Differential modeling of anaerobic and aerobic metabolism in the 800-m and 1,500-m run

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[1]*Faculty of Sport Sciences, University of Evry-Val d'Essonne, Evry, France;* [2]*Sport Medicine Center CCAS, Paris, France; and* [3]*Institute of Food, Nutrition, and Human Health, Massey University, Palmerston North, New Zealand*

Billat V, Hamard L, Koralsztein JP, Morton RH. Differential modeling of anaerobic and aerobic metabolism in the 800-m and 1,500-m run. *J Appl Physiol* 107: 478–487, 2009. First published May 28, 2009; doi:10.1152/japplphysiol.91296.2008.—This study examined the hypothesis that running speed over 800- and 1,500-m races is regulated by the prevailing anaerobic (oxygen independent) store (ANS) at each instant of the race up until the all-out phase of the race over the last several meters. Therefore, we hypothesized that the anaerobic power that allows running above the speed at maximal oxygen uptake ($\dot{V}O_{2max}$) is regulated by ANS, and as a consequence the time limit at the anaerobic power (tlim PAN = ANS/PAN) is constant until the final sprint. Eight 800-m and seven 1,500-m male runners performed an incremental test to measure $\dot{V}O_{2max}$ and the minimal velocity associated with the attainment of $\dot{V}O_{2max}$ ($v\dot{V}O_{2max}$), referred to as maximal aerobic power, and ran the 800-m or 1,500-m race with the intent of achieving the lowest time possible. Anaerobic power (PAN) was measured as the difference between total power and aerobic power, and instantaneous ANS as the difference between end-race and instantaneous accumulated oxygen deficits. In 800 m and 1,500 m, tlim PAN was constant during the first 70% of race time in both races. Furthermore, the 1,500-m performance was significantly correlated with tlim PAN during this period ($r = -0.92$, $P < 0.01$), but the 800-m performance was not ($r = -0.05$, $P = 0.89$), although it was correlated with the end-race oxygen deficit ($r = -0.70$, $P = 0.05$). In conclusion, this study shows that in middle-distance races over both 800 m and 1,500 m, the speed variations during the first 70% of the race time serve to maintain constant the time to exhaustion at the instantaneous anaerobic power. This observation is consistent with the hypothesis that at any instant running speed is controlled by the ANS remaining.

exercise; oxygen; pace; performance

THIS STUDY attempts to elucidate alterations in energetics during actual middle-distance track competition by examining how these fluctuations may be related to changes in running speed. For that purpose, since the best human performances in middle-distance running (800–10,000 m) are characterized by a speed variability of 5–10% (5, 15, 52, 57), the data were collected under actual race conditions. This is novel and extremely important as in many cases data collection using standard laboratory conditions may not truly reflect real-world performances. It is still not known how athletes regulate their speed to optimize performance in supramaximal races such as middle-distance events (26, 27). It is now possible to monitor athletes during real competitions on the track with a portable gas analyzer system coupled with a global positioning system (GPS) (5, 6, 55), and therefore we can simultaneously obtain both speed variations and energetics in the context of performance achievement. Even if control of speed and thus of power output is voluntary (5), the physiological signals that athletes receive for estimating their ability to sustain any instantaneously chosen speed have yet to be to elucidated.

For exhaustive constant-speed runs performed between 90 and 120% of the velocity associated with the attainment of maximal oxygen uptake ($v\dot{V}O_{2max}$) and eliciting maximal oxygen uptake ($\dot{V}O_{2max}$), i.e., above the critical speed (CS) that is the asymptote of the speed/time limit relationship (25), the estimation of the time limit to the end of the race has been shown to be accurate especially in well-trained subjects (26). Indeed, the Borg (9) rating of perceived exertion (RPE) vs. time limit scale was recently validated (27). When anaerobic power is elicited, both accumulated oxygen deficit (AOD) and lactate concentration increase as the exercise progresses, corresponding to the so-called "anaerobic capacity" i.e., a quantity of energy allowing some distance [the anaerobic distance capacity (ADC)] to be run without the resynthesis of ATP by oxidative phosphorylation (20, 29, 44). This anaerobic reserve called "anaerobic work capacity" is expressed in joules or in oxygen deficit or distance equivalent for a given energy cost of running in joules per kilogram per meter (19), and it has been demonstrated that the time to exhaustion performed at constant speeds between 90 and 140% of vvO_{2max} could be well predicted by this reserve (8). To be in accord with the common literature we regard anaerobic energy and oxygen-independent energy as synonymous terms. For exhaustive variable-speed runs, it has been demonstrated that the number of repetitions of intermittent exercise cycles could be calculated with a decrease of the anaerobic reserve during the hard running phases and an increase during the recovery phases (47). Furthermore, the range of speed variation has been reported to depend on the ratio CS/ADC. This ratio, called the "endurance parameter ratio," is considered to be an important determinant of the race-pace strategy, suggesting that the ability to vary running speed above the fatigue threshold speed depends on the ratio between the anaerobic reserve (ADC) and the fatigue threshold speed (CS) (25). In the same way, Ward-Smith (60) named the ratio between the anaerobic capacity and the maximal aerobic power as λ. Ward-Smith reported a λ value of 55 s, which is close to the duration of 400-m events. However, no studies have as yet examined the time course of this ratio during supramaximal exercise.

Middle-distance running of duration 2–4 min (800–1,500 m) elicits aerobic metabolism to its maximum power and anaerobic metabolism to its maximum capacity (6, 25, 55, 59). It has been demonstrated that $\dot{V}O_{2max}$ and maximal oxygen deficit are well correlated with performance in middle-distance races (800–1,500 m) (19). The power output above $\dot{V}O_{2max}$

elicited in 800- and 1,500-m races depends on the remaining anaerobic store as reflected by the accumulated oxygen deficit at each instant of the race. Therefore, sequential anaerobic power (PAN) that is momentarily elicited should depend on the remaining anaerobic stores (ANS) at that moment of the race and on the run duration at that sequential anaerobic power (tlim PAN) according to the following equation:

$$PAN = ANS/tlim\ PAN \qquad (1)$$

or, from a more physiological viewpoint, the time that an athlete can sustain an anaerobic power is given by the ratio between the anaerobic store at that moment of the race and the anaerobic power at the same moment. That is:

$$tlim\ PAN = ANS/PAN \qquad (2)$$

where PAN is in watts, ANS in joules and is estimated by the oxygen deficit during the race (6), and tlim PAN is in seconds. Given that the anaerobic stores are a finite quantity of energy, the middle-distance runner must elicit $\dot{V}_{O_{2max}}$ to minimize the ANS depletion before the final sprint. For that, the first part of the race must not be run too fast yet also be sufficient to achieve a good performance. Furthermore, it has recently been reported that 800-m runners demonstrated an oxygen uptake ($\dot{V}_{O_2}$) drop below $\dot{V}_{O_{2max}}$, which additionally taxes the anaerobic stores (55). This $\dot{V}_{O_2}$ drop could be due to the metabolic acidosis, which impairs mitochondrial respiration (30). Therefore, middle-distance speed must be as high as possible above the maximal aerobic power (i.e., the product of $v\dot{V}_{O_{2max}}$ by the oxygen cost of running) to achieve a good final performance but without depleting anaerobic stores too early and without decreasing $\dot{V}_{O_2}$ below $\dot{V}_{O_{2max}}$ by an inhibition of oxidative phosphorylation with early acidosis (11, 37, 53). Furthermore, the recent work of Jones et al. (32) on pacing strategy showed that a fast start would contribute to improved exercise tolerance because of a more rapid increase in oxygen uptake.

Noakes, St. Clair Gibson, and Lambert discuss the model of a central neural governor preventing the risk of anaerobiosis on oxygen-sensitive organs during maximal exercise (48, 49). Fatigue is hypothesized as being the result of the complex interaction of multiple peripheral physiological systems and the brain. In this model, all changes in peripheral physiological systems such as substrate depletion or metabolite accumulation act as afferent signalers that modulate control processes in the brain in a dynamic, nonlinear, integrative manner. A lot of the central governor theory is based on the work of Ulmer (57), who considered that afferent motor signals to skeletal muscles concerned not only the space/time pattern of motion but also the setting of muscular performance and through this the control of the current metabolic rate. He proposed that for an optimal adjustment of metabolic rate during heavy exercise, e.g., in athletic competitions, a feedback control system must exist, including a programmer that takes into consideration a finishing point (teleoanticipation). He showed different time delays between the perception of level of exertion (RPE scale) and those of the heart rate (HR), which support his hypothesis that perceived exertion is part of the feedback system for optimal adjustment of exertion. He concluded that when exercise is long enough there is enough time, such as when a plateau of HR for instance is reached, to include energy reserves for a final spurt. This "central governor" model proposes that the subconscious brain regulates power output (pacing strategy) by modulating motor unit recruitment to preserve body homeostasis and prevent catastrophic physiological failure such as rigor (48).

The present study examines the hypothesis that running speed is regulated by the prevailing anaerobic store at each instant of the race. If this hypothesis can be supported, despite the progressive depletion of the anaerobic stores, then PAN at each instant of the race would allow a time to exhaustion at PAN (tlim PAN) to be maintained constant until the last several meters of the race, whereupon it becomes an all-out rather than a controlled exercise.

MODELING RATIONALE

Equations 1 and *2* are interpreted in the context of a general two-component (aerobic and anaerobic) bioenergetic system. The simplest such system is the two-parameter critical power model (46). This simple model, however, does not incorporate any control over power output. The hypothesis that achievable power output or running speed may be controlled in some way by the remaining ANS has been suggested and modeled previously (43). Such modeling has been demonstrated, supported, and illustrated with constant-power exercise on a cycle ergometer (44). This three-parameter critical power model has been the subject of a number of subsequent studies (10, 13, 17, 46). This hypothesis has not to our knowledge been adequately examined with respect to actual track running, and it remains to be demonstrated whether a constant tlim PAN is indeed mathematically consistent with this model. Below we verify this consistency, in order that data collected in these circumstances and evidencing this constancy does indeed support the hypothesis.

Suppose, as suggested above, we hypothesize that

$$tlim\ PAN = ANS/PAN = k_1\text{(a constant)} \qquad (3)$$

where instantaneous ANS is given by the difference between end-race and instantaneous oxygen deficits. Now the end-race oxygen deficit is some fixed value (say k_2), and instantaneous oxygen deficit is the integral of PAN (denoted by the variable x) up to that instant. Consequently this simple equation takes the form:

$$(k_2 - x)/x' = k_1 \qquad (4)$$

where $x' = $ PAN is the derivative of x. That is:

$$x' = k_2/k_1 - x/k_1 \qquad (5)$$

This is a simple first-order linear differential equation whose solution is $x = k_2(1 - e^{-t/k_1})$, which is exactly the same form as that which has previously been shown to represent the optimal strategy for running a given distance in minimal time under the control system assumption hypothesized above (45). It follows therefore that if data on ANS and PAN are collected serially during a race and (if they change at the same rate) demonstrate a constant ratio over at least a significant part of that race (excluding maybe the final sprint), then our hypothesis would be supported.

POWER SYSTEMS ESTIMATION BY GAS EXCHANGE

We estimated the anaerobic power and anaerobic work capacities with gas exchange according to previous validation

studies (16, 39, 40, 41, 61). This is indirect information on power systems but provides noninvasive and continuous data throughout a race performed in actual racing conditions, as required for our approach to the estimation of the anaerobic work capacity at the instant $t(x')$ hypothesized to regulate anaerobic power.

METHODS

Subjects

The subjects included 15 male middle-distance runners; 8 were specialists over 800-m and 7 over 1,500-m races. The two groups had previously attained similar levels of achievements (in number of points on the IAAF scoring tables) and presented no significant difference in aerobic characteristics (included with race results in Table 1 for comparison of maximal $\dot{V}O_2$ reached during the races). Before participation, all subjects were informed of the risks and stresses associated with the protocol and gave their written voluntary informed consent. The present study conformed to the standards set by the Declaration of Helsinki, and all procedures were approved by the local ethics committee, the Hospital Saint Louis, Paris. As some subjects were under 18 years old, their parents provided informed consent. Height and weight of the subjects were measured (Table 2). Five skinfold measurements were taken (triceps, biceps, suprailiac, subscapular, and midthigh), and percent body fat was calculated using the formula of Durnin and Womersley (22).

Experimental Design

Experiments were conducted in May at the start of the competitive season. At first, the subjects performed a test to measure $v\dot{V}O_{2max}$ and

the energy cost of running for estimation of the oxygen required at speeds above $v\dot{V}O_{2max}$ (41). One week later each runner ran one race over 800 m or 1,500 m, according to their specialty, during a meeting on a synthetic 400-m track at 7 P.M. in a climate of 20°C without wind (<2 m/s, anemometer, Windwatch, Alba, Silva, Sweden) as performed in a prior study taking such measurements on an outdoor track (6). Given that it was a real competition, the athletes in each race all ran simultaneously.

Respiratory and velocity measurements. Throughout the test and the competition, respiratory and pulmonary gas exchange variables were measured using a breath-by-breath portable gas analyzer (Cosmed K4b², Cosmed, Rome, Italy) that was calibrated before each test according to the manufacturer's instructions (23). The device weighs 800 g and is placed near the center of mass of the body. Breath-by-breath data were later reduced to 5-s intervals (Data Management Software, Cosmed, Rome, Italy). Likewise, running speed and other variables measured by the K4b² were averaged every 5 s. Running speed was strictly verified throughout the tests with a GPS integrated in the K4b² (Garmin USA for Cosmed) (36). The accuracy and reliability of the Cosmed K4b² portable gas analysis system has previously been demonstrated (21, 23, 38), and we checked one of the coupled GPS (which was a new option of the K4b² system) by comparing the distance measured by the GPS with the real racing distance (800 or 1,500 m). The difference between the real and measured distance was less than 1% ($0.97 \pm 0.038\%$ and $0.92 \pm 0.026\%$ over 800 and 1,500 m, respectively). This was in accordance with prior studies performed with GPS for maximal races run by both humans and horses (35, 36).

Determination of blood lactate concentration. Fingertip capillary blood samples were collected into a capillary tube and were analyzed for lactate concentration using a lactate analyzer (Lactate Pro CT-

Table 1. *Maximal values of $\dot{V}O_2$ and HR of the race compared with the maximal values measured in the incremental test and anaerobic capacity during the races (estimated by the accumulated oxygen deficit at the end of the race) for the 800-m race and the 1,500-m race*

Subjects	$\dot{V}O_{2max}$; max $\dot{V}O_{2race}$, ml·kg⁻¹·min⁻¹	$v\dot{V}O_{2max}$; v_{race}, km/h	HR_{max}; max HR_{race}, beats/min	Lactate max$_{incr}$; Lactate$_{race}$, mM	v_{race}, %$v\dot{V}O_{2max}$	Cr, ml·kg⁻¹·m⁻¹	Racing Time t_{800} or t_{1500}, s; Rank in Race
			800-m race				t_{800}
1	70.0; 71.0	20.0; 21.2	190; 190	12.7; 14.4	105.9	0.210	136; 7
2	60.0; 57.4	19.0; 22.8	185; 183	14.2; 16.1	120.0	0.189	126; 3
3	64.8; 62.4	18.0; 20.6	196; 196	12.1; 15.8	114.3	0.216	140; 8
4	62.7; 60.6	19.0; 24.0	195; 194	11.4; 18.0	126.3	0.198	120; 1
5	66.0; 65.2	20.0; 22.6	195; 194	13.7; 20.8	113.0	0.198	127; 4
6	62.7; 60.8	19.0; 22.1	195; 193	12.0; 17.3	116.1	0.198	131; 6
7	66.0; 65.2	20.0; 23.0	199; 200	15.0; 16.3	115.0	0.198	125; 2
8	66.5; 68.0	19.0; 22.3	195; 194	16.0; 16.8	117.4	0.210	129; 5
Mean	64.8; 63.8	19.3; 22.3	194; 193	13.4; 16.9	116.0	0.202	129
	$P = 0.1$		$P = 0.08$	$P = 0.005$			
SD	3.0; 4.4	0.7; 1.1	4; 5	1.6; 1.9	5.9	0.009	
			1,500-m race				t_{1500}
1	63.0; 63.2	19.0; 20.5	199; 198	12.0; 11.4	108.1	0.198	263; 3
2	60.0; 57.6	18.0; 20.0	191; 191	11.9; 12.8	111.1	0.200	270; 7
3	73.9; 74.1	20.0; 20.1	182; 182	11.9; 15.6	100.7	0.222	268; 4
4	69.0; 66.3	21.0; 21.6	191; 192	13.2; 18.1	102.9	0.197	250; 1
5	63.0; 62.6	18.0; 17.2	194; 193	15.0; 16.8	95.5	0.210	314; 6
6	64.0; 61.7	18.5; 20.1	200; 199	14.0; 18.0	108.9	0.208	268; 4
7	65.0; 64.4	19.5; 21.1	188; 189	13.0; 14.6	108.2	0.200	256; 2
Mean	65.4; 64.3	19.1; 20.1	192; 192	13.0; 15.3	105.1	0.205	270
	$P = 0.06$		$P = 0.7$	$P = 0.02$			
SD	4.6; 5.1	1.1; 1.4	6; 6	1.2; 2.6	5.6	0.009	

For the 800-m or 1,500-m race. $\dot{V}O_{2max}$ is the maximal oxygen uptake achieved in the incremental test; max $\dot{V}O_{2race}$ is the maximal value of oxygen uptake achieved during the race; $v\dot{V}O_{2max}$ is the velocity associated with $\dot{V}O_{2max}$ in the incremental test; Lactate max$_{incr}$ is the maximal blood lactate accumulation measured at the end of the incremental test; Lactate$_{race}$ is the lactate at the end of the race; v_{race} is the average velocity over the 800-m or 1,500-m run expressed in km/h and in percentage of $v\dot{V}O_{2max}$; HR_{max} is the maximal heart rate reached during the incremental test; max HR_{race} is the maximal heart rate reached during the 800-m or 1,500-m race; and Cr is the energy cost of running. Subjects are different subjects over 800-m and 1,500-m run races.

Table 2. *Individual physical characteristics and performance of the metabolic power of athletes required to run the 800 m and 1,500 m at their personal best*

Subjects	Weight, kg	Height, cm	Age, yr	Fat mass, %	Racing Time, t_{800} or t_{1500}, s	Personal Best, s	% of Personal Best
				800-m race			
1	66	183	17	10.6	136.0	134.0	99
2	74	179	19	13.6	126.0	112.8	89
3	61	180	17	9.1	140.6	140.6	100
4	69	185	19	7.0	120.0	108.0	90
5	66	180	19	7.0	127.1	127.1	100
6	74	178	17	12.1	131.0	129.0	99
7	72	184	19	11.8	125.0	116.0	93
8	65	180	17	12.3	129.0	126.0	98
Mean	68	181	18	10.4	129.6	124.1	96
SD	5	3	1	2.5	6.0	11.0	4
				1,500-m race			
1	53	168	17	11.0	263	249	95
2	76	190	18	13.0	270	247	91
3	50	170	18	12.0	268	250	93
4	65	180	18	11.0	250	244	98
5	60	169	17	10.0	314	275	88
6	59	175	18	12.0	268	253	94
7	52	162	18	13.0	256	237	93
Mean	59	173	18	11.7	270	251	93
SD	9	9	1	1.1	21	12	3

Subjects are different subjects over 800-m and 1,500-m run races.

1710, Arkray, Kyoto, Japan). This lactate analyzer was calibrated before all tests (42).

Exercise Tests

Incremental test. To measure the energy cost of running at different speeds, the subjects first performed a paced incremental test with 3-min stages on a track (6). During the last 6 min of a 10-min warmup at a speed of 12 km/h, when anaerobic metabolism is negligible and when there is no slow component of oxygen uptake kinetics, the oxygen cost (Cr) at this submaximal speed was measured. Thereafter the subjects ran at 14 km/h and speed was progressively increased by 1 km/h at each stage. A fingertip capillary blood sample was collected immediately before and 3 min after the test. $\dot{V}_{O_2max}$ was defined as the plateau attained by oxygen uptake during this incremental test or if no plateau appeared we used secondary $\dot{V}_{O_2max}$ achievement criteria, i.e., a respiratory exchange ratio (RER = carbon dioxide output/$\dot{V}_{O_2}$) greater than 1.05, blood lactate greater than 8 mM/l, and a peak HR at least equal to 90% of the age-predicted maximum (2). The $v\dot{V}_{O_2max}$ was defined as the minimal velocity at which $\dot{V}_{O_2max}$ occurred (5). When $v\dot{V}_{O_2max}$ was maintained for at least half rather than for all of the last stage, it was then considered as the averaged velocity maintained during the last two stages (6).

Middle-distance (800 m and 1,500 m) races. One week later, the subjects competed in an 800-m or 1,500-m race in a competition (official meeting organized by the French Athletic Federation). Before the race subjects performed a 30-min warmup period at 60% $v\dot{V}_{O_2max}$ followed by two 100-m runs at a faster speed and a 5-min rest period. Their performance was defined as the time achieved over these distances (t_{800} or t_{1500}). A fingertip capillary blood sample was collected shortly before, immediately after, and 3 and 8 min after the race. The $\dot{V}_{O_2}$ drop phenomenon was considered to appear when the decrease in $\dot{V}_{O_2}$ was ≥5% during an interval of time of at least 15 s while the subjects continued to run at or above $v\dot{V}_{O_2max}$. Because of the competition period, the subjects were no longer available to perform tests to measure their maximal accumulated oxygen deficit [an all-out run of 2 min according to the protocol of Medbo et al. (41)]. Time limit at $\dot{V}_{O_2max}$ was computed as the total racing time minus the time delay for reaching $\dot{V}_{O_2max}$ and the $\dot{V}_{O_2}$ drop duration.

Description and Calculation of Physiological Data

Net oxygen cost of running. The net oxygen cost of running, Cr, is defined as the per kilogram body weight oxygen equivalent of the energy required above resting (estimated by $\dot{V}_{O_2} - \dot{V}_{O_2rest}$) to transport the subject's body over one unit of distance (19).

$$Cr = (\dot{V}_{O_2} - \dot{V}_{O_2rest})/v \qquad (6)$$

where $\dot{V}_{O_2}$ is the oxygen uptake at the mean velocity v and is expressed in milliliters per kilogram per minute. Given that the runners were not really at rest before the race we assumed a $\dot{V}_{O_2}$ at rest ($\dot{V}_{O_2rest}$) to be equal to 5 $ml \cdot kg^{-1} \cdot min^{-1}$ according to the intercept of the $\dot{V}_{O_2}$-speed regression line obtained by Medbo and Tabata (39, 41). v is the velocity in meters per minute, and thus Cr is the oxygen cost of running in milliliters O_2 per kilogram per meter. Cr is estimated by the oxygen uptake at submaximal speed, i.e., during the last 6 min of the 10-min warmup at 12 km/h in the incremental test. The oxygen uptake required according to the speed during the 800-m or 1,500-m races ($\dot{V}_{O_2demand}$) was calculated according to Eq. 7 (19):

$$\dot{V}_{O_2demand} = v_{race} \times Cr \qquad (7)$$

where v_{race} is the 800-m or 1,500-m racing speed. This formula assumes that the energy cost of running is independent of running velocity according to di Prampero (18) and other authors (51). This assumption is also a condition of the validity of the critical power (speed) model and its derivatives (46). At these speeds the aerodynamic component of the energy cost of running is still of the same order of magnitude as that of the experimental error of measurement (5%) (6).

Accumulated O_2 deficit calculation during the 800-m and 1,500-m races. Every 5 s, the oxygen deficit (O_2 deficit expressed in ml O_2/kg) was calculated as the difference between the oxygen demand ($\dot{V}_{O_2demand}$, $ml \cdot kg^{-1} \cdot min^{-1}$) according to the speed (m/min) multiplied by the energy cost of running (ml $O_2 \cdot kg^{-1} \cdot m^{-1}$), and the effective oxygen uptake ($\dot{V}_{O_2}$ in $ml \cdot kg^{-1} \cdot min^{-1}$). The accumulated O_2 deficit was the whole race oxygen deficit and was the sum of all the 5-s oxygen deficits during the race.

Instantaneous time limit at the anaerobic power (tlim PAN). The time limit at the anaerobic power (tlim PAN) was calculated according to *Eq. 2,* which represents the maximal duration that the runner could sustain at this anaerobic power at this instant of the race given the anaerobic stores at the time. Speed variability was defined using the coefficient of the variation (i.e., the ratio between the speed SD and the mean speed, multiplied by 100).

Statistics

Because of the small sample sizes in this study ($n = 7$ and $n = 8$), the normality of the distribution and the equality of the variance were checked by SigmaStat (Jandel Scientific, Chicago, IL). When the normality of the distribution and the equality of the variance were verified, an ANOVA test on one factor (racing distance effect, 800 vs. 1,500 m) or two factors (distance and the first vs. second part of the race) was applied to measure the racing distance and fatigue effect during each race on tlim PAN (Staview 5.5, Statsoft, Berkeley, CA); if not, a Mann-Whitney *U*-test was applied. The two parts of the race were split according to racing time and not running distance since we focused on tlim PAN and not on the distance limit at PAN. Correlations between $\dot{V}_{O_{2max}}$, total accumulated oxygen deficit (TAOD), %AN, speed variability, and performance were determined using Pearson's product-moment correlation coefficient. A chi-squared test was performed to test the association between racing distance and the occurrence of the $\dot{V}_{O_2}$ drop. We do not necessarily adopt the common but arbitrary 5% level for statistical significance. Exact *P* values are quoted for all tests, and statistical and practical significances are discussed on a case-by-case basis. This will also permit readers to form their own assessments as to the importance of our results. All results are presented as means ± SD.

RESULTS

Performance Times (t_{800} and t_{1500})

All the runners ran at a speed equal to or superior to 90 and 95% of their absolute personal best or equal to or superior to the performance accomplished at the same period of the year (in the early phase of the competition period) (96 ± 4 vs. 93 ± 3% for the 800-m and 1,500-m runners, $P = 0.19$) (Table 2). The runners elicited their maximal $\dot{V}_{O_2}$ and HR, average racing speed (v_{800} and v_{1500}) was above that of the speed associated with $\dot{V}_{O_{2max}}$ ($v\dot{V}_{O_{2max}}$) (116.0 ± 5.9 and 105.1 ± 5.6% of $v\dot{V}_{O_{2max}}$, $P = 0.002$), and the postrace maximal blood lactate concentrations were equal to 16.9 ± 1.9 and 15.3 ± 2.6 mM after the 800-m and 1,500-m races, respectively ($P = 0.18$) (Table 1).

Racing Speed Variations and Correlation with Performance

Running speed ranges were 5.8 ± 1.3 vs. 7.5 ± 2.3 m/s over 800 m and 1,500 m. However, when this coefficient of speed variation was expressed relative to the average speed (27.0 ± 7.1% and 52.8 ± 13.6%), the speed range was significantly higher during the 800-m race compared with the 1,500-m race ($P < 0.001$). Typical speed patterns of one 800-m runner (Fig. 1A) and one 1,500-m runner (Fig. 1B) showed that over 800 m, the speed continuously decreased as if in an all-out exercise (Fig. 1A), while over 1,500 m the speed reached a plateau with fluctuations above $v\dot{V}_{O_{2max}}$ (Fig. 1B). This higher speed amplitude over 800 vs. 1,500 m was confirmed by the higher coefficient of the 800-m speed variation (11.5 ± 4.1% vs. 8.3 ± 3.3% over 800 and 1,500 m, respectively, $P = 0.003$). In both races, the coefficients of variation of the speed during the second half of the races were significantly lower than those
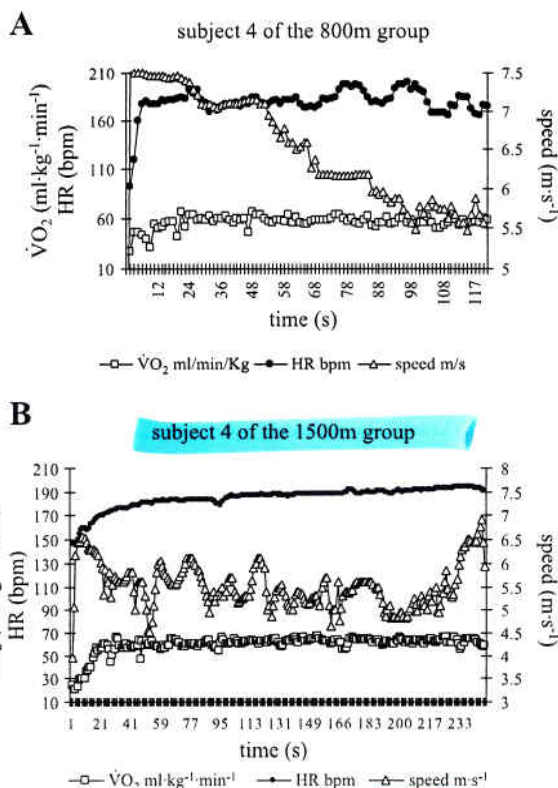
A

subject 4 of the 800m group

—□— $\dot{V}_{O_2}$ ml/min/Kg —●— HR bpm —△— speed m/s

B

subject 4 of the 1500m group

—□— $\dot{V}_{O_2}$, ml·kg⁻¹·min⁻¹ —●— HR bpm —△— speed m·s⁻¹

Fig. 1. Typical sequential oxygen uptake ($\dot{V}_{O_2}$), heart rate (HR), and speed over the 800 m (*A*) and 1,500 m (*B*) in two different runners (*subject 4* of the 800-m group and *subject 4* of the 1,500-m group, respectively). bpm, beats/min.

observed during the first half of the races (CVs = 3.2 ± 1.4% and 8.0 ± 3.3% for the last part of the 800 and 1,500 m, $P = 0.006$). Performance was related to the variability of running speed for the 800-m race ($r = -0.712$, $P = 0.047$) but not for the 1,500 m ($r = 0.24$, $P = 0.606$). Thus the higher the variability over 800 m, the better was the performance (i.e., lower t_{800}).

Time Limit at the Momentary Anaerobic Powers (tlim PAN) and at $\dot{V}_{O_{2max}}$ and Correlation with 800- and 1,500-m Performances

Sequential speeds elicited a PAN that the athlete was able to sustain for 32% of the final racing time (tlim PAN = 34.0 ± 8.0 and 31.9 ± 12.2% of t_{800} and t_{1500}, $P = 0.68$) (Table 3). However, after two-thirds of the racing time, tlim PAN had dropped (62 ± 13 and 63 ± 14% of t_{800} and t_{1500}, respectively, $P = 0.91$). The average value of tlim PAN was significantly longer in the first compared with the second half of the 800-m (57 ± 14 vs. 32 ± 6 s, $P = 0.01$) and 1,500-m (107 ± 36 vs. 74 ± 41 s, $P = 0.01$) races (Table 3). Over 1,500 m, tlim PAN was not influenced by the delay of attainment of $\dot{V}_{O_{2max}}$ since it was not significantly different before and after the attainment of $\dot{V}_{O_{2max}}$ (96 ± 32 vs. 78 ± 32 s, $P = 0.32$). In contrast, over 800 m tlim PAN appeared (considering the risk of type 1 error and the interindividual variation) to be related to the attainment of $\dot{V}_{O_{2max}}$ (57 ± 16 vs. 43 ± 11 s, $P = 0.06$). In addition, tlim

Table 3. *Time to exhaustion at $\dot{V}_{O_{2max}}$ during the 800-m and 1,500-m races in seconds and in % of t_{800} and t_{1500}, amplitude and duration of $\dot{V}_{O_2}$ drop at end of races, TAOD, and final speed*

Subjects	t$\dot{V}_{O_2}$ drop, s ($P = 0.59$)	tlim $\dot{V}_{O_{2max}}$, s ($P < 0.01$)	tlim$\dot{V}_{O_{2max}}$, % of time trial ($P = 0.13$)	Amplitude of $\dot{V}_{O_2}$ drop, ml·kg^{-1}·min^{-1} ($P = 0.79$ Mann Whitney)	TAOD, ml/kg	Final Speed, %$v\dot{V}_{O_{2max}}$ ($P = 0.09$)
800-m race						
1	2	82	60	1.0	36	105.0
2	24*	62	49	3.1*	44	83.8
3	6	86	61	0.6	41	76.2
4	10	86	72	0.8	44	105.2
5	2	93	73	0.9	35	104.3
6	3*	94	72	7.3*	44	107.3
7	6	70	56	1.1	33	105.2
8	21*	61	47	5.0*	43	122.2
Mean	16 ($n = 3$)	79	61	5.1 ($n = 3$)	40	101.1
SD	11 ($n = 3$)	13	10	2.1 ($n = 3$)	5	14.4
1,500-m race						
1	0	205	78	0.0	63	111.0
2	13†	147	54	11.5†	79	114.7
3	7†	214	80	4.6†	42	104.1
4	10†	209	84	6.3†	66	120.1
5	0	258	82	0.1	40	95.6
6	11†	176	66	6.8†	69	166.0
7	43†	136	53	6.2†	54	119.8
Mean	15 ($n = 5$)	202	71	7.1 ($n = 5$)	59	118.7
SD	16 ($n = 5$)	35	13	2.6 ($n = 5$)	14	22.6

tlim $\dot{V}_{O_{2max}}$, time to exhaustion at $\dot{V}_{O_{2max}}$; t$\dot{V}_{O_2}$ drop, duration of $\dot{V}_{O_2}$ drop; TAOD, total accumulated oxygen deficit. *Subject values used to calculate the mean and SD for $n = 3$ in 800-m race; †subject values used to calculate the mean and SD for $n = 5$ in 1,500-m race. In heading, P values are indicated for the significance of the difference between the 800-m and 1,500-m races except for the time trials. Subjects are different subjects over 800-m and 1,500-m run races.

PAN was not influenced by the $\dot{V}_{O_2}$ drop ($r = 0.455$, $P = 0.49$). These final two results are crucial and show that the ability to maintain $\dot{V}_{O_{2max}}$ at the end of the race did not influence the time to exhaustion at the momentary anaerobic power.

tlim PAN during the first ~70% of the race was correlated with the t_{1500} ($r = -0.915$, $P = 0.004$) but not with t_{800} ($r = -0.05$, $P = 0.892$). This means that over 1,500 m, the longer the time limit at any instantaneous anaerobic power (tlim PAN) in the first part of the race, the better the performance (i.e., shorter racing time).

The time limit at $\dot{V}_{O_{2max}}$ (tlim $\dot{V}_{O_{2max}}$) expressed as a percentage of the racing duration was also not significantly different between 800 m and 1,500 m (61 ± 10 vs. 71 ± 13% of the racing time over 800 m and 1,500 m, $P = 0.13$) (Table 4). In the final part of the race, half of the group (8/15) demonstrated a $\dot{V}_{O_2}$ drop below $\dot{V}_{O_{2max}}$ that appeared over the final 10% of the race, despite the fact that a speed exceeding $v\dot{V}_{O_{2max}}$ was maintained. This decrease did not depend on the racing distance since it was observed in both the 800- and 1,500-m races (3/8 and 5/7 runners over 800 m and 1,500 m; chi-squared = 1.73, $P = 0.2$) (Table 4). This decrease was 5.1 ± 2.1 vs. 7.1 ± 2.6 ml·kg^{-1}·min^{-1} ($P = 0.79$) or 9.3 ± 4.2 vs. 11.4 ± 5.6% of $\dot{V}_{O_{2max}}$, ($P = 0.46$) and its relative duration was not significantly different between the 800-m and 1,500-m races, respectively (16 ± 11 vs. 15 ± 16 s, $P = 0.59$, i.e., 12 ± 9 vs. 5 ± 6% of the racing time, $P = 0.13$). As detailed above, of the eight runners who evidenced a $\dot{V}_{O_2}$ decrease running at a speed exceeding $v\dot{V}_{O_{2max}}$, three of them increased their speed and two maintained it by increasing their speed and then eliciting their anaerobic power in the final sprint using the remaining anaerobic stores. Their performances were not correlated with the time limit at $\dot{V}_{O_{2max}}$ expressed either in seconds or in percent of the racing time ($P = 0.64$ and 0.80 for t_{800} and $P = 0.71$ and 0.22 for t_{1500}).

The AOD, which depends on the speed run above $v\dot{V}_{O_{2max}}$ and time sustained at $\dot{V}_{O_{2max}}$ considered beforehand, represents the progressive depletion of the anaerobic stores. AOD increased linearly throughout the race until the finish as shown in Fig. 2, *A* and *B*. The TAOD was negatively correlated with performance over 800 m (t_{800}) ($r = -0.70$, $P = 0.05$), meaning that for the 800 m, the higher the oxygen deficit, the better the performance (lower t_{800}), but not significantly correlated over 1,500 m (t_{1500}) ($r = -0.51$, $P = 0.26$).

DISCUSSION

This study has, for the first time, taken a bioenergetic approach to running speed variation and performance as measured during actual race conditions, despite the inherent practical difficulties in obtaining such measurements. We have taken this approach in an attempt to understand how a runner selects running speed so as to optimize real-world performance using energetic resources.

The originality of this study was to adapt the calculation to the data measured during an actual race providing continuous estimation of aerobic power from oxygen uptake and anaerobic power from the deficit in oxygen. It overcomes two major limits of the original approach based on the use of constant-power tests and assuming an infinitely fast increase in aerobic power. This is because the constant-power model does not incorporate any $\dot{V}_{O_2}$ kinetics but it has been demonstrated that a fast-start pacing strategy allows achievement of optimal performance under the assumptions of the three-parameter model (45).

This study shows that speed control in middle-distance races is such as to maintain the time to exhaustion at the instantaneous anaerobic power (tlim PAN = ANS/PAN) constant

Table 4. *Time to exhaustion at the anaerobic power in the whole race and in the first and second half part of the race*

Subjects	tlim PAN on Whole Race, s (% of t_{800} or t_{1500})	tlim PAN on First Half, s (% of t_{800} or t_{1500})	tlim PAN on Second Half, s (% of t_{800} or t_{1500})
	800-m race		
1	39.8 (29.3%)	49.4 (36.3%)	30.5 (22.4%)
2	47.0 (37.2%)	60.5 (48.0%)	35.2 (27.9%)
3	34.3 (24.5%)	39.6 (28.3%)	29.8 (21.3%)
4	37.8 (31.5%)	51.8 (43.2%)	24.7 (20.6%)
5	47.8 (37.5%)	59.9 (47.2%)	36.6 (28.8%)
6	54.5 (41.7%)	74.1 (56.6%)	36.3 (27.7%)
7	30.7 (24.6%)	39.6 (31.6%)	23.1 (18.5%)
8	59.5 (46.1%)	79.4 (61.6%)	40.7 (31.6%)
Mean	43.9 (34.0%)	56.7 (44.0%)	32.1 (25%)
SD	10.1 (8.0%)	14.7 (11.6%)	6.2 (4.7%)
	1,500-m race		
1	98.4 (37.4%)	131.3 (49.9%)	76.4 (29.0%)
2	99.5 (36.9%)	138.5 (51.3%)	65.2 (24.1%)
3	62.9 (23.5%)	81.2 (30.3%)	46.8 (17.5%)
4	108.2 (43.3%)	129.9 (52.0%)	147.8 (59.1%)
5	27.2 (8.7%)	38.6 (12.3%)	17.4 (5.5%)
6	85.3 (31.8%)	107.4 (40.1%)	66.8 (24.9%)
7	106.4 (41.6%)	119.2 (46.6%)	95.4 (37.3%)
Mean	83.9 (31.9%)	106.6 (40.3%)	73.7 (28.2%)
SD	29.5 (12.2%)	35.6 (14.6%)	40.8 (16.8%)

Whichever the race distance ($P = 0.69$), time to exhaustion at the anaerobic power (tlim PAN) is significantly lower in the second vs. the first half time of the race ($P = 0.013$). Considering the whole race, tlim PAN is lower over 800 m vs. 1,500 m ($P < 0.001$) in absolute but not in relative time to t_{800} and t_{1500} ($P = 0.81$). Subjects are different subjects over 800-m and 1,500-m run races.

during ~70% of the racing time. This result suggests that the time spent running at the chosen instantaneous anaerobic power during this portion of middle-distance races may be a consequence of an anaerobic energetic controller of speed. This may well be related to the perception of exhaustion as previously reported for blood lactate accumulation (9). Furthermore, 1,500-m performance is related to tlim PAN, which depends on a careful first half racing speed selection, while performance over 800 m is related to the total anaerobic stores. Furthermore, tlim PAN decreased almost significantly ($P = 0.06$) after the initial phase of $\dot{V}_{O_{2max}}$ steady-state achievement in the 800-m but not the 1,500-m race.

Time Limit at the Instant Racing Anaerobic Power (tlim PAN) is Maintained Constant During the First 70% of the Racing Duration

Our results show that the sequential time limit at the anaerobic power (tlim PAN) was constant during the first two-thirds of the racing time in both the 800 m and 1,500 m. This time limit is similar to the concept of the "endurance parameter ratio" proposed in a previous study by Fukuba and Whipp (25). This ratio has the dimension of duration (since it is a distance divided by speed) and has been interpreted to be a time limit before exhaustion (25). That is, speed variation has been reported to depend on the ratio of the anaerobic capacity (or the distance covered without the resynthesis of ATP by oxidative phosphorylation) to the critical speed. This index is considered to be an important determinant of the race-pace strategy (25), suggesting that the ability to vary running speed above the critical speed depends on the ratio between the anaerobic reserve, the anaerobic work capacity in joules (or distance equivalent for a given energy cost of running set in $J \cdot kg^{-1} \cdot m^{-1}$), and the fatigue threshold speed. The values of tlim PAN reported in the

present study for 1,500 m are close to the λ value Ward-Smith calculated (60) for long sprints (400 m). However that model was a constant-speed model, which is not necessarily optimal for achieving the best performance (i.e., the best average speed) (7, 24).

The present study showed that the time limit at the instantaneous anaerobic power remained constant until ~30% of the remaining racing time. These results indicate that this sequential time limit at the chosen anaerobic power may be a potential factor in regulating speed variations during supramaximal running races (800–1,500 m). Since the time limit at the instant anaerobic power is the ratio of the instant anaerobic stores and anaerobic power, we hypothesized that the reserves of anaerobic energy at each instant of the race could be one candidate for the feedback controllers of the power output, or more particularly of the anaerobic power. However, this does not exclude the possibility as reported for the marathon by Noakes (48), of the action of a central (brain) neural control that regulates performance "in anticipation" as recently suggested by the model of central neural control. Indeed, a large component of the complete central governor discusses and incorporates energetic feedback mechanisms, as described particularly in the manuscript of Noakes et al. (49). However, middle-distance events that are run in <5 min appear to have an energetic feedback mechanism that allows the last 30% of the racing time to be run without decreasing speed below the maximal aerobic speed. Our study may have been more complete if we had also examined the relationship between RPE, estimated time limit [ETL (24)], acidosis (pH), and the anaerobic deficit during race simulations on the treadmill, but the runners were not available for additional experiments as the competitive season had started. Garcin and Billat (26) previously demonstrated that an athlete was able to estimate his or
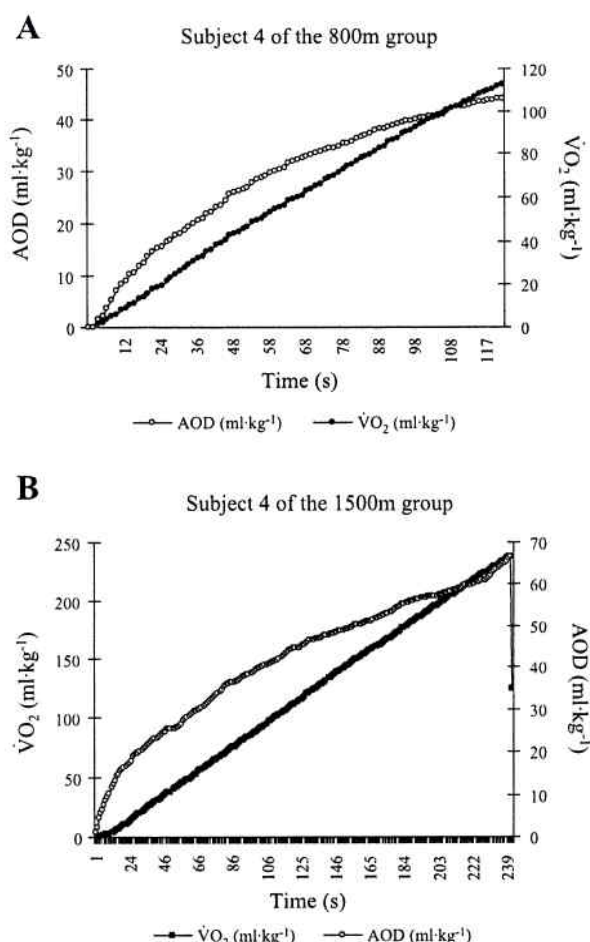
A

B

Fig. 2. Typical time course of the oxygen volume (Vo₂), and accumulated oxygen deficit (AOD) over 800 m (*A*) and 1,500 m (*B*) races for *subject 4* of the 800-m group and *subject 4* of the 1,500-m group. respectively.

her time remaining at each moment of an exhaustive run at $v\dot{V}o_{2max}$ and validated a scale of difficulty of exercise based on ETL. Nevertheless, the examination of physiological strain during real racing conditions, where there are continual variations in speed by athletes, is a new challenge to increasing our understanding of the limits of human performance. Such limits clearly do not depend only on energetic resources but also on the ability to control them (14, 28).

By reducing speed, as in interval training, the runner prevents significant early phosphocreatine depletion and high glycolytic flux and the consequent accumulation of H^+, which inhibits the rise of the signal activating oxidative phosphorylation, thereby restricting oxidative ATP supply to below the oxidative capacity (14, 34, 56). A subsequent acceleration will then decrease the PCr/Cr ratio, which in turn increases the sensitivity of mitochondrial respiration to ADP (56). The drop of tlim PAN was significantly lower after the attainment of $\dot{V}o_{2max}$ over 800 m but not over 1,500 m. The *P* value at 0.06 over 800 m may be due to a type 1 error due to small sample size and/or the high interindividual variation linked to the fast start and speed decrease over 800 m. The 800-m race is more like an all-out race during which the first 200 m are run in

lanes, which imposes a fast start for getting to the front to minimize the distance covered in races if runners wish to optimize their performance (33). During this starting phase of ~30 s, the initial oxygen deficit inherent in the delay of $\dot{V}o_{2max}$ achievement taxes tlim PAN significantly and as a consequence tlim PAN drops, as we observed after this initial unsteady $\dot{V}o_2$ phase while the O_2 demand is high. Furthermore, the interindividual difference between the initial and $\dot{V}o_{2max}$ steady state could be due to the different 800-m energetic profile. Indeed, 800-m race training is a balance between aerobic and anaerobic interval training (3, 4), but some runners are rather 400- to 800-m runners or 800- to 1,500-m runners and perform preferentially anaerobic or aerobic interval training, respectively. Furthermore, our 800-m runners ran the first part of the race at a different absolute speed, and it is well known that time to reach $\dot{V}o_{2max}$ is inversely related to exercise intensity (31).

The method of estimating the oxygen deficit by gas exchange has been demonstrated to enable noninvasive quantification of the relative aerobic/anaerobic metabolism contributions (36) and has been extensively used in previous studies (16, 39, 61). The accumulated oxygen deficit at any one instant of the race is proportional to lactate accumulation and HR increase and may be associated with the time limit that an athlete is still able to sustain at that instant of the race (20). The estimation of the time limit during exhaustive exercise between 90 and 120% of $v\dot{V}o_{2max}$ has been shown to be accurate especially in well-trained subjects. The estimation of a time limit scale has been validated for predicting the effective time limit at a given speed (27, 28). At any instant of the race, a runner is able to gauge the time limit at his or her running speed and in middle-distance running the time limit at the anaerobic power determines any speed fluctuation. Furthermore, it has been shown in an all-out 30- to 36-s exercise that there appeared to be a preprogrammed 30-s "end point" based on the anticipated exercise duration from previous experience, and that the changes in power output generated by the brain could be in response to peripheral metabolic changes in the active muscles (1). A minimal duration of 30 s may be required for efficacy of such controls. In the present study, the runner adopted a speed allowing him to elicit an anaerobic power that could be sustained for a time limit of 50 or 100 s, representing 30% of the remaining duration of the race, maintaining this until the last third part of the race. This capacity for estimating the time limit remaining has been reported to be fitness dependent since the runners who had the highest $\dot{V}o_{2max}$ were those who estimated ETL more accurately (28). However in the Garcin et al. studies (26, 28), running speed was imposed on the athlete and was maintained constant (at $v\dot{V}o_{2max}$). Therefore, the perception of the time limit remaining at a sequential speed maintained for only a few seconds remains an unexplored domain that could be solved through an interdisciplinary approach between physiology and perceptual motor skills. The data obtained from the present study suggest that the athlete perceives the relative time for the total duration of the race (tlim PAN). It would be relevant to examine whether this scale is valid when the choice of speed is free as during a race. Even if the runners were asked to adopt a speed of their own choice and not according to the speed of their opponents, it is impossible to deny the likelihood that tactical aspects take into account the other runners, especially among those who had similar per-

sonal best times. However this race was performed in the early stage of the competition season and was considered by coaches as fine tuning between the regional championships.

Time Limit at the Anaerobic Power (tlim PAN) and Performance in Middle-Distance Races

The question we asked was whether performance over middle-distance running was correlated with the momentary anaerobic power and its time to exhaustion and/or to the oxygen deficit. The best 1,500-m runners were those who recorded the higher time limits at the anaerobic power in the first two-thirds of the race thanks to a lower speed start. While this was the case for the 1,500-m runners, the best 800-m runners were those who demonstrated the highest anaerobic capacity (total oxygen deficit) at the end of the race. The 800-m performance has previously been reported to be related to the accumulated oxygen deficit in middle-distance runners (11, 53). The 800-m performance could rely on the capacity to buffer the H^+ inevitably produced during the race, which is rather more like an all-out race without any recovery and speed fluctuation around a plateau (55). Furthermore, high lactate exchange ability has been reported to be correlated with the 800-m but not with the 1,500-m performance in well-trained specialized subjects and could play a role in the athlete's capacity to sustain exercise of close to 2-min duration and specifically to run 800 m (12). The 1,500-m performance was neither correlated with the maximal oxygen deficit nor with the anaerobic power but with their ratio (tlim PAN) averaged in the first two-thirds of the race. This means that over 1,500 m the runners who had the longest limits at their anaerobic power in the first part of the race were those who achieved the best final performance. The 1,500-m run could therefore require a closer control of speed while the 800-m race is more like a long sprint, at least for the first two-thirds of the race.

Conclusion

The present study supports the contention that in supramaximal middle-distance races (800 and 1,500 m) eliciting $\dot{V}O_{2max}$, running speed varies according to the anaerobic power in such a way as to maintain the time limit at the given sequential anaerobic power constant until the last third of the racing time. This finding is independent of the appearance of a $\dot{V}O_2$ drop at the end of the race observed in half of our runners and previously reported in a study over 800 m (55) and in laboratory conditions with a standard cart system (50). Only two runners were unable to manage their speed to maintain their time limit at PAN above 0 before the end of the race. The best 1,500-m runners were those who achieved the highest time limits at the anaerobic power in the first two-thirds of the race, and the best over 800 m were those who achieved the highest total accumulated oxygen deficit. These results suggest that the best 1,500-m performance depends on the runner's ability not to start too fast involving a lower anaerobic power (keeping a longer time limit at the anaerobic power), while the 800-m run, which tends to be more like all-out exercise, may depend more on the total oxygen deficit that the athletes can bear before exhaustion. The anaerobic reserve may therefore determine the time to go at any instantaneous speed above $v\dot{V}O_{2max}$ and could be part of an energetic controller set to be included in a model of central fatigue that is currently under debate (54). The

present report has been a new approach to the energetics of middle-distance running, examining speed variation during real races. The present report can be viewed as a preliminary study before studies are carried out on the optimization of middle-distance performance in terms of speed management (5, 6, 7, 15).

We recognize that this was the only variable measured and uses indirect methods of measurement. Equally, a large number of other peripheral, cardiac, and/or neural factors could, and probably are, involved in creating variation in running speed during these events.

REFERENCES

1. **Ansley L, Robson PJ, St. Clair Gibson A, Noakes TD.** Anticipatory pacing strategies during supramaximal exercise lasting longer than 30 s. *Med Sci Sports Exerc* 36: 309–314, 2004.
2. **Astrand PO, Ryhming I.** A nomogram for calculation of aerobic (physical fitness) from pulse rate during submaximal work. *J Appl Physiol* 7: 218–221, 1954.
3. **Billat LV.** Interval training for performance: a scientific and empirical practice: special recommendations for middle- and long-distance running. I. Aerobic interval training. *Sports Med* 31: 13–31, 2001.
4. **Billat LV.** Interval training for performance: a scientific and empirical practice. Special recommendations for middle- and long-distance running. II. anaerobic interval training. *Sports Med* 31: 75–90, 2001.
5. **Billat VL, Slawinski J, Danel M, Koralsztein JP.** Effect of free versus constant pace on performance and oxygen kinetics in running. *Med Sci Sports Exerc* 33: 2082–2088, 2001.
6. **Billat VL, Lepretre PM, Heugas AM, Koralsztein JP.** Energetics of middle-distance running performances in male and female junior using track measurements. *Jpn J Physiol* 54: 125–135, 2004.
7. **Billat VL, Wesfreid E, Kapfer C, Koralsztein JP, Meyer Y.** Nonlinear dynamics of heart rate and oxygen uptake in exhaustive 10,000 m runs: influence of constant vs. freely paced. *J Physiol Sci* 56: 103–111, 2006.
8. **Blondel N, Berthoin S, Billat V, Lensel G.** Relationship between run times to exhaustion at 90, 100, 120, and 140% of v$\dot{V}O_{2max}$ and velocity expressed relatively to critical velocity and maximal velocity. *Int J Sports Med* 22: 27–33, 2001.
9. **Borg E, Kaijser L.** A comparison between three rating scales for perceived exertion and two different work tests. *Scand J Med Sci Sports* 16: 57–69, 2006.
10. **Bosquet L, Delhors PR, Duchene A, Dupont G, Leger L.** Anaerobic running capacity determined from a 3-parameter systems model: relationship with other anaerobic indices and with running performance in the 800 m-run. *Int J Sports Med* 28: 495–500, 2007.
11. **Brandon LJ, Boileau RA.** Influence of metabolic, mechanical and physique variables on middle distance running. *J Sports Med Phys Fitness* 32: 1–9, 1992.
12. **Bret C, Messonnier L, Nouck JM, Freund H, Dufour AB, Lacour JR.** Differences in lactate exchange and removal abilities in athletes specialised in different track running events (100 to 1500 m). *Int J Sports Med* 24: 108–113, 2003.
13. **Chatagnon M, Busso T.** Modelling of aerobic and anaerobic energy production during exhaustive exercise on a cycle ergometer. *Eur J Appl Physiol* 97: 755–760, 2006.
14. **Conley KE, Kemper WF, Crowther GJ.** Limits to sustainable muscle performance: interaction between glycolysis and oxidative phosphorylation. *J Exp Biol* 204: 3189–3194, 2001.
15. **Cottin F, Papelier Y, Durbin F, Koralsztein JP, Billat VL.** Effect of fatigue on spontaneous velocity variations in human middle-distance

running: use of short-term Fourier transformation. *Eur J Appl Physiol* 87: 17–27, 2002.

16. **Craig IS, Morgan DW.** Relationship between 800-m running performance and accumulated oxygen deficit in middle-distance runners. *Med Sci Sports Exerc* 30: 1631–1636, 1998.

17. **Dekerle J, Nesi X, Carter H.** The distance-time relationship over a century of running Olympic performances: a limit on the critical speed concept. *J Sport Sci* 24: 1213–1221, 2006.

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

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

20. **Doherty M, Smith PM, Hughes MG, Collins D.** Rating of perceived exertion during high-intensity treadmill running. *Med Sci Sports Exerc* 33: 1953–1958, 2001.

21. **Duffield R, Dawson B, Pinnington HC, Wong P.** Accuracy and reliability of a Cosmed K4b² portable gas analysis system. *J Sci Med Sport* 7: 11–22, 2004.

22. **Durnin JV, Womersley J.** Body fat assessed from total body density and its estimation from skinfold thickness: measurements on 481 men and women aged from 16 to 72 years. *Br J Nutr* 32: 77–97, 1974.

23. **Einsenmann JC, Brisko N, Shadrik D, Welsh S.** Comparative analysis of the Cosmed Quark b² and K4b² gas analysis systems during submaximal exercise. *J Sports Med Phys Fitness* 43: 150–155, 2003.

24. **Foster C, Hoyos J, Earnest C, Lucia A.** Regulation of energy expenditure during prolonged athletic competition. *Med Sci Sports Exerc* 37: 670–675, 2005.

25. **Fukuba Y, Whipp BJ.** A metabolic limit on the ability to make up for lost time in endurance events. *J Appl Physiol* 87: 853–861, 1999.

26. **Garcin M, Billat V.** Perceived exertion scales attest to both intensity and exercise duration. *Percept Mot Skills* 93: 661–671, 2001.

27. **Garcin M, Vandewalle H, Monod H.** A new rating scale of perceived exertion based on subjective estimation of exhaustion time: a preliminary study. *Int J Sports Med* 20: 40–43, 1999.

28. **Garcin M, Mille-Hamard L, Billat V.** Influence of aerobic fitness level on measured and estimated perceived exertion during exhausting runs. *Int J Sports Med* 25: 270–277, 2004.

29. **Gastin PB, Costill DL, Lawson DL, Krzeminski K, McConell GK.** Accumulated oxygen deficit during supramaximal all-out and constant intensity exercise. *Med Sci Sports Exerc* 27: 255–263, 1995.

30. **Gollnick PD, Bertocci LA, Kelso TB, Witt EH, Hodgson DR.** The effect of high intensity exercise on the respiratory capacity of skeletal muscle. *Pflügers Arch* 415: 407–413, 1990.

31. **Hill DW, Ferguson CS.** A physiological description of critical velocity. *Eur J Appl Physiol Occup Physiol* 79: 290–293, 1999.

32. **Jones AM, Wilkerson DP, Vanhatalo A, Burnley M.** Influence of pacing strategy on O₂ uptake and exercise tolerance. *Scand J Med Sci Sports* 18: 615–626, 2008.

33. **Jones AM, Whipp BJ.** Bioenergetic constraints on tactical decision making in middle distance running. *Br J Sports Med* 36: 102–104, 2002.

34. **Jubrias SA, Crowther GJ, Shankland EG, Gronka RK, Conley KE.** Acidosis inhibits oxidative phosphorylation in contracting human skeletal muscle in vivo. *J Physiol* 553: 589–599, 2003.

35. **Larsson P.** Global positioning system and sport-specific testing. *Sports Med* 33: 1093–1101, 2003.

36. **Larsson P, Henriksson-Larsen K.** Combined metabolic gas analyzer and GPS analysis of performance in cross-country skiing. *J Sports Sci* 23: 861–870, 2005.

37. **Maronski R.** Minimum-time running and swimming: an optimal control approach. *J Biomech* 29: 245–249, 1996.

38. **Mc Naughton LR, Sherman R, Roberts S, Bentley DJ.** Portable gas analyzer Cosmed K4b² compared to a laboratory based mass spectrometer system. *J Sports Med Phys Fitness* 45: 315–323, 2005.

39. **Medbo JI, Tabata I.** Relative importance of aerobic and anaerobic energy release during short-lasting exhausting bicycle exercise. *J Appl Physiol* 67: 1881–1886, 1989.

40. **Medbo JI, Burgers S.** Effect of training on the anaerobic capacity. *Med Sci Sports Exerc* 22: 501–507, 1990.

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

42. **Medbo JI, Mamen A, Holt Olsen O, Evertsen F.** Examination of four different instruments for measuring blood lactate concentration. *Scand J Clin Invest* 60: 367–380, 2000.

43. **Morton RH.** Modelling human power and endurance. *J Math Biol* 28: 49–64, 1990.

44. **Morton RH** A 3-parameter critical power model. *Ergonomics* 39: 611–619, 1996.

45. **Morton RH.** A new modelling approach demonstrating the inability to make up for lost time in endurance running events. *IMA J Mgmt Math* epub doi:10.1093/imaman/dpn022, 2008.

46. **Morton RH.** The critical power, and related whole-body bioenergetic models. *Eur J Appl Physiol* 96: 339–354, 2006.

47. **Morton RH, Billat LV.** The critical power model for intermittent exercise. *Eur J Appl Physiol* 91: 303–307, 2004.

48. **Noakes TD.** The central governor model of exercise regulation applied to the marathon. *Sports Med* 37: 374–377, 2007.

49. **Noakes TD, St. Clair Gibson A, Lambert EV.** From catastrophe to complexity: a novel model of integrative central neural regulation of effort and fatigue during exercise in humans: summary and conclusions. *Br J Sports Med* 39: 120–124, 2005.

50. **Perrey S, Candau R, Millet GY, Borrani F, Rouillon JD.** Decrease in oxygen uptake at the end of a high-intensity submaximal running in humans. *Int J Sports Med* 23: 298–304, 2002.

51. **Saunders P, Pyne D, Richard T, Hawley J.** Factors affecting running economy in trained distance runners. *Sports Med* 34: 465–485, 2004.

52. **Siler WL, Martin PE.** Changes in running pattern during a treadmill run to volitional exhaustion: fast versus slow runners. *J Appl Biomech* 7: 12–28, 1991.

53. **Snell PG, Mitchell JH.** The role of maximal oxygen uptake in exercise performance. *Clin Chest Med* 5: 51–62, 1984.

54. **St. Clair Gibson A, Noakes TD.** Evidence for complex system integration and dynamic neural regulation of skeletal muscle recruitment during exercise in humans. *Br J Sports Med* 38: 797–806, 2004.

55. **Thomas C, Hanon C, Perrey S, Le Chevalier JM, Couturier A, Vandewalle H.** Oxygen uptake response to an 800-m running race. *Int J Sports Med* 26: 268–273, 2005.

56. **Townsend MA.** Road-racing strategies. *Med Sci Sports Exerc* 14: 235–243, 1982.

57. **Ulmer HV.** Concept of an extracellular regulation of muscular metabolic rate during heavy exercise in humans by psychophysiological feedback. *Experientia* 52: 416–420, 1996.

58. **Walsh B, Tonkonogi M, Soderlund K, Hultman E, Saks V, Sahlin K.** The role of phosphorylcreatine and creatine in the regulation of mitochondrial respiration in human skeletal muscle. *J Physiol* 537: 971–978, 2001.

59. **Ward-Smith AJ.** The bioenergetics of optimal performances in middle-distance and long-distance track running. *J Biomech* 32: 461–465, 1999.

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

61. **Weber CL, Schneider DA.** Reliability of MAOD measured at 110% and 120% of peak oxygen uptake for cycling. *Med Sci Sports Exerc* 33: 1056–1059, 2001.