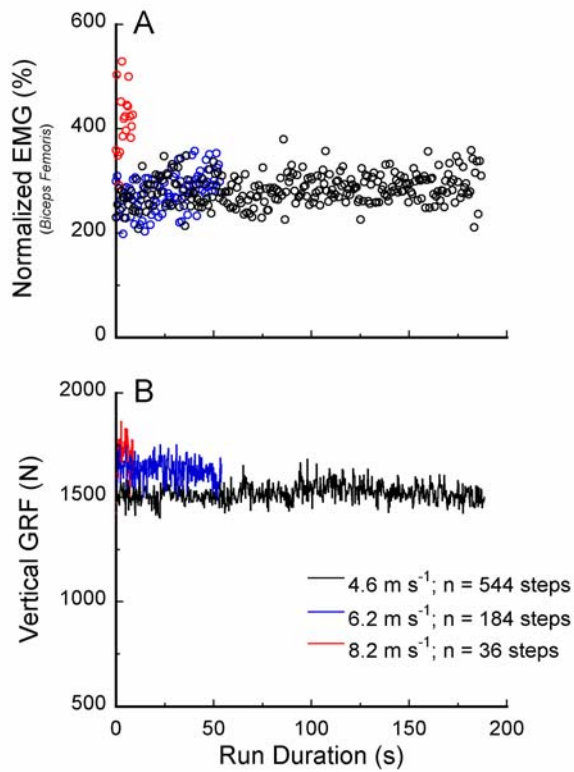


Figure 10. Surface electromyographic activity from the biceps femoris muscle (top panel, normalized as a percentage of the value during a standardized warm-up) and stance averaged vertical ground reaction force (bottom panel) from three fatiguing trials conducted at different treadmill speeds and therefore with differing times to volitional fatigue and the cessation of exercise. Note that the slope of the integrated IEMG-time relationship depended on the intensity of the effort with shorter, more fatiguing trials showing a much greater rate of increase in the surface EMG signal from this muscle.

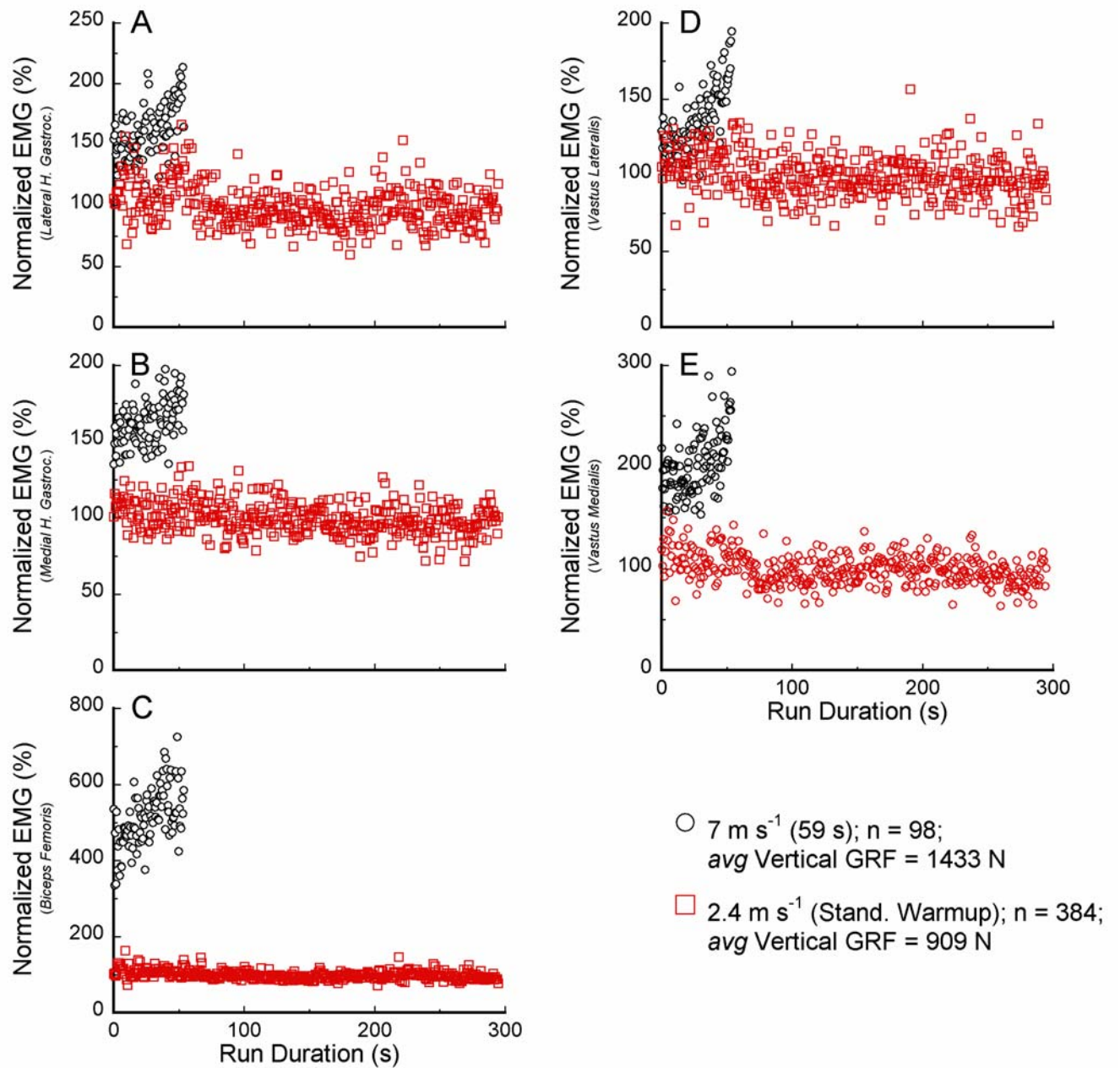


Figure 11. Normalized EMG activity from five different muscles vs. time (panels A-E; lateral gastrocnemius, medial gastrocnemius, biceps femoris, vastus lateralis and vastus medialis, respectively) during a standardized, steady-state warm-up run at 2.4 m/s and during a fatiguing running trial at a high speed of 7.0 m/s. Note that the activation of all five extensor muscles was constant or decreased slightly during the steady-state run and increased rapidly during the run at 7 m/s which resulted in fatigue and discontinuation in 59 s.

KEY RESEARCH ACCOMPLISHMENTS:

- Validation and extension of the anaerobic reserve model to two modes of whole-body exercise: cycling and locomotion.
- Development of two new techniques for quantifying anaerobic and aerobic fitness
 - o Two-trial procedure
 - o Modified Wingate (single trial)
- Establishing a mechanistic link between muscle fatigue and the exercise performance-duration relationship.
- Identification of muscle force decrements (i.e. fatigue) rather than metabolic power, as the factor limiting brief all-out exercise performance.
- Finding that rates of muscular fatigue during intense whole-body exercise: 1) vary directly with intensity, but 2) do not seem to vary between different muscles (i.e. no bottlenecks, all contributing muscles fatigue equally).

REPORTABLE OUTCOMES:

Manuscripts

Bundle, MW, Ernst, CL, Bellizzi, MJ, Wright, S and Weyand, P. A metabolic basis for impaired muscle force production and neuromuscular compensation during sprint cycling. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology*, **291**:R1457-64, 2006.

Weyand, P. Sandell, RF, Prime DN, Bundle, MW. Mechanical limits to running speed: set by limb force maximums or stance time minimums? *Journal of Applied Physiology*, in review.

Bundle, MW and Weyand P. Metabolism, force application and fatigue during brief, all-out exercise: I. Sprint cycling, in preparation for submission to the *Journal of Physiology*.

Bundle, MW and Weyand P. Metabolism, force application and fatigue during brief, all-out exercise: I. Sprint running, in preparation for submission to the *Journal of Physiology*.

Abstracts/Presentations

Weyand, P. Biological barriers and locomotor performance limits: what gives with maximum running speeds? Houston Society of Engineering and Medicine in Biology, Abstract submitted 11/2007, Oral presentation to follow in 2/2008.

Robb, R. and Weyand P. Biological barriers to running speeds: force or rate limited? Rice Undergraduate Research Symposium, 2006.

Sandell, R and Weyand P. Mechanical/metabolic limits to human locomotor performance I. Rice Undergraduate Research Symposium, 2007

Prime DN. and Weyand P. Mechanical/metabolic limits to locomotor performance II. Rice Undergraduate Research Symposium.

CONCLUSIONS:

Major conclusions (with specific respect to the three objectives in the original statement of work) from the full award period are as follows:

1. All-out locomotor efforts above the maximum intensities that can be supported aerobically cannot be sustained for shorter but not longer durations because: 1) anaerobic metabolism impairs the muscular force production necessary to maintain the intensity of the effort, and 2) impaired muscular force production ultimately compromises the external forces the limbs can apply thereby resulting in the cessation or termination of the effort. The exercise intensity
2. Our results suggest that a two-test protocol similar to that described previously (Bundlie et al, 2003) will suffice in determining the anaerobic and aerobic fitness of soldiers. Our results also raise the possibility that this might be accomplished with a single test that approximates the current standard of the Wingate test. Specifically, our results indicating that our anaerobic reserve model accurately describes the losses in power output that occur over the course of the Wingate test suggests a single 30 to 60 s test may provide a full profile of an individual's anaerobic and aerobic fitness. A full conclusion on this latter possibility brought about by our findings here awaits more comprehensive and detailed investigation.

3. The progressive recruitment of additional motor units during fatiguing exercise occurs in all the major muscles involved in the exercise effort. The latter stages of this process during which maximal volitional recruitment appears to be reached forces the cessation of exercise or a reduction in exercise intensity.

SO WHAT?

- broader conclusions, implications and applications of the work accomplished

Beyond the specific conclusions stated with respect to the statement of work for the grant provided above, the work accomplished has more general scientific implications and application.

Our data demonstrate a convincing link between non-oxidative pathways of ATP resynthesis (i.e. anaerobic) and muscular fatigue during locomotor efforts. Although muscular fatigue has been an area of extensive and even classic investigation in physiology, the vast majority of this work have been carried out with non-physiological preparations or using exercises that engage only a very small amount of muscle. We have compiled a data set that is novel in two regards: 1) our data includes, force, performance and an indirect measure of fatigue (continuous IEMG data) during whole-body locomotor efforts, and 2) we have all of these data on a continuous basis for many efforts taking place at different intensities and durations.

Thus far, we can confidently conclude that the upper limits for brief exercise performance reflect mechanical maximums. Additionally, performance during brief all-out efforts is not limited by metabolic power. Rather, these performances are determined by the maximum musculoskeletal intensity that can be attained in the non-fatigued state for 2-3 seconds and by the extent of the fatigue/force impairment that is induced by a reliance on anaerobic metabolism as the exercise continues. This stands in stark contrast to the prevailing view of a metabolic limit to these performances. This biological conclusion also suggests that the traditional and standard tests of anaerobic power and capacity are of questionable physiological relevance. Our anaerobic reserve model provides an alternative biological paradigm and concrete testing procedures that can accurately predict performance capabilities over a wide range of intensities and durations.

In addition, our data demonstrate that fatigue during brief, all-out locomotor efforts is a global rather than specific phenomenon.

For both running and cycling our data indicate that no single muscle or muscle groups fatigues and fails unilaterally. Rather, all of the muscles and muscle groups we have monitored fatigue in parallel. This likely reflects the integrated function of the cardiovascular and musculoskeletal systems under these physiological conditions.

List of Individuals paid on the grant (in addition to PI)

Jennifer Lin
Matthew Bundle
Laura Dominguez
Roland Robb
Bethany Smith
Rosalind Sandell
Danille Prime

REFERENCES:

1. Alexander, RM. Sprinting and endurance for runners and cyclists. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology*, 290(3):R757.
2. Bundle MW, Hoyt RW and Weyand PG. High speed running performance: a new approach to assessment and prediction. *Journal of Applied Physiology*, 95:1955-1962, 2003.
3. Bundle, MW, Ernst, CL, Bellizzi, MJ, Wright, S and Weyand PG. A metabolic basis for impaired muscle force production and neuromuscular compensation during sprint cycling. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology*, 291(5):R1457-64, 2006.
4. Weyand, P. Lin, J.E. and M. Bundle. Energetics of high-speed running: integrating classical theory and contemporary observations. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology*, 290(3): R758-65, 2006.
5. Weyand, P. and M. Bundle. Energetics of high-speed running: integrating classical theory and contemporary observations. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology*, 288: R956-R965, 2005.

APPENDICES:

1. Reference 2 above: Bundle et al, AJP, 2006
2. Weyand, Sandell, Prime and Bundle, Mechanical limits to running speed: set by limb force maximums or stance time minimums? in review



A metabolic basis for impaired muscle force production and neuromuscular compensation during sprint cycling

Matthew W. Bundle, Carrie L. Ernst, Matthew J. Bellizzi, Seth Wright and Peter G. Weyand

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A metabolic basis for impaired muscle force production and neuromuscular compensation during sprint cycling

Matthew W. Bundle,^{1,2} Carrie L. Ernst,¹ Matthew J. Bellizzi,¹ Seth Wright,¹ and Peter G. Weyand^{1,2,3}

¹Concord Field Station, Museum of Comparative Zoology, Harvard University, Old Causeway Rd., Bedford, Massachusetts; ²Locomotion Laboratory, Department of Kinesiology, Rice University, Houston Texas; and ³Center for Human Performance, Texas Medical Center, Houston, Texas

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Bundle, Matthew W., Carrie L. Ernst, Matthew J. Bellizzi, Seth Wright, and Peter G. Weyand. A metabolic basis for impaired muscle force production and neuromuscular compensation during sprint cycling. *Am J Physiol Regul Integr Comp Physiol* 291: R1457–R1464, 2006. First published July 13, 2006; doi:10.1152/ajpregu.00108.2006.—For both different individuals and modes of locomotion, the external forces determining all-out sprinting performances fall predictably with effort duration from the burst maximums attained for 3 s to those that can be supported aerobically as trial durations extend to roughly 300 s. The common time course of this relationship suggests a metabolic basis for the decrements in the force applied to the environment. However, the mechanical and neuromuscular responses to impaired force production (i.e., muscle fatigue) are generally considered in relation to fractions of the maximum force available, or the maximum voluntary contraction (MVC). We hypothesized that these duration-dependent decrements in external force application result from a reliance on anaerobic metabolism for force production rather than the absolute force produced. We tested this idea by examining neuromuscular activity during two modes of sprint cycling with similar external force requirements but differing aerobic and anaerobic contributions to force production: one- and two-legged cycling. In agreement with previous studies, we found greater peak per leg aerobic metabolic rates [59% (± 6 SD)] and pedal forces at $\dot{V}O_{2\text{ peak}}$ [30% (± 9)] during one- vs. two-legged cycling. We also determined downstroke pedal forces and neuromuscular activity by surface electromyography during 15 to 19 all-out constant load sprints lasting from 12 to 400 s for both modes of cycling. In support of our hypothesis, we found that the greater reliance on anaerobic metabolism for force production induced compensatory muscle recruitment at lower pedal forces during two- vs. one-legged sprint cycling. We conclude that impaired muscle force production and compensatory neuromuscular activity during sprinting are triggered by a reliance on anaerobic metabolism for force production.

motor control; aerobic and anaerobic contributions; performance

HUMAN LOCOMOTOR PERFORMANCE depends directly upon the forces that the musculoskeletal system can generate and transmit to the environment. For example, runners and cyclists modulate their speed and power output primarily by altering the respective forces they apply to the ground (61) or pedals (29). The maximum external forces applied at top running speed or at peak cycling power output can be supported by skeletal muscle for only 3 s or less (41, 61). As the duration of all-out efforts become more prolonged, the external forces that the musculoskeletal system can provide become progressively reduced. As a result, performances decline from the 3-s max-

imum to a nearly sustainable level as the duration of all-out efforts extends to 300 s (10, 17, 30). The reductions in force production responsible for the well-characterized performance-duration relationship have been considered by some investigators to be a whole-body manifestation of muscle fatigue (9, 62). Given the rapidity with which the duration-dependent decrements in force production occur, shorter-duration, all-out efforts provide a potentially powerful approach for examining the time course of muscle fatigue in vivo.

In contrast to the consistent decrements in all-out locomotor performance observed in humans and other species for efforts of increasing duration (17, 30), the extent and time course of fatigue measured from isolated muscle preparations are variable and appear to depend on the stimulation protocol (4, 11, 16, 42). Although the time courses can vary considerably, in vitro and in vivo decrements in force production may have a common metabolic basis. Isolated muscle fibers contracting at low frequencies in oxygenated solutions (31, 42) and in vivo muscle active at levels below the maximum rate of aerobic metabolism (13) show little indication of decrements in force production over time. In contrast, muscle fibers contracting in anoxic solutions (31, 38) and individuals relying heavily on anaerobic pathways of ATP resynthesis (60) experience impaired force production after relatively few contractions. The mechanism responsible for the rapid decrements in force has been studied extensively but remains incompletely understood (14, 18, 25, 49).

Regardless of the mechanism, during prolonged in vivo contractions at elevated fractions of the maximum force available, skeletal muscle fatigues rapidly. To maintain a constant external force output, the nervous system can compensate by either increasing the rate of stimulation or recruiting additional muscle fibers (24). The progressive increase in neuromuscular activity characteristic of high-force, intermittent contractions (33, 45) generally occurs via motor unit recruitment (43, 55). In contrast, at lower force levels, those equal to 30% or less of the maximum voluntary contraction (MVC), intermittent contractions can be sustained with steady levels of neuromuscular activation and do not appear to require compensatory muscle recruitment (21, 40).

Although the mechanical and neuromuscular responses to fatiguing contractions are generally considered with respect to the fraction of the MVC, the mechanism triggering compensatory recruitment may be metabolic. Our recent work with short-duration, all-out running and cycling efforts (10, 58, 60)

Address for reprint requests and other correspondence: P. G. Weyand, Locomotion Lab, Dept. of Kinesiology MS-545, Rice Univ., Houston TX 77005 (e-mail: pweyand@rice.edu).

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suggests that duration-dependent decrements in sprinting performance may be determined by the metabolic pathways supporting force production regardless of the absolute level of force generated. Accordingly, applying pedal forces greater than the maximums that can be supported by aerobic metabolism results in compensatory muscle recruitment to maintain performance (20, 45), whereas lower pedal forces are maintained with constant neuromuscular activity (45).

Here, we employed an experimental tool that allowed us to alter the aerobic and anaerobic contributions to the external forces produced during all-out sprint locomotion. Specifically, we took advantage of the greater pedal forces that could be supported aerobically during one- vs. two-legged cycling to evaluate whether compensatory recruitment would be triggered at the same absolute pedal force or by a reliance on anaerobic metabolism for force production. We knew from previous work that the timing of pedal force application (54) and muscle activation patterns (36) are similar during one- and two-legged cycling, but that the maximum pedal forces that can be supported by aerobic metabolism are not. On a per leg basis, rates of oxygen uptake during one-legged cycling have been found to be at least 40% greater than during two-legged cycling (15); thus, allowing greater muscle and pedal forces to be supported aerobically in the one-legged mode.

We hypothesized that the duration-dependent decrements in external force production that occur during all-out sprint cycling result from impaired muscle force production and that the impairment has a metabolic basis. We specifically predicted that a reliance on anaerobic metabolism for force production during locomotion compromises muscular force production, thereby triggering compensatory recruitment during all-out efforts. In accordance with the greater pedal forces that can be supported by the maximum rates of aerobic metabolism in one- vs. two-legged cycling, we expected the onset of compensatory neuromuscular activity to occur at a greater pedal force threshold in the one-legged mode. Conversely, for all-out sprint efforts requiring equivalent pedal forces, we anticipated that compensatory neuromuscular activity would be greater during two- vs. one-legged cycling.

MATERIALS AND METHODS

Subjects. Six males, 22–36 years of age [mass, 75.2 kg (± 7.2 SD)]; height, 179.5 cm (± 2.6) volunteered to participate in this study and provided their written informed consent in accordance with the protocol reviewed and approved by the Institutional Review Board of Harvard University. All of the subjects were moderately to highly fit. Five of the six subjects were actively engaged in endurance training at the time of the study; two subjects were trained cyclists, two were former competitive runners, one was a cross-country skier, and one was active but did not exercise regularly.

Testing protocol. Subjects completed a minimum of eight testing sessions, which were separated by at least 48 h of rest. In the first two sessions, subjects underwent progressive discontinuous tests to determine $\dot{V}O_{2\text{ peak}}$ and their steady-state rates of oxygen uptake at a series of different work rates with one- and two-legs, respectively. In sessions three through eight, subjects performed one- or two-legged all-out cycling bouts at work rates that elicited failure between 15 and 400 s. Subjects performed five sprints with one-leg during three of the sessions and five sprints with two-legs during the other three sessions. Within sessions, subjects were instructed to take as much rest between sprints as they deemed necessary to be fully recovered but were

required to take a minimum of 10 min. Subjects alternated one- and two-legged conditions between successive test sessions.

Mechanical power and pedal forces. All tests were completed on a stationary, friction-braked cycle ergometer (Monark Ergonomic 818 E) equipped with drop bars, a racing saddle, and pedal straps. Each ergometer trial was conducted at a constant cadence of 100 rpm. This ensured that differences in power output were due to differences in pedal force, rather than differences in both force and velocity.

One-legged tests were performed using the dominant leg with subjects sitting in the same position as for the two-legged tests with the inactive leg supported by a stool adjacent to the vacant pedal. During the one-legged tests, the vacant pedal was weighted with a 9.4-kg counterweight to facilitate a smooth pedaling motion. For the sprint trials, the ergometer was loaded over a 2-s period by gradually releasing a hand-held spring clamp to apply the desired tension to the flywheel. Timing of the sprint duration began immediately after the load had been applied. Subject feedback for pedal cadence was provided with a tachometer equipped with video display and a metronome that beat 100 times per minute. The tachometer measured the revolutions from reflective tape on the flywheel, which triggered a photocell (Banner Engineering, Valu-Beam SM912LV) mounted at the base of the ergometer. Pulses from the photocell were digitized (National Instruments model NB-MIO-16H) and recorded in custom-designed software (National Instruments, LabView 4.0). The software converted flywheel revolutions to pedal revolutions using the ergometer gear ratio (52:14).

During short-duration high-intensity efforts, measurements of mechanical power from friction-braked cycle ergometers underestimate the power supplied by the subject if the inertial work done to accelerate flywheel is omitted (37, 44). We accounted for this by using a post hoc correction modeled after Morin and Belli (44) that incorporates the flywheel velocity. For the one-legged trials, we also added the work done to accelerate the counterweight (radius = 0.175 m). The influence of these corrections is greatest for trials of very short duration. During the shortest sprints completed by the subjects, the corrected power output was 4.4% (± 1.6) (range: 7.3 to 2.4) greater than that to overcome friction alone.

We calculated the average force applied to the pedals per revolution (F_{avg}) from power output in accordance with

$$F_{\text{avg}} = \frac{\text{Power Output}}{\text{Radius} \cdot 2\pi(\text{Freq})} \quad (1)$$

where radius was the length of the crank arm (0.175 m) and Freq was the measured mean cadence in revolutions per second. Because the pattern of force application during two-legged cycling results in one of the two legs always being in a downstroke, $F_{\text{avg}} = F_{\text{ds}}$, where F_{ds} is the average force applied to the pedals during the downstroke period. However, for one-legged cycling, force can only be applied during the downstroke period of the active leg, and since revolutions with constant angular velocity have equal downstroke and upstroke periods, the F_{ds} at a given power output for one-legged cycling is

$$F_{\text{ds}} = 2 \cdot F_{\text{avg}} \quad (2)$$

This method provides the time-averaged force applied during each downstroke. Because our measures of electromyographic activity are also downstroke averages, this approach allows the most direct comparison between pedal force application and neuromuscular activity. The average pedal force during downstroke, F_{ds} , is referred to as pedal force throughout the manuscript, and these data are presented exclusively on a per-leg basis.

Maximal and submaximal rates of oxygen uptake ($\dot{V}O_{2\text{ peak}}$, $\dot{V}O_{2\text{ ml}}$, $O_{2\text{ kg/min}}$). One- and two-legged $\dot{V}O_{2\text{ peak}}$ values were determined from a progressive, discontinuous cycling test to failure. The peak rate of $O_{2\text{ uptake}}$ for each condition was the highest single-minute $\dot{V}O_{2\text{ value}}$ obtained during the progressive, discontinuous cycling test. The test consisted of a minimum of seven 5-min constant load, work bouts

on the ergometer, separated by at least 5 min of rest. Work rates were increased 10 to 30 W per workload in accordance with the estimated fitness level of the subject. The test was initiated at a power output estimated to be 30–40% of one- or two-legged $\dot{V}O_{2\text{ peak}}$ and was terminated when the subject was unable to complete a 5-min bout. Expired air was collected during the last 2 min of each 5-min bout using Douglas bags. A sample of air from each bag was analyzed for O_2 (Applied Electrochemistry SA-3), and CO_2 (Applied Electrochemistry CD-3A) fractions after calibration with gas of known concentrations. Gas volumes were determined with a dry gas meter (Parkinson-Cowan CD4) and digital thermometer (Wescor TH-65 TC). Rates of oxygen uptake were determined from O_2 and CO_2 fractions, and the expired volumes in accordance with Consolazio et al. (12).

Sprint cycling. Sprint tests for one- and two-legged cycling were constant load trials administered at intensities between 100% and 300% of the respective $\dot{V}O_{2\text{ peak}}$. Subjects completed 15–19 all-out trials for each cycling condition at pedal forces that were chosen to elicit failure in 15 to 400 s. Five sprints were performed per session; subjects were allowed the time necessary between sprints to fully recover. This was generally 20 min after long sprints (>180 s) and a minimum of 10 min after shorter sprint tests. Tests were initiated with a 2-s unloaded acceleration followed by the application of the frictional load. Tests were terminated when the subject could not maintain the desired cadence of 100 rpm for 5 s. Subjects were instructed to increase their cadence and allowed 3 s to do so at least once before the investigator stopped the test.

Pedal force provided anaerobically. The force supported by anaerobic metabolism was defined as the difference between the pedal force during each sprint trial (F_{ds}) and the minimum pedal force required to elicit $\dot{V}O_{2\text{ peak}}$ i.e., F_{aer} ($F_{ds} - F_{aer}$). Anaerobic pedal force (F_{an}) values should be regarded as lower limits because they assume the maximum pedal forces that can be supported aerobically in the respective modes are available to subjects throughout the one- and two-legged sprint trials.

In accordance with prior practice (10, 58, 60), we have quantified the mechanical performance supported by anaerobic metabolism to avoid relying on uncertain estimates of the quantities of anaerobic energy released. This approach offers two advantages. First, the mechanical end products of anaerobic metabolism can be accurately measured while the anaerobic energy released cannot be (6, 7, 48). Second, the mechanical measures provide accurate predictions of individual performance capabilities (10, 58, 60) that are not available from the quantitative estimates of the anaerobic energy released during these efforts.

Electromyography. Bipolar surface electromyography (EMG) electrodes were placed on the skin of the dominant leg overlying the muscle belly of the distal portion of vastus lateralis with an inter-electrode distance of 10–14 cm. The reference electrode was placed on the anterior medial aspect of the tibialis. Repeatable electrode placement was achieved by marking the location of each electrode during the first sprint session with indelible ink. Subjects were instructed to reapply the ink as necessary throughout their participation in the study. To reduce electrical impedance, the skin was lightly abraded and cleaned with rubbing alcohol before electrode placement. The surface EMG signals were amplified (1,000–5,000 times) and filtered (100–3,000 Hz half-amplitude band pass and 60 Hz notch filter) using a Grass P511 preamplifier. The analog output from the preamplifier was recorded throughout the duration of each one- and two-legged sprinting bout by a computer using the previously described A/D board with a sampling frequency of 6,000 Hz.

The recorded EMG data were rectified and integrated per contraction (iEMG). Because of the considerable variation in iEMG values that occur from one contraction to the next, we determined the rate of increase in iEMG over the course of the trial by comparing the average of the first five contractile bursts after the load was applied to the average of the last five bursts recorded during each all-out trial. Because we were interested in the increase in iEMG over the course

of the all-out sprint trials rather than the magnitude of the EMG signal, we normalized the start and end iEMG averages to the five contraction average from the start of each trial. We deemed all-out trials of less than 12 s to be too short to obtain consistent within-trial increases in iEMG using our averaging technique.

Data analysis and statistics. For the purpose of comparing condition means for one- and two-legged cycling at common standardized durations, we interpolated the mechanical performance data to durations of 15, 20, 30, 45, 60, 75, 90, 120, 180, 240, and 300 (58). For each subject and condition, the measures of power output and F_{ds} were fit with an iterative procedure in accordance with the general equations provided in Weyand et al. (59).

One- and two-legged means for $\dot{V}O_{2\text{ peak}}$, $\dot{V}O_{2\text{ peak/leg}}$, power output, power output/leg, and F_{ds} at the aerobic limits (F_{aer}) were compared using a paired *t*-test ($\alpha < 0.05$).

RESULTS

Pedal forces at $\dot{V}O_{2\text{ peak}}$. The mean absolute $\dot{V}O_{2\text{ peak}}$ values measured during cycling with one and two legs were 44.4 (± 5.6) and 55.9 (± 8.1) ml O_2 kg/min, respectively, with corresponding power outputs of 196 (± 32) and 305 (± 54) W, respectively. These power outputs were achieved with the significantly greater mean pedal forces (F_{aer}) of 214 (± 34) N during one-legged cycling compared with 166 (± 30) N for two-legged cycling (Fig. 1). When expressed on a per-leg basis, the aerobic limits and power outputs were significantly greater for one-legged cycling. Per-leg values of $\dot{V}O_{2\text{ peak}}$ and power output for two-legged cycling were 27.9 (± 4.0) ml O_2 kg/min and 152 (± 27) W. For efforts below 90% of $\dot{V}O_{2\text{ peak}}$, the relationship between metabolic rate and power output was linear for both one- ($\dot{V}O_2 = 0.20 \cdot \text{power output} + 6.9$) and two-legged ($\dot{V}O_2 = 0.15 \cdot \text{power output} + 10.9$) cycling.

Pedal forces during sprint cycling. The power output per leg and pedal forces (F_{ds}) during the one- and two-legged all-out sprinting bouts decreased with a time course similar to that measured previously for two-legged cycle ergometry (60). The decrements in mechanical performance for a typical subject as the duration of all-out sprinting became more prolonged are illustrated in Fig. 2.

For sprints of equal durations, F_{ds} was greater during one- than two-legged cycling. The power outputs for one-legged

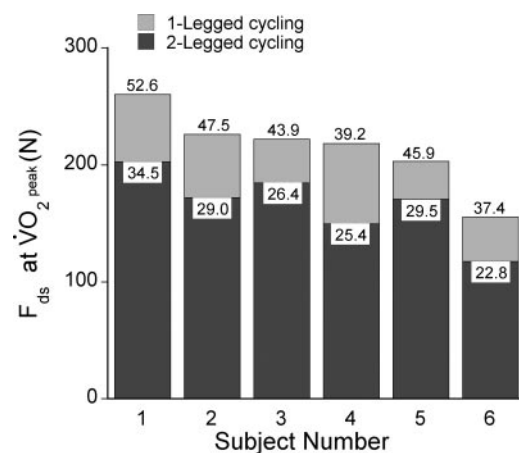


Fig. 1. Numeric values above (one leg) and within the bars (two legs) represent peak rates of oxygen uptake (ml $O_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) per leg for each subject. The minimum pedal force (F_{ds}) eliciting $\dot{V}O_{2\text{ peak}}$ was 30 (9.4)% greater during one- vs. two-legged cycling at a cadence of 100 rpm.

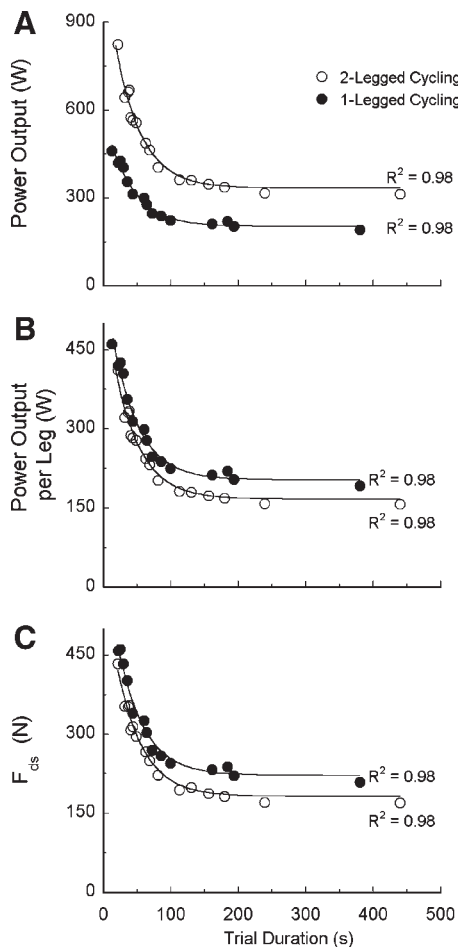


Fig. 2. The decrements in total mechanical power (A), per leg mechanical power (B) and pedal force, F_{ds} (C), vs. the duration of all-out constant load sprints for a representative subject during one- and two-legged cycling.

sprints longer than 120 s required pedal forces that were 24 (± 6)% greater than those of a two-legged sprint of equal duration. For the shortest sprints (i.e., 15 s) the difference in F_{ds} between the two conditions was 16 (10)%.

As anticipated for both one- and two-legged sprints, our estimates of the minimum contribution to force production from anaerobic energy sources decreased with increments in all-out trial duration (Fig. 3). The anaerobic contribution to pedal force for efforts of 15 s was 57 (± 7) and 61 (± 5)% of

Fig. 3. The decrements in pedal force (F_{ds}) vs. the duration of all-out one- (A) and two-legged (B) sprint trials. Shaded areas represent the minimum contribution to force production provided by anaerobic metabolism (F_{an}). The thick vertical line in each panel denotes sprints of equal pedal force ($F_{ds} = 224$ N). The greater maximum aerobic forces during one-legged cycling reduce the reliance on anaerobic metabolism, allowing the required pedal force to be sustained nearly four times as long.

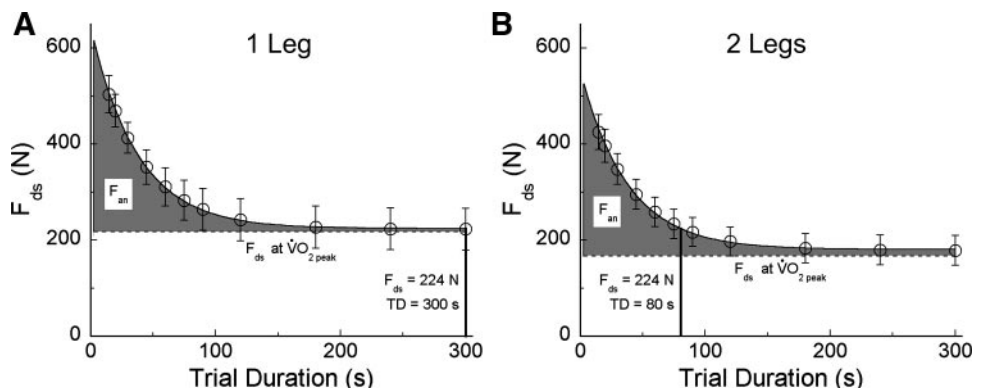


Table 1. Trial durations and F_{an} for one- and two-legged sprints at the same pedal forces

Pedal Force F_{ds} , N	Sprint Duration, s		Anaerobic Force, N		Percent Difference	
	One Leg	Two Legs	One Leg	Two Legs	Duration, %	F_{an} , %
225	241	80	11	59	201	-81
250	106	63	36	84	68	-57
275	80	52	61	109	54	-44
300	64	43	86	134	49	-36
400	33	20	186	234	65	-21

Sprint durations, anaerobic forces (F_{an}), and the respective percent differences [(1L-2L)/2L] for one- and two-legged sprint trial performed at equal pedal force (F_{ds}).

the total during the one- and two-legged conditions, respectively. For longer efforts, 300 s, the anaerobic contribution to force production was only 3 (± 6) and 7 (± 6)% of the total force requirements for the respective conditions.

When considered for trials of equal F_{ds} , two-legged sprints relied more heavily on anaerobic metabolism for force production than one-legged trials (Table 1). For those one- and two-legged trials conducted at equal pedal forces, the proportion of F_{ds} generated anaerobically during the least and most forceful trials was 22 (± 6)% and 11 (4)% greater, respectively, for two- vs. one-legged cycling.

EMG. EMG activity measured per contraction increased throughout the duration of each all-out trial (Fig. 4). Typically, we observed higher rates of iEMG increase (Δ iEMG/ Δ time) during shorter vs. longer trials (Fig. 5). When the rate of increase in iEMG was regressed against F_{ds} , the correlation coefficients of these regressions were high; average R^2 value for one-legged cycling was 0.91 and that for two-legged cycling was 0.93. Slopes for the one- and two-legged conditions varied between individuals but were essentially parallel for five of the six subjects (Fig. 6). The x-intercept of this relationship, the largest F_{ds} with no increase in iEMG, occurred at a greater F_{ds} during one- vs. two-legged cycling for all six subjects.

DISCUSSION

Our results support the hypothesis that the impairment of muscle force production during sprint locomotion has a metabolic basis. As expected, our one- vs. two-legged comparison provided per leg differences in peak rates of aerobic metabolism and pedal forces at $\dot{V}O_{2\text{ peak}}$ of 59 (± 6) and 30 (± 9)%,

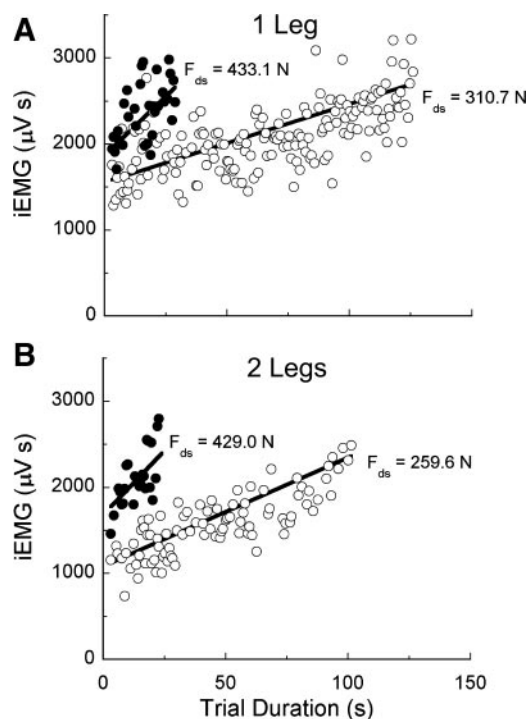


Fig. 4. Contraction-by-contraction rectified and integrated EMG (iEMG) values increased throughout the duration of an all-out sprint trial for both one- (A) and two-legs (B). The solid line joins the means of the first five contractions to that of the final five contractions for each of the sprints shown. Rates of iEMG increase were greater for trials with larger pedal force (F_{ds}) requirements and greater for two- vs. one-legged cycling at similar F_{ds} .

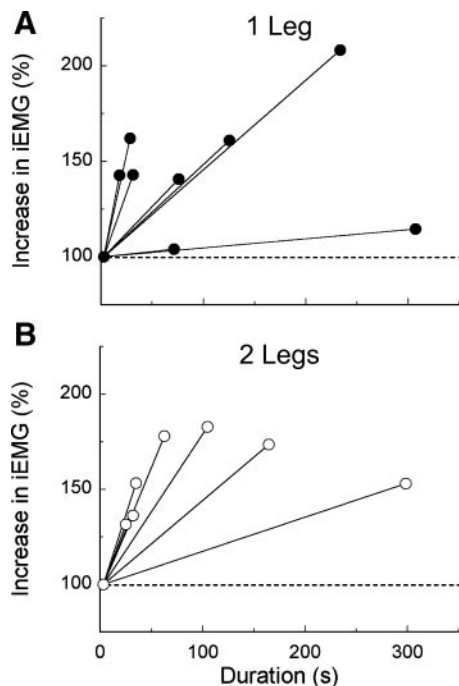


Fig. 5. Rates of iEMG increase from the first five contractions to the last five contractions during the even-numbered, all-out trials completed by subject #1 during one- (A) and two-legged (B) cycling. Rate of iEMG increase (slope of the line) were generally greater for shorter compared with longer trials.

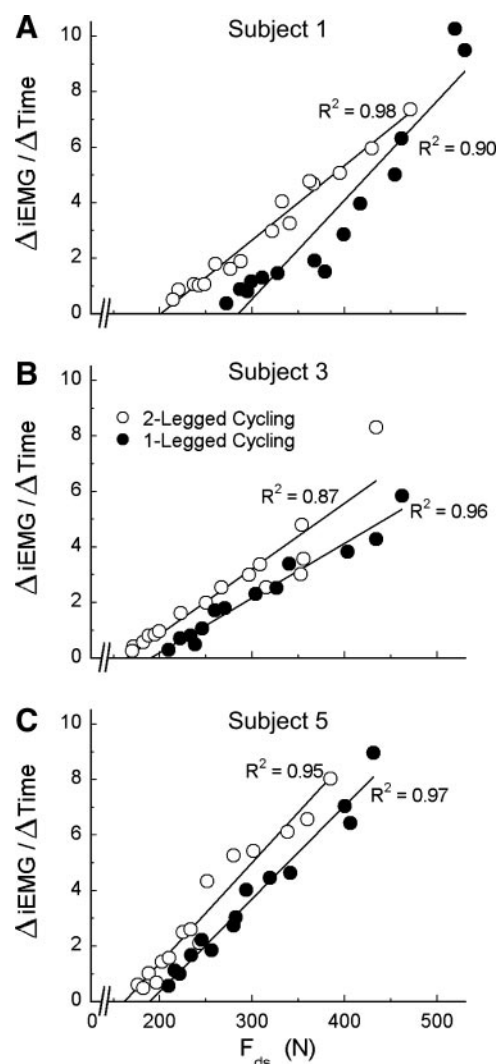


Fig. 6. Rates of iEMG increase ($\Delta iEMG / \Delta Time$) in relation to the pedal forces (F_{ds}) at which one- (A) and two-legged (B) sprint trials were conducted by the odd numbered subjects. At the same F_{ds} , rates of iEMG increase were greater for the mode during which a greater proportion of the force required was provided anaerobically (i.e., two- vs. one-leg condition) (C).

respectively. Additionally, during both one- and two-legged constant-load sprints performed at pedal forces greater than those provided aerobically, we observed the progressive increases in neuromuscular activation that were also expected. The latter result suggests that compensatory motor unit recruitment occurred throughout each trial to provide the muscle force necessary to maintain a constant pedal force. Because of the lesser pedal forces supported aerobically during two-legged cycling, the onset of compensatory muscle recruitment occurred at lower pedal force thresholds in this mode (Fig. 6). Similarly, at equivalent pedal forces, the rates of increase in compensatory neuromuscular activity were greater during two- vs. one-legged sprint cycling. We attribute these between-mode differences in the rates at which muscle force is impaired (i.e., muscle fatigue), and neuromuscular compensation occurs to the greater reliance on anaerobic pathways of ATP resynthesis for force production during two- vs. one-legged cycling.

Muscle recruitment. Our measures of muscle recruitment were determined from positive increments in the integrated surface electromyogram. Recordings from surface EMG are primarily influenced by the volume of active muscle adjacent to the electrodes and the discharge rate of the motor neurons that innervate the active fibers. Distinguishing between these components from surface EMG is not possible, and caution has long been urged when inferring motor control strategies from these measures (34, 39). However, because of the difficulties of identifying individual motor unit action potentials during strong dynamic contractions, very little experimental evidence exists to address which motor control strategy is used (19). During isometric contractions of unfatigued limb muscles, force production is modulated by recruitment for outputs of up to 85% of the maximum level (24), and the available data suggest that the neuromuscular strategy employed during concentric contractions conforms to the same trend (19).

During fatiguing submaximal contractions, measures of EMG are known to increase throughout the effort (8, 23, 33). This response has been attributed to motor unit recruitment because motor neuron firing rates during these contractions have generally decreased or exhibited little net change (1, 8, 27). In the absence of direct measurements, we have assumed that potential changes in firing rates during fatiguing concentric contractions are similar to those that have been measured during equivalent isometric contractions. Given this assumption and the observation that the measured force outputs from the shortest trials were 83 (± 2)% of the predicted maximums for sprint cycling (60), we infer that the measured increase in EMG (Fig. 4) is attributable primarily to motor unit recruitment. Regardless of whether the increase in EMG is achieved through rate coding, motor unit recruitment, or both, our primary finding would be unaffected; a reliance on anaerobic metabolism for force production during sprint efforts compromises muscular force production and triggers compensatory increases in neuromuscular activity.

For each subject, the onset of compensatory neuromuscular activity occurred at greater pedal forces during one- vs. two-legged cycling. Could the muscle force thresholds at which compensatory neuromuscular activity occurred have been the same even though pedal force thresholds were different? Two observations suggest this was not the case. First, within both individual muscles and muscle groups, both oxygen uptake and maximum aerobic force production are consistently greater when the exercise engages a lesser total mass of muscle (5, 15, 50, 53). Previous results from the many one- vs. two-legged cycle ergometry and knee-extension studies indicate greater aerobic force production occurs via higher rates of oxygen uptake in the working muscle (35, 51), rather than through the recruitment of synergist muscles. Supporting this, during one-legged knee-extensions neuromuscular activity has been found to be absent in synergistic muscle groups at work rates up to the aerobic maximum (5). Second, although we cannot exclude the possibility that synergistic muscles proximal to the knee might have been more active during one- vs. two-legged cycling, their anatomy would likely preclude meaningful contributions to the muscle forces required to extend the knee during downstroke. These observations indicate that the pedal force thresholds at which compensatory neuromuscular activity occurred were representative of differences in the quadriceps muscle forces required under the two conditions.

Force decrements and impaired muscle force production. During one- and two-legged all-out cycling trials, the pedal forces (F_{ds}) maintained for the shortest vs. longest sprints differed by 2.3 (± 0.4) fold. For trials lasting between 15 and 300 s, this decrement corresponded to pedal force differences of 250 (± 43) N. The rapid time course for the decrements in external force output supports the idea that the impairment of force production characteristic of muscle fatigue commences at the onset of activity (9). Our results here and elsewhere (60) suggest that duration-dependent decrements in force production are determined by the cumulative duration of the contractions involved and not by limitations in the rates at which ATP can be resynthesized from the metabolic pathways available (47, 52).

Much of the current understanding for the cellular basis of muscle fatigue stems from the rigorous work of Westerblad and colleagues (56, 57) and Allen and colleagues (3, 4). These authors have postulated that the fatiguing mechanisms they propose to be active in vitro can qualitatively account for whole-body performance loss (57). Several quantitative differences between the extent and time course of in vitro vs. in vivo rates of fatigue suggest that current cellular explanations may not generalize to whole-body performances. First, the initial loss of force that Allen and Westerblad (4) attribute to an accumulation of inorganic phosphate may be much less pronounced at physiological temperatures (14, 18). Second, the precipitation of calcium (Ca^{2+}) and inorganic phosphate (P_i) within the sarcoplasmic reticulum depends on a sequence of processes that occur with slow time courses (4, 22, 26). Therefore, this mechanism is unlikely to contribute to the impairment of force production during all-out efforts of durations less than 60 to 120 s (4). In contrast, 70% of the duration-dependent decrements we report here occur within 60 s. Third, there is no in vivo analog to the prolonged period of constant force generation between periods of force loss (3, 57) and because this period of stasis is not always observed in isolated muscle, whether this result is a product of stimulation protocol is unclear (e.g., 11, 32).

Although our results do not identify a cellular mechanism responsible for the impairment of force production during intense sequential contractions, they do provide direct experimental evidence that the onset of fatigue in vivo has a metabolic basis. Contractile inhibition by the metabolic byproducts generated through a reliance on anaerobic energy for ATP resynthesis has long been considered the most likely mechanism responsible for the decrements in force production that occur during fatigue (28, 31). However, experimental perturbations and tests at physiological temperatures have yet to definitively identify a mechanism (14, 18, 49). The results we present here indicate that a dependence on nonoxidative pathways of ATP resynthesis impairs muscle force production during locomotion.

Regardless of the mechanism, the metabolic basis for muscle force impairment and compensatory neuromuscular activity that we report here for one- and two-legged sprint cycling seems likely to be general (10, 58, 60) and to operate similarly in both more and less fit subjects. We expect that the individual force thresholds at which these phenomena are triggered will simply vary directly with the aerobic power of the individual.

Numerous investigators have suggested that there may be no single mechanism responsible for muscle fatigue. During com-

plex tasks (34, 46) and longer-duration efforts (25, 52), the mechanisms inducing failure may differ from those we describe here. However, we believe the mechanism of muscle fatigue that we identify here explains why the duration-dependent decrements in force production that occur during sprint locomotion can be described so accurately in metabolic terms (2, 10, 58, 60). During these and similar dynamic efforts, we suggest that common mechanisms of muscle fatigue are likely present at cellular, tissue, and systemic levels, although the specific mechanisms remain to be firmly established.

We conclude that impaired muscular force production and compensatory neuromuscular activity during sprint locomotion are triggered by a reliance on anaerobic metabolism for force production.

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REFERENCES

- Adam A and De Luca CJ. Firing rates of motor units in human vastus lateralis muscle during fatiguing isometric contractions. *J Appl Physiol* 99: 268–280, 2005.
- Alexander RM. Sprinting and endurance for cyclists and runners. *Am J Physiol Regul Integr Comp Physiol* 290: R757, 2006.
- Allen DG, Lännergren J, and Westerblad H. Muscle cell function during prolonged activity: Cellular mechanisms of fatigue. *Exp Physiol* 80: 497–527, 1995.
- Allen DG and Westerblad H. Role of phosphate and calcium stores in muscle fatigue. *J Physiol* 536: 657–665.
- Anderson P, Adams RP, Sjøgaard G, Thorboe A, and Saltin B. Dynamic knee extension as model for study isolated exercising muscle in humans. *J Appl Physiol* 59: 1647–1653, 1985.
- 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.
- Bangsbo J. Quantification of anaerobic energy production during intense exercise. *Med Sci Sports Exerc* 30: 47–52, 1998.
- Bigland-Ritchie B, Cafarelli E, and Vollestad NK. Fatigue of submaximal static contractions. *Acta Physiol Scand* 128 (Suppl 556): 137–148, 1986.
- Bigland-Ritchie B and Woods JJ. Changes in muscle contractile properties and neural control during human muscular fatigue. *Muscle Nerve* 7: 691–699, 1984.
- Bundle MW, Hoyt RW, and Weyand PG. High-speed running performance: a new approach to assessment and prediction. *J Appl Physiol* 95: 1955–1962, 2003.
- Burke RE, Levine DN, Zajac FE, Tsairis P, and Engel WK. Mammalian motor units: physiological-histochemical correlation in three types of cat gastrocnemius. *Science* 174: 709–712, 1971.
- Consolazio CF, Johnson RE, and Pecora LJ. *Physiological Measurements of Metabolic Functions in Man*. New York: McGraw-Hill, 1963.
- Costill DL. Physiology of marathon running. *JAMA* 221: 1024–1029, 1972.
- Coupland ME, Puchert E, and Ranatunga KW. Temperature dependence of active tension in mammalian (rabbit psoas) muscle fibers: effect of inorganic phosphate. *J Physiol* 536: 879–891, 2001.
- Davies CTM and Sargeant AJ. Physiological responses to one- and two-leg exercise breathing air and 45 percent oxygen. *J Appl Physiol* 36: 142–148, 1974.
- Dawson MJ, Gadian DG, and Wilkie DR. Muscular fatigue investigated by phosphorus nuclear magnetic resonance. *Nature* 274: 861–866, 1978.
- Dawson MJ and Wilkie DR. Human power production in relation to man-powered flight. *Proceedings of the J Roy Aeronaut Soc Symposium on Man-Powered Flight*, 1977.
- Debold EP, Dave H, and Fitts RH. Fiber type and temperature dependence of inorganic phosphate: implications for fatigue. *Am J Physiol Cell Physiol* 287: C673–C681, 2004.
- del Valle A and Thomas CK. Firing rates of motor units during strong dynamic contractions. *Muscle Nerve* 32: 316–325, 2005.
- deVries HA, Moritani T, Nagata A, and Magnussen K. The relation between critical power and neuromuscular fatigue as estimated from electromyographic data. *Ergonomics* 25: 783–791, 1982.
- Duchateau J, Balestra Carpentier AC, and Hainaut K. Reflex regulation during sustained and intermittent submaximal contractions in humans. *J Physiol* 541: 959–967, 2002.
- Duke AM and Steele DS. Mechanisms of reduced SR Ca²⁺ release induced by inorganic phosphate in rat skeletal muscle fibers. *Am J Physiol Cell Physiol* 281: C418–C429, 2001.
- Edwards RG and Lippold OCJ. The relation between force and integrated electrical activity in fatigued muscle. *J Physiol* 132: 677–681, 1956.
- Enoka RM and Fuglevand AJ. Motor unit physiology: some unresolved issues. *Muscle Nerve* 24: 4–17, 2001.
- Fitts RH. Mechanisms of muscular fatigue. In: *Principles of Exercise Biochemistry*, edited by Poortmans, JR. Karger, Basel, Switzerland: Karger, 2004, 3rd rev. ed., vol. 46, p. 279–300.
- Fryer MW, West JM, and Stephenson GD. Phosphate transport into the sarcoplasmic reticulum of skinned fibres from rat skeletal muscle. *J Muscle Res Cell Motil* 18: 161–167, 1997.
- Garland SJ, Enoka RM, Serrano LP, and Robinson GA. Behavior of motor units in human biceps brachii during a submaximal fatiguing contraction. *J Appl Physiol* 76: 2411–2419, 1994.
- Gollnick PD and Hermansen L. Biochemical adaptations to exercise: anaerobic metabolism. *Exerc Sport Sci Rev* 1: 1–43, 1973.
- Hagberg JM, Mullin JP, Giese MD, and Spitznagel E. Effect of pedaling rate on submaximal exercise responses of competitive cyclists. *J Appl Physiol* 51: 1–7, 1981.
- Hill AV. The dimensions of animals and their muscular dynamics. *Sci Prog* 150: 209–230, 1950.
- Hill AV and Kupalov. Anaerobic and aerobic activity in isolated muscle. *Proc R Soc Lond B Biol Sci* 105: 313–322, 1930.
- Hood DA, Gorski J, and Terjung RL. Oxygen cost of twitch and titanic isometric contractions of rat skeletal muscle. *Am J Physiol Endocrinol Metab* 250: E449–E456, 1986.
- Hunter SK, Critchlow A, Shin I, and Enoka RM. Men are more fatigable than strength-matched women performing intermittent submaximal contractions. *J Appl Physiol* 96: 2125–2132, 2004.
- Hunter SK, Duchateau J, and Enoka RM. Muscle fatigue and the mechanisms of task failure. *Exerc Sport Sci Rev* 32: 44–49, 2004.
- Klausen K, Secher NH, Clausen JP, Hartling O, and Trap-Jensen J. Central and regional circulatory adaptations to one-leg training. *J Appl Physiol* 52: 976–983, 1982.
- Koga S, Barstow TJ, Shiojiri T, Takaishi T, Fukuba Y, Kondo N, Shibasaki M, and Poole DC. Effect of muscle mass on VO₂ kinetics at the onset of work. *J Appl Physiol* 90: 461–468, 2001.
- Lakomy HKA. Measurement of work and power output using friction-loaded cycle ergometers. *Ergonomics* 29: 509–517, 1986.
- Lännergren J and Westerblad H. Force decline due to fatigue and intracellular acidification in isolated fibers from mouse skeletal muscle. *J Physiol* 434: 307–322, 1991.
- Lippold OCJ. The relation between integrated action potentials in a human muscle and its isometric tension. *J Physiol* 117: 492–499, 1952.
- Madeleine P, Jørgensen LV, Sjøgaard K, Arendt-Nielsen L, and Sjøgaard G. Development of muscle fatigue as assessed by electromyography and mechanomyography during continuous and intermittent low-force contractions: effects of the feedback mode. *Eur J Appl Physiol* 87: 28–37, 2002.
- Martin JC, Brown NA, Anderson FC, and Spirduso WW. A governing relationship for repetitive muscular contraction. *J Biomech* 33: 969–974, 2000.
- Meyer RA and Terjung RL. AMP deamination and IMP reamination in working skeletal muscle. *Am J Physiol Cell Physiol* 239: C32–C38, 1980.
- Meyers BM and Cafarelli E. Caffeine increases time to fatigue by maintaining force and not by altering firing rates during submaximal isometric contractions. *J Appl Physiol* 99: 1056–1063, 2005.

44. **Morin JB and Belli A.** A simple method for measurement of maximal downstroke power on friction-loaded cycle ergometer. *J Biomech* 37: 141–145, 2004.
45. **Moritani T, Takaishi T, and Matsumoto T.** Determination of maximal power output at neuromuscular fatigue threshold. *J Appl Physiol* 74: 1729–1734, 1993.
46. **Mottram CJ, Jakobi JM, Semmler JG, and Enoka RM.** Motor-unit activity differs with load type during a fatiguing contraction. *J Neurophysiol* 93: 1381–1392, 2005.
47. **Nevill ME, Bogdanis GC, Boobis LH, Lakomy HKA, and Williams C.** Muscle metabolism and performance during sprinting. In: *Biochemistry of Exercise IX*, edited by Maughan RJ and Shireffs SM. Champaign, IL: Human Kinetics, p. 243–259, 1996.
48. **Olesen HL.** Accumulated oxygen deficit increases with the inclination of inclined running. *J Appl Physiol* 73: 1130–1134, 1992.
49. **Pate E, Bhimani M, Franks-Skiba K, and Cooke R.** Reduced effect of pH on skinned rabbit psoas muscle mechanics at high temperatures: implications for fatigue. *J Physiol* 486: 689–694, 1995.
50. **Richardson RS, Kennedy B, Knight DR, and Wagner PD.** High muscle blood flows are not attenuated by recruitment of additional muscle mass. *Am J Physiol Heart Circ Physiol* 269: H1545–H1552, 1995.
51. **Rowell LB, Saltin B, Kiens B, and Christensen NJ.** Is peak quadriceps blood flow in humans even higher during exercise with hypoxemia? *Am J Physiol Heart Circ Physiol* 251: H1038–H1044, 1986.
52. **Sahlin K, Tonkonogi M, and Soderlund K.** Energy supply and muscle fatigue in humans. *Acta Physiol Scand* 162: 261–266, 1998.
53. **Saltin B, Nazar K, Costill DL, Stein E, Jansson E, Essén B, and Gollnick PD.** The nature of the training response; peripheral and central adaptations to one-legged exercise. *Acta Physiol Scand* 96: 289–305, 1976.
54. **Sargeant AJ and Davies CTM.** Forces applied to cranks of a bicycle ergometer during one- and two-leg cycling. *J Appl Physiol* 42: 514–518, 1977.
55. **Thomas CK, and del Valle A.** The role of motor unit rate modulation versus recruitment in repeated submaximal voluntary contractions performed by control and spinal cord injured subjects. *J Electromyogr Kinesiol* 11: 217–229, 2001.
56. **Westerblad H, Allen DG, and Lannergren J.** Muscle fatigue: lactic acid or inorganic phosphate the major cause? *News Physiol Sci* 17: 17–21, 2002.
57. **Westerblad H and Allen DG.** Cellular mechanisms of skeletal muscle fatigue. In: *Molecular and Cellular Aspects of Muscle Contraction*, edited by Sugi H. New York: Kluwer Academic/Plenum, 2003, p. 563–571.
58. **Weyand PG and Bundle MW.** Energetics of high-speed running: integrating classical theory and contemporary observations. *Am J Physiol Regul Integr Comp Physiol* 288: R956–R965, 2005.
59. **Weyand PG, Lee CS, Martinez-Ruiz R, Bundle MW, Bellizzi MJ, and Wright S.** High-speed running performance is largely unaffected by hypoxic reductions in aerobic power. *J Appl Physiol* 86: 2059–2064, 1999.
60. **Weyand PG, Lin JE, and 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.
61. **Weyand PG, Sternlight DB, Bellizzi MJ, and Wright S.** Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J Appl Physiol* 89: 1991–1999, 2000.
62. **Wilkie DR.** Shortage of chemical fuel as a cause of fatigue: studies by nuclear magnetic resonance and bicycle ergometry. *Ciba Found Symp* 82: 102–119, 1981.





Mechanical limits to running speed: set by limb force maximums or stance time minimums?

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**Mechanical limits to running speed:
set by limb force maximums or stance time minimums?**

Peter G. Weyand¹, Rosalind F. Sandell¹, Danille N.L. Prime¹
and *Matthew W. Bundle^{1,2}

¹Rice University, Locomotion Laboratory, Kinesiology Department
Houston, Texas 77005

²University of Wyoming, Biomechanics Laboratory, College of Health Sciences,
Laramie WY 82071

key words: skeletal muscle, muscle mechanics, twitch times, performance, locomotion

Running head: speed limits in bouncing gaits

*Address correspondence to:

Matthew W. Bundle
Biomechanics Laboratory
College of Health Sciences, Dept. 3196
1000 E. University Avenue
Laramie, WY 82071
email: mbundle@uwyo.edu

Abstract

Why are the swiftest human runners unable to reach running speeds of 50 to 65 kilometers per hour when canine and equine athletes do so routinely? We hypothesized that top running speeds are limited, not by how much force the limbs can apply to the ground, but by the minimum time needed to apply the forces necessary. One-legged hopping and backward running were used as experimental contrasts to forward running to test these respective hypotheses. In each of the three gaits, seven athletic subjects completed progressive discontinuous treadmill tests to failure to determine their top speeds. Vertical ground reaction forces (in body weights, W_b) and periods of ground force application (T_c) were measured using a custom, high-speed force treadmill. At top speed, we found that both the stance-averaged (F_{avg}) and peak (F_{peak}) vertical forces applied to the treadmill surface during one-legged hopping exceeded those applied during forward running by more than one-half of the body's weight [$F_{avg} = 2.71 \pm 0.15$ vs. $2.08 \pm 0.07 W_b$; $F_{peak} = 4.20 \pm 0.24$ vs. $3.62 \pm 0.24 W_b$] and that hopping periods of force application were significantly longer [$T_c = 0.160 \pm 0.006$ vs. 0.108 ± 0.004 s]. Next, we found that the periods of ground force application at top backward and forward running speeds were nearly identical, agreeing with one another to within an average of 0.006 s [$T_c = 0.116 \pm 0.004$ s vs. 0.110 ± 0.005 s]. We conclude that running speed is limited, not by the maximum forces that the limbs can apply to the ground, but rather by the minimum time they need to apply the large mass-specific forces necessary.

Introduction

The prospect of humans running at speeds in excess of 50 to 65 kilometers per hour seems science fictional, but why? Racing horses, dogs, and even hopping kangaroos can readily travel at these speeds. Moreover, these animals do so with biological tissues and gait mechanics that are similar to those of human runners. Their muscles, tendons and bones are made of the same materials and work in much the same way as those of humans (5, 13, 22, 30, 34). Additionally, these species, like humans, enhance locomotor performance by using their limbs in a spring-like manner to ‘bounce’ along the ground much like a rubber ball once they are up to speed (9, 10). These fundamental tissue and gait similarities beg a basic question: what factors prevent humans from running at much faster speeds than they actually do?

The explanation undoubtedly involves both the stride mechanics selected in bouncing gaits and the functional limits of the biological tissues used to execute them. However, how these factors interact to impose the speed limits of terrestrial animals is largely unknown. Conceivably, a limit could be imposed by either how rapidly the limbs can be repositioned, or by how much force they can apply to the ground during each step, or perhaps some combination of the two. Here, we reasoned that the skeletal muscles that confer performance capabilities would most likely operate at their functional limits during the portion of the stride cycle in which they are most active. Accordingly, we focused on the mechanics of applying force to the ground (25, 29, 31, 33, 40), and not the repositioning of the limbs in the air. We deemed a direct functional limitation imposed via swing mechanics unlikely given the similar swing times of fast and slow runners at their very different top speeds (40). In contrast, both the magnitude and duration of

ground force application differs markedly between runners who vary in sprinting ability. Moreover, the large and rapid ground forces required for running cannot be supplied passively. These forces must be provided by the contractile activity of the limb muscles and the skeletal transmission of the muscular forces to the ground.

The possibility that ground force requirements may impose a direct limit to human running speed is consistent with the fundamental mechanics established for terrestrial gaits over the last half century. The classical studies of Cavagna, Taylor and colleagues indicate that the primary challenge that running and hopping animals face when traveling at steady speeds on flat surfaces is elevating the body against gravity to prepare for the next step (9, 10, 25, 33, 35). Because the forces necessary to overcome air resistance are relatively minor, animals can maintain their forward speed by applying sufficient force during each ground contact period to get the body back up into the air. Indeed, the ground reaction forces measured for the many species tested thus far support this general strategy: the peak forces applied horizontally to the surface are only one-third to one-tenth of those applied vertically (10, 11). Thus, the limb and muscle forces required to maintain the horizontal velocity of the center of mass are relatively small, while those required to lift and support the body are considerable.

How might ground force requirements limit human running speed? Conceivably, a barrier to faster speeds could be imposed by either the maximum amount of force the limbs can apply to the ground or the minimum time needed to apply the force necessary. Although both requirements are plausible given the gait mechanics runners use to increase their speeds, the amounts of force required seem less likely to be limiting than the brief contact periods during which these forces must be applied. Consider that as

athletic humans increase their speeds from a jog of 2 m/s to a sprint of 10 m/s, the average vertical forces they apply during the period of foot-ground contact typically increase from roughly 1.4 to 2.2 times the body's weight (40, 41). Over the same speed range, the duration of foot-ground contact decreases from roughly 0.3 seconds to 0.1 seconds (40). Thus, to achieve this 5-fold increase in speed, human runners increase the amount of force they apply to the running surface by roughly one and one-half times and the rates at which these forces are applied by a factor of three.

We undertook this study to answer a basic question: what imposes the mechanical limit to human running speed? The relative force and rate requirements for increasing running speed, and the force (1, 36) and rate properties of the muscles of the human limb (19, 20, 23), led us to hypothesize that human speed is limited, not by how much force the limbs can apply to the ground, but rather by how rapidly the limbs can do so. We employed two gaits as experimental tools for evaluating the potential limits present during forward running. We used one-legged hopping to alter the amount of force applied to the ground, and backward running to alter the rates of ground force application. We anticipated that the alternative mechanics of these gaits would allow us to evaluate two specific expectations. First, in keeping with the expected absence of a limitation on maximal limb force, we predicted that the forces applied at top speed would be greater for one-legged hopping than for forward running. Second, in keeping with the expected rate limitation, we predicted that the periods of foot-ground contact during which force is applied would fall to the same minimum values at the different top speeds attained during backward and forward running.

Methods

Experimental Design

We began the quantitative evaluation of our two hypotheses by developing a relationship expressing speed in terms of the force and time variables we wished to test as potential limits. We recognized that we could accomplish this in a manner applicable to all 3 gaits by expressing the lengths of the step taken in terms of the ground forces applied, and the frequencies of these steps in terms of the durations of foot-ground force application. Hence, our first step was simply to express speed as the product of the length and frequency of the steps taken:

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

where L_{step} is the distance traveled in the air between consecutive footfalls and $\text{Freq}_{\text{step}}$ is the number of steps taken per unit time. Under conditions in which speed is constant and the center of mass has the same height at the first and last instants of the foot-ground contact period, the average vertical force applied during the contact period, when expressed in relation to the body's weight (F_{avg}/W_b), equals the ratio of the total step time (T_{step}) to contact time (T_c) and the ratio of the step length (L_{step}) to contact length (L_c):

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

By multiplying the far left and right-hand terms in eq. 2 through by L_c , the distance traveled in the air between consecutive footfalls, or L_{step} , can be expressed as the product

of the average vertical force applied to the surface in relation to the body's weight and the forward distance through which the body travels, respectively, during the time of foot-ground contact:

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

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

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

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

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

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

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

Eq. 6 expresses speed in terms of the respective force (F_{avg}/W_b) and time (T_c) variables we sought to test our maximum force and minimum time hypotheses.

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

We chose backward running as an experimental tool because we knew from prior experience at slower speeds (43) that runners apply similar ground forces (F_{avg}/W_b), but do so with shorter contact lengths, L_c , when running backward vs. forward. Because running speed is equal to L_c/T_c , and L_c was expected to be relatively shorter when traveling backward, we anticipated that our subjects would have shorter periods of foot-ground contact (T_c) during backward versus forward running at common speeds. In accordance with our second hypothesis that running speed is limited by the minimum periods during which the limbs can apply the force needed, we predicted that for each subject T_c would fall to the same minimum values at the respective top backward and forward running speeds.

Recognizing that *Eqs. 1-6* apply equally to male and female runners and hoppers, we recruited both male and female subjects thereby allowing our two hypotheses to be tested over a relatively broad range of top speeds, ground support forces and foot-ground contact times.

We evaluated our limb force hypothesis exclusively in terms of the forces applied to the treadmill surface in the vertical plane. Horizontal forces were not included because they were not necessary for testing either of our two hypotheses. In the first case, a limitation on limb force would most likely be incurred in the middle third of the stance phase when the greatest ground and muscle forces are required (6, 26, 31); the horizontal forces at this time of the stance phase are close to zero. In the second case, minimum periods of foot-ground force application can be measured with great precision from the vertical force signal alone (24, 40).

Finally, we conducted our experiments on a treadmill rather than an overground runway with an in-ground force plate because the considerable advantages the treadmill offered for our experimental objectives. In contrast to a runway, the treadmill allows trial data to be collected for numerous consecutive footfalls, at the precise speeds of interest, and at the constant speeds dictated by the treadmill rather than the more variable speeds selected by the subject. We were well-assured from previous studies that our treadmill data will generalize to overground conditions because neither the mechanics of ground force application (17) being tested, nor the sprint running performances (7) of athletic subjects vary under the two conditions.

Subjects and Participation

We undertook our first and second hypothesis tests sequentially, with our Part I comparison of the F_{avg}/W_b values obtained during top speed forward running and one-legged hopping concluding in the Winter of 2007, and our Part II comparison of the minimum T_c values obtained during top speed forward and backward running being

completed in the Spring of 2007. A total of ten subjects, five males and five females volunteered and provided written informed consent in accordance with the requirements of the Institutional Review Board of Rice University. Nine of the ten subjects had competitive athletic experience and nine were regularly active at the time of the study. Six subjects were competitive track athletes: two were competitive horizontal jumpers, two were combination sprint/jump specialists, one was a 400 meter runner, and one was a 400 meter hurdler. Three of the four remaining subjects were regularly active at the time of the study, with one each participating in rugby, basketball and step aerobics. The fourth subject was not active outside of her treadmill sessions at the time of the study.

Part I: One-legged Hopping vs. Forward Running: A total of 7 subjects, 4 male (mass 69.0 ± 2.0 kg; leg length (L_o) 0.93 ± 0.02 m, means $\pm$ SE) and 3 female (mass 63.3 ± 1.2 kg, L_o 0.90 ± 0.05 m) volunteered to serve as subjects in Part I. Subjects were habituated to treadmill running during one practice session and to one-legged hopping during either one or two habituation sessions before any top speed trials took place. The hopping habituation process was generally shorter for those subjects who were competitive jumpers ($n = 3$ in Part I) all of whom had extensive experience with plyometric and bounding drills.

Part II: Backward vs. Forward Running: A total of 7 subjects, 3 male (mass 67.2 ± 0.3 kg, L_o 0.97 ± 0.01 m) and 4 female (mass 61.9 ± 1.5 kg, L_o 0.97 ± 0.04 m) volunteered and participated in Part II. Four of these subjects continued their participation after Part I while 3 Part I subjects were no longer available for testing. Therefore, the three newly

recruited subjects in Part II completed the backward and forward running protocols without completing the one-legged hopping protocol. All 7 subjects in Part II were habituated to forward running with one practice session and backward running with two or more sessions. All subjects completed a minimum of three total backward running treadmill sessions.

Measurements

Top Speed (m s^{-1}): All testing was conducted on a custom high-speed force treadmill (AMTI, Watertown, MA, USA) in the Locomotion Laboratory of Rice University with the subjects strapped into a safety harness that would suspend them above the treadmill in the event of a fall. Top speeds in all three gaits were determined via a progressive, discontinuous test to failure as follows. After a brief warm-up, the tests for each gait began at a trial speed between 2.0 and 3.0 m s^{-1} . The speed for successive trials was typically increased by 0.5 to 1.0 m s^{-1} at slower speeds and 0.2 m s^{-1} at faster ones. All tests continued through a trial speed at which the subject was unable to complete the prescribed number of steps without drifting backward on the treadmill. Two to three attempts were typically made at the failure speed before the test was terminated. In every case, the top speed successfully attained was within 0.2 m s^{-1} of the failure speed. For each running and hopping trial, the treadmill belt was set at the desired trial speed while the subject stood on the treadmill platform straddling the moving belt. Once the belt had reached the desired speed, subjects transferred their weight onto the moving belt using the handrails adjacent to the treadmill and fixed at waist height. Subjects were allowed to take as many handrail-assisted steps as they chose prior to release. Trials were

considered successful if a minimum of eight running or four hopping steps were completed without backward drift after full release of the handrails. Non-top speed trials generally lasted 10 to 20 seconds. Subjects were encouraged to take as much rest as necessary for full recovery between trials. They generally chose to take less than one minute between trials at slow and intermediate speeds and from one to ten minutes between the fastest ones.

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

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

Forces (F_{avg}/F_{wb} , $\times W_b$): The average vertical ground reaction force applied during the contact period was determined from the time during which the vertical force signal exceeded a threshold of 40 N. Forces expressed as multiples of the body's weight were determined by dividing the force recorded during each trial by the weight of the subject recorded on a platform scale immediately prior to treadmill testing (Fig. 1).

F_{peak} (F_{peak}/F_{wb} , $\times W_b$): Peak forces were the highest vertical ground reaction force values recorded over a 0.005 s interval during the last 80% of the foot-ground contact period. This practice discounted the early impact force peaks that can, in some instances (see Fig. 1B) exceed the limb force peaks that typically occur in the middle third of the contact period (26).

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

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

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

Effective Impulse (Imp_{Eff} , $W_b \cdot s$): The effective impulse, or the product of the vertical force applied in excess of the body's weight [$(F_{avg}/W_b) - 1$; i.e. the force responsible for

elevating the body against gravity], and the period of foot-ground contact during which this force is applied.

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

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

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

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

Statistics

We evaluated the between gait comparisons (1-Leg Hop vs Fwd Run and Bwd Run vs Fwd Run) for top speeds as well as F_{avg}/W_b , F_{peak} , L_c , L_{step} , T_c , T_{aer} , and $\text{Freq}_{\text{step}}$ using Student's paired T-tests in accordance with the expectations and hypothesis explicitly stated in the Experimental Design. All tests of significance were conducted with a critical alpha level of $P < 0.05$.

Results

Gait Mechanics as a Function of Speed

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

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

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

Gait Mechanics at Top Speed

Top Speeds (m s^{-1}): Top speeds and mean values for all of the mechanical variables in equation 6 are presented in Table 1 for the two experimental gaits with their corresponding forward running comparisons.

Four and six subjects, respectively, completed second one-legged hopping and backward running top speed treadmill tests on different days. For one-legged hopping, all duplicate top speed trials agreed to within 0.2 m s^{-1} or less with two subjects each being faster and slower, respectively, on their second trial. For backward running, all tests agreed to within 0.1 m s^{-1} with four subjects attaining identical top speeds on both trial days, and the remaining two running 0.1 m/s faster on the day of the second trial.

Forces (F_{avg} and F_{peak} , $\times W_b$): Both the stance-averaged and peak vertical forces applied to the treadmill surface at the respective top speeds (Fig. 5) in our first gait comparison were, on average, more than $0.5 W_b$ greater during one-legged hopping than forward running (2.71 ± 0.15 vs. $2.08 \pm 0.07 W_b$ and 4.20 ± 0.24 vs. $3.62 \pm 0.24 W_b$, respectively). Stance-averaged and peak vertical forces were also lower during backward than forward running (1.75 ± 0.05 vs. $2.10 \pm 0.07 W_b$, and 3.05 ± 0.11 vs. $3.60 \pm 0.24 W_b$, respectively; Fig. 5 and 6).

Contact lengths (L_c , m): The forward distance the body traveled during the period of foot-ground contact was not significantly different during top speed one-legged hopping and forward running (0.89 ± 0.05 vs. $0.98 \pm 0.04 \text{ m}$, respectively). In contrast, top speed

backward running contact lengths were significantly shorter than those used during forward running (0.74 ± 0.05 vs. 0.99 ± 0.03 m, respectively).

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

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

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

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

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

Discussion

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

Hypothesis Test 1: One-legged hopping versus forward running

We selected one-legged hopping as an experimental gait to test the prevailing view that maximum limb extensor forces likely limit all-out running speeds on straight and moderately curved paths (12, 18, 37, 38). At common speeds, the need during one-legged hopping to reposition the same leg for consecutive periods of ground force

application (Fig. 1B), did elevate both the aerial times and vertical forces required to attain them in comparison to forward running (Fig. 1B and 2). However, the outcome of primary relevance was whether the ground forces applied at top speed would be greater in this gait versus those applied during forward running. This was the case (Fig. 3, 5 and 6A): the average and peak vertical forces applied to the treadmill were 30.3 and 16.0% greater, respectively, for one-legged hopping than forward running. Although individual variability was present in the difference in force observed between the two gaits (i.e. the force reserve, Fig. 3), every subject applied greater average and peak forces while hopping on one leg than while running forward. Clearly, the ground forces applied during top speed forward running are substantially less than the maximums their limbs are capable of delivering to the running surface.

Why would runners apply forces during all-out sprinting efforts that are substantially less than maximal, particularly if doing so would limit the very performances they are attempting to maximize? Simply because the periods of foot-ground force application at top forward running speeds are too brief to allow the limb extensor muscles to develop maximum force. The profile of the ground reaction force (Fig. 5), the posture of the limb during high-speed running (6) and *in vivo* muscle force data (31) indicate that the forces generated by the extensor muscles peak roughly halfway through the contact period. While these muscles are clearly activated well before the limb contacts the ground (29, 31), there is no appreciable development of muscular force until contact occurs (31). Accordingly, a reasonable approximation of the time to peak muscle tension is one-half of the measured periods of foot-ground contact. For the

athletic subjects tested here, this half-period was 55 ± 3 ms at their top forward running speeds.

Several pieces of experimental evidence support the conclusion that the periods of foot-ground force application during sprint running are too short to allow the forces produced by the limb muscles to reach their contractile maximums (19, 20, 23). The time course of the development and transmission of muscular force *in vivo* in response to a single electrical impulse, or twitch, in human knee and ankle extensors is 81 and 120 ms, respectively, in young adult males (19). Thus, the periods required for the limb muscles to generate and transmit peak twitch forces *in vivo* are roughly two times longer than the time available during top speed running (Fig. 5). Moreover, if we assume that the knee and ankle extensor muscles develop force at their maximal tetanic contraction rates (dP_{50} : 19) throughout the 55 ms first half the foot-ground contact period, these muscle groups would reach only 46 and 22%, respectively, of their force maximums.

Hypothesis Test II: Backward versus Forward Running

Our second primary finding that the periods of force application during top speed backward and forward running did not differ, is most easily interpreted if the ground force requirements of these gaits were equivalent. However, both the average and the peak forces observed in these two gaits at top speed were lower during backward vs. forward running (Table 1). The different patterns of ground force application in the two gaits (Fig. 5) results in part from a different orientation of the limb during backward running (43) that requires the extensor muscles to generate 1.14 times more force per unit ground force applied than during forward running. If we adjust for this factor, the

average and peak forces required of the limb extensor muscles at the respective top speeds in these gaits were not different and agreed to within 5.3 ± 0.06 and $3.4 \pm 0.06\%$, respectively. Thus, the minimum times of force application observed at the different respective top speeds in these two gaits were nearly identical when the forces required of the extensor muscles during the contact period were the same.

A logical question raised by our finding that the brief durations of ground force application limit the maximum ground forces that can be applied, is why runners do not choose to take the greater contact lengths and times that would allow them to apply greater ground forces? A considerable body of evidence indicates that the large ground and muscle forces required to support the body's weight constrain the excursions of the stance limb to a relatively narrow range of positions directly underneath the body (4, 6, 11, 25, 28). When limb excursion angles and contact lengths are increased beyond those selected naturally, performance suffers because both the limb's mechanical advantage and the natural spring-like rebound of the body in the latter portion of the contact period are compromised (16, 28).

Gait Mechanics and Sprinting Performance

Our findings here also offer insight into which gait mechanics can and cannot be modified to bring about changes in sprinting performance. Two features of bouncing gaits have emerged as being mechanically constrained: contact lengths and swing times. In a previous investigation, we reported that there was little to no difference in the time that fast and slow runners take to reposition their limbs at top speed (40). Although sprint athletes have muscle fibers with faster contractile kinetics (14), faster muscle fibers

do not appear to confer appreciable reductions in either aerial or swing periods at top speed. Nonetheless, the minimum time for completing the swing process (343 ± 6 ms), and the accompanying aerial times required for doing so, do have a direct effect on the top speeds attained (*Eq. 6*). As can be seen for the three gaits illustrated in Fig. 6, the greater the aerial time requirement of the gait, the greater the slope of the force-speed relationship and the greater the force required to attain a given top speed.

The third constraint that has emerged here is largely biological: the lower limit to the periods of foot-ground contact during which the necessary ground forces can be applied. This limit clearly varies between individuals, and likely does so in accordance with the individual differences in the contractile speeds of the fibers of the limb muscles. Here, within each of the three gaits examined (Fig. 6), and also previously (40), we found that faster subjects were able to apply greater mass-specific ground forces and to do so with shorter foot-ground contact times. Both capabilities would be expected to be conferred by limbs with faster muscle fibers (8, 39).

These results identify two interventions, one physiological and one anatomical, that would improve performance within the mechanical constraints that bouncing gaits impose. First, muscle fibers with more rapid contractile kinetics (32) would allow greater ground forces to be applied during the brief foot-ground contact periods that sprinting requires. How fast might these faster muscle fibers allow humans to run? The quantitative relationships established in the Methods can be used to estimate the top speeds that would be theoretically possible with muscle fibers sufficiently rapid to allow our subjects to apply their hopping ground force maximums while running. If we assume no change in contact lengths or the minimum aerial times needed to reposition the swing

limbs at top speed, the average and greatest individual top speed hopping forces of 2.71 and 3.35 W_b would allow respective top running speeds of 14.0 and 19.3 $m \cdot s^{-1}$ to be attained. Second, artificially lengthening the limbs, as would be theoretically possible in trans-tibial amputees, would substantially increase the top running speed attained at the minimum period of foot-ground force application. For example, a relatively small increase in leg length of 10 cm would increase contact lengths by nine cm and the top speeds of the subjects tested here from 9.1 to 9.8 $m \cdot s^{-1}$. The calculations and theoretical values that would result from these two interventions appear in the Appendix.

Concluding Remarks

Finally, while muscle fibers with relatively slow contractile kinetics do limit sprint running performance, slower fibers also economize the forces produced during standing and walking (3, 25, 39) and confer greater tendon and bone safety margins during rapid weight-bearing movements (4, 39). The latter benefits may explain why the fastest animal sprinters have adapted for running speed with little apparent alteration in muscle fiber speeds. The muscles of cheetahs and greyhounds function at rates that differ little from those of other running animals (15, 42). Rather, these animals have adapted for speed by developing gait mechanics that prolong their periods of ground force application. These quadrupeds gallop with pronounced backbone bending that markedly increases their foot-ground contact times and lengths (2, 21). As a result, these sprint specialists can have contact lengths (37) that approach those of humans even though their limbs are only half as long (27).

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Because humans have limbs of moderate length and cannot gallop, they lack similar options for prolonging periods of foot-ground force application in order to sprint faster. Consequently, human running speeds in excess of 50 kilometers per hour are likely to be limited to the realms of science fiction, and not inconceivably, gene doping.

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Appendix

Our results and the quantitative relationships provided in the Methods, permit a theoretical assessment of the top running speeds attained by limbs capable of applying greater forces to the ground or those that have been artificially lengthened. The estimates that appear in the Discussion and Appendix Table 1 were determined by:

substituting Eq. 4

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

into Eq. 2 to give

$$F_{\text{avg}} / W_b = \frac{T_c + T_{\text{aer}}}{T_c} \quad \text{Eq. 7}$$

which was solved with respect to T_c to yield

$$T_c = \frac{T_{\text{aer}}}{\left(\frac{F_{\text{avg}}}{W_b} - 1\right)} \quad \text{Eq. 8}$$

Eq. 8 was then substituted into Eq. 6

$$\text{Speed} = \left[\frac{F_{\text{avg}}}{W_b} \bullet L_c \right] \bullet \left[\frac{T_{\text{aer}}}{\left(\frac{F_{\text{avg}}}{W_b} - 1\right)} + T_{\text{aer}} \right]^{-1} \quad \text{Eq. 9}$$

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

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References

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

40: 149-154, 1976.

15. Dobson GP, Parkhouse WS, Weber JM, Stuttard E, Harman J, Snow DH and Hochachka PW. Metabolic changes in skeletal muscle and blood of greyhounds during 800-m track sprint *Am J Physiol Reg Int Comp* 255: R513-R519, 1988.

16. Farley CT and Gonzalez O. Leg stiffness and stride frequency in human running. *J Biomech* 29: 181-186, 1996.

17. Ferris DP, Louie M and Farley CT. Running in the real world: adjusting leg stiffness for different surfaces. *Proc R Soc Lond B Biol Sci* 265: 989-994, 1998.

18. Greene PR. Running on flat turns: experiments, theory and applications. *J Biomech Eng* 107: 96-103, 1985.

19. Harridge SDR, Bottinelli R, Canepari M, Pellegrino MA, Reggiani C, Esbjörnsson M and Saltin B. Whole-muscle and single fibre contractile properties and myosin heavy chain isoforms in humans *Pflugers Arch* 432: 913-920, 1996.

20. Harridge SDR, Bottinelli R, Canepari M, Pellegrino C, Reggiani C, Esbjörnsson M, Balsom PD and Saltin B. Sprint training, in vitro and in vivo muscle function and myosin heavy chain expression. *J Appl Physiol* 84: 442-449, 1998.

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

22. Hill AV. The dimensions of animals and their muscular dynamics. *Sci Prog* 38: 209-230, 1950.

23. Korhonen MT, Cristea A, Markku A, Hakkinen K, Sipila S, Mero A, Viitasalo JT, Larsson L and Suominen H. Aging, muscle fiber type and contractile function in sprint-trained athletes *J Appl Physiol* 101: 906-917, 2006.

24. Kram R and Powell AJ. A treadmill mounted force platform. *J Appl Physiol* 67: 1692-1698, 1989.

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

26. Kuitunen S, Komi PV and Kyrolainen H. Knee and ankle joint stiffness in sprint running. *Med Sci Sports Exerc* 34: 166-173, 2002.

27. Lee DV, Bertram JEA and Todhunter RJ. Acceleration and balance in trotting dogs. *J Exp Biol* 202: 3565-3573, 1999.

28. McMahon, TA, Valiant G and Frederick EC. Groucho running. *J Appl Physiol* 62: 2326-2337, 1987.

29. Mero A, Komi PV and Gregor RJ. Biomechanics of sprint running *Sports Med* 13: 376-392, 1992.
30. Pollock CM and Shadwick RE. Relationship between body mass and biomechanical properties of limb tendons in adult mammals. *Am J Physiol* 266: R1016-R1021, 1994.
31. Roberts TJ, Marsh RL, Weyand PG and Taylor CR. Muscular force in running turkeys: the economy of minimizing work. *Science* 275: 1113-1115, 1997.
32. Rome LC and Lindstedt SL. The quest for speed: muscles built for high-frequency contractions. *News Physiol Sci* 13: 261-268, 1998.
33. Taylor CR. Force development during sustained locomotion: a determinant of gait, speed and metabolic power. *J Exp Biol* 115: 253-262, 1980.
34. Taylor CR. Relating mechanics and energetics during exercise. *Adv Vet Sci Comp Med* 38A: 181-215, 1994.
35. Taylor CR, Heglund NC, McMahon TA and Looney TR. Energetic cost of generating muscular force during running: a comparison of large and small animals. *J Exp Biol* 63: 775-779, 1980.
36. Thorpe SK, Li Y, Crompton RH and Alexander RM. Stresses in human leg muscles in running and jumping determined by force plate analysis and from published magnetic resonance images. *J Exp Biol* 201: 63-70, 1998.
37. Usherwood JR and Wilson AM. No force limit on greyhound sprint speed. *Nature* 438: 753-754, 2005.
38. Usherwood JR and Wilson AM. Accounting for elite indoor 200 m sprint results *Biol Lett* 2: 47-50, 2006.
39. Walmsley B, Hodgson JA and Burke RE. Forces produced by medial gastrocnemius during locomotion in freely moving cats. *J Neurophys* 41: 1203-1216, 1978.
40. Weyand PG, Sternlight DB, Bellizzi MJ and Wright S. Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J Appl Physiol* 81: 1991-1999, 2000.
41. Weyand PG and Davis JA. Running performance has a structural basis. *J Exp Biol* 208: 2625-2631, 2005.
42. Williams TM, Dobson GP, Mathieu-Costello O, Morsbach D, Worley MB and Phillips JA. Skeletal muscle histology and biochemistry of an elite sprinter, the African cheetah. *J Comp Physiol B* 167: 527-535, 1997.

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43. Wright S and Weyand PG. The application of ground force explains the energetic cost of running backward and forward. *J Exp Biol* 204: 1805-15, 2001.

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Figure Captions

Fig. 1. Vertical ground reaction forces, and contact and aerial periods of the step cycle vs. time for forward running (A), one-legged hopping (B), and backward running (C) for a representative subject. The ground reaction forces for forward running from panel A are reproduced in panels B and C (dashed curves) to allow comparisons of the ground reaction forces, and contact and aerial phase durations of these gaits with forward running.

Fig. 2. Gait mechanics as a function of speed for a representative subject in all three gaits. In each gait, foot-ground contact times (T_c) decreased by a factor of roughly two or more while the average vertical force (F_{avg}) applied during the contact period increased moderately (A). The vertical impulse (B) smaller symbols, and the aerial times (T_{aer}) were considerably greater for one-legged hopping than for either forward or backward running (B). Step frequency and step length (C) as a function of speed for all three gaits. Error bars are obscured by most of the filled symbols.

Fig. 3. The average vertical force applied during the foot-ground contact period as a function of speed for six individual subjects during forward running and one-legged hopping. Data are presented through the top speed of each subject in both gaits. For each subject, the average vertical force applied at the top running speed was appreciably less than that applied at the top one-legged hopping speed (i.e. the force reserve). These same data for subject 1 appear in Figure 2.

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

Fig. 5. Vertical ground reaction forces vs. time for a single footfall from subject 1 at top speed in each of the three gaits. Foot-ground contact times are longer and both peak and stance-average forces are greater for one-legged hopping than for either forward or backward running. The upper panel illustrates the time to peak *in vivo* twitch force for the quadriceps (dark arrow) and triceps surae muscles (grey arrow, data from: Harridge *et al.*, 1996; N.B. top forward running speed and contact time for Subject 1 were, 8.0 m s⁻¹ and 0.106 s, respectively)

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

Table 1. Top Speed Gait Mechanics

Gait	F_{avg} (W_b)	L_c (m)	L_{step} (m)	T_c (s)	T_{aer} (s)	$Freq_{step}$ (s^{-1})	Top Speed ($m\ s^{-1}$)
Fwd Run (I)	2.08 ± 0.07	0.98 ± 0.04	2.05 ± 0.14	0.108 ± 0.004	0.119 ± 0.004	4.51 ± 0.08	9.20 ± 0.59
1-Leg Hop	$2.71 \pm 0.15^*$	0.89 ± 0.05	2.51 ± 0.26	$0.160 \pm 0.006^*$	$0.274 \pm 0.019^*$	$2.36 \pm 0.13^*$	$5.75 \pm 0.39^*$
Fwd Run (II)	2.10 ± 0.07	0.99 ± 0.03	2.06 ± 0.11	0.110 ± 0.005	0.121 ± 0.003	4.42 ± 0.19	9.10 ± 0.52
Bwd Run	$1.75 \pm 0.05^*$	$0.74 \pm 0.05^*$	$1.29 \pm 0.14^*$	0.116 ± 0.004	$0.091 \pm 0.007^*$	$5.05 \pm 0.19^*$	$6.42 \pm 0.57^*$

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

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

Measured/ Theoretical	F _{avg} (W _b)	L _c (m)	L _{step} (m)	T _c (s)	T _{aer} (s)	Freq _{step} (s ⁻¹)	Top Speed (m s ⁻¹)
Fwd Run (II) (measured)	2.10 ± 0.07	0.99 ± 0.03	2.06 ± 0.11	0.110 ± 0.005	0.121 ± 0.003	4.42 ± 0.19	9.10 ± 0.52
ΔF _{avg} [*] (theoretical)	2.71	0.99	2.68	0.071	0.121	5.22	14.0
ΔL _o [*] (theoretical)	2.10	1.08	2.27	0.110	0.121	4.32	9.80

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

Figure 1

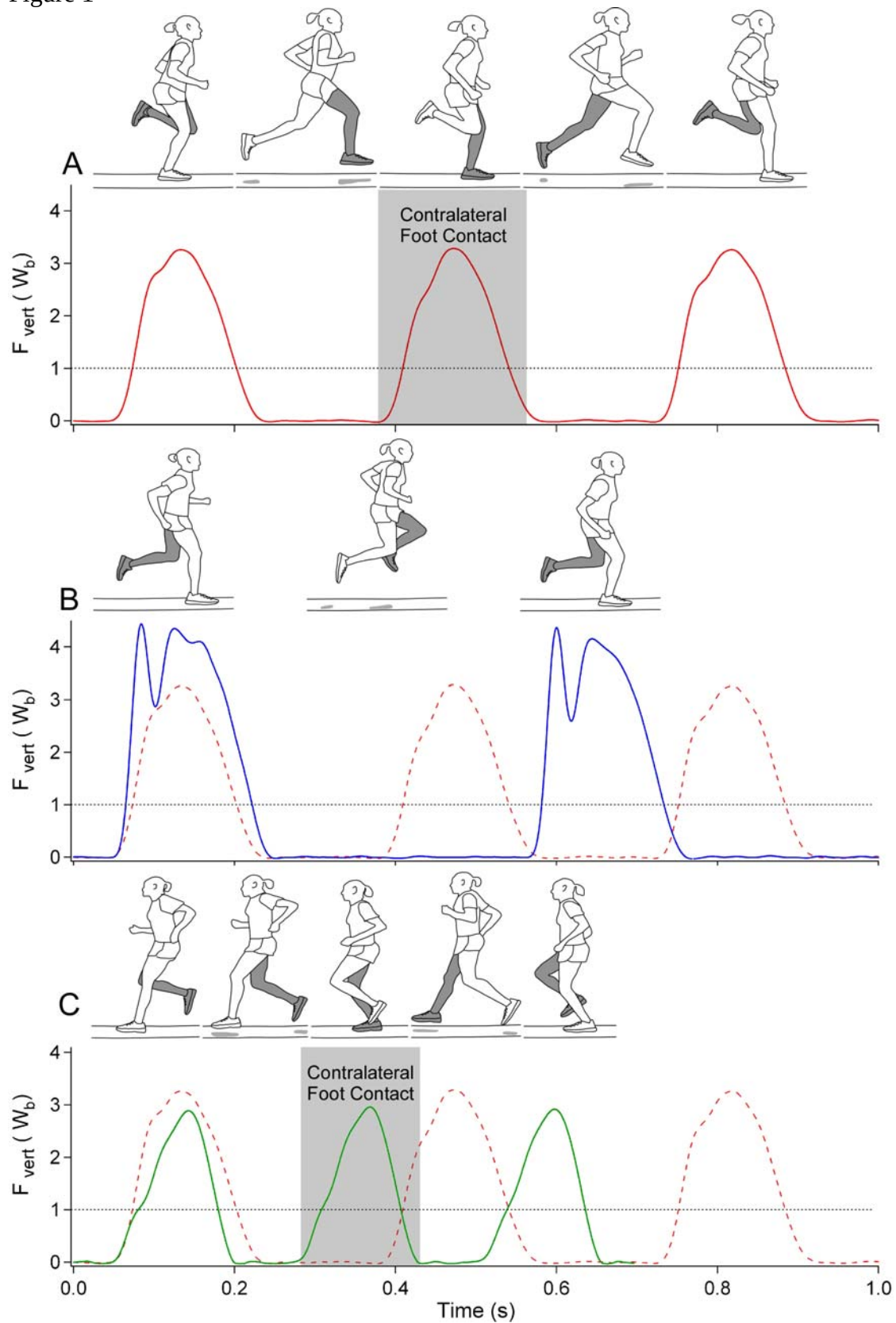


Figure 2

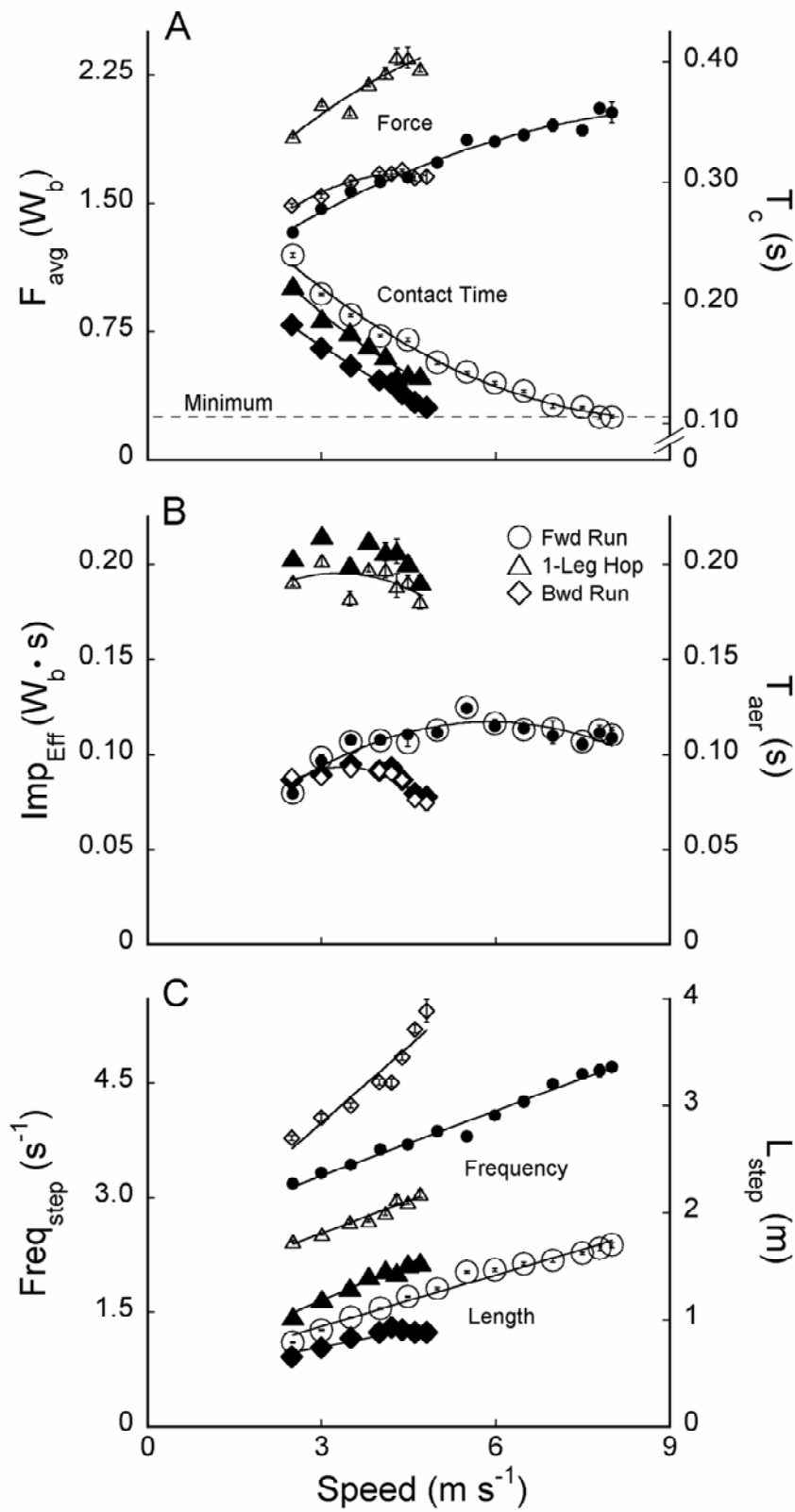


Figure 3

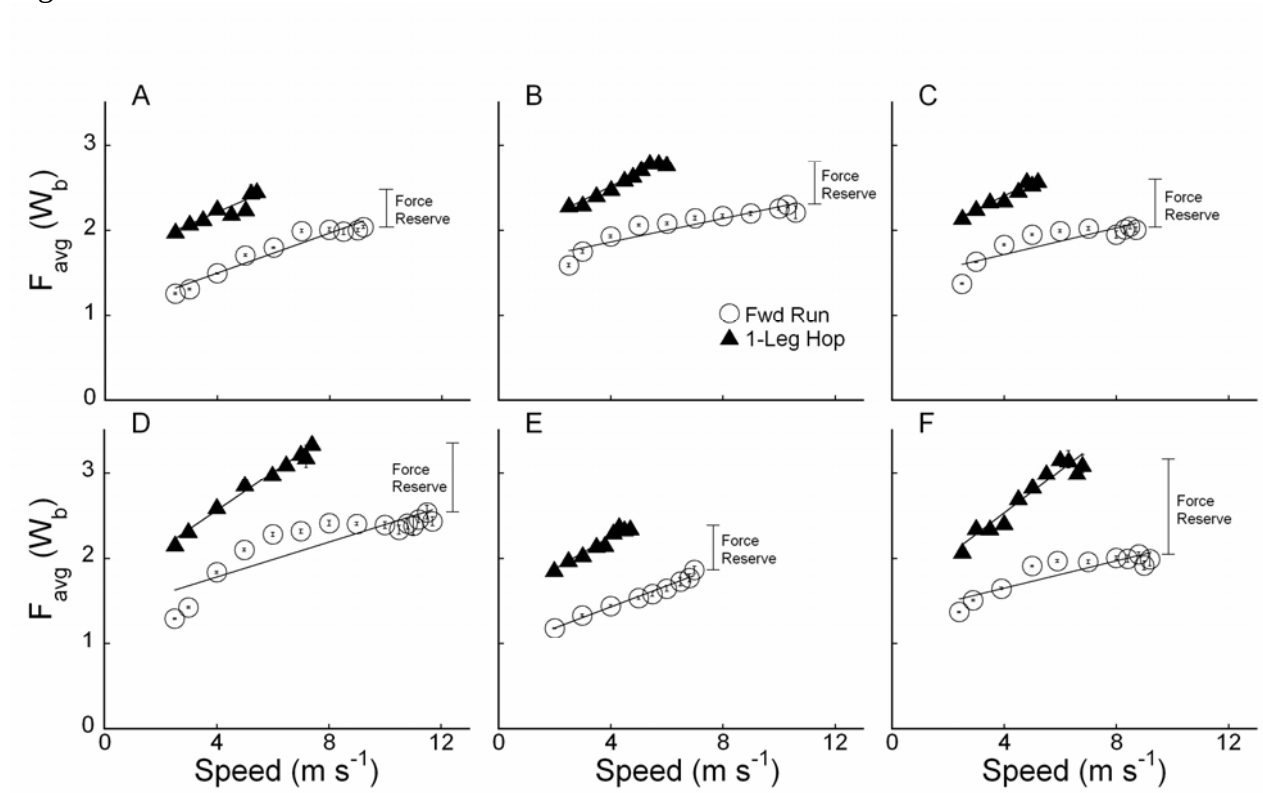


Figure 4

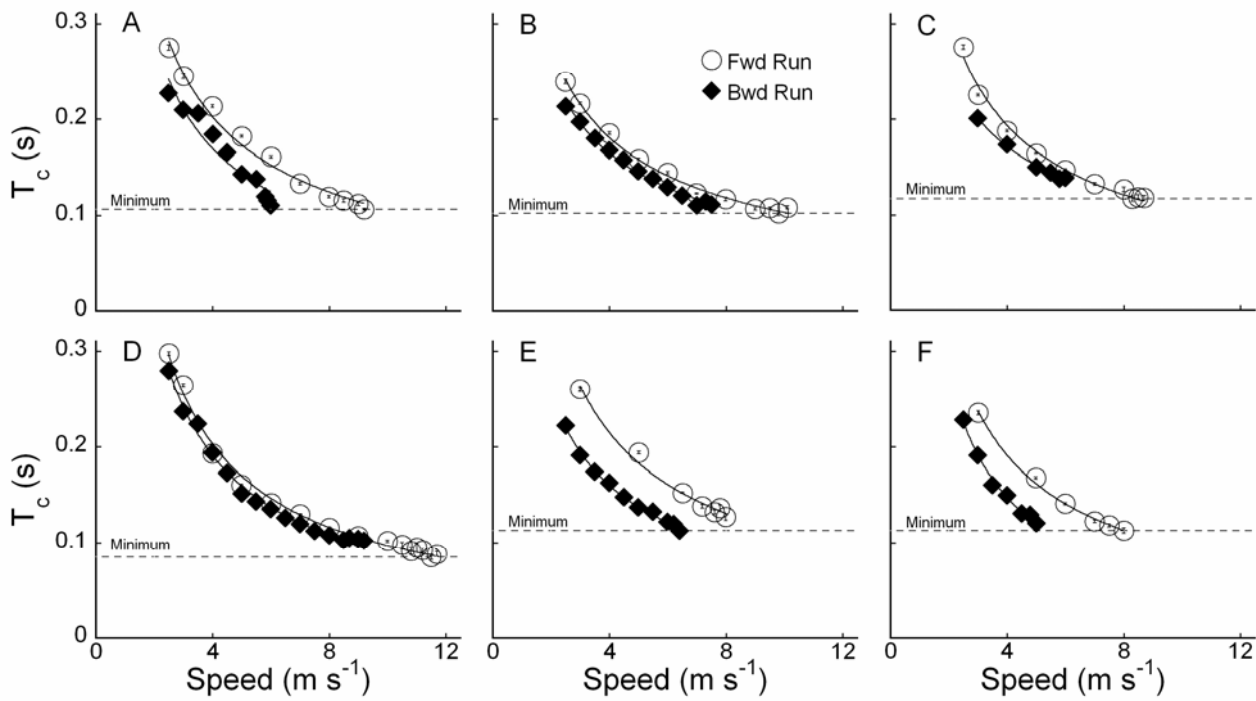


Figure 5

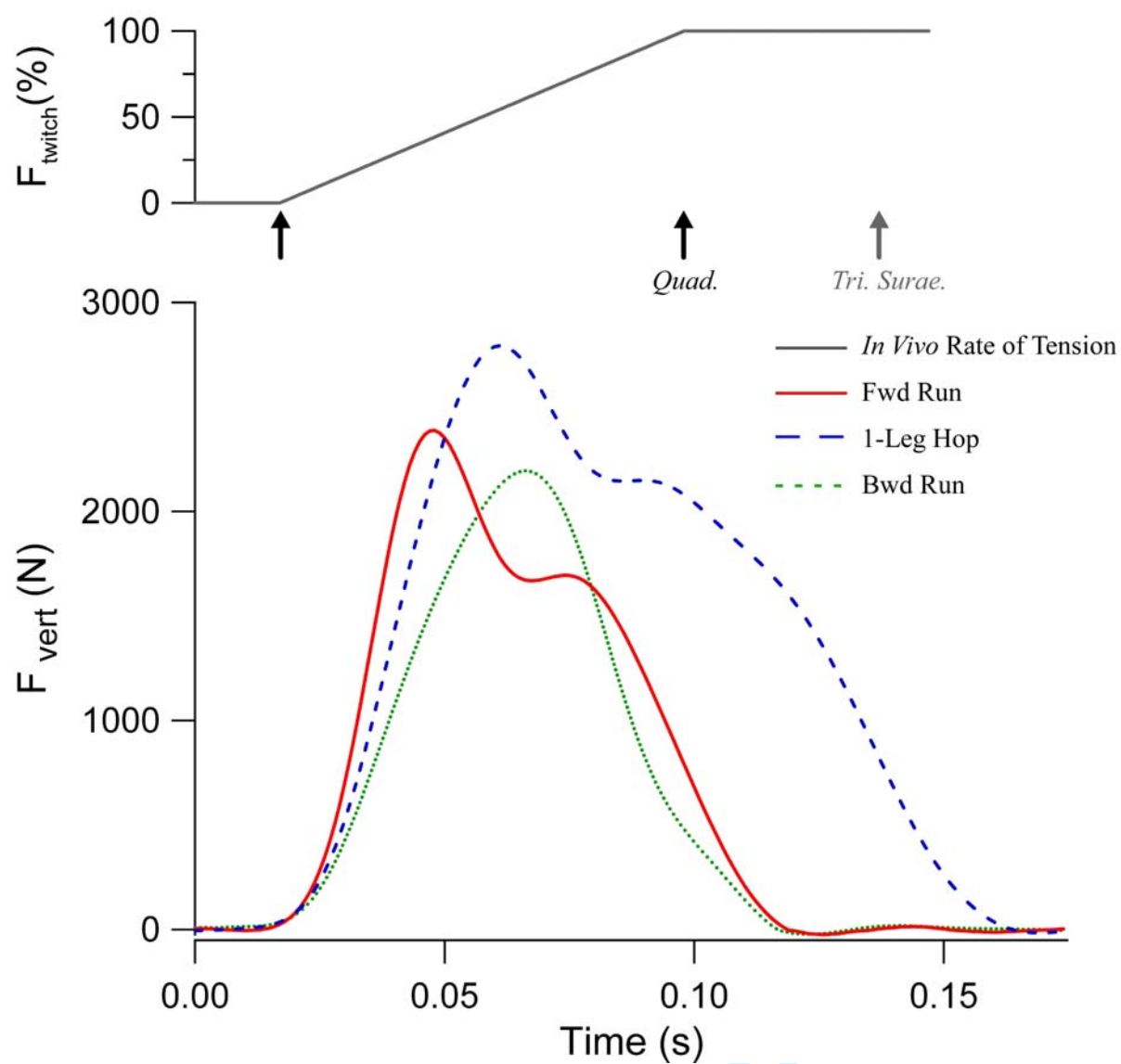


Figure 6

