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Sprint performance-duration relationships are set by the fractional duration of external force application

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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. First published October 27, 2005; doi:10.1152/ajpregu.00562.2005.—We hypothesized that the maximum mechanical power outputs that can be maintained during all-out sprint cycling efforts lasting from a few seconds to several minutes can be accurately estimated from a single exponential time constant (k_{cycle}) and two measurements on individual cyclists: the peak 3-s power output ($P_{mech\ max}$) and the maximum mechanical power output that can be supported aerobically (P_{aer}). Tests were conducted on seven subjects, four males and three females, on a stationary cycle ergometer at a pedal frequency of 100 rpm. Peak mechanical power output ($P_{mech\ max}$) was the highest mean power output attained during a 3-s burst; the maximum power output supported aerobically (P_{aer}) was determined from rates of oxygen uptake measured during a progressive, discontinuous cycling test to failure. Individual power output-duration relationships were determined from 13 to 16 all-out constant load sprints lasting from 5 to 350 s. In accordance with the above hypothesis, the power outputs measured during all-out sprinting efforts were estimated to within an average of 34 W or 6.6% from $P_{mech\ max}$, P_{aer}, and a single exponential constant ($k_{cycle} = 0.026\ s^{-1}$) across a sixfold range of power outputs and a 70-fold range of sprint trial durations ($R^2 = 0.96$ vs. identity, $n = 105$; range: 180 to 1,136 W). Duration-dependent decrements in sprint cycling power outputs were two times greater than those previously identified for sprint running speed ($k_{run} = 0.013\ s^{-1}$). When related to the respective times of pedal and ground force application rather than total sprint time, decrements in sprint cycling and running performance followed the same time course ($k = 0.054\ s^{-1}$). We conclude that the duration-dependent decrements in sprinting performance are set by the fractional duration of the relevant muscular contractions.

locomotion; cycling; running; anaerobic; aerobic; skeletal muscle; fatigue

THE MECHANICAL PERFORMANCE of skeletal muscle becomes progressively impaired during intense periods of contractile activity. The functional losses that are characteristic of skeletal muscle (5) can be observed at numerous levels of musculoskeletal organization. For example, the maximum speeds animals can attain during all-out locomotor efforts fall exponentially as the duration of the effort increases (18, 19, 25). Similarly, the force and power outputs of individual muscles and fibers drop off markedly with repeated stimulation (13, 14, 43). Although the mechanisms responsible are not well understood, performance is progressively compromised whenever skeletal muscle relies heavily on nonoxidative pathways of ATP resynthesis to fuel sequential contractions.

From a qualitative standpoint, the duration-dependent decrements in the mechanical performance of the musculoskeletal system during locomotion are generally more consistent than those observed in the various muscle and muscle fiber preparations. Peak locomotor performances, evaluated in terms of either the speed attained or mechanical power delivered to an external medium such as an ergometer, occur during efforts of 3 s or less (27, 37, 45). As the duration of an all-out effort is extended from seconds to minutes, performance declines in an exponential fashion. The characteristic negative exponential relationship between locomotor performance and effort duration was noted for both equine and human runners in the early work of A.V. Hill (18), and has been noted by Hill (19) and others (7, 10, 23, 47) subsequently for other modes of human locomotion such as swimming, cycling, and skating.

While the performance-duration relationship is qualitatively consistent for different modes of human locomotion, the quantitative relationships between burst and sustainable locomotor performances are not. For example, the maximum sprinting speeds human runners can attain for a burst of a few seconds are roughly twice as fast as the maximum speeds they can support aerobically (4, 46). In contrast, trained cyclists can achieve mechanical power outputs during short sprints that exceed the power outputs they can support aerobically by fourfold or more (27, 37, 47). The marked difference in the relative intensities that can be supported implies that the metabolic demands of sprinting may differ appreciably between these modes.

Our previous results may offer a general explanation for the decrements in sprinting performance that occur in relation to event duration. We recently found that the large absolute differences in sprint performance-duration relationships of sprint and endurance athletes are essentially invariant when expressed in the terms of our anaerobic reserve model. Specifically, when we expressed the speed-duration curves of these athletes in relation to the difference between their mechanical maxima for speed and the maximum that they could support aerobically (i.e., the anaerobic speed reserve), we found that they all conformed to the same relationship (4, 46). These results suggest that the performance of the musculoskeletal system may undergo duration-dependent performance decrements dictated by the relative reliance on anaerobic metabolism to provide mechanical function.

Here, we used the relatively greater intensities attained during sprint cycling to test this idea in two ways. First, we

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hypothesized that with increments in the duration of all-out efforts, the power outputs of different cyclists would decrease in the same relative manner from their mechanical maximum for 3 s to the metabolic maximum they could support aerobically. Second, we hypothesized that duration-dependent decrements in performance would follow the same time course for different modes of sprint locomotion, in the same manner that the decrements of individual specialists do (4, 46). Accordingly, we predicted that the exponential time constant describing the duration-dependent decrements in sprint cycling power outputs would be identical to that previously identified for sprint running speed.

MATERIALS AND METHODS

Experimental Design

Testing our two hypotheses required adapting the anaerobic reserve model we originally developed for running (4) to the following form for cycling:

$$P(t) = P_{aer} + (P_{mech\ max} - P_{aer}) \cdot e^{(-k_{cycle} \cdot t)} \quad (1)$$

where P(t) is the power output maintained for a trial of duration t, $P_{mech\ max}$ is the maximum power output for a trial of 3 s, P_{aer} is the maximum mechanical power output that can be supported by aerobic metabolism, the quantity $P_{mech\ max} - P_{aer}$ is the anaerobic reserve, e is the base of the natural logarithm, and k_{cycle} is the exponent that describes the decrements in power output occurring with increments in the duration of all-out cycling efforts. We expect that a single value of the exponent k_{cycle} will describe duration-dependent decrements in power output of any cyclist regardless of their mechanical and aerobic maxima.

The quantitative basis for the equations and relationships in our model is provided in greater detail elsewhere (46). $P_{mech\ max}$ and P_{aer} are empirically determined quantities that are representative of the body's functional limits for burst and endurance performance. However, when exercising at these specific intensities, the body does not exclusively rely on the pathways of either anaerobic or aerobic ATP resynthesis.

We evaluated our first hypothesis that our anaerobic reserve model would accurately estimate sprint cycling power outputs for efforts of 3 to 300 s regardless of the ability of the performer by 1) obtaining measurements of the respective maximum mechanical power outputs that could be attained for 3 s and supported aerobically by each cyclist, 2) establishing the individual power output-duration curve for each cyclist, and 3) evaluating the agreement between the all-out power outputs measured during the sprint cycling trials and those estimated by our anaerobic reserve model (eq. 1).

We evaluated our second hypothesis that performance decrements from the mechanical maximum to the aerobic maximum would follow the same time course for sprint cycling and sprint running by assessing whether the mean values for k_{cycle} and k_{run} are equal. The value for k_{cycle} was the mean of the individual values determined from an iterative best-fit procedure using eq. 1 and the measured $P_{mech\ max}$ and P_{aer} of the individual cyclist (Kaleidagraph 3.51, Synergy Software). The value for k_{run} was previously determined for seven subjects during all-out sprint running over a similar range of trial durations ($k = 0.013 \pm 0.001^{-1}$; Ref 4). The respective means were compared with an unpaired Student's t-test.

We recruited both male and female subjects to maximize the range of values obtained for $P_{mech\ max}$, P_{aer}, and power outputs during sprint cycling trials. We conducted all cycling tests at a pedal frequency of 100 revolutions per minute. Although marginally greater peak power output values are obtained at frequencies greater than 100 rpm, this strategy allowed power output differences to be a direct function of force rather than a more complicated function of force and velocity.

Subjects and Protocol

Seven subjects, four males and three females (mean age = 26 ± 2.7 yr) of varying fitness levels from recreational cyclists to trained, competitive cyclists volunteered and provided written, informed consent in accordance with the guidelines of the local institutional review board. Body masses and aerobic power maxima appear in Table 1.

Testing was generally completed in five laboratory sessions. All tests were conducted on a stationary cycle (SRM Indoor trainer; Königskamp, Germany) equipped with a strain gauge-based ergometer (Powercontrol IV, SRM). The ergometer has a large, aluminum flywheel to which rotational resistance is offered by an external magnetic brake aligned along the flywheel's outer rim. Brake position and resistance can be adjusted via cable and a lever mounted on the handlebars. Power output and cadence were continuously displayed on a PC monitor during all tests. The primary record of this data was recorded to the ergometer computer with a sampling frequency of 10 Hz and was downloaded to a PC following each trial. The zero torque output and slope settings of the ergometer were checked prior to each testing session.

The first testing session consisted of a progressive, discontinuous test to determine the maximum rate of oxygen uptake ($\dot{E}_{aer\ max}$). During the next three sessions, subjects completed a total of 13–16 all-out sprint cycling bouts of varying power outputs and durations to establish their individual power output-trial duration curves. Four to six all-out cycling bouts were generally completed per test session, in accordance with subject performance and verbal feedback regarding recovery. The last session consisted of six to eight all-out burst efforts of ≥ 3 s. During all trials subjects were restrained in the saddle with use of a seat belt that did not hinder leg movement.

Measurements

Metabolic rate during cycling ($\dot{E}_{metab}$). Rates of metabolic energy expenditure were determined from the rates of oxygen uptake measured with a computerized metabolic system (TrueMax 2400, Parvo Medics; Sandy, Utah). Each subject completed a progressive, discontinuous, power-output-incremented cycling test that consisted of 5-min bouts of cycling at 100 rpm interspersed with rest periods of ~3 to 5 min. Initial power outputs generally ranged from 70 to 150 W, depending on the estimated fitness level of the subject. Power outputs for subsequent bouts were increased by 20–40 W until a power output was reached at which the subject could not maintain the required 100 rpm pedal frequency for the full 5 min while putting forth a maximal effort. Expired air was directed via a one-way breathing valve and corrugated tubing through a pneumotach into a mixing chamber. Aliquots were drawn from the mixing chamber and analyzed for O_2 and CO_2 fractions using paramagnetic and infrared analyzers, respectively. Rates of oxygen uptake at each power output were averaged over the 4th and 5th min of each bout.

Mechanical and Metabolic Maxima

Peak power output at 100 rpm ($P_{mech\ max}$). Peak power outputs were determined from the highest power output that subjects were

Table 1. *Subject characteristics and aerobic maxima*

Subject, No.	Gender	Mass, kg	$\dot{E}_{aer\ max}$
1	M	79	54.2
2	M	77	54.2
3	M	82	59.3
4	M	82	59.8
5	F	63	37.7
6	F	70	40.9
7	F	74	38.3

Gender, mass, and maximum aerobic power ($\dot{E}_{aer\ max}$ in milliliters of oxygen per kilogram per minute) of the subjects.

able to maintain for 3 s at a pedal cadence of 100 rpm while strapped into the saddle. This value was determined from a series of all-out trials of ≥3 s at varying resistances. Subjects were allowed to cycle for 4 unloaded revolutions to accelerate the flywheel before the load was applied with simultaneous verbal cue. The greatest power output attained for 3 s at 100 ± 5 rpm for any of the trials was considered the peak mechanical power output of the subject ($P_{mech\ max}$). The corresponding metabolic rate ($\dot{E}_{an\ max}$) was estimated from linear extrapolation of the submaximal power output and oxygen uptake relationship of each individual. The validity of this extrapolation is not known.

Maximal aerobic power ($\dot{E}_{aer\ max}$). Maximal aerobic power was determined from the progressive, discontinuous cycling test previously described. The greatest $\dot{E}_{aer}$ value measured during any 15-s interval during the progressive test was considered $\dot{E}_{aer\ max}$. The maximum mechanical power that could be supported aerobically (P_{aer}), a calculated value, was computed from a linear extrapolation of each individual's oxygen uptake-power output relationship to the measured value of $\dot{E}_{aer\ max}$. In general, six submaximal bouts were completed before subjects reached $\dot{E}_{aer\ max}$. A minimum of five steady-state values no greater than 90% of $\dot{E}_{aer\ max}$ was used to formulate each subject's oxygen uptake-power output relationship.
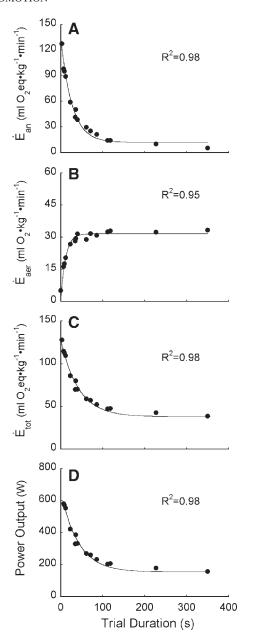
Sprint Cycling Trials

Sprinting trials were initiated by the subject performing 4 unloaded pedal revolutions before the prescribed resistance was applied to the ergometer's flywheel. Subjects were instructed to maintain a pedal frequency of 100 rpm throughout the trial using a metronome and/or visual feedback from the PC monitor. When the cadence fell below that prescribed, subjects were exhorted to restore the cadence to 100 rpm. If they were unable to do so within 2 s, the trial was halted. Each subject completed a minimum of 13 all-out trials. Flywheel resistance and power outputs for individual trials were chosen to obtain all-out trial durations throughout the desired target range of 5 to 300 s. Subjects were instructed to take as much time as necessary for a full recovery between sprint trials but were required to take a minimum of 10 min.

Rates of anaerobic energy release ($\dot{E}_{an}$). Estimated rates of anaerobic energy release, averaged over the duration of each sprint cycle bout, were determined from the oxygen deficits (ml O_2 eq·kg^{-1}·min^{-1}) incurred during each all-out sprint trial in accordance with Medbø et al. (31). The oxygen taken up during the cycling trial was subtracted from the estimated total demand. The total oxygen demand of each trial was estimated using a linear extrapolation of the subject's steady-state oxygen uptake-power output relationship to the power output of the sprint trial. The limitations of this technique have been discussed at great length (1, 2, 34). Although widely used, the validity of this technique is not known.

Rates of aerobic energy release ($\dot{E}_{aer}$). Rates of aerobic metabolism were determined from the rates of oxygen uptake using the Douglas bag technique in accordance with Consolazio et al. (8). Expired air was collected in individual bags for 60 or 90 s, or for a final bag interval determined by the duration of the subject's performance on the particular trial. Aliquots from each bag were analyzed for O_2 and CO_2 fractions after the analyzers were calibrated with a gas of known O_2 and CO_2 concentrations. Minute volumes and expired air temperatures were determined using a 120-liter Tissot wet spirometer with simultaneous temperature measurement. Rates of oxygen uptake, corrected to STPD, were averaged for the duration of each all-out cycling trial. Values for $\dot{E}_{an}$, $\dot{E}_{aer}$, $\dot{E}_{tot}$, and P for all the sprint cycle trials completed by subject 5 appear in Fig. 1. The curve-fit equations were the same as those previously described (46).

Run-Cycle Comparisons

The exponential value (k_{cycle}) best describing the power output-trial duration relationship for each subject was determined using an

Fig. 1. Estimated rates of anaerobic ($\dot{E}_{an}$; *A*), aerobic ($\dot{E}_{aer}$; *B*), and total ($\dot{E}_{tot}$; *C*) energy release and cycling mechanical power output (*D*) as a function of the duration of all-out sprint cycling trials for *subject 5*.

iterative best-fit procedure (KaleidaGraph, Version 3.6, Fig. 1*D*), given the measured values for $P_{mech\ max}$, P_{aer}, and *Eq. 1*. The same procedure was previously employed to determine k_{run} for 7 male runners from their maximum burst sprint speeds and running velocities at $\dot{E}_{aer\ max}$ (4).

RESULTS

Mechanical and Metabolic Maxima

Peak power output ($P_{mech\ max}$). For male subjects the maximum mechanical power output attained for 3 s was 1,127 ± 143 W (mean ± SE are reported throughout). The estimates for the corresponding metabolic power, $\dot{E}_{an\ max}$, which were obtained via linear extrapolation, were 217.3 ± 27.2 ml O_2 eq·kg^{-1}·min^{-1} (range = 193–256 ml O_2 eq·kg^{-1}·min^{-1}).

For female subjects the maximum mechanical power output for 3 s was 639 ± 56 W with corresponding estimates for $\dot{E}_{an\ max}$ of 116.3 ± 11.5 ml O_2 eq·kg^{-1}·min^{-1} (range = 103–123 ml O_2 eq·kg^{-1}·min^{-1}).

Aerobic power output (P_{aer}). The male mean for the maximum mechanical power output supported aerobically was 328 ± 39 W, and the corresponding mean $\dot{E}_{aer\ max}$ was 56.9 ± 3.1 ml O_2·kg^{-1}·min^{-1}. For females, the maximum mechanical power output that could be supported aerobically was 187 ± 32 W, and their mean $\dot{E}_{aer\ max}$ was 39.0 ± 1.7 ml O_2·kg^{-1}·min^{-1}.

Anaerobic power reserve ($P_{an\ res}$). The quantity $P_{mech\ max} - P_{aer}$, or the mean $P_{an\ res}$ was 799 ± 149 W for males and 452 ± 78 W (Fig. 2) for females, respectively. On average, the maximum mechanical power outputs attained for 3 s were 3.5 ± 0.6 times higher than the maximum power outputs that could be supported by aerobic power (Fig. 2).

Power Output vs. Trial Duration

Although individual subjects differed considerably in absolute power outputs maintained during the sprint trials (Fig. 3*A*), when these power outputs were expressed as a fraction of the individual's anaerobic power reserve (($P(t) - P_{aer}$)/$P_{an\ res}$), the power output decrements of different subjects were essentially identical (Fig. 3*B*). The mean k_{cycle} exponent of the 7 individual values providing the best fit to the measured power output-duration curves using *Eq. 1* was 0.026 ± 0.005 s^{-1} (range = 0.020–0.033).

The 105 sprint trials completed spanned a 70-fold range (5–350 s) of durations and sixfold range of mechanical power outputs (range: 180–1,136 W). For these trials the power outputs measured matched those estimated from the individual $P_{mech\ max}$ and P_{aer} values of each cyclist and the mean k_{cycle} value of 0.026 s^{-1} (eq. 1; Fig. 4) to within an average of 6.6% and 34 W per trial. Across the sixfold range in mechanical power output, our anaerobic reserve model accounted for 96% of the variance measured in all sprint trials, with a standard error of estimate (SEE) of 48.4 W. The predictions generated using the highest (0.033 s^{-1}) and lowest (0.020 s^{-1}) individual k_{cycle} values agreed with those measured to within an average

of 10.1 and 8.8%, respectively (SEE = 70.2 W and 58.7 W, resectively).

Sprint Cycling vs. Running

Mean values for $\dot{E}_{an}$, $\dot{E}_{aer}$, and $\dot{E}_{tot}$ in relation to trial duration for both cycling and running appear in Fig. 5A. To compare cyclists and runners of similar aerobic power, the means of the male cyclists only ($n = 4$) were compared with those of 7 similarly athletic male runners who were tested previously (cycle vs. run group $\dot{E}_{aer\ max}$ means = 56.9 ± 3.1 vs. 61.7 ± 2.0 ml O_2·kg^{-1}·min^{-1}). For sprint trials of all

Fig. 3. All-out mechanical power outputs in relation to cycling trial duration for 3 subjects with different absolute maxima for $P_{mech\ max}$ and P_{aer} (*A*). Individual differences in absolute power outputs at any given duration were virtually eliminated when power outputs were expressed in relation to the anaerobic power reserve (*B*). The curves were fit with the following equations: for *A*, $P(t) = P_{aer\ max} + (P_{an\ max} - P_{aer\ max})\cdot e^{-kt}$, for *B*, relative $P(t) = e^{-kt}$.
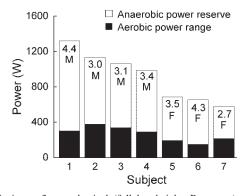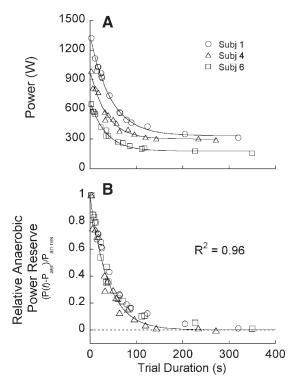

Fig. 2. Maximum 3-s mechanical (full bar height, $P_{mech\ max}$) and aerobic (height of the dark lower portion, P_{aer}) power outputs for each of the 7 subjects (male: 1–4; female: 5–7). The difference between these respective power outputs (the anaerobic power reserve, $P_{an\ res}$) is illustrated by the white upper portion of each bar. Duration-dependent decrements in mechanical power outputs are determined by the respective anaerobic power reserves of each cyclist. Numeric values for the ratio of $P_{mech\ max}$/P_{aer} appear within the bars of each subject.
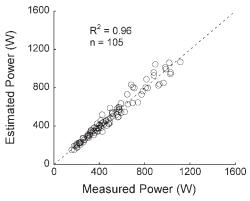

Fig. 4. Measured sprint cycling mechanical power outputs for all trials completed vs. those estimated using *Eq. 1*, the measured $P_{mech\ max}$ and P_{aer}, and the average value of $k = 0.026$ derived from the 7 subjects.
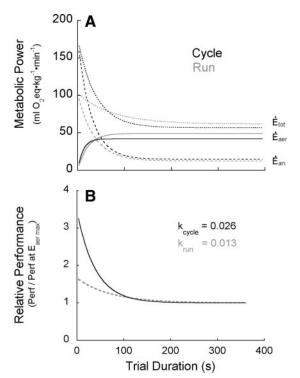
Fig. 5. Estimated rates of anaerobic ($\dot{E}_{an}$), aerobic ($\dot{E}_{aer}$), and total ($\dot{E}_{tot}$) energy release (*A*) and relative performance (*B*) as a function of the duration of all-out sprinting trials of male cyclists (*n* = 4) and male runners (*n* = 7). Respective cycle and run curves were formulated using group mean values for $\dot{E}_{an\ max}$ and $\dot{E}_{aer\ max}$. $\dot{E}_{tot}$ and relative performance curves were generated using values for k_{cycle} and k_{run} that were determined empirically during the respective modes of sprinting. Relative performances are expressed as power outputs and speeds divided by those supported by $\dot{E}_{aer\ max}$ in the respective modes (i.e., $P_{mech\ max}/P_{aer\ max}$ and $Spd_{mech\ max}/Spd_{aer}$).

durations, estimated rates of $\dot{E}_{an}$, during sprint cycling were two times greater than those estimated during sprint running. Values of $\dot{E}_{an}$, were estimated as the difference between the linear extrapolation of each individual subject's submaximal oxygen uptake-power output relationship and the measured values of oxygen uptake. Unlike $\dot{E}_{an}$, $\dot{E}_{aer}$ values were similar between the different modes across all trial durations. Accordingly, between mode differences in $\dot{E}_{tot}$, the sum of $\dot{E}_{an}$ plus $\dot{E}_{aer}$ depended on the duration of the all-out trial.

Sprinting performance, expressed in relation to the intensity of the maximum aerobic performance in the respective modes ($P(t)/P_{aer}$ and $Spd(t)/Spd_{aer}$), was also two times greater for sprint cycling than sprint running for the shortest trials of less than 10 s (Fig. 5*B*). For all-out efforts of longer durations, cycling values for $P(t)/P_{aer}$ were also greater than the corresponding running values for $Spd(t)/Spd_{aer}$, with between-mode differences being smaller for trials of progressively longer durations. For all trial durations of 100 s and longer, the relative performance values from the two modes were nearly identical.

Sprint Cycling vs. Running: Exponential Time Constants

Expressed as a fraction of the respective anaerobic reserves for the two modes of locomotion, the decrements in sprinting performance in relation to trial duration were two times greater for sprint cycling than sprint running. Accordingly, the expo-

nent providing the best-fit descriptions for the duration-dependent performance decrements in cycling was twice that previously identified for running (k_{cycle} = 0.026 ± 0.005 and k_{run} = 0.013 ± 0.001 s^{-1}; $P < 0.001$).

DISCUSSION

The results of our hypothesis tests were mixed: one positive, one negative. First, as expected, we found that decrements in sprint cycling power outputs of different individuals, although different in absolute terms, were the same when expressed in relation to their anaerobic reserves for power. Second, as not expected, we found that the sprint performance-duration relationships of cycling and running did not follow the same time course: duration-dependent decrements in sprint cycling power output were two times greater than those in sprint running speed. Thus the value of the exponent in our model that describes these decrements is mode-specific rather than universal (Fig. 6*A*). Why is this so?

We postulated that the greater duration-dependent performance decrements in sprint cycling vs. running might somehow be related to the greater relative intensities attained for the shorter cycling bouts. Accordingly, we focused on the timing of the muscular contractions that ultimately determine performance in the respective modes: those periods during which the limbs apply force to either the pedal or the ground. During cycling, each limb applies force to the pedal during the downstroke portion of the revolution (duty factor = 0.50) regardless of pedal frequency (9, 33, 39). During running at the speeds tested (4), each limb applies force to the running surface for 0.24 ± 0.02 of the total stride time, with negligible variation between subjects or speeds (45). We did not include the
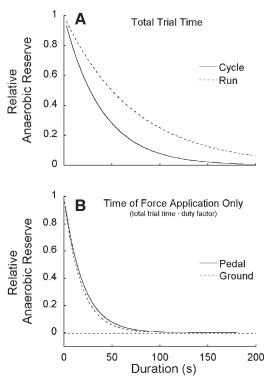

Fig. 6. Cycling power outputs and running speeds, expressed as fractions of the respective anaerobic reserves vs. total sprint trial duration (*A*) and vs. the cumulative time of force application to the pedals and ground (*B*).

muscular activity that can occur during the upstroke of the pedal revolution or the aerial phase of the running stride because the direct influence of this activity on performance appears to be negligible (9, 26, 45). When performance decrements in the two modes were expressed in relation to the durations for which the muscles were activated to apply force to the environment (i.e., total trial time·duty factor), they were essentially identical (cycle $= 0.052 \pm 0.01^{-1}$; run $= 0.054 \pm 0.01^{-1}$; $P = 0.85$; Fig. 6B).

A direct relationship between performance and the contractile durations during which the limb muscles convert chemical energy into external power and force is compatible with the current understanding of skeletal muscle fatigue (13, 14, 43) and mechanistically more logical. Our findings indicate that the qualitative similarity long observed for different performance-duration relationships (3, 7, 10, 11, 18, 19, 25, 35, 38, 39b, 40, 41) can be quantitatively explained by two factors: the anaerobic power or speed reserve available, and the proportion of the total sprint time that the muscles are activated to apply force to the environment.

In contrast to other investigations (7, 11, 16, 35, 39a, 39b, 40, 41) of performance capabilities for efforts of up to a few minutes, the performance outcomes provided by our model do not rely on quantitative estimates of the anaerobic energy released. Our anaerobic reserve model simply quantifies that portion of the power output or speed that is provided anaerobically. Thus the common performance-duration relationship we report is completely independent of the uncertainties associated with estimates of the anaerobic energy released during exercise.

How Well Does the Anaerobic Reserve Model Apply to Cycling?

Because the all-out power outputs of different cyclists did fall in the same relative manner from their mechanical to their aerobic maxima as trial durations increased, the estimated power outputs from our model closely matched those that we measured (Fig. 4). Across a 70-fold range of trial durations and a sixfold range of power outputs, our anaerobic reserve model estimated the actual power outputs of our subjects to within an average of $\pm$ 6.6% ($R^2 = 0.96$ vs. identity). Performance estimates were similarly accurate for individual subjects regardless of their mechanical and aerobic power maxima (R^2 range for individuals: 0.92–0.98; Fig. 3). The overall accuracy of the model for cycling was similar to that we previously reported for running ($R^2 = 0.97$; Ref 46). These positive results for a second mode of locomotion suggest that our model will accurately describe the performance-duration relationship for other whole-body exercises with measurable mechanical and aerobic maxima.

Our test of the accuracy of our model for sprint cycling performance was not completely independent as was the case with our prior running tests. Here, in contrast to previous practice (4, 46), we derived the value of our exponential time constant (k_{cycle}) from the same subjects whose performances were subsequently estimated. Our primary interest here was the general validity of the model rather than the specific degree of predictive accuracy. Thus we deemed a goodness-of-fit approach to be valid, and our data supported this premise. When we generated performance estimates using the highest and lowest individual k_{cycle} values (0.020 and 0.033, respectively) rather than the overall mean (0.026), the agreement of the performance estimates was virtually unaffected ($R^2 = 0.90$ and 0.95, respectively).

The similarly accurate performance estimations obtained for cycling and running indicate that the model's general applicability is independent of the mechanical differences that exist between sprint locomotor modes. In contrast to running, cycling is a non-weight-bearing exercise in which performance depends on the delivery of mechanical power to the pedals (27, 28) rather than the rapid application of force to the ground (26, 45). The external forces applied to the pedals during cycling (27, 28) are roughly an order of magnitude less than those applied to the ground during sprint running (45). Much lower external force outputs are consistent with the active muscles operating at greater strains, greater relative shortening velocities (i.e., V/V_{max}), and lesser stresses during cycling (19, 27, 36). Although these and accompanying differences in rates of cross-bridge detachment and ATP hydrolysis (21, 30) could have affected the time course of the sprint performance decrements examined in a variety of ways, they did not. Regardless of the requirements for power and force in the different modes, decrements in the proportion of the performance provided anaerobically were all but identically related to the cumulative duration of the contractions involved (Fig. 6).

Metabolic Power and Sprint Performance Limits: General Implications

Our cycle-run comparisons offer additional evidence that the reserves of chemical energy within the active muscles have flexible release rates that meet the metabolic demands generated by all-out sprint efforts, whatever those demands might be. Generally, the rates of anaerobic energy release during all-out sprint efforts have been assumed to be maximal (3, 7, 10, 12, 19, 25, 35, 38, 40–42). However, when hypoxic conditions are created to reduce the aerobic contributions to all-out sprint efforts, rates of anaerobic energy release compensate (6, 44) and considerably exceed the normoxic values that have been traditionally regarded as maxima. Here, we found when expressed in relation to the maximum cycling power outputs and running speeds supported aerobically, the mechanical maxima for burst sprint performance were two times greater for cycling than running. Additionally, we found that the estimated rates of anaerobic energy release were from 22 to 67% greater during sprint cycling vs. running for those trials that lasted from 3 to 60 s. Given that the extensor muscle mass recruited was not likely to be any greater during sprint cycling than sprint running (32), our results suggest that the rates of anaerobic energy release, within individual fibers, muscles, and throughout the whole body, can vary considerably during all-out sprinting efforts, and do so in accordance with the metabolic demands incurred by the contractions involved in the activity.

These results do not support the widely held view that performance-duration relationships can be explained by the maximum rates at which ATP can be made available (3, 7, 10, 12, 19, 25, 35, 38, 39a, 39b, 40–42). Rather, a reliance on anaerobic metabolism somehow induces decrements in the mechanical performance of the musculoskeletal system as the cumulative duration of the contractile activity becomes more

prolonged. The mechanism almost certainly involves the progressive inhibition of intracellular force production that occurs with intense sequential contractions (13, 14, 43), but it may also include reductions in the muscle volumes available (15), and perhaps other factors.

The absence of a direct metabolic limitation is well supported by interventions that have enhanced sprinting performance by prolonging the timing of the muscular contractions involved. The peak power outputs measured during single leg cycling sprints were elevated by elliptical pedal orbits that increased the duty factor by prolonging the downward phase of the pedal stroke (29). Similarly, the racing speeds attained by competitive speed skaters were enhanced by the invention of the klapskate. The klapskate has a hinged blade that prolongs the period of blade-ice interaction during which propulsion occurs (20, 39c). The prolonged periods of propulsion and greater duty factors provided by the klapskates allowed skaters to increase the mechanical power they deliver to the ice (39c) thereby producing improvements in the sprinting speed records.

A General Performance-Duration Relationship?

Our findings raise the possibility that a general quantitative description of the performance-duration relationship for the human musculoskeletal system may now be possible for these non-steady-state efforts. Given a dynamic activity engaging an appreciable fraction of the body's musculature with a known duty factor (d), we can express duration-dependent performance decrements using our anaerobic reserve model and a single exponential constant as

$$\mathrm{Perf}(t) = \mathrm{Perf}_{aer} + (\mathrm{Perf}_{mech\,max} - \mathrm{Perf}_{aer}) \cdot e^{(-k_{muscle} \cdot t \cdot d)} \qquad (2)$$

where Perf is expressed as an intensity and therefore with units of speed, power, etc., d is expressed as a fraction, and the exponential constant, k_{muscle} ($= 0.054$ s^{-1}) quantifies performance decrements in relation to the cumulative duration of the contractions involved in the all-out effort.

Two aspects of our findings warrant further comment. First, the time course with which nonoxidative pathways of ATP resynthesis impair musculoskeletal performance in vivo is quite rapid. When expressed in the nondynamic terms of uninterrupted contractile durations, 50% of the maximum mechanical function that can be provided anaerobically is unavailable at an effort duration of 15 s. Second, in contrast to previous suggestions prompted by the varied results obtained from muscle and fiber preparations outside the body, the fatigue process may not be beyond quantitative understanding (17). Under the in vivo conditions examined here, both the operative mechanisms and time course over which mechanical function of muscle is impaired appear to be extremely consistent.

REFERENCES

1. **Bangsbo J.** Is the O_2 deficit an accurate quantitative measure of the anaerobic energy production during intense exercise? *J Appl Physiol* 73: 1207–1209, 1992.

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

3. **Billat V, Koralsztein JP, and Morton RH.** Time in human endurance models: from empirical models to physiological models. *Sports Med* 27: 359–379, 1999.

4. **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.

5. **Burke RE and Levine DN.** Mammalian motor units: physiological-histochemical correlation in three types in cat gastrocnemius. *Science* 174: 709–712, 1971.

6. **Calbet JA, De Paz JA, Garatachea N, Cabeza de Vaca S, and Chavarren J.** Anaerobic energy provision does not limit Wingate exercise performance in endurance-trained cyclists. *J Appl Physiol* 94: 668–676, 2003.

7. **Capelli C.** Physiological determinants of best performances in human locomotion. *Eur J Appl Physiol* 80: 298–307, 1999.

8. **Consolazio CF, Johnson RE, and Pecora LJ.** *Physiological Measurements of Metabolic Functions in Man.* New York: McGraw-Hill, 1963.

9. **Coyle EF, Feltner ME, Kautz SA, Hamilton MT, Montain SJ, Baylor AM, Abraham LD, and Petrek GW.** Physiological and biomechanical factors associated with elite endurance cycling performance. *Med Sci Sports Exerc* 23: 93–107, 1991.

10. **di Prampero PE.** Factors limiting maximal performance in humans. *Eur J Appl Physiol* 90: 420–429, 2003.

11. **di Prampero PE, Capelli C, Pagliaro P, Antonutto G, Girardis M, Zamparo P, and Soule RG.** Energetics of best performances in middle-distance running. *J Appl Physiol* 74: 2318–2324, 1993.

12. **Ettema JH.** Limits of human performance and energy-production. *Int Z Angew Physiol Einschl Arbeitsphysiol* 22: 45–54, 1966.

13. **Fitts RH.** Cellular mechanisms of muscle fatigue. *Physiol Rev* 74: 49–94, 1994.

14. **Fitts RH.** Mechanisms of muscular fatigue. In: *Principles of Exercise Biochemistry* (3rd ed.), edited by Poortmans JR. New York: Karger, *Med Sport Sci* 46: 279–300, 2004.

15. **Garland J.** Role of small diameter afferents in reflex inhibition during human muscle fatigue. *J Physiol* 435: 547–558, 1991.

16. **Gastin PB.** Energy system interaction and relative contribution during maximal exercise. *Sports Med* 31: 725–741, 2001.

17. **Green HJ.** Metabolic determinants of activity induced muscular fatigue. In: *Exercise Metabolism,* edited by Hargreaves M. Champaign, IL: Human Kinetics, p. 211–256, 1995.

18. **Hill AV.** The physiological basis of athletic records. In: *British Association for the Advancement of Science: Report of the 93rd Meeting*, 1925, 156–173.

19. **Hill AV.** The dimensions of animals and their muscular dynamics. *Sci Prog* 150: 209–230, 1950.

20. **Houdijk H, de Koning JJ, de Groot G, Bobbert MF, and van Ingen Schenau GJ.** Push-off mechanics in speed skating with conventional skates and klapskates. *Med Sci Sports Exerc* 32: 635–41, 2000.

21. **Huxley AF.** Muscular contraction. *J Physiol* 243: 1–43, 1974.

25. **Jones JH and Lindstedt SL.** Limits to maximal performance. *Annu Rev Physiol* 55: 547–569, 1993.

26. **Kram R and Taylor CR.** Energetics of running: a new perspective. *Nature* 346: 265–267, 1990.

27. **Martin JC, Brown NA, Anderson FC, Spirduso WW.** A governing relationship for repetitive muscular contraction. *J Biomech* 33: 969–974, 2000.

28. **Martin JC and Spirduso WW.** Determinants of maximal cycling power: crank length, pedaling rate and pedal speed. *Eur J Appl Physiol* 84: 413–418, 2001.

29. **Martin JC, Lamb SM, and Brown NA.** Pedal trajectory alters maximal single-leg cycling power. *Med Sci Sports Exerc* 34: 1332–1336, 2002.

30. **McMahon TA.** *Muscles, Reflexes and Locomotion.* Princeton NJ: Princeton University Press, 1984.

31. **Medbø JI, Mohn AC, Tabata I, Bahr R, Vaage O, and Sejersted OM.** Anaerobic capacity determined by maximal accumulated O_2 deficit. *J Appl Physiol* 64: 50–60, 1988.

32. **Medbø JI and Tabata I.** Anaerobic energy release in working muscle during 30 s to 3 min of exhausting bicycling. *J Appl Physiol* 75: 1654–1660, 1993.

33. **Neptune RR and van den Bogart AJ.** Standard mechanical energy analyses do not correlate with muscle work in cycling. *J Biomech* 31: 239–245, 1998.

34. **Olesen HL.** Accumulated oxygen deficit increases with the inclination of inclined running. *J Appl Physiol* 73: 1130–1134, 1992.

35. **Perronet F and Thibault G.** Mathematical analysis of running performance and world running records. *J Appl Physiol* 67:453–465, 1989.

36. **Roberts TJ, Marsh RL, Weyand PG, and Taylor CR.** Muscular force in running turkeys: the economy of minimizing work. *Science* 275: 1113–1115, 1997.

37. **Sargeant AJ, Hoinville E, and Young A.** Maximum leg force and power output during short-term dynamic exercise. *J Appl Physiol* 51: 1175–1182, 1981.

38. **Savaglio S and Carbone V.** Scaling in athletic world records. *Nature* 16: 244, 2000.

39. **Smak W, Neptune RR, and Hull MJ.** The influence of pedaling rate on bilateral asymmetry in cycling. *J Biomech* 32: 899–906, 1999.

39a.**van Ingen Schenau, GJ, Jacobs R, and Koning JJ.** Can cycle power predict sprint running performance? *Eur J Appl Physiol Occup Physiol* 63: 255–260, 1991.

39b.**van Ingen Schenau, GJ, Koning J, and Groot G.** Optimisation of sprinting performance in running, cycling and speed skating. *Sports Med* 17: 259–275, 1994.

39c.**van Ingen Schenau GJ, De Groot G, Scheurs AW, Meester H, and De Koning JJ.** A new skate allowing powerful plantar flexions improves performance. *Med Sci Sports Exerc* 28: 531–535, 1996.

40. **Ward-Smith JA.** A mathematical theory of running, based on the first law of thermodynamics, and its application to the performance of world-class athletes. *J Biomech* 18: 337–349, 1985.

41. **Ward-Smith JA.** Aerobic and anaerobic energy conversion during high-intensity running. *Med Sci Sports Exerc* 31: 1855–1860, 1999.

42. **Ward-Smith AJ and Radford PF.** Investigation of the kinetics of anaerobic metabolism by analysis of the performance of elite sprinters. *J Biomech* 33: 997–1004, 2000.

43. **Westerblad H, Allen DG, and Lannergren J.** Muscle fatigue: lactic acid or inorganic phosphate the major cause? *News Physiol Sci* 17: 17–21, 2002.

44. **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, 1998.

45. **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.

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

47. **Wilkie DR.** Equations describing power input by humans as a function of duration of exercise. In: *Exercise Bioenergetics and Gas Exchange*, edited by Cerretelli P and Whipp BJ. Amsterdam: Elsevier, 1980, p. 75–80.