Physiological Differences Between Cycling and Running

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REVIEW ARTICLE

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Physiological Differences Between Cycling and Running

Lessons from Triathletes

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Abstract

The purpose of this review was to provide a synopsis of the literature concerning the physiological differences between cycling and running. By comparing physiological variables such as maximal oxygen consumption ($\dot{V}O_{2max}$), anaerobic threshold (AT), heart rate, economy or delta efficiency measured in cycling and running in triathletes, runners or cyclists, this review aims to identify the effects of exercise modality on the underlying mechanisms (ventilatory responses, blood flow, muscle oxidative capacity, peripheral innervation and neuromuscular fatigue) of adaptation. The majority of studies indicate that runners achieve a higher $\dot{V}O_{2max}$ on treadmill whereas cyclists can achieve a $\dot{V}O_{2max}$ value in cycle ergometry similar to that in treadmill running. Hence, $\dot{V}O_{2max}$ is specific to the exercise modality. In addition, the muscles adapt specifically to a given exercise task over a period of time, resulting in an improvement in submaximal physiological variables such as the ventilatory threshold, in some cases without a change in $\dot{V}O_{2max}$. However, this effect is probably larger in cycling than in running. At the same time, skill influencing motor unit recruitment patterns is an important influence on the anaerobic threshold in cycling. Furthermore, it is likely that there is more physiological training transfer from running to cycling than *vice versa*. In triathletes, there is generally no difference in $\dot{V}O_{2max}$ measured in cycle ergometry and treadmill running. The data concerning the anaerobic threshold in cycling and running in triathletes are conflicting. This is likely to be due to a combination of actual training load and prior training history in each discipline. The mechanisms surrounding the differences in the AT together with $\dot{V}O_{2max}$ in cycling and running are not largely understood but are probably due to the relative adaptation of cardiac output influencing $\dot{V}O_{2max}$ and also the recruitment of muscle mass in combination with the oxidative capacity of this mass influencing the AT. Several other physiological differences between cycling and running are addressed: heart rate is different between the two activities both for maximal and submaximal intensities. The delta efficiency is higher in running. Ventilation is more impaired in cycling than in running. It has also been shown that pedalling cadence affects the metabolic responses during cycling but also during a subsequent running bout. However, the optimal cadence is still debated. Central fatigue and decrease in maximal strength are more important after prolonged exercise in running than in cycling.

Exercise physiologists working with multisport athletes such as triathletes or duathletes who undergo both cycle and run training often use incremental exercise tests to monitor maximal oxygen uptake ($\dot{V}O_{2max}$), the anaerobic threshold (AT) and related physiological variables for both cycling and running. 'Performance $\dot{V}O_{2max}$' (i.e. how long a given rate of aerobic and anaerobic metabolism can be sustained) is determined by the interaction between $\dot{V}O_{2max}$ and lactate threshold (LT), whereas efficiency determines how much speed or power (i.e. 'performance velocity') can be achieved for a given amount of energy consumption.[1] However, these physiological variables measured in either cycling or running may adapt indifferently as a consequence of cross training in cycling and running;[2-13] cross training is defined as 'combined alternative training modes within a sport specific regimen'. The physiological adaptations to cross training in previously untrained athletes have been reviewed.[2,3]

It is also possible that the results of such physiological tests in cycling and running may be influenced by the athlete's original training background. However, no in-depth analysis has been carried out examining the differences in selected physiological parameters such as $\dot{V}O_{2max}$ and the AT, measured in cycling and running in athletes participating in either cycling or running or in triathletes actively participating in both cycling and running.

This review aims to provide a synopsis of the literature concerning the mechanisms associated with physiological differences between cycling and running. This article is not intended to review performance in triathlons or the physiological characteristics of triathletes. The comparison between triathletes, runners and cyclists is shown to identify the training acclimation triggered by mode of exercise. By comparing physiological variables such as $\dot{V}O_{2max}$, AT, heart rate, economy or delta efficiency measured in cycling and running in triathletes, runners or cyclists, we aim to identify the effects of exercise modality on the underlying mechanisms (ventilatory responses, blood flow, muscle oxidative capacity, peripheral innervation, neuromuscular fatigue) of adaptation.

1. Maximal Aerobic Power and the Anaerobic Threshold: Comparison between Cycling and Running

1.1 Trained Cyclists and Runners

1.1.1 Maximal Aerobic Power

Whole body $\dot{V}O_{2max}$ typically reflects a heightened capacity for cellular oxygen utilization within a specific activity.[14-16] The accepted hypothesis concerning $\dot{V}O_{2max}$ is that the greater the muscle mass used in an incremental task, the higher the measured $\dot{V}O_{2max}$.[17-19] For example, Gleser et al.[17] found an ~10% higher $\dot{V}O_{2max}$ for arm cranking in combination with lower limb muscle contractions compared with arm cranking alone. Other authors have reported no difference in $\dot{V}O_{2max}$ when upper limb activity is compared with lower limb and upper limb work.[14,20] It is generally accepted that in exercise situations involving a greater muscle mass, as in running, the higher the $\dot{V}O_{2max}$ value is observed in untrained subjects. Table I shows the studies that have reported maximal oxygen uptake for cycling and running in cyclists and runners.[5-7,14,18,21-36] However, direct comparison between studies is difficult since it is known that the incremental test protocol design (e.g. starting work rate, increments and duration of each stage) or the analysis performed on the data (e.g. exhaustion criteria, mathematical modeling) can greatly influence the values of physiological variables such as $\dot{V}O_{2max}$ or maximal aerobic power so obtained.[37,38]

Pechar et al.[5] concluded that athletes with previous experience in cycling may exhibit $\dot{V}O_{2max}$ values that are either equal to or approach those obtained in treadmill running. Various studies that have compared $\dot{V}O_{2max}$ in cycling and treadmill running in trained cyclists and runners support their premise.[30,39] Stromme et al.[39] reported a significantly higher (5.6%) $\dot{V}O_{2max}$ in cycling compared with treadmill running in male elite cyclists. Ricci and Leger[40] also found a higher $\dot{V}O_{2max}$ in cycle ergometry when compared with treadmill running (62.4 ± 8.1 vs 54.7 ± 8.1 mL/kg/min). Bouckaert et al.[34] later compared $\dot{V}O_{2max}$ in cyclists and runners completing incremental treadmill and cycling activity. These authors reported the $\dot{V}O_{2max}$ was 14% higher in treadmill running compared with bicycle ergometry in runners and 11% higher on the bicycle ergometer than on the treadmill in cyclists. Moreira-da-Costa et al.[32] found that $\dot{V}O_{2max}$ was highest in the exercise mode that the athletes had trained exclusively in. These authors reported a higher $\dot{V}O_{2max}$ value in treadmill exercise for runners and cycle ergometry in cyclists, respectively. Other research groups have found no significant difference in the $\dot{V}O_{2max}$ obtained in an incremental cycle test when compared with an incremental running test in trained cyclists.[6,7,27,41,42] Thus well trained cyclists can exhibit a $\dot{V}O_{2max}$ similar to that observed in treadmill running. Therefore, a training history and its accompanying adaptations in cycling may elicit a $\dot{V}O_{2max}$ value that is similar to that for treadmill running despite treadmill running potentially requiring a greater muscle mass. In only one study have trained cyclists been shown to exhibit a higher $\dot{V}O_{2max}$ value in treadmill running than in cycle ergometry;[8] a surprising result considering that the $\dot{V}O_{2max}$ of the subjects was well developed (i.e. in excess of 70 mL/kg/min) for both such exercise modes.

1.1.2 Submaximal Intensity/Anaerobic Threshold

It is generally described that submaximal running exercise induces a higher oxygen uptake and, probably, energy expenditure than cycling at the same intensity.[43-45] However, since the post-exercise oxygen consumption (EPOC) is similar in cycling and running[45] but the lactate concentration was shown to be higher after cycling at the same submaximal intensity,[29] one can speculate that the metabolic demands, i.e. the relative contribution of the glycolytic and oxidative processes, are different. In a recent experiment, Scott et al.[36] reported that during a short bout at the same intensity (1 minute at 250 W; treadmill

Table I. Studies (n = 21) that have assessed maximal oxygen uptake for cycling and running in cyclists and runners

Sport	n/sex	Level/details	Age (y)	Mass (kg)	Relative $\dot{V}O_{2max}$ bike (mL/kg/min)[a]	Absolute $\dot{V}O_{2max}$ bike (L/min)[a]	Relative $\dot{V}O_{2max}$ run (mL/kg/min)[a]	Absolute $\dot{V}O_{2max}$ run (L/min)[a]	Reference[b]
PE	5 M		30 ± 5.2	76.4 ± 4.7		4.5		4.7	[14]
R&C	5 M, 3 F	High/national	23	69		4.6***		5.0***	[21] NDP
S	5 M	2–3 sessions/wk	22	69.0		4.0*		4.3*	
None	6 M		25	72.1		3.2*		3.5*	
R	10 M	High/national	23	67.4		4.6*		4.8*	
R	14 M	Active	14–68	67.3		3.4*		3.7*	
R	7 M	2 mo running	43	73.7		3.4		3.4	
S	4 M	1 well trained	19–21			3.8 ± 0.6		4.1 ± 0.7	[22]
V	9 M	Well trained	24–34			4.6 ± 0.5*		4.8 ± 0.4*	
S	23 M	Trained	20.4 ± 1.8	77.3 ± 12.7	38.5 ± 4.3	3.0 ± 0.5	42.7 ± 4.9	3.3 ± 0.5	[23] SF
V	8 M		29.6 ± 7.6	77.5 ± 4.8		3.4 ± 0.5		3.8 ± 0.7	[24] NDP
V	3 M, 1 F					5.2*		4.8 ± 1.4*	[18]
Pre C	20 M		19.1 ± 3.9	73.3 ± 9.9		3.5 ± 0.5		4.0 ± 0.5	[5]
Post C						3.7 ± 0.4#		4.1 ± 0.5#	
Pre R	20 M		19.6 ± 1.4	72.3 ± 6.2		3.5 ± 0.3		3.5 ± 0.5	
Post R						3.8 ± 0.3#		3.7 ± 0.4#	
None	20 M		22.4 ± 3.9	73.7 ± 9.5		3.5 ± 0.4		3.9 ± 0.5	
None		8 wk post				3.4 ± 0.3		3.9 ± 0.4	
PE	50 M		21.2 ± 1.6	71.6 ± 8.5	48.1 ± 5.1	3.4 ± 0.4	54.8 ± 4.9	3.9 ± 0.5	[25]
None	30 M	Low	22.5 ± 2.6	75.5 ± 9	48.8 ± 5.4	3.7 ± 4.0	52.9 ± 4.7	4.0 ± 0.5	[26]
C	6 M	High		73.4 ± 2	65 ± 3.4	4.6 ± 0.2	62.9 ± 1.7	4.6 ± 0.2	[27] SF
None	18 M		19–24			2.7 ± 0.1***		3.3 ± 0.1***	[28] SF
V	6 F		19.4 ± 1.9	57.9 ± 6.61	32.1 ± 6.1*	1.8 ± 0.3*	34.9 ± 4.2*	1.9 ± 0.2*	[29] NDP

Continued next page

Table I. Contd

Sport	n/sex	Level/details	Age (y)	Mass (kg)	Relative $\dot{V}O_{2max}$ bike (mL/kg/min)^{a}	Absolute $\dot{V}O_{2max}$ bike (L/min)^{a}	Relative $\dot{V}O_{2max}$ run (mL/kg/min)^{a}	Absolute $\dot{V}O_{2max}$ run (L/min)^{a}	Reference^{b}
C	10 M	Steady training		69.2 ± 7	65.9 ± 6.5	4.5 ± 0.4	62.8 ± 3.5	4.2 ± 0.3*	[6] H
R	10 M			68.4 ± 8.5	61.7 ± 6.2*	4.3	68.1 ± 6.3*	4.6 ± 0.4	
None	10 M	Non-athletes	26 ± 6	72.8 ± 11.8	40.0 ± 5.5*	2.9 ± 0.4*	45.1 ± 3.9*	3.2 ± 0.4*	[30] SF, DP, BLA, HR
R	12 M	National	22.7 ± 4.0	61.7 ± 8.7	61.9 ± 4.9*	4.1 ± 0.5*	57.3 ± 4.5*	3.8 ± 0.6*	
C	10 M	National	20.6 ± 2.1	67.3 ± 9.2	56.5 ± 5.8*	3.6 ± 0.34*	64.3 ± 7.3*	4.0 ± 0.3*	
	12 M	No details	23 ± 5	75 ± 9	60 ± 6*		66 ± 8*		[32] BLA, DP, H90
R	10 M	2 y specific training	22.7 ± 4.0	61.7 ± 8.7		3.5 ± 0.4*		4.0 ± 0.3*	[32]
C	9 M		20.6 ± 2.1	67.3 ± 9.2		4.2 ± 0.6*		3.9 ± 0.6*	
V					46.7 ± 1.5		56.9 ± 1.8		[33]
R	9 M		23.5 ± 2.3	62.4 ± 5.3	67.7 ± 5.4*	4.2 ± 0.4*	77.1 ± 4.1*	4.8 ± 0.4*	[34] H
C	8 M		22.3 ± 2.7	68.1 ± 5.4	75.5 ± 8.2*	5.1 ± 0.5*	68 ± 4.1*	4.6 ± 0.4*	
PE	9 M	PE students	22.3 ± 1.2	69.8 ± 5.8	53.5 ± 3.2	3.7 ± 0.3	54 ± 4.6	3.8 ± 0.5	
R	7 M	Low-middle	28.1 ± 3.6	70.3 ± 7.8	50.1 ± 8.5*		59.6 ± 8.3*		[7]
C	7 M		24.3 ± 4.6	70.9 ± 11.2	55.1 ± 7.2*		59.5 ± 8.2*		
	6 F, 6 M					2.9 ± 0.7*		3.1 ± 0.8*	[35] DP
	13 M,1 F	Active	28.6 ± 9.6	77.5 ± 14.2	57 ± 12.9		59.3 ± 13.7		[36]

a Values are reported as mean ± SD. Where the original study reported the standard error of the mean, the standard deviation was calculated using the formula $SEM\sqrt{n}$, where SEM is the standard error of the mean and n is the sample size.

b Criteria for $\dot{V}O_{2max}$ are presented as a superscript in this column.

BLA = blood lactate concentration > 8 mM; **C** = cycle trained; **DP** = defined plateau; **F** = females; **H** = highest averaged value reached within last stage; **H90** = HR ≥90% of age predicted maximum; **H95** = HR ≥95% of age predicted maximum; **HR** = heart rate; **M** = males; **NDP** = non-defined plateau in $\dot{V}O_2$ despite increase in speed or work rate; **PE** = physical education students; **R** = run trained; **S** = students; **SF** = subjective/volitional exhaustion; **V** = various; $\dot{V}\mathbf{O_{2max}}$ = maximal oxygen consumption. $*$ $p < 0.05$: differences between running vs cycling, # $p < 0.05$: differences in the same sex, within subgroups, $***$ $p < 0.05$ cyclists < runners.

speed was calculated to elicit 250 W based on subject weight), total energy expenditure was similar between cycling and uphill running but the extent of aerobic and anaerobic energy transfer was different: the glycolytic component was 28% in cycling and 17% in running. If confirmed, this different metabolic contribution would directly influence the determination of the critical anaerobic threshold.

The physiological mechanisms surrounding the AT are complex and may be influenced by both neurological and peripheral muscle factors.[46] In addition, there is no biochemical evidence to support the fact that lactate production causes acidosis.[47] It is beyond the scope of this article to present and discuss the numerous (19 invasive and 15 non-invasive) techniques that could be used to determine the AT (for reviews see Bentley et al.[37] and Loat and Rhodes[48]). Training of specific muscle groups may facilitate O_2 transport and improve the metabolic profile of the specific muscles involved in the training thereby affecting the $\dot{V}O_{2max}$ as well as the AT. The AT can be expressed at an absolute work rate or as a percentage (%) of a maximal value. Also, the methods that are used to measure and define the AT are diverse and often confuse comparison of any variables associated with the concept.[49] Information concerning the AT measured in trained cyclists or runners completing incremental treadmill running and cycle ergometry tests seems to indicate that, similar to $\dot{V}O_{2max}$, training background may influence the observed response during incremental exercise in cycling or running. Davis et al.[26] investigated the comparability of the AT and $\dot{V}O_{2max}$ obtained from cycling and treadmill exercise (walking and running) in college students. No significant difference was found between cycling and treadmill exercise modes for the AT (63.8 ± 9.0 and $58.6 \pm 5.8\%$ $\dot{V}O_{2max}$ for cycling and treadmill exercise, respectively). However, the subjects in this study were not trained in either cycling or running. Withers et al.[6] later showed the AT was similar when expressed as a percentage of $\dot{V}O_{2max}$ in both the runners and the cyclists when obtained from an incremental cycle or treadmill running test. Coyle et al.[41] were also able to compare the LT measured in well trained cyclists completing both incremental cycle ergometer and treadmill running tests, and found no difference in $\dot{V}O_{2max}$ in cycling and running. However, they found that subjects with the highest LT ($\%\dot{V}O_{2max}$) in cycling had a similar LT in treadmill running. In contrast, the subjects with the lowest LT possessed an LT in treadmill running that closely matched the subjects in the high LT group. These data indicate that in well trained cyclists the LT may not necessarily be different when measured in running but this is probably due to specific adaptations in cycling rather than to any lack of adaptation to running.[50] However, more importantly, the conclusion drawn from this study is that cycling skill, muscle recruitment patterns and coordination in part influences the LT in cycling but not in running.

Mazzeo and Marshall[42] compared a group of trained cyclists completing both incremental cycling and running tests. These authors confirmed that the cyclists obtained similar $\dot{V}O_{2max}$ values in both tests, whereas in the distance runners treadmill $\dot{V}O_{2max}$ was higher than cycle $\dot{V}O_{2max}$. LT and VT occurred at a lower % $\dot{V}O_{2max}$ in both the cyclists and runners in the exercise mode in which they had not trained in extensively. However, the difference in the LT and VT was larger in the runners than in the cyclists. In addition, these authors found that the inflection point in plasma catecholamines also shifted in a similar manner to the blood lactate concentration between exercise modes, indicating the muscle metabolic response also changed with the different exercise modes. They suggested that the runners were not familiar with cycling, which may explain the differences in the LT and VT in cycling in trained runners.

In line with this suggestion, Bouckaert et al.[34] found the blood lactate response to incremental exercise was markedly different during incremental exercise in trained runners and cyclists performing exercise testing with the absolute $\dot{V}O_2$ corresponding to the onset of blood lactate accumulation (OBLA) lower in the exercise mode that they were not accustomed. However, the effect was much greater in the runners performing the incremental cycle testing, indicating the nature of the exercise was more unfamiliar than the cyclists performing running exercise. In another study, Hassmen[51] examined the effect of specialized training upon both physiological performance and perceptual responses to incremental cycling or running exercise. It was shown that the OBLA was much lower in the exercise mode that the subjects were not training in. In addition, the perception of effort and discomfort was far greater for the runners completing incremental cycle exercise at each submaximal workload. Therefore, these findings suggest that the perception of discomfort and peripheral fatigue is much greater in runners completing incremental cycle exercise. Although in this study the HR corresponding to the set lactate inflection points was not directly measured, the data indicate that calculation of HR corresponding to the OBLA would have been far higher in cycling relative to running in the runners, but similar in cyclists completing the two exercise tests.

1.2 Triathletes Performing Cycle Ergometry and Treadmill Running

1.2.1 Maximal Aerobic Power

Table II shows the studies that have reported maximal oxygen uptake and peak work load or power for cycling and running in triathletes.[8-10,12,52-89]

Kohrt et al.[53] and O'Toole et al.[54] were among the first groups of researchers to compare $\dot{V}O_{2max}$ of triathletes measured in both cycle ergometry and treadmill running. Kohrt et al.[53] assessed 13 triathletes in preparation for an Ironman triathlon. They found that $\dot{V}O_{2max}$ was significantly lower in cycle ergometry as compared with treadmill running (57.9 ± 5.7 vs 60.5 ± 5.6 mL/kg/min). In contrast, O'Toole et al.[54] reported similar $\dot{V}O_{2max}$ values in treadmill running and cycling. Therefore, these data are inconclusive with regard to differences in $\dot{V}O_{2max}$ between cycling and running in triathletes. In light of the data showing trained cyclists are able to achieve a $\dot{V}O_{2max}$ in cycling comparable with running,[5,30,39] it is possible that these subjects had adapted more to cycle training, effectively reducing the difference in $\dot{V}O_{2max}$ between the exercise modes. However, the subjects recruited for each investigation were of very mixed ability level (as evidenced by a relatively low $\dot{V}O_{2max}$), which could also have confounded the results. However, others have reported similar values for $\dot{V}O_{2max}$ in cycling and running in short distance specialist triathletes.[9,68,72] For example, Sleivert and Wenger[68] reported similar values for cycling and running $\dot{V}O_{2max}$ in 18 triathletes of mixed ability. In another study, Miura et al.[80] examined two groups of triathletes whom they characterized as either 'superior' or 'slower' level. They found no significant difference in $\dot{V}O_{2max}$ in cycling and running in both groups. Therefore, the differences in $\dot{V}O_{2max}$ between exercise modes may not be due to ability level. However, Schabort et al.[81] found $\dot{V}O_{2max}$ to be significantly higher in treadmill running then cycle ergometry (68.9 ± 7.4 vs 65.6 ± 6.3 mL/kg/min) in national level triathletes. Most studies have also shown that $\dot{V}O_{2max}$ is similar in cycling and running for triathletes of a wide range of competitive level performing incremental tests.[9,60,67,68,72,77] In only one study has a significantly higher $\dot{V}O_{2max}$ value been reported in cycling than in treadmill running (65.4 ± 4.2 vs 62.1 ± 6.3 mL/kg/min) in well trained triathletes.[78] This seems to be an exceptional result compared with the body of scientific evidence.

1.2.2 Anaerobic Threshold

Despite there still being controversy over the validity of the AT and LT determined via different procedures (invasive vs non-invasive, lactic vs ventilatory) [for reviews see Bentley et al.[37] and Loat and Rhodes[48]], a number of studies in triathletes have extended on initial studies by comparing both $\dot{V}O_{2max}$ and a measure of the AT in cycling and running in triathletes.[9,10,68,90,91] Table III shows the studies with ventilatory or anaerobic threshold data in cycling and running for cyclists, runners and triathletes.[6,9,10,26,30,31,52,58,68,72,73,78,80,87,89,90,92-97]

Kohrt et al.[62] conducted a 6- to 8-month longitudinal investigation of 14 moderately trained triathletes in training for a long distance triathlon. The researchers quantified $\dot{V}O_{2max}$ and the LT in both cycling and running. $\dot{V}O_{2max}$ remained relatively constant in both cycling and running until the latter stages of the training

Table II. Studies (n = 42) that have assessed maximal oxygen uptake for cycling and running in triathletes

Sport	n/sex	Level/details	Age (y)	Mass (kg)	Relative $\dot{V}O_{2max}$ bike (mL/kg/min/)[a]	Absolute $\dot{V}O_{2max}$ bike (L/min)[a]	Relative $\dot{V}O_{2max}$ run (mL/kg/min)[a]	Absolute $\dot{V}O_{2max}$ run (L/min)[a]	Reference[b]
T	9 M	Experienced			56.3		57.6		[52]
LDT	13 M	Competitive	29.5±4.8	69.8±5.6	57.9±5.6*		60.5±5.7*		[53] H
LDT	8 M	SA	30.5±8.8	74.7±10	66.7±10.1		68.8±10.4	5.1±0.9	[54] H, SF
	6 F	WC	31.3±5.6	60.3±4.6	61.6±7		65.9±8.1	3.9±0.4	
	5 F	WC subgroup			67.0±7.7		61.0±8.5		
	1 F	SA subgroup			60.6		64.6		
	6 M	SA subgroup			66.1±9.2		63.9±9.2		
	2 M	WC subgroup			77.0±10.0		75.1±10.0		
LDT	8 M	Highly trained	30.5±8.8	74.7±10.0	66.7±10.1		68.8±10.4		[55] SF
	7 F		31.3±5.6	58.8±5.7	64.0±8.9		68.1±9.4		
LDT	8 F				56.9		61.0		[56]
	10 M	Not clear			64.3		67.2		
LDT	11 M	Top 200 finishers	31.4±5.9	74.5±7.6		4.7±0.3		4.8±0.3	[57]
SDT	10 M	None given				4.6±0.5		4.9±0.8	[12]
LDT	9 M	Varied			64.3±8.5		68.1±11.9		[58]
SDT	14 M	Competitive			43.6±8.1		49.7±7.5		[59]
LDT	11 M	Not clear	31.4±1.8	74.5±2.3	63.2±1.7	4.81	65.3±1.3	4.7±0.1	[60] H, DP, R > 1.0 S
SDT	4 M	‘Elite’				4.7±0.4		4.8±0.4*	[61]
									[62] H
LDT	8 M 6 F	(I, Feb)	29.4±5.1	M 55.3–56.4 F 69.9–71.3	53.4±1.5*		57.4±1.4		
		(II, 6–8 wk post I)			55.5±1.5*		57.8±1.5		
		(III, 6–8 wk post II)			54.2±1.5*		57.2±1.5		
		(IV, 6–8 wk post III)			56.0±1.3*		58.4±1.4		
SDT	10 M	Highly trained	27.6±6.3	72±5.4	70.3±6*	5.1*	75.4±7.3*	5.4±0.6*	[10] H, SF

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Table II. Contd

Sport	n/sex	Level/details	Age (y)	Mass (kg)	Relative $\dot{V}O_{2max}$ bike (mL/kg/min/)^{a}	Absolute $\dot{V}O_{2max}$ bike (L/min)^{a}	Relative $\dot{V}O_{2max}$ run (mL/kg/min)^{a}	Absolute $\dot{V}O_{2max}$ run (L/min)^{a}	Reference^{b}
SDT	10 M	Competitive			62.9±3.8		67.0±4.2		[63]
LDT	10 M	Not clear			60.8±1.4		61.6±1.1		[64]
SDT	7 F	Recreational			48.2±3.8	2.9±0.3	50.7±2.6	3.1±0.2	[65]
	16 M	Not clear			56.5±8.5		62.0±8.4		
SDT	7 M	Competitive			60.5±6.2^{MW}		69.9±5.5 ^{MW}		[66]
	7 M	Competitive			51.9±3.9^{HW}		55.6±4.1^{HW}		
T	7 M	Horizontal TR	24±3	75±10	66.4±1		66.1±7.9		[67]
T	18 M	Recreational	27.7±1.3	76.2±2.1	60.1±1.5	4.6±0.1	63.7±1.6	4.8±0.1	[68] H, NDP
	7 F		28.3±2.3	59.3±2.1	51.1±2	3.0±0.1	51.4±1.3	3.1±0.1	
SDT	9 M				57.9±4.5		59.3±6.9		[69]
T	8 M				67.1±2.6		68.1±5.4		[70]
SDT	14 M				58.5±6.8		61.3±6.6		[71]
SDT	10 M	Amateur	27.4±5.7	78.4±8	61.3±10.1	4.75±0.5	63.3±8.9	4.9±0.2	[72] H, SF, DP
T	7 F				54.3±3.6		57.3±3.6		[73]
	7 F				63.2±3.9		65.4±2.9		
T	6 F	10 wk R	20.3±0.9	58.2±3.3		2.3±0.1		2.6±0.1	[74] NDP, R>1.15
	6 F	10 wk C	20.5±1.0	61.6±3.6		2.3±0.1		2.5±0.1	
	6 F	10 wk C+R	21.3±0.6	62.4±3.0		2.5±0.2*		2.6±0.2	
SDT	5 M	Competitive			60.8±3.0		64.3±4.7		[75]
SDT	6 M					4.53±0.1		4.5±0.1	[76]
SDT	17 M		26.5±8.2	62.8±5.1	61.1±8.1		63.8±8.1		[77] NDP, R<1.05
SDT	7 M	Competitive	20.8± 2.9	69.7±4.5	65.4±4.2		62.1±6.3		[78] H, DP HRm, I
SDT	9 M	Competitive			70±4.8		71.7±4.9		[79]
SDT	8 M	Superior	27.3±6.8	65.4±5.8	67.8±6.1$^{\#}$		69.7±5.4$^{\#}$		[80] H, NDP
	8 M	Lower	26±10.3	60.8±3.2	54.9±3.8$^{\#}$		59.3±7.1$^{\#}$		
T	4 M 2 F		21.3±1.6	65.7±5.6	64.6±2.6*	4.2±0.6*	66.9±3.7*	4.4±0.4*	[8]

Continued next page

Table II. Contd

Sport	n/sex	Level/details	Age (y)	Mass (kg)	Relative $\dot{V}O_{2max}$ bike (mL/kg/min/)[a]	Absolute $\dot{V}O_{2max}$ bike (L/min)[a]	Relative $\dot{V}O_{2max}$ run (mL/kg/min)[a]	Absolute $\dot{V}O_{2max}$ run (L/min)[a]	Reference[b]
C	6 M		24.3 ± 7.5	72.5 ± 3.7	71.2 ± 3.9*	5.2 ± 0.5*	75.3 ± 3.8*	5.3 ± 0.4*	
R	4 M 2 F		21.0 ± 2.4	64.8 ± 13.8	61.7 ± 5*	4.0 ± 1.1*	68.4 ± 4.1*	4.5 ± 1.1*	
All	14 M 2 F		22.2 ± 5	67.7 ± 9.1	65.8 ± 4.8*	4.4 ± 0.1*	70.2 ± 4.3*	4.7 ± 0.8*	
SDT	29 M	Competitive	20.9 ± 2.6	68 ± 7.8	69.1 ± 7.2	4.7	70.2 ± 6.2	4.8 ± 0.4	[9]
	6 M	Elite	21.8 ± 2.4	69.9 ± 7.3	75.9 ± 5.2	5.3	78.5 ± 3.6	5.5 ± 0.3	
SDT	5 M	National squad	23 ± 4	72.1 ± 4.7	69.9 ± 4.5*	5.0 ± 0.4	74.7 ± 5.3*	5.3 ± 0.5	[81] H
	5 F		25 ± 7	59.3 ± 5.8	61.3 ± 4.6	3.6 ± 0.4	63.2 ± 3.6	3.7 ± 0.3	
	5 M 5 F				65.6 ± 6.3*	4.3 ± 0.8	68.9 ± 7.4*	4.5 ± 1	
SDT	8 M	Competitive	21.7 ± 1.7	71.4 ± 2.2	64.7 ± 2.4		64.2 ± 2.1		[82]
	5 M	Elite senior	25.4 ± 0.8	72.2 ± 3.4	75.7 ± 2.3		76.3 ± 3.2		
SDT	12 M	Good level			70.7 ± 3.8		61.0 ± 6.2		[83]
	12 M	Middle level			67.7 ± 6.4		56.9 ± 5.5		
SDT	13 M	University team	23.1 ± 1.2	71.7 ± 1.8	67.2 ± 1.6		68.8 ± 1.8		[84]
T	10 M				67.1 ± 1.6		68.7 ± 2.6		[85]
SDT	13 M	Competitive			67.2 ± 1.6		68.8 ± 1.8		[86]
SDT	8 M	University team	24.0 ± 3.0	71.1 ± 6.5	68.7 ± 3.2		69.9 ± 5.5		[87] SF
T	4 M 4 F	Preparatory training	22 ± 2	60.7 ± 10	60.9 ± 6.7*		64.8 ± 5.8*		[88] NDP, R > 1.05
		Specific training			61.9 ± 6.4*		66.1 ± 6.9*		
		Pre-competition			62.8 ± 7.2*		67.1 ± 5.9*		
SDT	8 M		28.9 ± 7.4	73.3 ± 6.0	67.6 ± 3.6	4.9 ± 0.4	68.9 ± 4.6	5.0 ± 0.5	[89] SF

a Values are reported as mean ± SD. Where the original study reported the standard error of the mean, the standard deviation was calculated using the formula SEM$\sqrt{n}$, where SEM is the standard error of the mean and n is the sample size.

b Criteria for $\dot{V}O_{2max}$ are presented as a superscript in this column.

Feb = February; **C** = cycle trained; **DP** = defined plateau; **F** = females; **H** = highest averaged value reached within last stage; **HRm** = HR > age predicted HR_{max}; **HW** = heavy weight; **LDT** = long distance triathletes; **M** = males; **MW** = medium weight; **NDP** = non-defined plateau in $\dot{V}O_2$ despite increase in speed or work rate; **R** = run trained; R > 1.05 RER > 1.05, R > 1.15 RER > 1.15**;** **S** = students; **SA** = serious amateur; **SDT** = short distance triathletes; **Sept** = September; **SF** = subjective/volitional exhaustion; **T** = triathletes; **TR** = treadmill; **$\dot{V}O_{2max}$** = maximal oxygen consumption; **WC** = world class. * $p < 0.05$: differences between running vs cycling, # $p < 0.05$: differences in the same sex, within subgroups.

Table III. Studies (n = 21) showing ventilatory (VT)/anaerobic threshold-related data for cycling and running in cyclists, runners and triathletes

Sport	Performance level	n/sex	VT $\dot{V}O_2$ bike (L/min)	VT $\dot{V}O_2$ run (L/min)	VT $\dot{V}O_2$ bike (mL/kg/min)	VT $\dot{V}O_2$ run (mL/kg/min)	VT bike (% $\dot{V}O_{2max}$)	VT run (% $\dot{V}O_{2max}$)	Reference[a]
S	Previously untrained	30 M		2.4±0.3			63.8±9	58.6±5.8	[26]1,4,6
C	Steady training	10 M	3.0±0.5*	3.2±2.7*	43.7±6.2*	46.8±3.2*	66.3±6.9	74.3±6.1	[6]
R		10 M	2.6±0.3*	3.6±0.4*	37.8±5.3*	52.7±6.2*	61.2±4.9	77.3±2.6	
		12 M			48±5	57±5	79±7	85±5	[31]
T	Experienced	9 M			44.3	45.7			[52]
T		10 M	3.9*	4.42*			85	90	[58]8
							71.0±3.5	71.0±2.4	[92]
R	2 y training	10 M	2.6±0.3*	3.2±0.3*			74.8±5.7*	80.8±6.9*	[30]5
C		9 M	3.3±0.4	3.1±4.3			79.78±4.9	79.78±4.3	
T	Highly trained	10 M	3.0±0.5*	3.9±0.3*	46.9±4.3*	53.9±3.8*	66.8±3.7	71.9±6.6	[10]5
T	Highly trained	10 F	2.2±0.1	2.8±0.1	37.7±1.9	47.2±2	62.7±2.1*	74.0±2.0*	[90]
T		7 F					74.8±1.9*	85.0±2.1*	[68]5
T		18 M					81.4±1.3*	85.0±1.3*	
T	Well trained	6 M		4.0±0.5		57.8±5.3		84.6±5.0	[93]3
		SwBK		4.1±0.7		53.5±3.5		84.6±2.5	
		RBK		4.0±0.2		63.5±3.5		87.0±7.0	
T	Elite	7 M					71.8	86.2	[73]
T	Amateur	10 M	4.0±0.2*	4.5±0.2*	52.2±3.2*	57.7±2.7*	85.0±1.3*	91.1±1.0*	[72]6
T	Competitive	7 M			42.5±6.5	46.4±6.3	65.0±9.9	74.7±10.1	[78]
T	Competitive						72.5±0.4	84.9±0.6	[94]
T	Superior	8 M			48.7±3.8#	50.9±4.8#			[80]
T	Lower	8 M			39.7±2.9#	40.4±4.8#			
T	All	29 M	3.0±0.6*	2.6±0.4*	45.1±8.2	46.7±4.1	65.3	66.4	[9]2
T	Elite	6 M	3.0±0.6	2.8±0.3	49±10.9	50.9±4.3	64.5	64.8	
T	Well trained	8 M					69.9±3.3	70.1±3.4	[87]5
T	Well trained	9 M				67.0±3.6			[95]5
T	(Pre-competitive)	7 M 1 F	3.7±0.2#,°		55.8±2.8#		88.9±0.2#		[96]5,7
	(Competitive)	7 M 1 F	3.7±0.2		55.4±3.3		88.6±0.2#		
	(Post-competitive)	7 M 1 F	3.3±0.2#,°		49.0±4.1		79.0±0.2		
T		8 M	(LT) 3.8±0.4*	(LT) 4.4±0.5*					[89]

a VT determination by method of: 1 = abrupt FEO_2 increase; 2 = V slope; 3 = VT equivalent; 4 = abrupt R increase; 5 = nonlinear increase equivalent in O_2 determined by a computerized algorithm; 6 = non-linear increment in minute VE to exercise time identified by computerized analysis, checked from VT equivalents; 7 = determined visually from VE time-course curve; 8 = subjectively determined via VT breakpoint.

C = cycling; **F** = female; **LT** = lactate threshold modified Dmax method; **M** = male; **R** = running; **RBK** = run background; **S** = student; **SwBK** = swim background; **T** = triathlete; $\dot{V}O_2$ = oxygen consumption; $\dot{V}O_{2max}$ = maximal oxygen consumption; * $p < 0.05$: differences between running vs cycling, # or ° $p < 0.05$: differences in the same sex, within subgroups.

period, possibly reflecting an increase in training intensity at that time. However, $\dot{V}O_{2max}$ together with the LT in cycling was consistently lower than that obtained for treadmill running. These findings suggest that adaptation of the LT is specific to the muscles involved in training in a particular exercise mode. It may also be that the subjects' training background was more extensive in cycling than running. This study also indicates the nature of training in either exercise mode may influence adaptation in cycling or running. In a more recent longitudinal study[98] over one season in trained Olympic distance triathletes, the relative stability of $\dot{V}O_{2max}$ and the larger change in VT under the influence of specific training has been confirmed. However, Albrecht et al.[52] found no difference between the VT (expressed as % $\dot{V}O_{2max}$) obtained in cycling (78.8%) or running (79.3%). In accordance with this, Kreider[12] showed no significant difference in the VT in triathletes completing incremental tests in cycling and treadmill running. The study methodology and the training background of the subjects that these studies involved, however, were not clear.

Interestingly, these authors found that the exercise intensity sustained during the cycle and running stages of a short distance triathlon was similar. In single sport endurance competitions it is generally thought that the AT reflects the ability to sustain a set percentage of maximum capacity.[99] Kreider's data,[12] collected for a triathlon event, imply otherwise. Despite the VT of the athletes occurring at a different exercise intensity within isolated incremental running and cycling tests (90% vs 85% of $\dot{V}O_{2max}$), the exercise intensity that they sustained during a race was similar for both exercise modes. However, De Vito et al.[93] showed the VT in running to be lower after prior cycle exercise. These results and those reported by Zhou et al.[72] suggest that the cycle stage of a triathlon influences the ability to sustain a set percentage of maximal capacity during the subsequent running stage. This has implications for training prescription on the basis of incremental tests that have been performed in isolation.

Hue et al.[9] examined $\dot{V}O_{2max}$ and the VT in triathletes competing in short distance events. They found that the $\dot{V}O_{2max}$ (75.9 ± 5.2 vs 78.5 ± 3.6 mL/kg/min) values of international standard triathletes were similar in cycling and running but higher than in competitive triathletes (69.1 ± 7.2 vs 70.2 ± 6.3 mL/kg/min). Similarly, VT (expressed as % $\dot{V}O_{2max}$) was also similar in cycling and running in the two groups. Miura et al.[80] also reported VT measured in cycling and running to be similar, in absolute terms, in two groups of triathletes who varied in short distance triathlon race time. Schneider et al.[10] were able to confirm these findings and found that whilst $\dot{V}O_{2max}$ was significantly higher in running when compared with cycle exercise (75.4 ± 7.3 vs 70.3 ± 6.0 mL/kg/min), the VT was not significantly different between cycling and running when expressed as an absolute $\dot{V}O_2$ value but did differ relative to $\dot{V}O_{2max}$ (66.8 ± 3.7 vs 71.9 ± 6.6%).

In contrast, some reports do show differences in the AT between cycling and running.[67,72,90] It is possible that the volume or intensity of training in either cycling or running may influence the AT in either exercise mode. However, Schneider and Pollack[90] quantified training volume and intensity in cycling and running completed by 'elite' triathletes and found no significant differences in these variables despite a significant difference in the VT (% $\dot{V}O_{2max}$) in cycling versus running (74.0 ± 2.0 vs 62.7 ± 2.1%). On the other hand, Medelli et al.[67] quantified both the 'aerobic' (corresponding to VT) and 'anaerobic' threshold in both treadmill running and cycling in triathletes that they reported as 'elite'. These authors found that the AT occurred at a significantly greater % $\dot{V}O_{2max}$ (88.8%) during inclined (1.5% slope) treadmill running as compared with cycle ergometry (83.3%). However, the *aerobic* threshold was not significantly different between inclined running and cycle ergometry. Since Sloniger et al.[100] reported a greater activation of the vastus and soleus in uphill than in level running, inclined treadmill running may elicit different recruitment patterns in the calf and quadriceps muscle groups during progressive incremental exercise. This may partly explain the results observed by Medelli et al.[67] In another study, Zhou et al.[72] found no significant differences in treadmill or ergometry $\dot{V}O_{2max}$. However, the VT was significantly higher in running compared with cycling (91.1 ± 1.0 vs 85.0 ± 1.3% $\dot{V}O_{2max}$). There are also limited data available comparing $\dot{V}O_{2max}$ and the AT in cycling and running exercise modes for 'duathletes'. In one study, Bolognesi[101] found a significant difference in $\dot{V}O_{2max}$ measured in cycle ergometry (66.3 ± 9.0 mL/kg/min) and treadmill running (71.4 ± 10.3 mL/kg/min) in eight male duathletes. In this study a significant difference was also observed between the VT (expressed as % $\dot{V}O_{2max}$) in cycling (68.8 ± 3.7%) and treadmill running (73.9 ± 6.6%).

1.2.3 Sex Differences

There are limited reports comparing $\dot{V}O_{2max}$ and the AT obtained within cycling and running between males and females. Sleivert and Wenger[68] found both male and female triathletes to exhibit no differences in $\dot{V}O_{2max}$ between running and cycling. O'Toole et al.[54] also found no significant differences in cycling and running $\dot{V}O_{2max}$ in male (68.8 ± 10.4 vs 66.7 ± 10.1 mL/kg/min) or female (65.9 ± 8.1 vs 61.6 ± 7.0 mL/kg/min) triathletes. Therefore, the difference in $\dot{V}O_{2max}$ between cycling and running does not seem to vary appreciably between males and females. Similarly, Sleivert and Wenger[68] reported that the AT was not significantly different in cycling and running in male athletes. However, there was a significant difference in the VT between cycling and running in female athletes. Millet and Bentley[97] have also investigated if the differences in performance between elite junior and elite senior triathletes were due to the same physiological differences in men and women. Irrespective of sex, there were no differences in $\dot{V}O_{2max}$ (74.7 ± 5.7 vs 74.3 ± 4.4 and 60.1 ± 1.8 vs 61.0 ± 5.0 mL/kg/min) and cycling economy (72.5 ± 4.5 vs 73.8 ± 4.3 and 75.6 ± 4.5 vs 79.8 ± 9.8 W/L/min) between junior and senior triathletes. However, the difference in performance between juniors and seniors was due to different reasons in male and female triathletes: senior males had a higher VT than junior males whereas VT was similar in female junior and senior triathletes. In female triathletes, senior triathletes had a higher PPO and a lower increase in the energy cost of running after cycling. These differences between males and females are probably induced by different training characteristics. The hypothesized differences in training between elite male and female triathletes is likely influenced by the characteristics of the competition at this level: the cycling bout (where the number and density of athletes is lower than in males [102]) has a stronger influence on the overall race result in females.

From the limited literature available, it appears that in general males and females exhibit the same differences between running and cycling $\dot{V}O_{2max}$ and AT.

1.2.4 Heart Rate

Maximal heart rate (HR_{max}) is generally reported to be slightly (~5%) higher when obtained from an incremental treadmill test as compared with an incremental cycle test in untrained subjects.[7,23,103] In addition, the relationship between HR and exercise intensity or $\dot{V}O_2$ is exercise dependent[14,104,105] and is influenced by training mode, postural position[106] or laboratory environment.[107] In triathletes, the HR_{max} observed in cycling is often lower by 6–10 beats/min than that obtained during running.[62,78,79,103] Longitudinal investigations have demonstrated HR_{max} to remain relatively stable over the course of a season,[98] with higher values (~5 beats/min) observed in running than in cycling.[62] In contrast, there is also evidence suggesting that HR_{max} is similar between cycling and running modes.[53,67,72,88,99] Although this appears to hold for males, differences were observed for this variable in females by some authors.[55] Schneider and Pollack,[90] however, found no such significant differences between cycling and running HR_{max} in elite female triathletes.

The HR corresponding to the AT is used to prescribe submaximal exercise training loads.[105,108] The data concerning triathletes indicate that the HR corresponding to certain inflection points associated with the AT is always higher in running than cycling, both when expressed in absolute terms and relative to HR_{max}.[10,72,78,79,90,103] Schneider et al.[10] reported a significant difference in the HR corresponding to the VT in cycling and running (145.0 ± 9.0 vs 156.0 ± 8.0) in 'highly trained' triathletes. This corresponded to 80.9 ± 3.4 versus 85.4 ± 4.1% HR_{max}. In another study by the same research group and conducted on elite female triathletes,[90] a higher HR was recorded at the VT in running than in cycling (164.7 ± 4.0 vs 148.2 ± 3.4) and this difference was also evident when HR was expressed as a percent of HR_{max} (87.3 ± 1.6 vs 79.7 ± 1.5%). Similarly, Roecker et al.[103] found a difference of 20 beats/min between HR determined at the LT on cycling ergometer (149.9 ± 18.0 beats/min) and treadmill (169.6 ± 15.7 beats/min). However, recreational subjects (–22 beats/min) and cyclists (–14 beats/min) exhibited lower differences than triathletes and runners. Additionally, the differences were not influenced by sex.

There is some evidence that HR may not differ between cycling and running when it is determined from a submaximal inflection point. Medelli et al.[67] reported HR values corresponding to the 'aerobic' but not those corresponding to the 'anaerobic' threshold in well trained triathletes to be different in cycling compared with running. In another study, Bolognesi[101] reported no significant difference in the HR corresponding to the VT in cycling and running (152.0 ± 8.0 vs 158.0 ± 9.0) in duathletes. Similarly, Hue et al.[9] found a non-significant difference in the HR corresponding to the VT in elite triathletes. However, in both these two latter studies the mean difference between cycling and running was ~7 beats/min, which is quite large and practically relevant in terms of training prescription. Basset and Boulay[8] have reported that the relationship between HR and % $\dot{V}O_{2max}$ did not differ when calculated either from a treadmill or from a cycle ergometer test. These authors also showed that HR was similar between running and cycle ergometer tests throughout the training year and concluded that triathletes could use a single mode of testing for prescribing their training HR in running and cycling throughout the year.[88]

Zhou et al.[72] showed that the HR corresponding to the VT was significantly higher in running (174.6 ± 4.5) as compared with cycling (166.4 ± 7.6). However, these authors found that the HR measured in a triathlon race was similar to the HR at the VT in cycling but much lower in running. Other studies have also shown a decrease in the HR_{max} and the HR corresponding to the VT during an incremental running test performed after submaximal cycling.[48] Hue et al.[78] have also demonstrated that the HR during a 10 km run after 40 km of cycling is higher when compared with the same run without cycling. Therefore, even though the HR corresponding to the AT or HR_{max} may be similar in running compared with cycling (in exercise tests performed in isolation), the HR corresponding to the AT determined from an incremental running test may be different to that observed in a race situation, especially in running. At the elite level, because of the stochastic pace, there is no demand to control the exercise intensity for the run in an Olympic distance triathlon via HR. Within Ironman, the potential use of HR for controlling the running pace might be of interest, at least at the beginning of the marathon. However, to our knowledge there is no published protocol for determining HR for this purpose. Furthermore, the effect of prior cycling on HR during running should be considered when prescribing HR during running training on its own.

1.2.5 Running Economy

Running economy can be defined by the $\dot{V}O_2$ (in mL O_2/kg/min) of running at a certain speed, and is usually expressed by the energy cost (EC) of running a distance of 1 km (in mL/kg/km) calculated as $\dot{V}O_2$ divided by the velocity. It is known that training-induced, genetic, physiological and anthropometric factors influence economy (for reviews see Foster and Lucia[109] and Saunders et al.[110]).

EC has been reported in triathletes within both the conditions of isolated running and 'triathlon running'.[11,58,60,78,97,111-117] It is generally reported that in trained triathletes, EC measured at the end of an Olympic distance triathlon is higher by ~10% when compared with an isolated run, e.g. 224 versus 204 mL/kg/km,[115] 224 versus 207 mL/kg/km.[111] It has also been reported that the extent of any change in EC subsequent to an exhaustive cycling bout is influenced by athlete performance level, event distance, sex and age. The effect of a fatiguing cycling bout on the subsequent running energy cost was different between elite (−3.7 ± 4.8%, when compared to an isolated run) and middle-level (2.3 ± 4.6%) triathletes.[116] Elite long-distance triathletes had slightly (but not significantly) lower EC values than short-distance triathletes (163.8 vs 172.9 and 163.0 vs 177.4 mL/kg/km during an isolated and a 'triathlon' run, respectively).[11] Surprisingly, no difference has been observed in EC between elite junior and senior triathletes, whether male or female, during an isolated run and a 'triathlon' run (173–185 mL/kg/km).[97] However, the increase in EC subsequent to cycling was higher in juniors than in seniors in females (5.8 vs −1.6%) but not in males (3.1 vs 2.6%).[97]

The mechanisms underlying the deterioration in economy in the 'triathlon run' when compared with an isolated run are various: both reported changes in the ventilatory pattern[79] leading to a higher $\dot{V}O_2$ of the respiratory muscles,[116,118] and neuromuscular alterations reducing the efficiency of the stretch-shortening-cycle[113,116,119] have been proposed. Some metabolic factors such as shift in circulating fluids, hypovolaemia and increase in body temperature have also been suggested.[111,114,115] Of interest are the studies of Hausswirth et al.[112-114] comparing EC at the end of a short-distance triathlon and at the end of a marathon of similar duration: EC was more increased during the marathon (+11.7%) than during the triathlon (+3.2%) running when compared with a 45-minute isolated run. The differences are due mainly to a higher decrease in bodyweight related to fluid losses, a larger increase in core temperature during the long run and significant mechanical alterations during the long run when compared with the running part of a triathlon.

Interestingly, recent values of EC in world-level distance runners have been reported:[120-122] Jones[120] showed a continuous decrease in EC of Paula Radcliffe, the current world record holder for the women's marathon between 1992 (~205 mL/kg/km) and 2003 (~175 mL/kg/km) corresponding to a 15% improvement, whereas $\dot{V}O_{2max}$ (~70 mL/kg/min) and body mass (~54 kg) remained unchanged over the period. Jones reported also that her EC was more recently measured at 165 mL/kg/km. Billat et al.[123,124] reported higher values in elite female Portuguese and French (196 ± 17 mL/kg/km)[124] or Kenyan (208 ± 17 mL/kg/km)[123] distance runners. Overall, this compares favourably with values obtained for elite female triathletes: Millet and Bentley[97] reported in nine elite females (including one long-distance world champion, second at the Hawaii Ironman and five European medallists) an average value of 176.4 mL/kg/km, whereas the average $\dot{V}O_{2max}$ was 61.0 mL/kg/min for a body mass of 60.3 kg.

In males, Lucia et al.[121,122] reported a value of 150–153 mL/kg/km in Zersenay Tadese, the current long cross-country and half-marathon world champion for a $\dot{V}O_{2max}$ of 83 mL/min/kg. The EC of Tadese is lower (the lowest reported so far) than previously reported values in elite runners: 180 mL/kg/km for Steve Scott;[125] 203–214 mL/kg/km in elite French and Portuguese[124] or Kenyan[123] runners; ~190–192 mL/kg/km in elite East-African runners;[121,126] ~211 mL/kg/km in elite Spanish runners.[121] So, similar to females, with the exception of Tadese, running economy in male distance runners does not appear to be better than the ones reported in elite triathletes: 174 ± 9 and 164 ± 8 mL/kg/km for short-distance and long-distance triathletes, respectively.[11] However, further investigation with Elite Ironman triathletes is required to confirm such partial results. Since EC is calculated as $\dot{V}O_2$ divided by the running velocity, it is unclear how this later parameter influences the comparison between elite triathletes and elite runners who have higher absolute training and competition velocities and therefore a biased lower EC. To our knowledge, there are no values of EC measured at the same absolute or relative (percentage of velocity at $\dot{V}O_{2max}$) speed in the two groups.

Overall, from these data, it appears that the main difference in running performance between elite runners and triathletes comes mainly from a higher body mass in triathletes (affecting proportional $\dot{V}O_{2max}$) rather than from differences in running economy. Since mean lower leg thickness and calf mass have been shown to be related to running economy,[127] one may speculate that the higher body mass in triathletes comes mainly from the upper body muscles more and – probably –

from the higher skinfold thicknesses that are associated with swimming.

1.2.6 Delta Efficiency

Delta efficiency represents the ratio in the changes of external mechanical work to energy expenditure respectively within an incremental stage test.[128,129]

Delta efficiency is consistently reported to be higher in running than in cycling;[129-131] however, the mechanisms underlying such a difference are not clear. It is speculated that it comes mainly from the storage-recoil of elastic energy in the series of elastic components of the knee extensors that exists in running[132,133] but not in cycling.[130,131] The acceleration-deceleration of the limbs (internal mechanical power) is higher in running than in cycling. Similarly the metabolic cost of running has been shown to be mainly dependent on the cost of generating peak force during the stance phase and inversely proportional to the contact time.[134,135] The increase in contribution of muscles not directly involved in the force production (arms and trunk) might be higher in cycling than in running and this may therefore influence the delta efficiency. Finally, it cannot be excluded that this later mechanism is related to the described differences in ventilatory pattern between cycling and running (see section 2.1).

By comparing delta efficiency between cycling and running in a protocol that excluded several confounding factors such as differences in the metabolic power, extra external load and cycle (pedalling or stride) frequency, Bijker et al.[129] confirmed that delta efficiency is lower in cycling (25.7 ± 1.3%) than in running (45.5%). They did not provide strong evidence about the respective contributions of the different mechanisms that they discussed. Efficiency has important consequences in terms of physiological testing (section 1.2), development of fatigue (section 2.4.3) or training content. Efficiency determines the 'performance velocity'[1] and is therefore of high interest for the coaches. Secondly, the knowledge on the physiological determinants of running and cycling efficiency is relatively lacking in comparison to $\dot{V}O_{2max}$ and the lactate threshold. So this area is also of the highest interest for the scientists investigating cross-training adaptations.

2. Physiological Mechanisms Associated with Differences between Cycling and Running

The $\dot{V}O_{2max}$ is thought to be influenced by a combination of factors of central and peripheral origin, and their respective contributions have been the subject of considerable debate in recent years.[99,136-139] The reader is directed to these reviews for more comprehensive appreciation of this area. In contrast to the concept of $\dot{V}O_{2max}$, there is surprisingly little research examining the mechanisms associated with the AT. Also, minimal research into the factors surrounding differences in the AT or $\dot{V}O_{2max}$ between cycling and running has taken place.

2.1 Ventilatory Responses

Differences in ventilatory responses to exercise (exercise-induced arterial hypoxaemia, O_2 diffusion capacity, ventilatory fatigue, pulmonary mechanics) have been reported between running and cycling in the literature.

It is well documented that there is a drop in partial pressure of oxygen in arterial blood (P_aO_2) associated with a widening (A-a) DO2 that begins at around 60–70% $\dot{V}O_{2max}$ during incremental exercise both in running and in cycling. EAIH is associated with a decrease to 10 mmHg in P_aO_2 and can be indirectly diagnosed by a decrease in pulse oximetry saturation in oxygen (S_pO_2) below 90% (for a review, see Prefaut et al.[140]). Exercise-induced arterial hypoxaemia (EAIH) is associated with relative hypoventilation and therefore might occur more often in cycling than in running.[140] In addition, in multisport athletes, EAIH is exercise dependent and influenced by the order of the running and cycling bout.[141]

Arterial saturation in oxygen (S_aO_2) does not directly influence $\dot{V}O_{2max}$. However it has been hypothesized that $\dot{V}O_{2max}$ decreases by ~1% for each 1% decrease in S_aO_2.[142] However, it is unlikely that the observed differences in S_aO_2 between cycling and running are linked to the differences in $\dot{V}O_{2max}$. Green et al.[143] compared oxygen desaturation of cyclists and runners in incremental exercise testing. These authors found no differences for this variable at maximal exertion. However, this study did not compare the different athlete groups in both cycling and running tasks. Galy et al.[141] showed that in trained triathletes the desaturation was higher in running (S_pO_2 = 93.0–93.5%; P_aO_2 = 86.6–88.7 mmHg) than in cycling (S_pO_2 = 94.8–95.4%; P_aO_2 = 91.4–93.7 mmHg), irrespective of the order of bouts (running followed by cycling or *vice versa*). In addition, to the higher desaturation during running, a higher decrease in pulmonary diffusing capacity was reported after cycling.[96] This was explained by several factors, such as the crouched position on the bicycle (in turn inducing higher intrathoracic pressure), a decrease in thorax volume due to the 'triathlete' position on the handlebars and a lower efficiency of the peripheral muscular pump. These latter factors would limit the venous return to the heart and would therefore induce a low pulmonary blood volume after cycling. These different ventilatory/haemodynamic factors were concomitant to different blood rheological responses: cycling was associated with an important decrease in blood volume and running with an increase in the erythrocyte rigidity.[144] The incidence and relationships between these different mechanisms are still unclear, but this group[9,78,79,96,141,144-148] provided convincing arguments that pulmonary diffusion is different between cycling and running.

Smith et al.[149] found no difference in O_2 saturation between the two exercise modes in combination. However, it has also been shown that at maximum exertion there is a lower O_2 saturation in treadmill running compared with cycle ergometry.[150] In this study, a lower pulmonary ventilation during treadmill running was associated with higher breathing frequency and no change in tidal volume, indicating breathing mechanics were not altered by the different exercise modalities. These results were not confirmed by Boussana et al.[147] They reported that ventilation was more impaired in cycling than running, therefore inducing a greater decrease in ventilatory kinetics.[141,144-146,148] Boussana et al.[146] also reported that the ventilatory fatigue was higher in recreational triathletes when compared with their elite counterparts and that the order of successive submaximal bouts of cycling and running influenced the kinetics of the respiratory fatigue that was experienced.[145] After a cycling or a cycle-run bout, respiratory fatigue was significant, whereas after a running exercise, the signs of fatigue (i.e. decrease in maximal inspiratory pressure or the time to exhaustion that a respiratory load can be sustained) were not apparent. These results show that specific ventilatory adaptations occur as a result of the order of the cycle and run bouts during a triathlon event and that these may be partly compensated for by training.

Only a few studies have compared the O_2 concentration of arterial blood during maximal exercise testing in cycling and running.[22,141,143,149,150] Hermansen et al.[22] found no difference in the arteriovenous difference of O_2 between running and cycling.

Hopkins et al.[151] found trained female cyclists to exhibit higher pulmonary ventilation at maximal exertion, despite no difference in $\dot{V}O_{2max}$, during an incremental cycle test compared with a running test. It was suggested that differences in ventilation were associated with changes in pulmonary mechanics between cycling and running. The difference in mechanics was thought to be associated with differences in entrainment of the muscles of the diaphragm between the two exercise modes.[147,148,152] Indeed, another study has shown that entrainment of these muscles is higher in cycling than in running in triathletes.[153] Therefore, the degree of adaptation of pulmonary mechanics in response to combined cycling and running training may affect breathing mechanics during incremental cycle or running exercise, thereby influencing observed $\dot{V}O_{2max}$.

To summarize, a conclusive set of studies have shown that ventilatory pattern is more altered in cycling than in running.

2.2 Central and Peripheral Blood Flow

There are some studies in untrained subjects that have demonstrated that an increase in

$\dot{V}O_{2max}$ with endurance training is associated predominantly with an increase in maximum cardiac output (CO) induced by increase in stroke volume (SV), as compared with increases in arteriovenous (a-v) O_2 difference.[154,155] The data presented by Hermansen et al.[22] suggest that CO influenced by SV has an important influence on cycling or running $\dot{V}O_{2max}$. These researchers showed SV to be higher during treadmill running than during cycling. This result reflected the differences in $\dot{V}O_{2max}$ that were observed between the two exercise modes. Faulkner et al.[24] also measured SV during maximal running and cycling exercise. They found that a lower $\dot{V}O_{2max}$ was associated with a lower SV. Furthermore, a-v differences in arterial O_2 concentration were similar between the two exercise modes. Therefore, both these studies provide evidence that a lower $\dot{V}O_{2max}$ in cycling is associated with a lower SV influencing CO. However, an older study has suggested that the lower $\dot{V}O_{2max}$ in cycling is thought to be due to a lower a-v O_2 difference together with a lower maximal CO.[5]

The lower CO observed in cycling compared with running could be due to a reduced rate of cardiac filling influenced by limited venous return thereby influencing $\dot{V}O_{2max}$.[21] The reduced venous return may be due in part to peripheral muscle blood flow. Some evidence suggests that peripheral blood flow is different in the lower extremities during cycling as compared with running.[28,156-158] It has been suggested that "factors influencing venous return to the heart 'drive' the circulation during exercise".[158] Extravascular compression expels blood from the venous vasculature and impedes inflow of blood into the arterial vasculatures. This mechanism, called the 'muscle pump', which facilitates venous return to the heart and perfusion of skeletal muscle (in addition to suction at ventricular level or during muscle relaxation, vasodilator chemicals and decrease in peripheral resistances), occurs to a greater extent during locomotory muscle rhythmic contractions than during twitch or isometric contractions, and has therefore been reported both in cycling and running. The efficiency of this 'muscle pump' that is assumed to increase the local muscle blood flow is influenced by the type of activity performed.[156] To our knowledge, there has been no direct comparison of muscle pump efficiency between cycling and running. However, there are several mechanisms suggesting that the muscle pump efficiency is greater in running than in cycling: first, there is a direct mechanical coupling between contraction frequency and muscle blood flow and therefore muscle pump is directly influenced by the strides frequency;[159] secondly, its efficiency is greater in erect position; finally the type of contraction during running (stretch-shortening cycle) induces some pro-inflammatory processes that *per se* increase the muscle blood flow.[157] In addition, Matsui et al.[28] found that total lower limb blood flow was significantly lower immediately post-exercise after cycle exercise than after running exercise. However, the measurements that they took were indirect. The adaptation of blood flow in the calf and quadriceps muscle groups to training in cycling and running is a potentially interesting area of research in triathletes.

It has also been suggested that maximum CO is influenced by coronary blood flow or is mediated by the CNS.[160,161] Indeed, incremental exercise to exhaustion at altitude does not induce skeletal muscle acidosis or even a maximal cardiac output relative to sea level conditions.[33] Hence, fatigue at maximal exertion and in turn $\dot{V}O_{2max}$ may be influenced by blood flow to the heart or central neural innervation. However, to our knowledge, it is not known whether this differs in cycling compared with running.

2.3 Skeletal Muscle Oxidative Capacity

The peripheral muscle mitochondria are the site of cellular respiration and electron transport. An increase in mitochondria content and enzyme activity with endurance training is thought to result in an increase in the potential for cellular O_2 uptake.[162] Endurance athletes typically possess a greater number of slow twitch (ST) fibres than non-endurance trained athletes. ST fibres are known to be higher in mitochondria and oxidative enzymes, which could be associated with an increased whole body $\dot{V}O_{2max}$ or AT.[41,163,164] In contrast, an increase in skeletal muscle mitochondria may occur without the same corresponding increase in $\dot{V}O_{2max}$,[165] suggesting that muscle oxidative capacity is not a factor related to $\dot{V}O_{2max}$. However, a number of studies have reported significant correlations between a number of skeletal muscle characteristics, $\dot{V}O_{2max}$ and the AT.[163,166,167] Other investigators have shown a significant relationship between % ST fibres and mechanical efficiency during cycle exercise.[168,169] A few research groups have shown that muscle buffering capacity has a positive influence on endurance rowing, cycling and running performance.[127,164,170] Whilst this data should not be viewed as evidence of 'cause and effect', it provides evidence that skeletal muscle has some influence on the $\dot{V}O_{2max}$ and the AT together with endurance performance. However, whether these findings are replicated in both cycling and running modes in triathletes or even single sport athletes when muscle is analysed from both quadriceps and the calf muscle groups is not clear.

In line with this, there are limited data available regarding the skeletal muscle characteristics of triathletes and how they may impact on cycle and run AT and $\dot{V}O_{2max}$. Only one study has compared the oxidative capacity of skeletal muscle and the AT in both cycling and running.[31] These authors found that in untrained subjects the $\dot{V}O_{2max}$ and OBLA (% $\dot{V}O_{2max}$) was higher in running than cycling. The % ST fibre and oxidative enzyme capacity (determined in the vastus lateralis and gastrocnemius muscles) was not related to either the OBLA or $\dot{V}O_{2max}$ in cycling or running. However, subject numbers and the training status of the subjects limit the validity of the results from this study. Flynn et al.[57] also obtained muscle tissue from the gastrocnemius, vastus lateralis and posterior deltoid muscles of 11 triathletes and four normally active controls. Muscle fibre type, respiratory capacity and citrate synthase (CS) activity were examined in the samples. There was no significant difference in the % ST fibres (59 ± 4.0 vs 63 ± 3.3%) in the gastrocnemius and vastus lateralis muscles. The respiratory capacity also did not differ between the gastrocnemius and vastus lateralis muscles. However, CS activity of the vastus lateralis and the gastrocnemius were significantly different. Therefore, adaptation of oxidative enzyme activity in these muscles may occur independently. The significance of this in triathletes and performance in cycling and running is not known. Further studies are required to determine the influence of muscle fibre type and enzyme capacity in the calf and quadriceps on physiological variables measured in cycling and running.

2.4 Central and Peripheral Innervation

2.4.1 Muscle Recruitment Patterns

Running and cycling activity is performed by muscle contraction of the lower limbs. The main muscle groups that are involved in cycling and running are the quadriceps and plantar flexors, respectively.[171] An exception to this is during uphill running when the recruitment of the quadriceps muscle is increased.[100] Some researchers have suggested that any observed differences in the AT for cycling and running are a reflection of differences in muscle recruitment during exercise[46] between such exercise modes.

Coyle et al.[41] have stated that skill level may influence the LT (% $\dot{V}O_{2max}$) measured in cycling but not in running exercise. The same research group has shown that both the LT and performance level in cycling is influenced by differences in force application to the bicycle crank system.[163] Whether this was associated with modified recruitment patterns of the quadriceps or even calf muscles is not known. However, the authors suggested that the better cyclists were able to generate more pedalling force, at a lower metabolic cost, due to recruitment of the hip flexor muscles. Therefore, the different involvement of the different muscle groups in conjunction with specific training adaptations induced by a combination of cycling and running programmes may be influential on the AT in triathletes or single sport athletes. Marcinik et al.[172] found that a short-term strength training programme resulted in an improvement in the LT in cycling regardless of any cycle training. It was concluded that the strength training resulted in an improvement in muscle recruitment patterns during exercise. This could have influenced the pattern of muscle recruitment during incremental exercise thereby resulting in a change in the LT. However, the results of Marcinik et al.[172] together with the conclusions drawn by Coyle et al.[163] seem to indicate that the AT is influenced to some extent by the muscle recruitment of the lower limbs. However, longitudinal studies involving different running and cycling training interventions are required in this area.

In elite triathletes, it was shown that the mechanical alterations during the first minutes of the running bout subsequent to cycling were minimal[118] and lower than in their recreational counterparts. These mechanical changes were brief and disappeared in less than 6 minutes.[119] However, these alterations induced a higher increase in running energy cost in non-elite than in elite triathletes.[116] Recently it was confirmed that running mechanics are only slightly modified in elite triathletes when compared with an isolated run: Chapman et al.[173] reported that leg kinematics (as measured via 3-D analysis) were not modified in running after cycling at moderate intensity whereas *tibialis anterior* muscle activity was modified only in 35% of the group and was not associated with any fatigue variables. Therefore, even in elite triathletes, leg muscle activity during running can be influenced by cycling but this is presumably of little influence on race performance.

2.4.2 Pedalling Frequency

It has been reported that differences in physiological variables measured in cycling and running could be due to a greater perception of difficulty in cycling as compared with running.[51,174] The greater perception of effort observed in cycling by some researchers may be in part due to the interaction between optimal pedalling frequency and muscular strength.[172] It has been reported that cycling requires a considerable muscular strength component to performance in the activity.[25,172] The relative volume of training performed in running and cycling respectively may affect these responses in cycling. In terms of performance in cycling, these processes may be an important component to exercise adaptation during exercise.

Classically, it is described that the 'energetically optimal cadence' (EOC; ~50–75 rpm) does not match the preferred or 'freely chosen cadence' (FCC; ~80–100 rpm), although these two cadences are influenced by the performance level and skills of the cyclists.[175] FCC seems to be influenced by perceptual feedback related to objective or subjective neuromuscular fatigue, the decrease in joint loads or in force on cranks.[176,177]

It is generally reported that trained cyclists have a higher FCC than untrained subjects,[178,179] but the differences between elite cyclists and either cyclists of lower ability or runners are not always observed.[179,180] At the same time, FCC seems to decrease during prolonged exercise.[181,182] This may indicate that cycling cadence may influence performance when other physiological variables are similar within a group of trained subjects. Furthermore, the cadence selected at the start of a cycling trial together with the reduction of this variable during the trial may be related to the training completed in either running or cycling in triathletes. However, Marsh et al.[179] found no significant differences in preferred cycling cadence during an incremental exercise test between trained runners and cyclists. In this study,[179] delta efficiency did not differ between the athletic groups. These data suggest that cycling cadence may not be influential when primarily running training is performed. This possibly indicates that pedalling cadence is not affected by a training history in either cycling or running. In contrast, during prolonged exercise (2 hours), the preferred cadence is relatively stable (83 rpm) in triathletes.[183] However, the time course of changes in cadence during prolonged exercise has not been compared in athletes specializing in running, cycling or triathlon training.

Most of the studies have shown that performance and the stride patterns during running after cycling are greatly influenced by the pedalling frequency during cycling.[87,89,95,182,184] However, the conclusions drawn from such studies are equivocal: Gottschall and Palmer[184] reported that by using a high cadence (FCC +20%) during a 30-minute cycle time trial, the subsequent 3 km running performance was

1 minute faster than by cycling at slow cadence (FCC –20%). This was due to an increased stride frequency whereas stride length was unchanged. Bernard et al.[95] reported that pedalling cadence (60, 80 or 100 rpm) has a short-term effect since during the first 500 m of a subsequent run, stride rate and running velocity were significantly higher after cycling at 80 or 100 rpm than at 60 rpm. Interestingly, the low cadence induced a deteriorated economy during the first part of the running bout. However, pedalling cadence did not influence overall subsequent 3 km performance. The same group reported contradictory results, since Vercruyssen et al.[87,89] recommended the use of low pedalling cadences. By comparing low (EOC; 75 rpm), medium (FCC; 81 rpm) and high pedalling cadence (‘mechanical optimal cadence’ [MOC], 90 rpm), they showed oxygen consumption during a subsequent 15-minute treadmill run to be increased only in the MOC (+4.1%) and FCC (+3.6%) conditions when compared with an isolated run. Recently by comparing the metabolic responses and time to exhaustion during a running test at 85% of $\dot{V}O_{2max}$ following three conditions of 30-minute cycling with the last 10 minutes performed at different pedalling cadence (FCC = 94 rpm; FCC –20% = 74 rpm and FCC +20% = 109 rpm), Vercruyssen et al.[89] confirmed that the low cadence (FCC –20%) induces a lower energy expenditure during cycling, leading to an increased time to exhaustion during running. It is unclear how these later results are relevant in ‘real triathlon’, where running performance might be limited by other factors than metabolic ones. In addition, the stochastic nature of the cycling bout in triathlon is now well described[185-187] and there is an acceleration in the final portion of the cycling bout to enter the transition area in a good position. How the change in speed affects the change in pedalling cadence and how the FCC influences the subsequent run is still under debate. Whether differences in muscle contraction frequency influenced by different volume and intensity during cycling and running training affect the physiological adaptation in these exercise modes is also not known.

2.4.3 Neuromuscular Fatigue

Since the type of muscle contraction and potential muscle damage are different between cycling and running, the neuromuscular fatigue induced by prolonged exercise probably originates from different sites (central, i.e. spinal and supraspinal, vs peripheral) and leads to a different level of strength loss (for a review see Millet and Lepers[188]). In running, the decrease in isometric strength loss is proportional to the duration of the exercise,[188-190] whereas it is less obvious in cycling.[191,192] The decrease in concentric strength is less than in isometric strength but the reasons are unclear.

By using different methods such as the ratio of the root mean square (RMS) of the EMG recorded during MVC normalized by the muscle compound action potential (M-wave) amplitude (RMS/M), recent experiments have shown that there is a difference in the contribution of central fatigue between cycling and running. After 2 hours of prolonged cycling, the decrease in RMS (vastus lateralis and vastus medialis) was of the same extent (10%) as the decrease in M-wave amplitude,[181] showing that central fatigue did not contribute to the observed 13% decrease in strength. Contradictory central fatigue was observed after a prolonged 30 km run.[190] Two methods have been recently used to evidence deficit in muscle activation and therefore central fatigue after prolonged exercise; first, the change in the ratio between MVC and the mechanical response to an electrically evoked contraction at high frequency (80 Hz), and, second, the twitch interpolation technique where the ratio between a twitch superposed to a MCV and the twitch evoked on the muscle relaxed indicates the extent of the activation deficit. After a prolonged run, the activation deficit was shown in several studies in knee extensors[189,190] and plantar flexors,[193] whereas for the same long duration (>4 hours), this central fatigue was not observed in cycling.[181,194] However, the activation deficit was observed in cycling at higher intensity[192,195] and is probably induced at the spinal level by the presynaptic inhibition of the α-motoneuron due to metabolic causes.

The activity of electromyography (EMG) has been used to examine muscle recruitment patterns during exercise. Various authors have used EMG to establish a central fatigue component during prolonged endurance exercise.[191,196] EMG recorded during evoked contraction (M-wave) has also been used to identify peripheral fatigue as evidenced by a decrease in the action potential propagation on sarcolemna (increase in duration of M-wave) or lesser sarcolemna excitability (decrease in M-wave amplitude). There is no difference in the change in neuromuscular propagation induced by prolonged exercise between cycling and running since the decreases in amplitude (1–13%) and duration (1–24%) of M-wave are similar.[132,181,189-193,196] During prolonged exercise either in running or in cycling, the sarcolemna excitability appears to not be an important factor of peripheral fatigue. The changes in evoked twitch mechanical responses (ΔP; %) at low (20 Hz) and high (80 Hz) frequency tetanus and their ratio (P20/P80) indicates change in excitation-contraction coupling. High-frequency fatigue was observed after prolonged running[190] but not cycling,[194] whereas low-frequency fatigue has not been observed either after prolonged cycling or – surprisingly – after running. One may therefore speculate that the muscle damages induced by running are not important enough for inducing greater low-frequency fatigue than in cycling. However, further experiments are required. EMG measurements have not been obtained and compared during incremental cycling and running tests in triathletes or in single sport athletes. Therefore using EMG in combination with metabolic variables, it is possible that there is a difference in CNS or peripheral muscle innervation limiting muscle contraction during incremental running or cycling tasks. In one study, Bijker et al.[171] measured the relationship between mechanical power output, efficiency and EMG activity of the quadriceps muscle during incremental exercise in cycling and running. The results demonstrated that in contrast to cycling, during running EMG was not related to mechanical power output. These authors concluded that series elastic energy dictated recruitment pattern during running. This can be viewed as a considerable influence on the physiological responses during maximum running and cycling exercise. It would be of interest to replicate this study in trained cyclists, runners and triathletes.

3. Summary and Conclusions

Despite treadmill running potentially utilizing more muscle mass, the majority of studies indicate that runners achieve a higher $\dot{V}O_{2max}$ on treadmill whereas cyclists can achieve a $\dot{V}O_{2max}$ value in cycle ergometry similar to that in treadmill running. Hence, $\dot{V}O_{2max}$ is specific to the exercise mode (i.e. running or cycling). The data from the available studies also seems to indicate that the muscles adapt specifically to a given exercise task over a period of time resulting in an improvement in submaximal physiological variables such as the anaerobic threshold in some cases without a change in $\dot{V}O_{2max}$. However, this effect is probably larger in cycling than in running. At the same time, skill influencing motor unit recruitment patterns is an important influence on the AT in cycling. Furthermore, it is likely that there is more physiological training transfer from running to cycling than *vice versa*. In triathletes, the majority of data demonstrate that there are generally no large differences in $\dot{V}O_{2max}$ measured in cycle ergometry and treadmill running. Therefore, it seems likely that triathletes adapt in a similar way to cyclists and exhibit a $\dot{V}O_{2max}$ in cycling that is similar to that in treadmill running. The data concerning the AT in cycling and running in triathletes are conflicting. This is likely to be due to a combination of athlete actual training load and past training history in these particular sports. The mechanisms surrounding the differences in the AT together with $\dot{V}O_{2max}$ in cycling and running are not largely understood but are probably due to the relative adaptation of cardiac output influencing $\dot{V}O_{2max}$ and also the recruitment of muscle mass in combination with the oxidative capacity of this mass influencing the AT. Several other physiological differences between cycling and running have been addressed since they are potential important factors at exhaustion: HR is different between the two activities both for maximal and submaximal intensities. The delta efficiency is higher in running. Differences in ventilatory responses to exercise (exercise-induced arterial hypoxaemia, O_2 diffusion capacity, ventilatory fatigue and pulmonary mechanics) have been reported between running and cycling, and ventilation is more impaired in cycling than running. Several mechanisms suggest that the muscle pump efficiency is greater in running than in cycling. It has also been shown that pedalling cadence affects the metabolic response during cycling but also during a subsequent running bout. However, the optimal cadence is still debated. Central fatigue and decrease in maximal force are more important after prolonged exercise in running than in cycling. All these findings might influence the training content and cross-training effects in triathletes. However, to date very little information on volume/intensity of training in elite triathletes has been reported and there is no experiment that investigates the effects of changing one training parameter on overall triathlon performance.

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