

Energy System Interaction and Relative Contribution During Maximal Exercise

Paul B. Gastin

Victorian Institute of Sport, Melbourne, Australia

Contents

Abstract	725
1. Historical Overview	726
2. Methods Used to Evaluate Energy Release	727
3. Power Output, Fatigue and Anaerobic Energy Supply	729
4. Aerobic Energy Supply	730
5. Interaction and Relative Contribution of the Energy Systems	735
6. Conclusion	738

Abstract

There are 3 distinct yet closely integrated processes that operate together to satisfy the energy requirements of muscle. The anaerobic energy system is divided into alactic and lactic components, referring to the processes involved in the splitting of the stored phosphagens, ATP and phosphocreatine (PCr), and the nonaerobic breakdown of carbohydrate to lactic acid through glycolysis. The aerobic energy system refers to the combustion of carbohydrates and fats in the presence of oxygen. The anaerobic pathways are capable of regenerating ATP at high rates yet are limited by the amount of energy that can be released in a single bout of intense exercise. In contrast, the aerobic system has an enormous capacity yet is somewhat hampered in its ability to delivery energy quickly. The focus of this review is on the interaction and relative contribution of the energy systems during single bouts of maximal exercise. A particular emphasis has been placed on the role of the aerobic energy system during high intensity exercise.

Attempts to depict the interaction and relative contribution of the energy systems during maximal exercise first appeared in the 1960s and 1970s. While insightful at the time, these representations were based on calculations of anaerobic energy release that now appear questionable. Given repeated reproduction over the years, these early attempts have lead to 2 common misconceptions in the exercise science and coaching professions. First, that the energy systems respond to the demands of intense exercise in an almost sequential manner, and secondly, that the aerobic system responds slowly to these energy demands, thereby playing little role in determining performance over short durations. More recent research suggests that energy is derived from each of the energy-producing pathways during almost all exercise activities. The duration of maximal exercise at which

equal contributions are derived from the anaerobic and aerobic energy systems appears to occur between 1 to 2 minutes and most probably around 75 seconds, a time that is considerably earlier than has traditionally been suggested.

The immediate source of energy for muscle contraction comes from the hydrolysis of ATP. As ATP exists in very low concentration in the muscle, and regulatory mechanisms appear to prevent its complete degradation, the body has evolved well regulated chemical pathways to regenerate ATP to allow muscle contraction to continue. There are 3 distinct yet closely integrated processes that operate together to satisfy the energy requirements of the muscle.

The first process involves the splitting of the high-energy phosphagen, phosphocreatine (PCr), which together with the stored ATP in the cell provides the immediate energy in the initial stages of intense or explosive exercise. The second process involves the nonaerobic breakdown of carbohydrate, mainly in the form of muscle glycogen, to pyruvic acid and then lactic acid through glycolysis. The third process, aerobic or oxidative metabolism, involves the combustion of carbohydrates and fats, and under some circumstances proteins, in the presence of oxygen.

The splitting of the stored phosphagens, ATP and PCr, and the nonaerobic breakdown of carbohydrate comprise the anaerobic energy system. The terms alactic (lactic acid is not formed) and lactic are often used to describe these anaerobic (without oxygen) pathways. These pathways are capable of regenerating ATP at high rates, resulting in large muscle power outputs. The capacity of the anaerobic system is, however, limited by the amount of energy that can be released in a single exercise bout. A rapid reduction of stored PCr and an accumulation of lactic acid with a concomitant reduction in pH brings about either a cessation of exercise or a forced reduction in the work output. In contrast, the aerobic energy system is capable of producing extremely large amounts of ATP, yet is rate-limited by the limits of oxidative phosphorylation

and of the respiratory and cardiovascular systems to deliver oxygen to the muscle. In many instances throughout this review, only 2 energy systems are referred to, namely the aerobic and anaerobic systems. Reference to a three-system dichotomy further divides the anaerobic system into ATP-PCr (alactic) and glycolytic (lactic) components.

Together these 3 energy processes are well suited to cope with the high, often sustained, and usually diverse energy demands placed on them during our daily lives and sporting endeavours. Their contrasting powers and capacities represent not a disadvantage but an advantage as they interact smoothly and efficiently to replenish ATP. The interaction and relative contribution of the energy systems during single bouts of maximal, and usually exhaustive, exercise is the focus of this review. A particular emphasis has been placed on the contribution of the aerobic energy system to high intensity exercise. The traditionally held view that the aerobic energy system plays an insignificant role during high intensity exercise seems to warrant re-evaluation.

1. Historical Overview

Attempts to depict the interaction and relative contribution of the energy systems during maximal exercise first appeared in the literature in the 1960s and 1970s. Based on a study by Fox and co-workers,^[1] which used oxygen debt and lactic acid production to determine relative energy release, Fox^[2] introduced a conceptual figure of the relationship between the 3 energy systems in reference to performance time and power output. At a similar time, Howald et al.^[3] presented a figure that attempted to summarise the sequence and quantitative relationship between the energy-supplying processes in human skeletal muscle. Fox^[2] and Mathews and Fox^[4] discussed the concept of an

energy continuum, dividing up this continuum into areas of activity based on exercise duration. The power and capacity of each system was calculated such that the system likely to predominate during a particular activity was given. Selected activities appeared along this contribution scale. However, literal interpretation of many of the concepts presented has unfortunately often led to the misconception that the energy systems operate in discrete time periods.

Astrand and Rodahl^[5] drew on earlier data^[6,7] to present a table of the relative contribution from the aerobic and anaerobic systems during maximal work efforts ranging from 10 seconds up to 120 minutes. Energy release during the shorter more intense exercise periods was estimated from measures of oxygen deficit, using an assumed mechanical efficiency of 22%. Graphical representation of this data indicated that a 2 minute maximal effort derived equal contributions from the aerobic and anaerobic energy systems. Similar representations by Mathews and Fox^[4] suggested that the point of equal contribution did not occur until somewhere between 3 to 4 minutes. Such a marked difference appears to be related to the method by which each of these groups estimated anaerobic energy release.

Variations of these original figures and tables have, and continue to, appear in most exercise physiology and coaching texts. Few updated versions, however, have been presented that take into account the significant amount of research that has taken place in this and related areas more recently. While such data does not discredit the nature of the interaction between the energy systems during exhaustive exercise, it does warrant a review of the time sequence with which these interactions take place. Of most interest is the method by which energy release is determined as it can have a significant influence on the calculated relative contribution of the energy systems during periods of maximal exercise.

2. Methods Used to Evaluate Energy Release

Aerobic energy release from the combustion of carbohydrates and fats is readily quantified, as there is a direct relationship between the oxygen uptake ($\dot{V}O_2$) measured at the mouth and the whole-body aerobic production of ATP.^[8] For each litre of oxygen [at standard temperature, pressure and density (STPD)] utilised in the respiratory chain, approximately 20kJ is yielded. Determination of the metabolic respiratory quotient (ratio of expired CO_2 to $\dot{V}O_2$) to quantify the proportion of carbohydrate and fat broken down provides an exact measurement of the aerobic energy yield.

Unfortunately, methods to quantify anaerobic energy release are less precise. A variety of procedures have been used; however, as anaerobic ATP production is an intracellular process with little reliance on central processes, a universally accepted method does not exist as there is no direct mechanism for its validation. Methods that have been used in the past that are now less favourable because of known inaccuracies include oxygen debt, blood lactate measures and power output from ergometric tests.

The peak blood lactate concentration is often used as a measure of anaerobic energy release during exercise.^[9] Although lactate in the blood may provide an indication of the extent of glycolysis, it cannot be used to quantify muscle lactate production nor does it provide any indication of the energy derived from the stored phosphagens, ATP and PCr. Blood lactate concentration has been demonstrated to be clearly lower than muscle lactate concentration.^[10,11] The common observation that blood lactate reaches a peak at varying times after termination of intense exercise indicates that muscle and blood lactate are not in equilibrium.^[12,13]

The amount of oxygen taken up in excess of the resting value during the recovery period has been referred to as the oxygen debt. The classical oxygen debt hypothesis predicted that the volume of oxygen consumed after exercise was linked to the metabolism of lactate during the post-exercise re-

covery period.^[14] Margaria et al.^[13] modified the hypothesis by partitioning the oxygen debt into alactic and lactic components. However, the use of oxygen debt as a measure of anaerobic energy release has been discredited by several authors.^[15-17] Bangsbo et al.^[18] found that the oxygen debt markedly overestimated anaerobic energy release, and could only account for approximately a third of the oxygen debt from the resynthesis of nucleotides and PCr and the elimination of lactate during 60 minutes of recovery. It appears that the dissociation between the recovery oxygen consumption and the accumulation and fate of lactate, along with the influence of a number of factors that stimulate mitochondrial respiration after exercise, undermine its use.^[19,20] This discredits the traditional concept of paying back a debt that was incurred during exercise by restoring anaerobic stores. Factors known to elevate oxygen consumption during recovery that are not directly related to anaerobic energy release during exercise include an elevation in temperature, increases in hormonal activity and the general elevated energy needs associated with a return to homeostasis.^[16,19]

Ergometric assessments of mechanical work are frequently used as noninvasive, indirect and performance-based measures of the power and capacity of the 3 energy systems. Examples include force-velocity, vertical jump, staircase and bicycle ergometer tests.^[16] Contribution of the energy systems is dependent on the intensity and duration of the work effort, such that tests generally attempt to select a duration that maximises the contribution of one particular energy system while minimising the contribution of the others. In theory, the assessment of the power and the capacity of each system is required to comprehensively evaluate the energy potential of a muscle.^[21] In practice, 2 types of tests are used for the assessment of the anaerobic energy system. Bouchard et al.^[21] proposes that a maximal effort lasting 10 to 15 seconds be used to assess alactic anaerobic power and capacity and a maximal effort of 60 to 90 seconds be used to assess lactic anaerobic capacity. Unfortunately, the acti-

vation and subsequent contribution of each of the energy systems during both types of tests makes it difficult to provide relative measures, even if the mechanical work could be accurately converted to an energy equivalent. It is now known that glycolytic processes leading to lactate formation are initiated within the first few seconds of maximal dynamic exercise,^[22,23] making it almost impossible to distinguish between alactic and lactic components. The issue is further complicated by the fact that aerobic processes contribute significantly to the energy supply, even in maximal efforts as short as 30 seconds.^[24-26]

The re-introduction of the needle biopsy technique^[27] has enabled direct measurement of the decrease in muscle ATP and PCr, as well as accumulation of metabolites like pyruvate and lactate, thereby allowing an assessment of the anaerobic energy production of the biopsied muscle. The muscle biopsy technique provides measurement of concentrations and not amounts. Having determined changes in ATP, PCr and lactate concentrations, the total anaerobic energy release during whole-body exercise is calculated by estimating the active muscle mass involved in exercise. This has been assumed to be about 25 to 30% of the total bodyweight,^[21,28] although this figure is likely to vary for different modes of exercise and in individuals of varying bodyweights. Concern may also be raised over the representativeness of the biopsy sample^[29] and a possible underestimation of the anaerobic energy release because of changes occurring between the cessation of exercise and the attainment of the biopsy sample.^[30,31] Many of these problems seem to be overcome in the one-legged knee extensor model employed by Bangsbo and colleagues.^[18,32]

The concept of oxygen deficit was first introduced by Krogh and Lindhard^[33] in 1920, and has been used since as a means to determine anaerobic energy production during both sub- and supramaximal exercise. During supramaximal exercise, the appropriateness of its use relies on the validity of the assumption that supramaximal energy demand can be determined from the relationship between

submaximal work intensity and oxygen consumption. Theoretical calculations by Medbø et al.,^[28] favourably comparing the maximal accumulated oxygen deficit with estimates in the literature of the anaerobic energy release during similar high intensity efforts, have since been supported in small muscle group^[18] and whole-body^[26] exercise. Notwithstanding these reports, much debate has taken place regarding the validity of the method and its underlying assumptions.^[34-36] For example, although Bangsbo has demonstrated a close relationship between the oxygen deficit and estimates from changes in muscle metabolites in a single muscle group, he has repeatedly raised concerns over the ability of the method to accurately quantify anaerobic energy release during whole-body exercise.^[30,35]

Bangsbo^[30] has suggested that the anaerobic energy production obtained from both the biopsied muscle and the oxygen deficit method are underestimated. The extent to which this may be the case is not known. In their one-legged knee extensor model, the underestimation as a result of lactate release from the quadriceps muscle was estimated to be about 3% and is probably higher in whole-body exercise.^[30] Quantification of anaerobic energy release using the oxygen deficit method is more likely to be underestimated during very short, intense exercise where average power outputs are well above maximal aerobic power, as the efficiency relationship used to predict energy demand may not remain linear.^[5,30] Several investigators have reported decreasing efficiencies with increasing power output.^[37-39]

However, the linear extrapolation of submaximal work may inherently compensate for this changing efficiency as it is similar to the calculation of a delta efficiency in that it reflects each additional increment in work.^[31,40] In so doing, it follows changes at any point along the regression of energy release and exercise intensity.^[38] In considering the efficiency changes from submaximal to maximal work, Gladden and Welch^[38] reported a decrease in efficiency but noted that the pattern was also evident in progressive submaximal inten-

sities predominantly aerobic in nature. Although the issue of efficiency during supramaximal exercise remains unresolved, some of our data suggest that the oxygen deficit is relatively unaffected by possible changes in efficiency at increasing supra-maximal exercise intensities.^[31]

The accurate determination of anaerobic energy release during intense whole-body exercise continues to pose a problem. Until such time as alternative methods become available or the use of ³¹P magnetic resonance spectroscopy becomes possible in whole-body, dynamic exercise, our understanding of energy system response to exercise will remain limited. At present, however, the muscle biopsy technique and the oxygen deficit method provide the best possible insights into anaerobic energy production during intense exercise. Combined with measures of $\dot{V}O_2$, and by piecing together information from a range of investigations, estimations of the interaction and relative contribution of the 3 energy systems to varying intensities and durations of exercise may be attempted.

3. Power Output, Fatigue and Anaerobic Energy Supply

Rate of energy release is critical to success in sports that require the development and short term maintenance of high power outputs. Lamb^[41] has estimated that world-class weightlifters can produce power outputs that are 10 to 20 times that required to elicit the maximal rate of aerobic energy supply [maximal oxygen uptake ($\dot{V}O_{2max}$)]. Such power outputs are almost instantaneous. Sprinters may be able to achieve 3 to 5 times the power output that elicits $\dot{V}O_{2max}$ yet cannot sustain such high power outputs.^[41] Ward-Smith,^[42] using mathematical modelling techniques on running performances of elite male athletes, has estimated that the ratio between maximal anaerobic power to maximum sustainable aerobic power is in the range of 2.0 to 2.6, a value consistent with the 2 to 4 range suggested by Spriet.^[43] During the acceleration phase of the sprint, the average power output over a complete running stride may exceed 1000W, with

values of over 3kW being reported during the propulsive phase of the stride.^[44]

The rate of anaerobic provision of ATP is critical to the development of high power output. Peak rates for ATP synthesis from both the degradation of PCr and glycolysis during various modes of exercise lasting 10 seconds or less appear to be in the range of 6 to 9 mmol ATP · kg dry mass⁻¹ · sec⁻¹.^[43] Together, these 2 energy pathways may combine to provide approximately 15 mmol ATP · kg dry mass⁻¹ · sec⁻¹ over the first 6 seconds of sprint exercise, with some 50% of the ATP being supplied from the degradation of PCr.^[44] The rate of PCr degradation is at its maximum immediately after the initiation of contraction and begins to decline after only 1.3 seconds.^[45] ATP production from glycolysis, on the other hand, does not reach its maximal rate until after 5 seconds and is maintained at this rate for several seconds.^[45]

The decreasing force generation during brief, intense exercise is the result of either a reduced rate of ATP resynthesis or a decreasing rate of ATP utilisation by the contractile apparatus.^[46,47] The resting levels of ATP and PCr in skeletal muscle are in the range of 25 and 70 to 80 mmol · kg dry mass⁻¹,^[43,45] respectively, and appear to be relatively unaffected by the state of training.^[48] A total depletion of ATP does not occur even in extreme exercise conditions, although a 30 to 40% decrease in muscle ATP has been reported.^[18,49] In contrast, almost complete depletion of PCr stores is possible.^[47,50,51] Energy derived from the stores of ATP and PCr, considered the alactic component, have been estimated to contribute between 20 to 30% of the anaerobic energy release during intense exhaustive exercise of 2 to 3 minutes in duration.^[17,18,28]

Fatigue is the transient decrease in performance capacity of the muscles, usually seen as a failure to maintain or develop expected force or power output. Both central and peripheral mechanisms have been postulated as causes of muscle fatigue. Any one of the many links in the long chain from the voluntary motor centres in the brain to the contractile apparatus in the single muscle fibres may con-

tribute.^[52] While evidence does point to the central nervous system as a possible site of fatigue, most research implicates changes in the periphery as the major limiting factor.^[53]

Although the stores and energy derived from ATP and PCr are limited, it appears that the rate and total energy release from anaerobic glycolysis may also be limited,^[28] due either to inhibition of glycolytic enzymes or to a lack of activation of glycolysis.^[47] During maximal exercise, the rate of glycolysis may be increased up to 100 times that of rest,^[54] although this rate cannot be sustained. A gradually decreasing pH^[47] is likely to reduce the activity of the glycolytic enzymes, in particular phosphorylase and phosphofructokinase, and result in a reduced rate of ATP resynthesis.^[46] An alternative explanation suggests that a decrease in the sarcoplasmic concentration of free adenosine monophosphate results in a diminished activation of phosphorylase a.^[45] The decreasing rate of glycolysis may also be in response to a reduced energy demand,^[55] resulting from either inhibition of the motoneuron, changes in the activation or force-generating capacity of individual cross-bridges or alteration of the ability of the sarcoplasmic reticulum to load and release Ca²⁺.^[55-57]

4. Aerobic Energy Supply

It has long been assumed that the aerobic energy system responds slowly to the demands of high intensity exercise and plays little role in determining performance over short durations. Indeed many laboratory and field tests ranging in duration up to 90 seconds are described as tests of anaerobic performance.^[21] The popular 30-second Wingate test is one such example. However, the development of techniques to more closely evaluate $\dot{V}O_2$ kinetics and relative aerobic contribution to total energy supply during intense exercise has provided a means to challenge some of the assumptions surrounding the role of aerobic metabolism during high intensity exercise.

The rate of $\dot{V}O_2$ kinetics at the onset of exercise reflects the adjustment of both systemic oxygen

transport and muscle metabolism.^[58] When exercise is performed at a work rate below anaerobic threshold, $\dot{V}O_2$ increases exponentially to a steady-state level.^[59] Exercise at higher intensities sees an additional slow component developed after a few minutes which either delays the attainment of the steady state or drives $\dot{V}O_2$ to the maximum level.^[58,60,61] During supramaximal exercise, $\dot{V}O_2$ cannot stabilise and continues to increase until the point of fatigue,^[58] which may or may not see $\dot{V}O_2$ rise to a maximum.^[62] The attainment of near $\dot{V}O_{2max}$ during high intensity exercise of only a few minutes has been consistently documented.^[7,62-64] After only 30 to 60 seconds of exercise, the $\dot{V}O_2$ can be as high as 90% of the athlete's maximum.^[62,64]

Kavanagh and Jacobs^[64] investigated oxygen consumption during the Wingate test after noting conflicting data that reported aerobic contributions ranging from 13 to 44% during the 30-second test. Based on an assumed mechanical efficiency of 25% for cycle exercise, they estimated the aerobic contribution to be 18.5%. Smith and Hill,^[65] using similar procedures, estimated the aerobic contribution to be 16%. In contrast to these rather low estimates, 5 studies that used the accumulated oxygen deficit to quantify energy supply reported values between 23 to 33% for 30 seconds of maximal, exhaustive exercise.^[26,62,66-68] In line with these estimates, Bogdanis et al.,^[69] using direct muscle measures, reported a 29% aerobic contribution. Interestingly, when a second maximal 30-second sprint was performed after 4 minutes of passive recovery, the estimated aerobic contribution increased to 44%. In comparison to the first sprint, power output and anaerobic ATP resynthesis were reduced by 18 and 41%, respectively. The apparent mismatch between anaerobic ATP provision and decrease in power output can primarily be explained by a 19% increase in $\dot{V}O_2$.^[24,69] During repeated sprint exercise, the significant reduction in anaerobic ATP turnover appears to be partially compensated for by an increase in $\dot{V}O_2$ in subsequent sprints.^[69-71] It has also been demonstrated that the local depletion of oxygen and/or phosphagen stores, either

through priming exercise or blood flow occlusion, significantly improves the oxygen kinetics in response to exercise.^[72]

The mismatch between the decline in power output during sprint cycle exercise and the decrease in anaerobic ATP utilisation has also been observed during repeated sprints as short as 6 seconds in duration. During ten 6-second cycle sprints,^[23] the decline in power output from sprint 1 to 10 was 27%. However, the decline in anaerobic ATP utilisation was 64%, due largely to an almost complete inhibition of the glycolytic rate by sprint 10. Although an increase in efficiency as exercise continued was suggested as a partial explanation, aerobic metabolism was acknowledged as an important contributor to the energy supply.^[24] It now seems evident that all 3 energy systems make a contribution to the energy supply during sprinting, even during efforts as short as 6 seconds.

Table I provides a summary of over 30 studies in the literature that have reported aerobic energy system contribution during single bouts of maximal (for a given duration) exhaustive exercise. The methods used to estimate energy release vary, yet fall into 3 main categories. The accumulated oxygen deficit has been used extensively; however, in all but one instance, only studies that have employed individual efficiency relationships have been included as assumed mechanical efficiencies are known to provide less valid estimates of anaerobic energy release.^[28] Under the broad category of direct measures, estimates of energy release have been obtained from direct measures of changes in intramuscular substrates and metabolites. In some instances, investigators have used values cited by others in the literature using similar techniques or have combined their own measures with data from the literature. Finally, a group of studies that have employed mathematical modelling techniques to predict world class running performances have been included.

Mathematical analyses of world record and Olympic running performances based on satisfying the first law of thermodynamics have proved to be

Table I. Estimates of relative aerobic energy system contribution during single bouts of dynamic high intensity exercise

Study	Exercise	Participants	Method	Duration (sec)	% Aerobic
Bangsbo et al. ^[73]	Cycle	3 ST cyclists	ODI	179	74
	Run	14 ET runners		181	78
	Run	15 T soccer		205	78
	Run	5 T oarsmen		243	83
Calbet et al. ^[66]	Cycle ^a	19 UT	ODI	30	23
				45	31
				148	59
Craig et al. ^[74]	Cycle	6 ST cyclists	ODI	70	50
		6 ET cyclists		70	55
		6 ST cyclists		120	63
		6 ET cyclists		120	67
		6 ST cyclists		300	86
		6 ET cyclists		300	85
Di Prampero et al. ^[75]	Run	MD runners	MM	102	62
				132	69
				209	78
		452		89	
		778		93	
Faina et al. ^[56]	Cycle	8 T cyclists	ODI	225	85
	Swim flume	8 T swimmers		302	82
	Kayak	7 T kayakers		356	88
Gastin & Lawson ^[62]	Cycle ^a	8 UT	ODI	15	19
				30	29
				45	39
				60	46
				75	52
				90	58
Gastin & Lawson ^[76]	Cycle ^a	6 ST cyclists	ODI	90	53
		8 ET triathletes		90	56
		8 UT		90	58
Gastin et al. ^[40]	Cycle ^a	9 UT	ODI	62	51
		6 UT/6 ET		90	57
		9 UT		94	59
		186		76	
		208		74	
Green et al. ^[77]	Cycle	10 T cyclists	ODI	173	76
Hermansen & Medbø ^[67]	Run	1 ST		15	22
				30	29
				60	43
				60	51
				60	46
				120	59
				240	75
Hill ^[78]	Run	6 MD runners	DM	49	37
		7 MD ^b runners		61	38
		5 MD runners		120	61
		9 MD ^b runners		146	67
				246	80
				309	83

Table I. Contd

Study	Exercise	Participants	Method	Duration (sec)	% Aerobic
Kavanagh & Jacobs ^[64]	Cycle ^a	5 UT	ODA	30	18
Locatelli & Arsac ^[79]	Run ^a	4/4 ^b ST runners	DM	11	3
Medbø & Sejersted ^[80]	Run	6 ET	ODI	55	50
		6 ST		57	44
Medbø & Tabata ^[25]	Cycle	14 UT	ODI	34	30
		13 UT		75	47
				156	65
Morton & Gastin ^[81]	Swim bench ^a	7 UT	ODI	60	40
		7 ST		60	46
Morton ^[82]	Swim bench ^a	UT	ODI	45	50
				60	44
Nummela & Rusko ^[83]	Run	8 ET	ODI	49	46
		8 ST runners		50	37
O'Brien et al. ^[68]	Cycle ^a	9 UT	ODI	30	30
				30	33
				60	46
				60	48
Olesen et al. ^[84]	Run	6 runners	ODI	62	37
		8 SMD runners		64	44
				139	60
				146	72
		6 runners		148	57
				148	68
Péronnet & Thibault ^[85]	Run	ST runners	MM	6	5
				10	8
		MD runners		20	14
				44	30
				102	57
				132	65
				209	76
				226	78
				291	82
				452	88
Ramsbottom et al. ^[86]	Run	11/1 ^b runners	ODI	171	69
				182	71
Ramsbottom et al. ^[87]	Run	32/17 ^b UT	ODI	173	68
				178	70
Serresse et al. ^[88]	Cycle ^a	23 T	DM	10	3
		21 T		30	28
		20 T		90	46
Smith & Hill ^[65]	Cycle ^a	6 UT	DM	30	16
Spencer & Gastin ^[89]	Run	3 ST runners	ODI	22	29
		6 MD runners		49	43
		5 MD runners		113	66
		6 MD runners		235	84

Continued over page

Table I. Contd

Study	Exercise	Participants	Method	Duration (sec)	% Aerobic
Spencer et al. ^[90]	Run	4 ST runners	ODI	52	46
		5 MD runners		118	69
				242	83
van Ingen Schenau et al. ^[91]	Run	ST runners	MM	10	4
				20	8
		MD runners		44	17
Ward-Smith ^[92]	Run	ST runners	MM	10	7
				20	14
		MD runners		45	28
				105	52
		ET runners		218	72
Withers et al. ^[26]	Cycle ^a	3 UT	ODI	816	96
				30	28
				60	49
Withers et al. ^[93]	Cycle ^a	12 ET	ODI	90	61
				45	40
				60	47
				75	54
				90	60

a All-out.

b Female.

DM = direct measures; **ET** = endurance trained; **MD** = middle distance; **MM** = mathematical model; **ODA** = oxygen deficit using an assumed mechanical efficiency; **ODI** = oxygen deficit using individual mechanical efficiency; **SMD** = sprint and middle distance; **ST** = sprint trained; **T** = trained, unspecified; **UT** = untrained.

very successful in predicting performance^[75,85,91,92] and have been suggested to be generally more consistent than the body of experimental data.^[42] Péronnet and Thibault,^[85] covering 16 distances from 60m to the marathon, correlated 1987 male records with an average absolute prediction error of only 0.7% and a maximum error of 2.3%. Ward-Smith^[92] reported similar prediction errors (0.9 and 1.5%, respectively) for Olympic Games results over 7 distances and 4 Olympiads. These methods attempt to account for each energy exchange during running, including changes in chemical, mechanical, potential, kinetic and thermal energy with each stride.^[92] Inherent in the method is the separate estimation of aerobic and anaerobic contribution to each race distance. Ward-Smith^[42] argues that because of excellent agreement between prediction and performance, there are good grounds for confidence that

the energy contributions are modeled with considerable precision.

Although the available data suggests a significant aerobic contribution during intense exercise, the perceptions of coaches and scientists continue to reflect disagreement. In a recent round table discussion featuring 8 coaches and sport scientists, expert opinion on the aerobic contribution to the 800m running event (1.5 to 2 minutes in duration) ranged from 35 to 65%.^[94] The lower estimates given by some members of this group are somewhat typical and reflect the misconceptions that still exist as a result of early concepts becoming entrenched in the exercise science and coaching professions (see section 1).

Recent investigations specifically evaluating the relative energy contribution during track running events indicate that the aerobic contribution to the 800m event is around 55 to 65% aero-

bic.^[75,78,85,89,90] This relatively high aerobic contribution is indirectly supported by the strong relationship between laboratory-determined maximal oxygen deficit and performance times over 100 and 400m, but not 800m, which suggests that the importance of the anaerobic energy supply diminishes, and consequently the aerobic energy supply increases, as running distance increases.^[86] This is clearly illustrated in figure 1, which summarises the findings of Spencer and Gastin^[89] who attempted to evaluate the energy system contribution, using the accumulated oxygen deficit method, to simulated sprint and middle distance running events.

5. Interaction and Relative Contribution of the Energy Systems

In an effort to move beyond a simple presentation of findings, data from table I have been further summarised using iterative curve fitting techniques (fig. 2). This analysis has enabled a table of the aerobic contribution to cumulative periods of exhaustive exercise to be developed (table II). Such a table offers an updated alternative to the many that have appeared in textbooks over the years, many based on the early calculations of Fox and colleagues^[1,2,4] who used the oxygen debt as the measure of anaerobic energy release, a method which is no longer in favour and which has been shown to considerably overestimate the anaerobic metabolism.

Howald et al.^[3] introduced a figure attempting to summarise the sequence and quantitative relationships between the 3 energy-supplying processes in human skeletal muscle. A logarithmic scale was used for exercise duration up to 120 minutes, with total energy output, given in kcal · min, decreasing with time. The figure suggested that equal contribution from the aerobic system occurs at around 3 to 4 minutes. Fox et al.^[95] reproduced a figure developed over 20 years earlier^[4] that suggested an effort needed to be about 3.5 minutes in duration before it derived equal energy from the aerobic system. Astrand and Rodahl^[5] presented data that calculated relative energy system contribution during

maximal work efforts ranging from 10 seconds up to 120 minutes. It was noted that a 2-minute maximal effort derived about 50% from each system, such that both processes were equally important for success. Bouchard et al.^[21] presented their own version of the interaction between the energy systems, with equal contributions from the aerobic and anaerobic systems occurring around 100 seconds. Lamb,^[41] in summarising data from Bangsbo et al.,^[18] suggested the point of equal contribution occurred somewhere between 2 to 3 minutes.

In contrast to these estimates, many of the earlier ones based on calculations of anaerobic energy release which now appear questionable, the summary analysis presented in table II suggests that the duration of maximal exercise that results in an equal contribution from the aerobic and anaerobic energy systems is between 1 to 2 minutes, and most probably around 75 seconds. Thus, it appears that the aerobic contribution during intense exercise has been consistently underestimated, such that figures used even quite recently to describe the in-

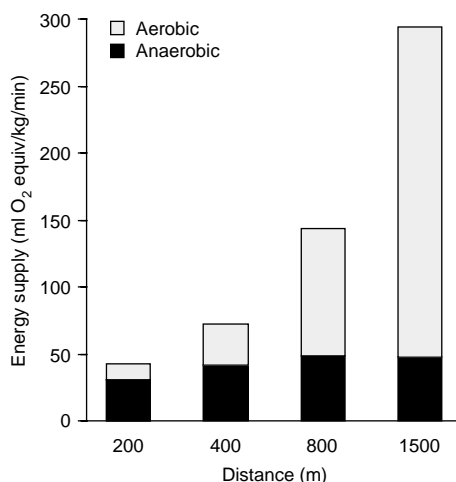


Fig. 1. Energy system contribution to the total energy supply during sprint and middle distance running. The 200m (n = 3), 400m (n = 6), 800m (n = 5) and 1500m (n = 6) running events were simulated on a treadmill. Energy release was evaluated using the accumulated oxygen deficit method (from Spencer and Gastin,^[89] with permission). $\dot{V}O_{2max}$ = maximal oxygen uptake.

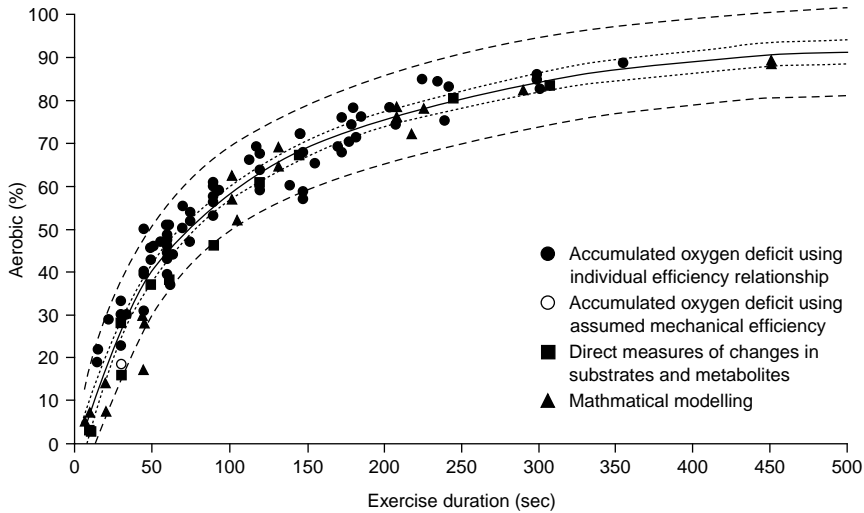


Fig. 2. Summary analysis of data in the literature of the relative aerobic contribution to the total energy supply during periods of maximal exercise. Both 95% confidence intervals (inner band) and 95% prediction intervals (outer band) are shown ($r^2 = 0.96$). Techniques used to estimate relative aerobic energy release include the accumulated oxygen deficit using an individual efficiency relationship or assumed mechanical efficiency, direct measures of changes in substrates and metabolites, and mathematical modelling. Data from table I.

teraction between the energy systems^[95,96] are too far skewed to the right. In a given exercise bout, the cross-over point to predominantly aerobic energy supply may occur between 20 to 30 seconds,^[76,89] with the aerobic contribution to each continuing period of exercise increasing while the anaerobic contribution continues to diminish. While not seemingly so, this is in fact consistent with the suggestion that a maximal effort of about 75 seconds derives equal energy from both the aerobic and anaerobic energy systems.

An alternative to evaluating the energy system contribution to a given period of maximal exercise (table II) is to consider the relative aerobic and anaerobic contribution to sequential phases within a given period of maximal exercise. The interaction and contribution of the energy systems will be dependent on the intensity, duration and mode of exercise. Small, insignificant differences exist for training status. Table III provides 5 contrasting examples, with estimates of the sequential energy system contribution during 90 seconds of all-out exer-

cise,^[76] 800 and 1500m running,^[89] and exercise to exhaustion during cycling at 110% $\dot{V}O_{2max}$ ^[40] and one-legged, knee-extension at 65W.^[18]

Figure 3 illustrates the relative energy system contribution to the total energy supply for any given duration of maximal exercise. The figure graphi-

Table II. Estimates of anaerobic and aerobic energy contribution during selected periods of maximal exercise

Duration of exhaustive exercise (sec)	% Anaerobic	% Aerobic ^a
0-10	94	6
0-15	88	12
0-20	82	18
0-30	73	27
0-45	63	37
0-60	55	45
0-75	49	51
0-90	44	56
0-120	37	63
0-180	27	73
0-240	21	79

a Approximately $\pm 10\%$ at the 95% prediction level (refer table I and fig. 2).

Table III. Estimates of aerobic energy system contribution (%) for sequential phases during varying modes and intensities of exercise

Sequential phase of exercise (sec)	90 sec all-out cycling ^[76]	800m running ^[89]	1500m running ^[89]	110% $\dot{V}O_{2max}$ cycling ^[40]	One-legged knee-extension at 65W ^[18]
0-30	30	41	57	35	20
30-60	73	73	84	66	44
60-90	91	76	87	76	57
90-120		76	88	81	62
120-150			89	85	70
150-180			89	89	70

$\dot{V}O_{2max}$ = maximal oxygen uptake.

cally represents information more often presented in tabular form for periods of maximal exercise from 5 to 300 seconds; it does not illustrate the time course of each of the energy systems. Aerobic contribution is based on the summary analysis (fig. 2) of the data presented in table I. The corresponding percentage of anaerobic contribution has been further divided into estimates of ATP-PCr and glycolytic components based on rates of anaerobic ATP turnover and relative contribution (see table I in Bangsbo^[30]). In all, data from over 40 investigations have been used to develop this figure.

Over the years, most figures that have been presented in the literature to describe the interactions between the energy systems have been conceptual in nature.^[3,96,98] Attempts to describe the individual kinetics of each of the energy supplying processes in relation to actual power output do not appear to have been undertaken. Figure 4 presents a re-working of original data from Gastin and Lawson^[76] during 90 seconds of all-out cycle ergometer exercise. All-out cycle exercise is characterised by the attainment of peak power output in the first 5 to 10 seconds followed by a progressively declining power output until either completion of the test or voluntary cessation. Energy supply is given in oxygen equivalents, having been derived from actual measures of $\dot{V}O_2$ and estimates of energy demand using the accumulated oxygen deficit method. The anaerobic component has been divided into ATP-PCr and glycolytic contributions based on the assumption that the ATP-PCr system is maximal in the first 1 to 2 seconds of exercise, that approximately 75 to 85% of the decline in PCr occurs dur-

ing the first 10 seconds, and that little if any ATP resynthesis from PCr occurs after 20 seconds of maximal exercise.^[44,45] Having established the kinetics of the ATP-PCr system, the remaining anaerobic contribution was then attributed to anaerobic glycolysis. The resultant peak in glycolytic rate presented in the figure is consistent with the notion that ATP production from glycolysis reaches a maximal rate after 5 seconds and is maintained at this rate for several seconds.^[45]

Figure 4 also contrasts the kinetics of both the power output and energy supplying processes for

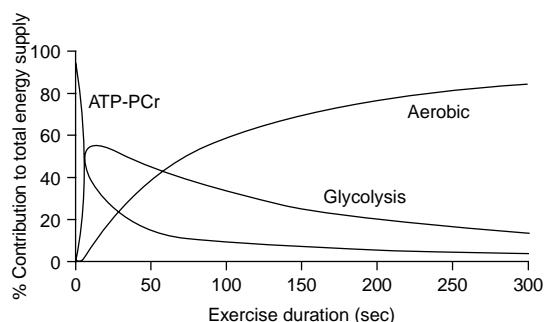


Fig. 3. Relative energy system contribution to the total energy supply for any given duration of maximal exercise. The figure graphically represents information often presented in tabular form for any given exercise duration; it does not illustrate the time course of the energy systems. Aerobic contribution data taken from table I and figure 2. Anaerobic contribution based on a similar presentation of data in the literature by Bangsbo^[30] [Updated and adapted with permission from J. Finn, P. Gastin, R. Withers and S. Green, 2000, 'Estimation of peak power and anaerobic capacity of athletes' in *Physiological tests for elite athletes*, Australian Sports Commission, edited by C.J. Gore (Champaign, IL: Human Kinetics), 45].^[97] ATP-PCr = alactic component of the anaerobic energy system.

a group of sprint trained cyclists and endurance trained triathletes. The significantly higher peak power output in the sprint trained group is supported by higher peak rates of ATP resynthesis from the ATP-PCr and glycolytic systems. Although the final $\dot{V}O_2$ during the test and the separately measured $\dot{V}O_{2max}$ in the sprint group were lower than in the endurance group, $\dot{V}O_2$ kinetics were surprisingly faster in the sprint trained athletes.^[76] Interestingly, in both groups the final power output is almost directly attributable to the rate of aerobic energy supply, providing clear support for the existence of an anaerobic capacity.

The kinetics of each of the energy supplying systems during constant intensity exercise is of considerable interest, given that few sporting events are truly all-out in nature. Figure 5 contrasts the power output and energy supply for an endurance trained triathlete during both 90-second all-out and exhaustive exercise at a constant intensity equivalent to 110% $\dot{V}O_{2max}$. The peak rate of ATP resynthesis from ATP-PCr and glycolysis in the all-out test is

more than double that of the constant intensity test. The kinetics of $\dot{V}O_2$ in this athlete are faster in response to the higher supramaximal intensity of all-out exercise, which is in keeping with the findings of others.^[7,40] The onset of fatigue in the constant intensity test results in an inability to maintain the required power output, and appears closely related to the inability of anaerobic glycolysis to continue to supply ATP.

6. Conclusion

The interaction and relative contribution of the 3 energy systems during periods of maximal exhaustive exercise is of considerable theoretical and practical interest. Early attempts in the 1960s and 1970s to describe these relationships, while insightful at the time, have since been found to be somewhat misleading. Given repeated reproduction over the years, these early attempts have led to 2 common misconceptions in the exercise science and coaching professions. First, that the energy systems respond to the demands of intense exercise in an almost sequential manner, and secondly, that the aerobic system responds slowly to these energy demands, thereby playing little role in determining performance over short durations.

The assessment of anaerobic energy release during exercise is much less precise than the assessment of aerobic energy release, as measured by the $\dot{V}O_2$. Measures of changes in muscle substrates and metabolites and the accumulated oxygen deficit, combined with measures of $\dot{V}O_2$, have more recently been used to proportion energy system contribution during varying periods of maximal exercise. Mathematical modelling techniques, which attempt to account for each energy exchange during exercise, have also been employed. Together the 3 energy systems appear well suited to cope with the high, often sustained and usually diverse energy demands placed on them during daily and sporting activities. Analysis of the current literature suggests that virtually all physical activities derive some energy from each of the 3 energy-supplying processes. There is no doubt that each system is

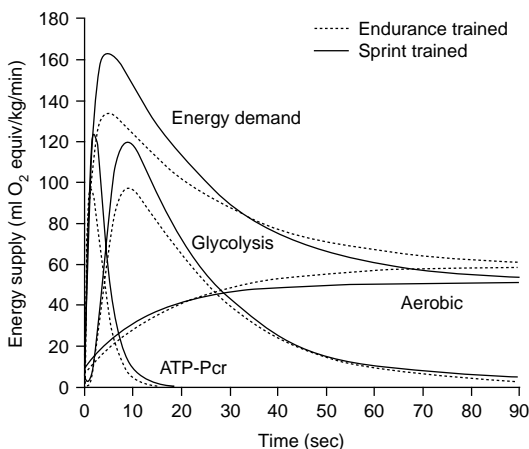


Fig. 4. Relative contribution of the 3 energy systems to the total energy supply during 90 seconds of all-out cycle exercise. Participants were 6 male sprint-trained cyclists [mean maximal oxygen uptake ($\dot{V}O_{2max}$) = 58 ml/kg/min] and 8 endurance-trained triathletes (mean $\dot{V}O_{2max}$ = 65 ml/kg/min). Data from Gastin and Lawson.^[76] **ATP-PCr** = alactic component of the anaerobic energy system.

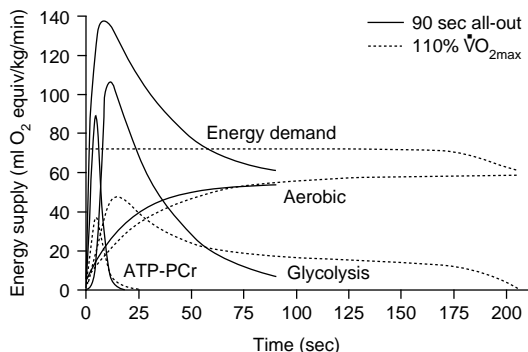


Fig. 5. Relative contribution of the 3 energy systems to the total energy supply during 90 seconds of all-out cycle exercise and exhaustive constant intensity exercise at 110% maximal oxygen uptake ($\dot{V}O_{2max}$). Participant was a male endurance-trained triathlete ($\dot{V}O_{2max} = 64.9$ ml/kg/min; 90 seconds all-out oxygen deficit = 65.8 ml/kg; 110% $\dot{V}O_{2max}$ oxygen deficit = 69.2 ml/kg). Data from Gastin et al.^[40] ATP-PCr = alactic component of the anaerobic energy system.

best suited to providing energy for a different type of event or activity, yet this does not imply exclusivity. Similarly, the energy systems contribute sequentially but in an overlapping fashion to the energy demands of exercise.

The anaerobic system is capable of responding immediately to the energy demands of exercise and is able to support extremely high muscle power outputs. Unfortunately the anaerobic system is limited in its capacity, such that either a cessation of work or a reduction in power output to a level that can be met by aerobic metabolism is seen during extended periods of intense exercise. The aerobic energy system responds surprisingly quickly to the demands of intense exercise, yet is incapable of meeting the energy demands at the beginning of exercise, irrespective of the exercise intensity. It now seems evident that the aerobic system plays a significant role in determining performance during high intensity exercise, with a maximal exercise effort of 75 seconds deriving approximately equal energy from the aerobic and anaerobic energy systems.

References

1. Fox EL, Robinson S, Wiegman DL. Metabolic energy sources during continuous and interval running. *J Appl Physiol* 1969; 27 (2): 174-8
2. Fox EL. *Sports physiology*. 1st ed. London: Saunders College Publishing, 1979
3. Howald H, von Glutz G, Billeter R. Energy stores and substrate utilization in muscle during exercise. In: Landry F, Orban WAR, editors. *The Third International Symposium on Biochemistry of Exercise*; Miami (FL). Miami (FL): Miami Symposia Specialists, 1978: 75-86
4. Mathews DK, Fox EL. *The physiological basis of physical education and athletics*. Philadelphia (PA): W.B. Saunders, 1971
5. Astrand P-O, Rodahl K. *Textbook of work physiology*. New York: McGraw-Hill, 1970
6. Astrand I, Astrand P-O, Christensen EH, et al. Myohemoglobin as an oxygen-store in man. *Acta Physiol Scand* 1960; 48: 454-60
7. Astrand P-O, Saltin B. Oxygen uptake during the first minutes of heavy muscular exercise. *J Appl Physiol* 1961; 16: 971-6
8. Astrand P-O. Aerobic and anaerobic energy sources in exercise. *Med Sport Sci* 1981; 13: 22-37
9. Jacobs I. Blood lactate: implications for training and sports performance. *Sports Med* 1986; 3: 10-25
10. Jacobs I, Kaiser P. Lactate in blood, mixed skeletal muscle, and FT or ST fibres during cycle exercise in man. *Acta Physiol Scand* 1982; 114: 461-6
11. Tesch PA, Daniels WL, Sharp DS. Lactate accumulation in muscle and blood during submaximal exercise. *Acta Physiol Scand* 1982; 114: 441-6
12. Gollnick PD, Bayly WM, Hodgson DR. Exercise intensity, training, diet, and lactate concentration in muscle and blood. *Med Sci Sports Exerc* 1986; 18 (3): 334-40
13. Margaria R, Edwards HT, Dill DB. The possible mechanisms of contracting and paying the oxygen debt and the role of lactic acid in muscular contraction. *Am J Physiol* 1933; 106: 689-715
14. Hill AV, Lupton H. Muscular exercise, lactic acid and the supply and utilization of oxygen. *Q J Med* 1923; 16: 135-71
15. Hermansen L. Anaerobic energy release. *Med Sci Sports* 1969; 1 (1): 32-8
16. Vandewalle H, Peres G, Monod H. Standard anaerobic exercise tests. *Sports Med* 1987; 4: 268-89
17. Saltin B. Anaerobic capacity: past, present, and future. In: Taylor AW, editor. *Biochemistry of exercise VII: international series on sport sciences*. Champaign (IL): Human Kinetics, 1990: 387-412
18. Bangsbo J, Gollnick PD, Graham TE, et al. Anaerobic energy production and O_2 deficit-debt relationships during exhaustive exercise in humans. *J Physiol* 1990; 422: 539-59
19. Gaesser GA, Brooks GA. Metabolic bases of excess post-exercise oxygen consumption: a review. *Med Sci Sports Exerc* 1984; 16 (1): 29-43
20. Rieu M, Duvallet A, Scharapan L, et al. Blood lactate accumulation in intermittent supramaximal exercise. *Eur J Appl Physiol* 1988; 57: 235-42
21. Bouchard C, Taylor AW, Simoneau J, et al. Testing anaerobic power and capacity. In: MacDougall JD, Wenger HA, Green HJ, editors. *Physiological testing of the high-performance athlete*. Champaign (IL): Human Kinetics, 1991

22. Jacobs I, Tesch PA, Bar-Or O, et al. Lactate in human skeletal muscle after 10 and 30 s of supramaximal exercise. *J Appl Physiol* 1983; 55 (2): 365-7
23. Gaitanos GC, Williams C, Boobis LH, et al. Human muscle metabolism during intermittent maximal exercise. *J Appl Physiol* 1993; 75 (2): 712-9
24. Nevill ME, Bogdanis GC, Boobis LH, et al. Muscle metabolism and performance during sprinting. Champaign (IL): Human Kinetics, 1996; 243-59
25. Medbø JI, Tabata I. Relative importance of aerobic and anaerobic energy release during short-lasting exhaustive bicycle exercise. *J Appl Physiol* 1989; 67 (5): 1881-6
26. Withers RT, Sherman WM, Clark DG, et al. Muscle metabolism during 30, 60, and 90 s of maximum cycling on an air-braked ergometer. *Eur J Appl Physiol* 1991; 63: 354-62
27. Bergström J. Muscle electrolytes in man, determined by neutron activation analysis on needle biopsy specimens: a study on normal subjects, kidney patients and patients with chronic diarrhoea. *Scand J Clin Lab Invest* 1962; 14 Suppl. 68: 1
28. Medbø JI, Mohn A, Tabata I, et al. Anaerobic capacity determined by maximal accumulated O₂ deficit. *J Appl Physiol* 1988; 64 (1): 50-60
29. Blomstrand E, Ekblom B. The needle biopsy technique for fibre type determination in human skeletal muscle: a methodological study. *Acta Physiol Scand* 1982; 116: 437-42
30. Bangsbo J. Quantification of anaerobic energy production during intense exercise. *Med Sci Sports Exerc* 1998; 30 (1): 47-52
31. Gastin PB. Quantification of anaerobic capacity. *Scand J Med Sci Sports* 1994; 4: 91-112
32. Bangsbo J, Johansen L, Graham T, et al. Lactate and H⁺ effluxes from human skeletal muscles during intense, dynamic exercise. *J Physiol* 1993; 462: 115-33
33. Krogh A, Lindhard J. The changes in respiration at the transition from work to rest. *J Physiol* 1920; 53: 431-7
34. Graham TE. Oxygen deficit: introduction to the assumptions and the skepticism. *Can J Appl Physiol* 1996; 21 (5): 347-9
35. Bangsbo J. Oxygen deficit: a measure of the anaerobic energy production during intense exercise. *Can J Appl Physiol* 1996; 21 (5): 350-63
36. Medbø JI. Is the maximal accumulated oxygen deficit an adequate measure of the anaerobic capacity. *Can J Appl Physiol* 1996; 21 (5): 370-83
37. Gaesser GA, Brooks GA. Muscular efficiency during steady-rate exercise: effects of speed and work rate. *J Appl Physiol* 1975; 38 (6): 1132-9
38. Gladden LB, Welch HG. Efficiency of anaerobic work. *J Appl Physiol* 1978; 44 (4): 564-70
39. Luhtanen P, Rahkila P, Rusko H, et al. Mechanical work and efficiency in ergometer bicycling at aerobic and anaerobic thresholds. *Acta Physiol Scand* 1987; 131: 331-7
40. Gastin PB, Costill DL, Lawson DL, et al. Accumulated oxygen deficit during supramaximal all-out and constant intensity exercise. *Med Sci Sports Exerc* 1995; 27 (2): 255-63
41. Lamb DR. Basic principles for improving sport performance. *GSSI Sports Sci Exch* 1995; 8 (2): 1-6
42. Ward-Smith AJ. Aerobic and anaerobic energy conversion during high-intensity exercise. *Med Sci Sports Exerc* 1999; 31 (12): 1855-60
43. Spriet LL. Anaerobic metabolism during high-intensity exercise. In: Hargreaves M, editor. *Exercise metabolism*. Champaign (IL): Human Kinetics, 1995: 1-39
44. Lakomy HKA. Physiology and biochemistry of sprinting. In: Hawley JA, editor. *Running: handbook of sports medicine and science*. Oxford: Blackwell Science, 2000: 1-13
45. Maughan RJ, Gleeson M, Greenhaff PL. *Biochemistry of exercise and training*. Oxford: Oxford University Press, 1997
46. Hermansen L. Muscular fatigue during maximal exercise of short duration. *Med Sport Sci* 1981; 13: 45-52
47. Hultman E, Bergström M, Spriet LL, et al. Energy metabolism and fatigue. In: Taylor AW, editor. *Biochemistry of exercise VII: international series on sport sciences*. Champaign (IL): Human Kinetics, 1990: 73-92
48. Saltin B, Gollnick PD. Skeletal muscle adaptability: significance for metabolism and performance. In: Peachey LD, Adrian R, Geiger SR, editors. *Handbook of physiology*. Baltimore (MD): Williams & Wilkins, 1983: 555-631
49. Jacobs I, Bar-Or O, Karlsson J, et al. Changes in muscle metabolites in females with 30-s exhaustive exercise. *Med Sci Sports Exerc* 1982; 14 (6): 457-60
50. Bogdanis GC, Nevill ME, Boobis LH, et al. Recovery of power output and muscle metabolites following 30 s of maximal sprint cycling in man. *J Physiol* 1995; 482 (2): 467-80
51. Vollestad NK, Sejersted OM. Biochemical correlates of fatigue. *Eur J Appl Physiol* 1988; 57: 336-47
52. Asmussen E. Muscle fatigue. *Med Sci Sports* 1979; 11 (4): 313-21
53. McLester JR. Muscle contraction and fatigue: the role of adenosine 5'-diphosphate and inorganic phosphate. *Sports Med* 1997; 23 (5): 287-305
54. Newsholme EA, Start C. *Regulation in metabolism*. London: Wiley & Sons, 1973
55. Green HJ. Manifestations and sites of neuromuscular fatigue. In: Taylor AW, editor. *Biochemistry of exercise VII: international series on sport sciences*. Champaign (IL): Human Kinetics, 1990: 13-35
56. Faina M, Billat V, Squadrone R, et al. Anaerobic contribution to the time to exhaustion at the minimal exercise intensity at which maximal oxygen uptake occurs in elite cyclists, kayakers and swimmers. *Eur J Appl Physiol* 1997; 76: 13-20
57. Fitts RH, Kim DH, Witzmann FA. The development of fatigue during high intensity and endurance exercise. In: Nagle FJ, Montoye HJ, editors. *Exercise in health and disease*. Springfield (IL): Charles C. Thomas, 1981: 118-35
58. Xu F, Rhodes EC. Oxygen uptake kinetics during exercise. *Sports Med* 1999; 27 (5): 313-27
59. Whipp BJ. Rate constant for the kinetics of oxygen uptake during light exercise. *J Appl Physiol* 1971; 30 (2): 261-3
60. Armon Y, Cooper DM, Flores R, et al. Oxygen uptake dynamics during high-intensity exercise in children and adults. *J Appl Physiol* 1991; 70 (2): 841-8
61. Paterson DH, Whipp BJ. Asymmetries of oxygen uptake transients at the on- and offset of heavy exercise in humans. *J Physiol* 1991; 443: 575-86
62. Gastin PB, Lawson DL. Variable resistance all-out test to generate accumulated oxygen deficit and predict anaerobic capacity. *Eur J Appl Physiol* 1994; 69: 331-6

63. Katch VL. Kinetics of oxygen uptake and recovery for supra-maximal work of short duration. *Int Z Angew Physiol* 1973; 31: 197-207
64. Kavanagh MH, Jacobs I. Breath-by-breath oxygen consumption during performance of the Wingate test. *Can J Appl Sport Sci* 1988; 13 (1): 91-3
65. Smith JC, Hill DW. Contribution of energy systems during a Wingate power test. *Br J Sports Med* 1991; 25 (4): 196-9
66. Calbet JAL, Chavarren J, Dorado C. Fractional use of anaerobic capacity during a 30- and a 45-s Wingate test. *Eur J Appl Physiol* 1997; 76: 308-13
67. Hermansen L, Medbø JI. The relative significance of aerobic and anaerobic processes during maximal exercise of short duration. *Med Sport Sci* 1984; 17: 56-67
68. O'Brien B, Payne W, Gastin P, et al. A comparison of active and passive warm ups on energy system contribution and performance in moderate heat. *Aust J Sci Med Sport* 1997; 29 (4): 106-9
69. Bogdanis GC, Nevill ME, Boobis LH, et al. Contribution of phosphocreatine and aerobic metabolism to energy supply during repeated sprint exercise. *J Appl Physiol* 1996; 80 (3): 876-84
70. Bogdanis GC, Nevill ME, Lakomy HKA, et al. Power output and muscle metabolism during and following recovery from 10 and 20 s of maximal sprint exercise in humans. *Acta Physiol Scand* 1998; 163: 261-72
71. Bogdanis GC, Nevill ME, Lakomy HKA, et al. Effects of active recovery on power output during repeated maximal sprint cycling. *Eur J Appl Physiol* 1996; 74: 461-9
72. Pagenelli W, Pendergast DR, Koness J, et al. The effect of decreased muscle energy stores on the $\dot{V}O_2$ kinetics at the onset of exercise. *Eur J Appl Physiol* 1989; 59: 321-6
73. Bangsbo J, Michalsik L, Petersen A. Accumulated O_2 deficit during intense exercise and muscle characteristics of elite athletes. *Int J Sports Med* 1993; 14 (4): 207-13
74. Craig NP, Norton KI, Conyers RAJ, et al. Influence of test duration and event specificity on maximal accumulated oxygen deficit on high performance track cyclists. *Int J Sports Med* 1995; 16 (8): 534-40
75. Di Prampero PE, Capelli C, Pagliaro P, et al. Energetics of best performances in middle-distance running. *J Appl Physiol* 1993; 74 (5): 2318-24
76. Gastin PB, Lawson DL. Influence of training status on maximal accumulated oxygen deficit during all-out exercise. *Eur J Appl Physiol* 1994; 69: 321-30
77. Green S, Dawson BT, Goodman C, et al. Anaerobic ATP production and accumulated O_2 deficit in cyclists. *Med Sci Sports Exerc* 1996; 28 (3): 315-21
78. Hill DW. Energy system contributions in middle-distance running events. *J Sports Sci* 1999; 17: 477-83
79. Locatelli E, Arsac L. The mechanics and energetics of the 100m sprint. *New Stud Athlet* 1995; 10 (1): 81-7
80. Medbø JI, Sejersted OM. Acid-base and electrolyte balance after exhausting exercise in endurance-trained and sprint-trained subjects. *Acta Physiol Scand* 1985; 125: 97-109
81. Morton DP, Gastin PB. Effect of high intensity board training on upper body anaerobic capacity and short-lasting exercise performance. *Aust J Sci Med Sport* 1997; 29 (1): 17-21
82. Morton DP. Quantification of anaerobic capacity on the swim bench ergometer [masters thesis]. Ballarat (VIC): Ballarat University College, 1992
83. Nummela A, Rusko H. Time course of anaerobic and aerobic energy expenditure during short-term exhaustive running in athletes. *Int J Sports Med* 1995; 16 (8): 522-7
84. Olesen HL, Raabo E, Bangsbo J, et al. Maximal oxygen deficit of sprint and middle distance runners. *Eur J Appl Physiol* 1994; 69: 140-6
85. Péronnet F, Thibault G. Mathematical analysis of running performance and world running records. *J Appl Physiol* 1989; 67 (1): 453-65
86. Ramsbottom R, Nevill AM, Nevill ME, et al. Accumulated oxygen deficit and short-distance running performance. *J Sports Sci* 1994; 12: 447-53
87. Ramsbottom R, Nevill ME, Nevill AM, et al. Accumulated oxygen deficit and shuttle run performance in physically active men and women. *J Sports Sci* 1997; 15: 207-14
88. Serresse O, Lortie G, Bouchard C, et al. Estimation of the contribution of the various energy systems during maximal work of short duration. *Int J Sports Med* 1988; 9 (6): 456-60
89. Spencer MR, Gastin PB. Energy system contribution during 200 to 1500m running in highly trained athletes. *Med Sci Sports Exerc* 2001; 33 (1): 157-62
90. Spencer MR, Gastin PB, Payne WR. Energy system contribution during 400 to 1500 metres running. *New Stud Athlet* 1996; 11 (4): 59-65
91. van Ingen Schenau GJ, Jacobs R, de Koning JJ. Can cycle power predict sprint running performance. *Eur J Appl Physiol* 1991; 63: 255-60
92. Ward-Smith AJ. A mathematical theory of running, based on the first law of thermodynamics, and its application to the performance of world-class athletes. *J Biomech* 1985; 18 (5): 337-49
93. Withers RT, Van Der Ploeg G, Finn JP. Oxygen deficits incurred during 45, 60, 75 and 90-s maximal cycling on an air-braked ergometer. *Eur J Appl Physiol* 1993; 67: 185-91
94. New Studies in Athletics Round Table. Speed in the 800 metres. *New Stud Athlet* 1996; 11 (4): 7-22
95. Fox EL, Bowers RW, Foss ML. The physiological basis for exercise and sport. 5th ed. Dubuque (IA): Wm. C. Brown Communications, 1993
96. McArdle WD, Katch FI, Katch VL. Essentials of exercise physiology. 2nd ed. Philadelphia (PA): Lippincott, Williams and Wilkins, 2000
97. Finn J, Gastin P, Withers R, et al. Estimation of peak power and anaerobic capacity of athletes. In: Gore C, editor. Physiological tests for elite athletes. Champaign (IL): Human Kinetics, 2000: 37-49
98. Bouchard C, Taylor AW, Dulac S. Testing maximal anaerobic power and capacity. In: MacDougall JD, Wenger HA, Green HJ, editors. Physiological testing of the elite athlete. Champaign (IL): Human Kinetics, 1982

Correspondence and offprints: Dr *Paul Gastin*, UK Sports Institute, 40 Bernard Street, London WC1N 1ST, England. E-mail: Paul.Gastin@uk.sport.gov.uk