

Modeling and Analysis of the Effect of Training on $\dot{V}O_2$ Kinetics and Anaerobic Capacity

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Abstract In this paper, we present an application of a number of tools and concepts for modeling and analyzing raw, unaveraged, and unedited breath-by-breath oxygen uptake data. A method for calculating anaerobic capacity is used together with a model, in the form of a set of coupled nonlinear ordinary differential equations to make predictions of the $\dot{V}O_2$ kinetics, the time to achieve a percentage of a certain constant oxygen demand, and the time limit to exhaustion at intensities other than those in which we have data. Speeded oxygen kinetics and increased time limit to exhaustion are also investigated using the eigenvalues of the fixed points of our model. We also use a way of analyzing the oxygen uptake kinetics using a plot of $\ddot{V}O_2(t)$ vs $\dot{V}O_2(t)$ which allows one to observe both the fixed point solutions and also the presence of speeded oxygen kinetics following training. A method of plotting the eigenvalue versus oxygen demand is also used which allows one to observe where the maximum amplitude of the so-called slow component will be and also how training has changed the oxygen uptake kinetics by changing the strength of the attracting fixed point for a particular demand.

Keywords Oxygen uptake kinetics · Anaerobic capacity · Nonlinear dynamical systems · Athletic performance analysis · Modeling

1. Introduction

In this paper, we show how the model of Stirling et al. (2005) can be used to analyze and model the oxygen uptake kinetics $\dot{V}O_2(t)$ in response to exercise and provide insights into the changes in fitness of an individual. A number of values have been developed in the

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past which allow one to quantify important aspects of the oxygen uptake kinetics which can be related to fitness levels. In this section, we introduce the physiological concepts that will be used later on in the paper.

The model of Stirling et al. (2005) (see also Stirling et al., 2007b) is an alternative model to the currently used 3 phase model (Barstow and Mole, 1991; Davies et al., 1972; Gaesser and Poole, 1996; Jones and Poole, 2005; Linnarsson, 1974; Whipp and Wasserman, 1972). The main difference between the two models is that the model of Stirling et al. (2005) contains no phases or time delays, instead they model the oxygen uptake kinetics over the continuum of exercise intensities using a set of coupled ordinary differential equations which are smooth functions of $\dot{V}O_2$, time and exercise intensity (see Section 2.3.1). It is also shown in Stirling et al. (2005) that it is possible to model the slowing down of the oxygen uptake kinetics, or the so-called slow component behavior without the use of phases starting after a specific time delay. Stirling et al. (2005) also present a means of estimating the oxygen demand, and hence calculating the oxygen deficit and debt which does not rely on extrapolation from submaximal values. Another new and extremely useful feature of the model of Stirling et al. (2005) is the ability to make predictions of the oxygen uptake kinetics in response to exercise that we do not have data for.

The maximum oxygen uptake or $\dot{V}O_{2\max}$ is one of the fundamental indicators of fitness. A high $\dot{V}O_{2\max}$ is required for the highest levels of performance and much of the training programs of athletes are designed to elevate this quantity. However, it has also been found that two subjects with the same $\dot{V}O_{2\max}$ can have different performance levels. This is due mainly to differences in biomechanical efficiency of the subject. As a result, the minimum velocity to achieve $\dot{V}O_{2\max}$, the so-called velocity at $\dot{V}O_{2\max}$ or $v\dot{V}O_{2\max}$ (Daniels, 2005; Billat and Koralsztein, 1996) is also often calculated so as to be able to separate performance levels amongst groups of identical $\dot{V}O_{2\max}$. Another way of separating such groups, which is far more basic but in many ways essentially the same, is by comparing race times of the same distance and conditions (i.e., for two subjects with the same $\dot{V}O_{2\max}$ the most biomechanically efficient athlete will have the lower race time). This is probably the oldest and most classical means of showing increased fitness. It can be used to separate groups of individuals or to show improvements in an individual's level of fitness resulting in a decrease in the time to complete a given distance in the same conditions. In this paper, we are interested in looking at improvements in a individual. It should be noted that over different race distances, the same athlete can show different levels of performance. A sprint athlete, for example, is efficient over the sprint distances, but not necessarily so over very long distances. Therefore, in general, a race provides information about efficiency and fitness over the race distance, but not necessarily over vastly different distances, due to differences in the physiological and biomechanical demands.

Increased physical fitness leads to significantly altered pulmonary $\dot{V}O_2$ kinetics. Endurance training is believed to be one of the best means of altering the kinetics (Carter et al., 2000; Casaburi et al., 1987; Jones and Carter, 2000; Womack et al., 1995). Many studies in which oxygen uptake kinetics of an individual have been compared following a period of training have been carried out to investigate various aspects of the effects of the training methods used (see Jones and Carter, 2000; Jones and Koppo, 2005; Jones and Poole, 2005 for a review). One of the main alterations believed to be observable is a speeding of the uptake kinetics. This has been observed in both healthy (Bell et al., 2001; Cerretelli et al., 1979; Gollnick and Saltin, 1982; Hagberg et al., 1980; Hickson et al., 1978; Phillips et al., 1995) and clinical patient populations (Brandenburg et al., 1999;

Otsuka et al., 1997; Puente-Maestu et al., 2003). Speeded kinetics can be measured as a reduction in the time to achieve a certain percentage (i.e., 95%) of a given absolute oxygen demand. Factors which affect the magnitude of the changes due to training include the initial training status of the subject, training program duration and the frequency, and duration and intensity of the individual sessions making up the program (Daniels, 2005; Martin and Coe, 1997; Wenger and Bell, 1986). Another effect of increased fitness is that for the same absolute work rate, in our case, expressed as oxygen demand given as an absolute value of oxygen uptake, the classification of the intensity can change, for example, from heavy (i.e., above the so-called lactate threshold) to moderate (i.e., below the so-called lactate threshold). The two reasons that can be found for this from a study of the oxygen uptake kinetics are an increase in the $\dot{V}O_{2\max}$ or speeded oxygen uptake kinetics, Jones and Koppo (2005).

With training, it is possible to increase the anaerobic capacity, calculated as the maximum accumulated oxygen deficit in a run to exhaustion lasting longer than 2 minutes (Astrand and Saltin, 1961; Karlsson and Saltin, 1970; Medbo et al., 1988). For more information regarding the oxygen deficit, see Bangsbo (1992, 1996a, 1996b, 1998), Saltin (1987, 1990), Stirling et al. (2005). Increasing the anaerobic capacity has the effect of increasing the maximum anaerobic energy yield, which in turn assuming the same efficiency of movement would lead to a longer run time to exhaustion at a given absolute exercise intensity or oxygen demand (i.e., one which would exhaust the anaerobic capacity) see Billat et al. (2002), Demarle et al. (2001). Speeded oxygen uptake kinetics also has the effect of increasing the run time to exhaustion at an absolute exercise intensity which exhausts the anaerobic capacity (Faina et al., 1997). This is because the speeded kinetics result in a slower use of the anaerobic capacity at the same exercise intensity (i.e., in our case the same absolute oxygen demand), see Jones and Koppo (2005). Training also has the effect of decreasing the oxygen deficit and debt for a particular absolute exercise intensity (Hagberg et al., 1980; Hultman et al., 1967; Karlsson et al., 1972).

In the following sections, we investigate how these concepts can be studied using the model of Stirling et al. (2005). We show what is possible to conclude with the help of this model and how the tools the authors in Stirling et al. (2005) developed can give important information regarding the individuals fitness levels.

2. Method

2.1. Experimental protocol

The experiment consisted of both a running race to exhaustion at a free speed over a fixed course and a constant speed run to exhaustion, before and after a period of training, with the subjects being male adolescents. The $\dot{V}O_{2\max}^b$ and $\dot{V}O_{2\max}^a$ is found from the peak $\dot{V}O_2$ of either the free race or the constant speed runs to exhaustion before and after training, respectively. In what follows, the superscript *a* and *b* denote before and after training, respectively. The $\dot{V}O_{2\max}$ is used along with the run time T_f for the free speed race over the course, as a classical means of determining increased fitness levels. The speed for the constant speed run was such that it would exhaust the anaerobic capacity if the subject

Table 1 Physical characteristics of the individuals taking part in the study

Subject	Age (Years)	Height (m)	Weight (Kg)	$\dot{V}O_{2\max}^b$ (ml/min/Kg)	$\dot{V}O_{2\max}^a$ (ml/min/Kg)
1	14.0	1.64	56.6	47	55
2	14.5	1.67	55.4	60	65
3	14.0	1.83	61.5	59	63
4	14.7	1.80	71.9	60	60

Table 2 Individual time incurred for the free speed tests, for both before and after training

Subject	T_f^b (s)	T_f^a (s)
1	481	436
2	392	372
3	393	372
4	348	326

ran to exhaustion. The run is to a good approximation constant speed (as the subject had to follow a pacing cyclist) once the subject has accelerated from rest to this speed.

The period of training that the subjects underwent consisted of 6 weeks of twice a week interval training (for more information on interval training, see Billat 2001a, 2001b) with the repetitions done at the free race speed. The training was specifically designed to improve the performance over the free race distance. In this paper, we are interested in showing how the model of Stirling et al. (2005) can be used to detect whether the subjects level of fitness has changed. We are not interested in determining if a particular training method is effective. As a result, we have used a small group of subjects which is obviously not large enough to make a proper analysis of training methods, and, therefore, the details of training methods have not been discussed in detail.

For both the free and the constant speed tests, breath by breath data was recorded, using a $K4b^2$ Cosmed, Rome, Italy, for all the subjects. Simultaneously running speed data was also recorded using a GPS system (Cosmed, Rome, ITALY).

2.2. Individual characteristics

Four male teenagers were used as subjects, with written consent being obtained from their parents before the participation in any experiment. The subjects' age, height, and weight is given in Table 1. The $\dot{V}O_{2\max}$ is equal to the peak $\dot{V}O_2$ observed in either the free race or constant speed runs to exhaustion.

Table 2 shows the free speed race times, where T_f is the time to cover the course (all subjects run the same course both before and after training) in a running race to exhaustion at free speed.

The change in T_f^b and T_f^a from the free race can be used with the $\dot{V}O_{2\max}^b$ and $\dot{V}O_{2\max}^a$ as a classical means of determining if the athletes are fitter with training. In Table 2, it can be seen that all of the subjects improved their time following training, and in Table 1,

it can be seen that three of these individuals also showed improvement in their $\dot{V}O_{2\max}$, while one showed no improvement in $\dot{V}O_{2\max}$.

2.3. Modeling methodology

2.3.1. The differential equations model for $\dot{V}O_2(t)$

The model (Stirling et al., 2005) is given by the following set of coupled ordinary differential equations:

$$\ddot{V}O_2(v, t) = A[\dot{V}O_2(v, t) - \dot{V}O_{2\min}]^B \times [\dot{V}O_{2\max} - \dot{V}O_2(v, t)]^C [D(v, t) - \dot{V}O_2(v, t)]^E, \quad (1)$$

$$\dot{v} = I(t), \quad (2)$$

where $\ddot{V}O_2(v, t)$ represents the rate of change of $\dot{V}O_2(v, t)$ with respect to time and $\dot{v} = I(t)$ defines the rate of change of velocity with respect to time. $\dot{V}O_{2\min}$ and $\dot{V}O_{2\max}$ are the minimum and maximum $\dot{V}O_2$ values, respectively, and the function $D(v, t)$ represents the time and velocity dependent demand of the exercise. The three brackets in Eq. (1) (i.e., $(\dot{V}O_2(v, t) - \dot{V}O_{2\min})$, $(\dot{V}O_{2\max} - \dot{V}O_2(v, t))$, $(D(v, t) - \dot{V}O_2(v, t))$), model the three physiologically possible steady state conditions. These conditions are standard in exercise physiology and correspond respectively to the cases where $\dot{V}O_2(v, t) = \dot{V}O_{2\min}$, $\dot{V}O_2(v, t) = \dot{V}O_{2\max}$ and $\dot{V}O_2(v, t) = D(v, t)$. The first two brackets also prevent us from exceeding the bounds defined by $\dot{V}O_{2\min} \leq \dot{V}O_2(v, t) \leq \dot{V}O_{2\max}$ which is also obviously physiologically correct. For the case where $D(v, t) \geq \dot{V}O_{2\max}$, then the oxygen uptake will not exceed the $\dot{V}O_{2\max}$, but it will approach it asymptotically given sufficient time. Baseline resting values of $\dot{V}O_2(v, t) = \dot{V}O_{2\min}$ will only occur if we have the $D(v, t) = \dot{V}O_{2\min}$. All of the phenomena mentioned above are standard observations in exercise physiology.

The positive parameters A , B , C , and E control the shape of the curve which describes the model (Stirling et al., 2005). Note that in Eq. (1), the parameters B , C , and E are dimensionless while parameter A has dimensions of $(m^3 s^{-1})^{(1-B-C-E)} s^{-1}$. Parameter A controls the overall rate of change of $\dot{V}O_2(t)$. B controls how quickly we leave or approach the minimum value $\dot{V}O_{2\min}$, and C controls how quickly we approach or leave the maximum value $\dot{V}O_{2\max}$. E cannot be even or a fraction. Following the results of the analysis provided in Stirling et al. (2005), the value of the parameter E was kept constant and equal to $E = 1$.

In the present study, we model data sets of constant velocity v . The rate of change of v is, therefore, zero, i.e., we can write $\dot{v} = 0$. This also allows us to write $\dot{V}O_2(t)$ instead of the general expression $\dot{V}O_2(v, t)$ in Eq. (1). As $\dot{v} = 0$, we make the classic assumption that the demand $D(v, t)$ is not a function of time but depends only on the magnitude of the constant exercise velocity v , therefore, there is $D(v, t) = D(v)$. We then assume that for a particular data set that corresponds to a constant velocity v , the demand $D(v)$ is a constant and its value D characterizes the intensity of this particular data set. The dynamical system governing the kinetics of $\dot{V}O_2(t)$ is thus reduced to

$$\ddot{V}O_2(t) = A[\dot{V}O_2(t) - \dot{V}O_{2\min}]^B [\dot{V}O_{2\max} - \dot{V}O_2(t)]^C [D - \dot{V}O_2(t)]^E. \quad (3)$$

As the parameters A, B, C, D, E and the values $\dot{V}O_{2_{\min}}$ and $\dot{V}O_{2_{\max}}$ are all constants, then $\ddot{V}O_2(t)$ is said to be autonomous as $\ddot{V}O_2(t)$ is governed by $\dot{V}O_2(t)$ alone. Note that this is not true in general; it is only the case for the experiment we model here where we have $\dot{v} = 0$, and we assume the demand D is a constant.

For modeling purposes, simplicity, and numerical reasons, we can also assume dimensionless quantities and use the normalized variable $\dot{V}O_{2_n}(t)$, see also Stirling et al. (2005), such that

$$\dot{V}O_{2_n}(t) \equiv \frac{\dot{V}O_2(t) - \dot{V}O_{2_{\min}}}{\dot{V}O_{2_{\max}} - \dot{V}O_{2_{\min}}} \tag{4}$$

and $0 \leq \dot{V}O_{2_n}(t) \leq 1$. Note that the normalized variable $\dot{V}O_{2_n}(t)$ provides the fractional use of the so-called $\dot{V}O_2(t)$ reserve and is of much use practically as it gives an individual's usable $\dot{V}O_2(t)$ range. Substituting Eq. (4) into Eq. (3), we obtain:

$$\begin{aligned} \ddot{V}O_{2_n}(t) &= A[\dot{V}O_{2_{\max}} - \dot{V}O_{2_{\min}}]^{B+C+E-1} \\ &\times [\dot{V}O_{2_n}(t)]^B [1 - \dot{V}O_{2_n}(t)]^C [D_n - \dot{V}O_{2_n}(t)]^E, \end{aligned} \tag{5}$$

where D_n is the normalized demand, according to Eq. (4).

Denoting

$$A_n \equiv A[\dot{V}O_{2_{\max}} - \dot{V}O_{2_{\min}}]^{B+C+E-1}$$

the parameter A_n is dimensionless and Eqs. (1) and (2) of the model take the normalized form

$$\dot{V}O_{2_n}(t) = A_n [\dot{V}O_{2_n}(t)]^B [1 - \dot{V}O_{2_n}(t)]^C [D_n - \dot{V}O_{2_n}(t)]^E, \tag{6}$$

$$\dot{v} = 0. \tag{7}$$

The ramifications of the model presented in Eqs. (1) and (2) are discussed in detail in Stirling et al. (2005, 2007a, 2007b), however, we mention some of the main ones below. One of the most important ramification is that as we can fit the model of Stirling et al. (2005) to the raw oxygen uptake data, it can be seen that the phases and time delays used in the 3 or n phase model are not necessary (for a review of the 3 or n phase model, see Barstow and Mole, 1991; Davies et al., 1972; Gaesser and Poole, 1996; Jones and Poole, 2005; Linnarsson, 1974; Stirling et al. 2005, 2007a; Whipp and Wasserman, 1972 and Whipp et al., 2002). This has very important implications as these phases are a statistical artifact of usually averaged systems and not a proven physiological artifact. As a result, when looking for physiological mechanisms for some of the features of the oxygen uptake kinetics, it is now no longer necessary to discount mechanisms which do not show time delayed phase like behavior. Another feature that we shall use is that the parameters in the model of Stirling et al. (2005) do not change with exercise intensity for an individual; they only change with changes in the level of fitness for that individual. This has an important implication as it allows us to predict for an individual at a given level of fitness the response to exercise intensities that we do not have data for, once the parameters are fit to that individual.

2.3.2. *Fourier low-pass filtering of the raw data*

As mentioned before, the data sets under study consist of breath-by-breath recordings. The data points oscillate with a high frequency and large amplitude around a smooth curve, which describes the basic response pattern, or underlying dynamics (Linnarsson, 1974). Such oscillations can be the result of noise due to the measuring device or can be physiological, including abnormal breathing during exercise including shallow breathing or breath holding (Borrani et al., 2001). It has been shown that physiological systems fluctuate in a nonlinear manner, even under resting conditions (Billat et al., 2003; Goldberger et al., 2002). Mathematically it is well known that such nonlinear systems produce signals which appear noisy (Kantz and Schreiber, 1999; Guckenheimer and Holmes, 1983), though what is attributed to noise could be an inherent feature of the system being studied.

In order to derive a smooth curve that provides the basic response pattern of the data, we implement a Fourier low-pass filtering method (Stirling et al., 2005; Zakyntinaki and Stirling, 2007; Zakyntinaki et al., 2007). By the use of such a method, a smooth curve is provided by removing the high frequency oscillations (higher harmonics) and reconstruct the signal from the lowest harmonics, while at the same time utilizing all the information contained in the original data set. For a detailed discussion of the Fourier transform and its properties, see, for example, Mitra (2005), Proakis and Manolakis (1992), Press et al. (1993).

It is worth noticing here that the process of obtaining the basic response pattern of the data is not sensitive to the level of experimental noise. The application of a low-pass filter successfully calculates the basic response pattern of the time series data, since it was observed that

- The basic response pattern of the data consists of frequencies that lie in the low part of the spectrum
- As the time series data was recorded in a breath-by-breath basis, the signal components of the data due to experimental error consist of frequencies that lie far from those of the basic response pattern, in the high end of the spectrum
- The experimental error of the data recorded as described in Section 2.1 is normally distributed, and
- The size of the data set for each individual subject is very large.

For the purposes of the present study, the FFT algorithm was adopted from Press et al. (1993). When the number of data points is not an integer power of 2, as is the general case of physiological data, the length of the time series can be artificially increased by adding zero values, a method that is referred to as zero-padding (Press et al., 1993). It is worth noticing here that after the calculation of a discrete Fourier transform, it is possible to achieve the desired smoothing by applying a rectangular window filter (Mitra, 2005; Proakis and Manolakis, 1992) that truncates the frequency time series after the some term. The application of such a rectangular window can, however, result in the introduction of “ripples” of infinite duration in the resulting smoothed curve (Mitra, 2005; Proakis and Manolakis, 1992). The way to avoid these oscillatory effects is by providing a smooth transition between the pass-band of frequencies and the stop-band. This can be achieved by use of windows that does not contain abrupt discontinuities but decay to zero gradually (Mitra, 2005; Proakis and Manolakis, 1992; Zakyntinaki and Stirling, 2007).

2.3.3. Derivation of the optimal parameter values

As discussed in Section 2.3.2, the process of low-pass filtering calculates the basic response pattern of the data and at the same time removes the high frequency oscillations caused by experimental error. Since the model is fit to the smooth, free of experimental noise, curve of the basic response pattern, experimental error plays a role in the modeling process only in the first step of low-pass filtering (for a discussion on the sensitivity of the filter to experimental error, see Section 2.3.2).

Once a smooth curve describing the data has been calculated, the optimal values of the parameters A , B and C ($E = 1$) of the model are found by optimizing the fit of the curve provided by the model to the curve describing the basic response pattern of the data set. A curve provided by the model is considered to be an optimal fit to the basic response pattern of the data when the sum of the squared vertical residuals (calculated at the discrete time intervals of the data sets), between the curve of the model and the curve of the filtered data, is the minimum possible (Zakynthinaki and Stirling, 2007).

In our study, the problem of optimization of the parameters of the model (minimization of the sum of the residuals) is solved numerically via the implementation of a stochastic optimization method. In the present study, the value of the demand D is also considered to be a parameter, the optimal value of which is to be optimized so that the fit of the curve provided by the model is optimal. The algorithm we used is the one of ALOPEX IV stochastic optimization (Zakynthinaki and Saridakis, 2003; Zakynthinaki and Stirling, 2007) which has been proven to be a very powerful tool for the calculation of the optimal values of the control variables of dynamical systems. The main advantage of this method is that no knowledge of the dynamics of the system or of the functional dependence of the cost function on the control variables is required. As an optimization algorithm, ALOPEX IV is very easy in its implementation. It is worth noticing that it is characterized by its effectiveness and speed of convergence in real time.

To give a brief description of the process of calculation of the optimal parameter values, we note that the process starts with a random set of values for the parameters A , B , C , and D . The curve provided by the model is then calculated (by integration of Eq. (6), as described in Stirling et al., 2005) and the sum of the residuals is numerically evaluated. The process continues iteratively by changing the parameter values by small increments (of the order of 1% of the parameter values) and the residuals are evaluated at each iteration. We note here that as will be explained in Section 3.1.3, the calculated values of parameter C have to be within the range $\cos(C\pi) > 0$. As mentioned before, the optimization process is considered to be successful and the values of the parameters optimal when a best fit is reached, between the curve provided by the model and the curve that describes the basic response pattern of the data.

3. Results

3.1. Parameters in our model, and what they result in

3.1.1. The parameters resulting from optimizing the fit the model to the raw data

In Figs. 1 and 2, we present as an example, the curves produced by the model of Stirling et al. (2005) (see Eqs. (1) and (2)), the Fourier filtered data, and the raw data of the constant speed run to exhaustion of Subject 3, before and after training. Note that the data

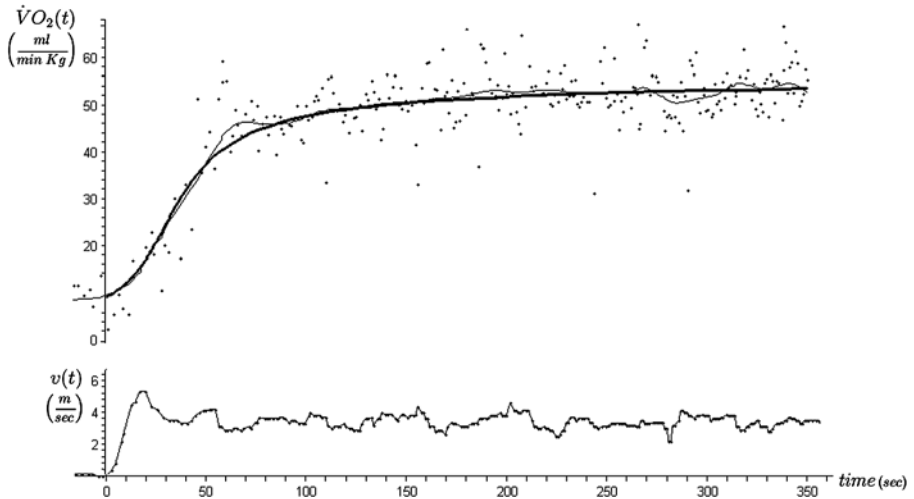


Fig. 1 Oxygen uptake and velocity time series, for the before training constant intensity run to exhaustion of Subject 3. The $\dot{V}O_2(t)$ is seen as points, while the thick curve represents the model and the thin curve represents the Fourier filtering of the data.

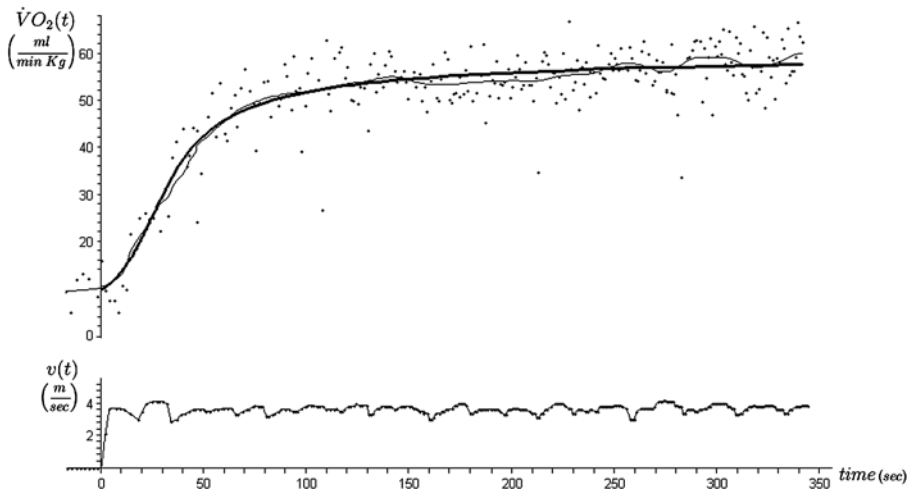


Fig. 2 Oxygen uptake and velocity time series, for the after training constant intensity run to exhaustion of Subject 3. The $\dot{V}O_2(t)$ is seen as points, while the thick curve represents the model and the thin curve represents the Fourier filtering of the data.

is unaveraged and unedited for an individual during a single exercise bout. In the same figures, we also show the time series for the speed at which Subject 3 ran to produce the corresponding $\dot{V}O_2(t)$ time series. It can easily be seen that even though efforts were made to ensure a constant speed time series, in reality, the speed is only approximately constant. It should also be noted that some of these oscillations in the speed time series

Table 3 Table of (normalized) parameter values and demands (see Eqs. (6) and (7)) before and after training

Subject	A_n		B		C		D	
	Before	After	Before	After	Before	After	Before	After
1	0.62	0.64	1.99	1.91	1.73	1.97	0.93	0.95
2	0.32	0.49	1.82	1.71	1.89	1.95	0.93	0.96
3	0.35	0.37	1.81	1.72	1.89	1.95	0.93	0.95
4	0.38	0.38	1.49	1.49	1.63	1.63	0.94	1.07

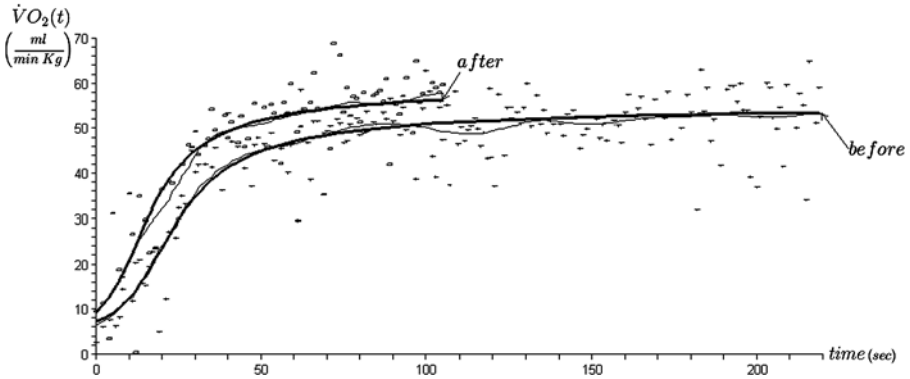


Fig. 3 Oxygen uptake for the before and after training constant intensity run to exhaustion of Subject 4. The $\dot{V}O_2(t)$ is seen as points (crosses for before training and squares for after training), while the thick curve represents the model and the thin curve represents the Fourier filtering of the data.

are probably the cause of the some of the oscillations of the smooth Fourier curve about the curve produced by the model. Distance measurement errors in the GPS unit, resulting from errors in the calculation of position and hence displacement, are also a source of some of the oscillations in the speed time series.

In Table 3, we show the parameters we obtain from optimizing the fit of the model to the data, both before and after training. As expected, it can be seen that the parameters change with changes in levels of fitness. It can also be seen that the patterns for the changes in the parameters (for our small population group) can be divided into two groups. Either all the parameters stay the same value, or else A_n increases, B decreases, and C increases. With the number of parameters and the type of nonlinear system we study, it should be remembered, however, that it is the combined effect of these parameters and the model which governs the kinetics, not just the individual isolated parameters.

In Fig. 3, we show the fit of our model for both before and after training to the data of Subject 4, the only subject whose parameters did not change with training. As can be seen, the fit of the model is good for both data sets. It is also important to notice that the curve representing the after training data is ran for less time and at a higher demand (see Table 3 for the normalized demands) than the before training curve. This is due to the fact that the subject ran at a faster speed, however, as can be observed in Fig. 3, the model provides a good fit without a change in the parameters. This fact along with the lack of change in the $\dot{V}O_{2max}$, indicates that Subject 4 did not get fitter following the training,

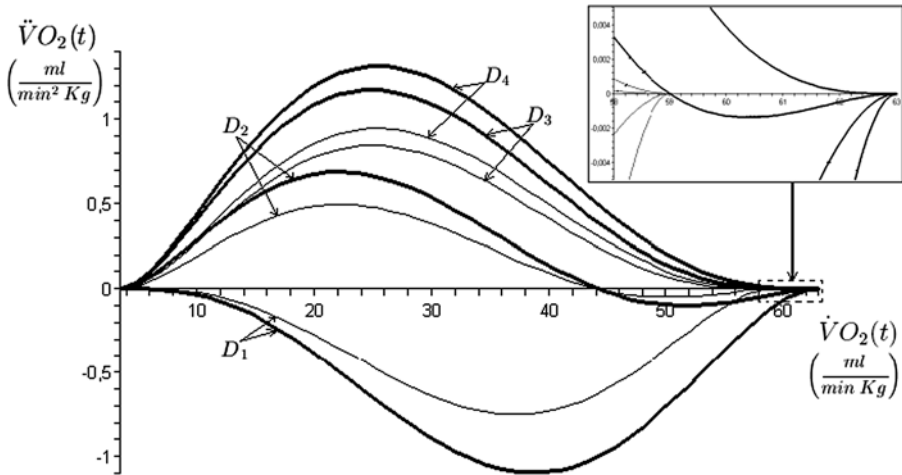


Fig. 4 Phase portrait, or plot of $\ddot{V}O_2(t)$ vs. $\dot{V}O_2(t)$, showing the fixed points (i.e., $\ddot{V}O_2(t) = 0$ as $\dot{v} = 0$ for all time) at $\dot{V}O_2(t) = \dot{V}O_{2min}$, $\dot{V}O_2(t) = \dot{V}O_{2max}$ and $\dot{V}O_2(t) = D$. The plot also shows the size of the vector field for different demands, both before and after training. The thin lines correspond to the before training state and the thick to the after training state. Detail of the region near $\dot{V}O_{2max}^a$ and $\dot{V}O_{2max}^b$ is also shown.

even though he ran faster in the free test. We will look for more evidence regarding this in the proceeding sections.

To get a better understanding of the combined effect of these changes in parameters, we examine the effect on the oxygen uptake kinetics. More specifically, we now proceed to investigate whether the new parameters result in an speeding up of the kinetics, as would be expected for improved levels of fitness.

3.1.2. Model parameters, fixed points and the phase portrait following training

In this section, we show using Subject 3 as an example, how the parameters for before and after training affect the plot of $\ddot{V}O_2(t)$ vs $\dot{V}O_2(t)$. We also present the fixed points of this graph for before and after training and show the relationship with on and off transient kinetics, for values of the demand $D_1 = 6.3 \text{ ml/min/Kg}$, $D_2 = 0.75\dot{V}O_{2max}^b$, $D_3 = \dot{V}O_{2max}^b$ and $D_4 = \dot{V}O_{2max}^a$ as examples.

Fixed points can be observed in Fig. 4 as the points where $\ddot{V}O_2(t) = 0$, which correspond to the condition where $\dot{V}O_2(t)$ is constant or, in other words, the oxygen uptake has reached steady state. In the before training state, this occurs in Fig. 4 when $\dot{V}O_2(t) = D = \dot{V}O_{2min}^b$ or $\dot{V}O_2(t) = D = \dot{V}O_{2max}^b$ and when $\dot{V}O_2(t) = D$ where the demand D equals 6.3 ml/min/Kg or $0.75\dot{V}O_{2max}^b$. For the demand $D = \dot{V}O_{2max}^a$ in the before training state, the fixed point is at $\dot{V}O_2(t) = \dot{V}O_{2max}^b$, (see the corresponding detail in Fig. 4 where this can clearly be seen). In the after training state where for Subject 3 we have $\dot{V}O_{2max}^b < \dot{V}O_{2max}^a$, the fixed points are at $\dot{V}O_2(t) = D = \dot{V}O_{2min}^a$ or $\dot{V}O_2(t) = D = \dot{V}O_{2max}^a$, and at $\dot{V}O_2(t) = D$ where in Fig. 4 the demand equals either 6.3 ml/min/Kg , $0.75\dot{V}O_{2max}^b$ or $\dot{V}O_{2max}^b$. For the demand $D \geq \dot{V}O_{2max}^a$ in the after training

state, the fixed point is at $\dot{V}O_2(t) = \dot{V}O_{2\max}^a$. We go on to discuss the nature of fixed points in the following Section 3.1.3.

Regarding the physiological meaning of the sign of $\ddot{V}O_2(t)$, we note the following. When $\ddot{V}O_2(t) < 0$, we will have off transient kinetics, where the $\dot{V}O_2(t)$ reduces to meet the decreased demand, as is observed during recovery from exercise (see, for example, the curves labeled D_1 in Figs. 4 and 5). When $\ddot{V}O_2(t) > 0$, we will have on transient kinetics where the $\dot{V}O_2(t)$ increases to meet the increase in demand, as is observed in the response to increases in exercise intensity (see, for example, the curves labeled D_2, D_3 , and D_4 in Figs. 4 and 5).

As $\ddot{V}O_2(t)$ is the rate of change of $\dot{V}O_2(t)$ with respect to time, t , then it can be observed that the larger the absolute value $|\ddot{V}O_2(t)|$, the larger the change in $\dot{V}O_2(t)$ with time. When one looks at the detail in Fig. 4, it can be seen that when the demand $D = \dot{V}O_{2\max}^b$ or $D = \dot{V}O_{2\max}^a$, in the before and after training conditions, respectively, then the rate of change of $\dot{V}O_2(t)$ with respect to $\dot{V}O_2(t)$ as one approaches $\dot{V}O_2(t) = \dot{V}O_{2\max}^b$ or $\dot{V}O_2(t) = \dot{V}O_{2\max}^a$ is very small. We shall (in Section 3.1.3) by looking at the eigenvalues of these fixed points, show that this is a minimum for $D = \dot{V}O_{2\max}^b$ or $D = \dot{V}O_{2\max}^a$ in the before and after training conditions, respectively. This is of much interest as it is another way of observing the slowing down of the oxygen uptake kinetics, or the so-called slow component behavior. It shows that the maximum amplitude of the so-called slow component will occur when $D = \dot{V}O_{2\max}$ and this will be the case for which it takes the maximum amount of time to reach steady state conditions. The same is also true when one observes the off transient kinetics during recovery to $D = \dot{V}O_{2\min}$.

If one looks at the four sets of two curves (labeled $D_1 \dots D_4$) corresponding to the before and after oxygen uptake kinetics for the same demand D , one can see that the curves corresponding to the after training conditions are above the equivalent curve corresponding to the before conditions for on transient kinetics. For off transient kinetics, the curve for the after training conditions is below that for the before training conditions. This is another graphical way of seeing that for this individual the oxygen uptake kinetics have speeded following training (i.e., the individuals oxygen uptake reacts quicker to changes in oxygen demand following training). As we shall quantify and discuss in the proceeding sections, this has important implications regarding improved fitness levels.

Figures 4 and 5 show for Subject 3 the effect of improved fitness via training on the oxygen uptake kinetics. It can be seen that for all of the demands the on transients are quicker following training, while the off transient is also quicker to reach recovery levels following training. These predictions from the model are as would be expected physiologically for an athlete who has improved fitness levels. Obviously, if the same curves were drawn for Subject 4, then no changes would be observed, as the parameters did not change following training.

3.1.3. *The parameters, the corresponding eigenvalues and the time to achieve 95% of 95% $\dot{V}O_{2\max}^b$, while running at $D = 95\% \dot{V}O_{2\max}^b$, following training*

To get an understanding of what the changes in the parameters mean, we perform a linear stability analysis and look at the eigenvalue of the fixed point of the system of Eqs. (1) and (2) for $\dot{V}O_2 = D^a = D^b = 95\% \dot{V}O_{2\max}^b$, both before and after training, respectively (see Section 2.3.1). We chose a demand D equal to $95\% \dot{V}O_{2\max}^b$ because if we chose a demand equal to $\dot{V}O_{2\max}^b$, we have (as shall be explained below) $\lambda_1 = \lambda_2 = 0$. This will cause a

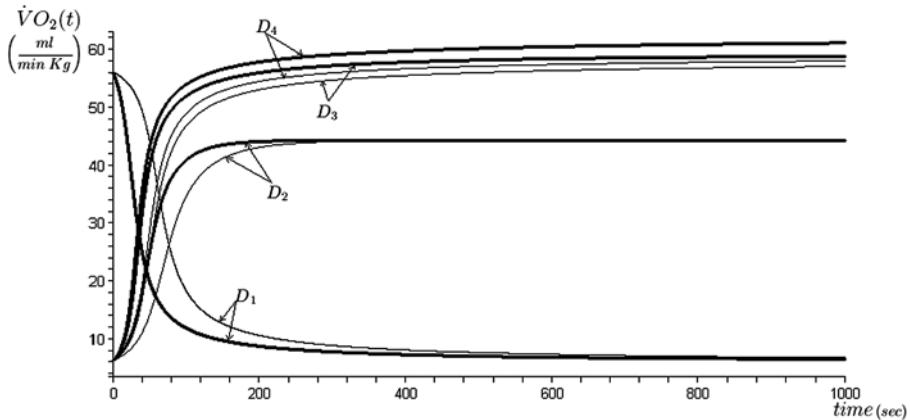


Fig. 5 Plot of $\dot{V}O_2(t)$ vs. time t , showing the oxygen uptake kinetics both before and after training for the different demands shown in Fig. 4. The thin lines correspond to the before training state and the thick to the after training state.

problem for an individual whose $\dot{V}O_{2max}$ does not change with training (i.e., $\dot{V}O_{2max}^b = \dot{V}O_{2max}^a$) but their oxygen uptake kinetics, and hence the model parameters do change (i.e., the $\dot{V}O_{2max}$ is constant but the oxygen uptake kinetics are speeded). The problem in choosing a value of $D = \dot{V}O_{2max}^b$ is that the resulting changes in fitness indicated by changes in the model parameters would not be picked by λ_2 as this would remain equal to zero (i.e., $\lambda_2^b = \lambda_2^a = 0$). It should be noted, however, that in this group of subjects, we don't have such an individual.

It is important to remember here that as discussed in Section 2.3.1, there is $\dot{v} = 0$ and $\dot{D} = 0$. We can, therefore, assume that the demand D is a constant which is not a function of time, t or speed v .

The eigenvalues λ of the Jacobian matrix J (see Stirling et al., 2005) are

$$\lambda = \frac{\frac{\partial \dot{V}O_2(t)}{\partial \dot{V}O_2(t)} + \frac{\partial \dot{v}}{\partial v} \pm \sqrt{\left(\frac{\partial \dot{V}O_2(t)}{\partial \dot{V}O_2(t)} - \frac{\partial \dot{v}}{\partial v}\right)^2 + 4 \frac{\partial \dot{V}O_2(t)}{\partial v} \frac{\partial \dot{v}}{\partial \dot{V}O_2(t)}}}{2}.$$

As, however, \dot{v} is neither a function of $\dot{V}O_2(t)$ or v , then we have $\frac{\partial \dot{v}}{\partial \dot{V}O_2(t)} = 0$ and $\frac{\partial \dot{v}}{\partial v} = 0$ hence,

$$\lambda_1 = 0.$$

According to the linear stability analysis of the model presented in Stirling et al. (2005), in the case $B \neq 1$, $C \neq 1$, and $E = 1$ that is our case (see in particular Eq. (27) in Stirling et al., 2005 for the case where $E = 1$ and D is a constant) the solution for λ_2 (the eigenvalue that controls the strength of the attractor at $\dot{V}O_2(t) = D$) is given by

$$\lambda_2 = -A(D - \dot{V}O_{2min})^B(\dot{V}O_{2max} - D)^C. \tag{8}$$

Note that when $D = \dot{V}O_{2min}$ or $D = \dot{V}O_{2max}$, there is $\lambda_2 = 0$. According to Eq. (8), the solution at $\dot{V}O_2(t) = D$ is attracting for $\dot{V}O_{2min} < D < \dot{V}O_{2max}$, as there is $A > 0$. For

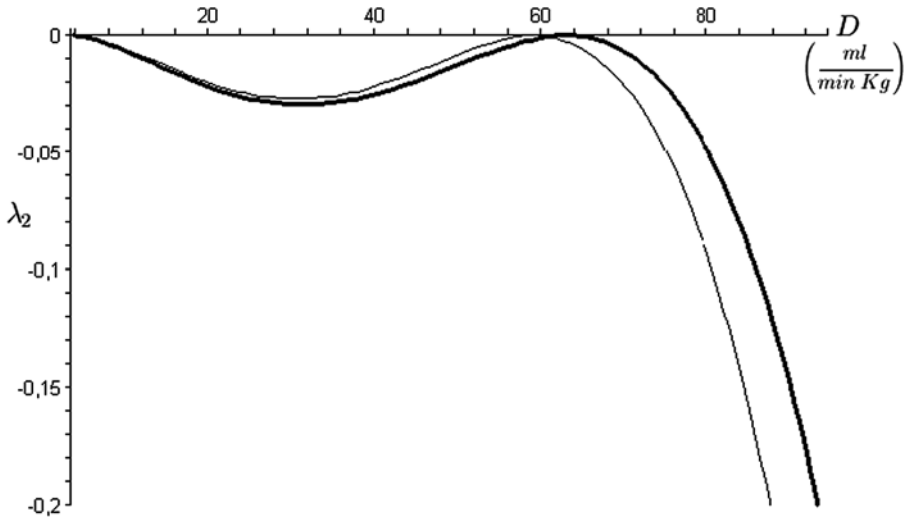


Fig. 6 Plot of λ_2 vs. D from Eq. (8) showing how the size of the eigenvalue, and hence the strength of the attractor change with the oxygen demand for Subject 3. The thick line corresponds to after training and the thin line to before training. Note that $\lambda_2 = 0$ when $D = \dot{V}O_{2\min}$ and $D = \dot{V}O_{2\max}^b$ or $D = \dot{V}O_{2\min}^a$ in the before and after training state, respectively.

higher exercise demands, $D > \dot{V}O_{2\max}$, however, the eigenvalue is complex and the solution is attracting when the real part of the complex eigenvalue is negative. As mentioned in Section 2.3.3, due to the fact that for $D > \dot{V}O_{2\max}$, there is

$$\begin{aligned} \text{real}(\lambda_2) &= \text{real}[-A(D - \dot{V}O_{2\min})^B(\dot{V}O_{2\max} - D)^C] \\ &= -A(D - \dot{V}O_{2\min})^B(D - \dot{V}O_{2\max})^C \cos(C\pi). \end{aligned}$$

It is necessary, therefore, that the value of the parameter C is such that $\cos(C\pi) > 0$, for $\text{real}(\lambda_2) < 0$. This constraint provides a range for the values of C that are appropriate for the implementation of the model of Eqs. (6) and (7).

The more negative the real part of the eigenvalue λ_2 , the greater the strength of the attractor and as a result, the quicker one approaches the steady state solution. It should be noted that the physiology and eigenvalues predict that the slowest on transient rate of approach for the steady state solutions in our model is the case where the $D = \dot{V}O_{2\max}$. Hence, $\lambda_2 = 0$ corresponds to the largest so-called slow component (the same is also true for off transient kinetics to a demand $D = \dot{V}O_{2\min}$). It can be seen in Fig. 6 that for $D > \dot{V}O_{2\max}$ and $\cos(C\pi) > 0$, the eigenvalue λ_2 of the fixed point at $\dot{V}O_{2\max}$ rapidly becomes more negative the greater D is compared to $\dot{V}O_{2\max}$. Or, in physiological terms, the greater the oxygen demand is than $\dot{V}O_{2\max}$, the quicker one approaches $\dot{V}O_{2\max}$. In Fig. 6, we can also see that (for Subject 3) following a period of training, the eigenvalues λ_2 have become more negative for values of oxygen demand $\dot{V}O_{2\min} < D \leq \dot{V}O_{2\max}^b$. This means that the fixed point solutions are more attracting or, physiologically speaking, the

Table 4 Time to achieve 95% of the demand $D = 95\% \dot{V} O_{2\max}^b$ both before and after training (i.e., $TA95\%_{0.95^b}^b$ and $TA95\%_{0.95^b}^a$, respectively, where the subscript 0.95^b refers to the demand $D = 95\% \dot{V} O_{2\max}^b$). $D_{0.95^b}^a$ corresponds to the normalized demand for a subject running at a demand D following a period of training which has resulted in a change in the maximum oxygen uptake to $\dot{V} O_{2\max}^a$. $\lambda_{2,0.95^b}^b$ and $\lambda_{2,0.95^b}^a$ are the eigenvalues of the fixed point of Eqs. (6) and (7), both before and after training, respectively

Subject	D (ml/min/Kg)	$TA95\%_{0.95^b}^b$ (s)	$\lambda_{2,0.95^b}^b$	$D_{0.95^b}^a$ (ml/min/Kg)	$TA95\%_{0.95^b}^a$ (s)	$\lambda_{2,0.95^b}^a$
1	44.825	140	-0.0035625	0.802	56	-0.0176704
2	57.175	328	-0.0011283	0.873	109	-0.0069462
3	56.225	297	-0.0012370	0.866	160	-0.0045392
4	57.175	158	-0.0029265	0.95	158	-0.0029265

oxygen uptake kinetics have speeded up, and hence steady state values are reached in less time.

As can be seen in Table 4, Subjects 1, 2, and 3 can all be observed to have more negative values of λ_2 for a demand $D = 95\% \dot{V} O_{2\max}^b$ following training, and hence have more strongly attracting solutions for the corresponding fixed point. It can also be seen that this correlates with a corresponding decrease in the time to achieve 95% of $95\% \dot{V} O_{2\max}^b$ following training. This can be interpreted as an indication that these three individuals did improve their fitness following training as observed by the faster oxygen uptake kinetics. It can also be seen that Subject 4 shows no change in λ_2 following training (as a result of the fact that their parameters did not change), and hence no change in the time to achieve 95% of $95\% \dot{V} O_{2\max}^b$. This can be interpreted as an indication that he did not improve his fitness following training.

3.2. Analysis of the constant speed test

3.2.1. Oxygen deficit and the anaerobic capacity in the constants speed tests

Table 5 shows the performance in the constant speed test before and after training. The speed is chosen for each individual to be a speed that will be sufficiently intense so as to exhaust the anaerobic capacity of the individual if they continue running to exhaustion. It should be noted that the distance covered in this case is not necessarily the same between individuals as they stop when they are exhausted. As before, we assume the speed and also the oxygen demand to be to a good approximation constant (see Figs. 1 and 2) and, therefore, the resulting oxygen uptake kinetics is easier to model than that from the free race, in which the speed, and hence the demand change with time.

As there are many variables changing at the same time in Table 5, it is difficult to understand what changes have occurred fitness wise with the subjects, hence, now in Table 6, we take a closer look at the data presented in Table 5 and the results (which we present in Table 3) of fitting our model to this data. Using the optimal values of the parameters given in Table 3, the Eqs. (1) and (2) for our model and Eq. (9) shown below, we calculate the oxygen deficit.

Table 5 Performance in the constant speed test before and after training. In this table, v_c is the actual constant speed achieved in the test, T_c is the time to exhaustion at this speed and d_c is the distance covered

Subject	v_c^b (Km/h)	T_c^b (s)	d_c^b (m)	v_c^a (Km/h)	T_c^a (s)	d_c^a (m)
1	9.73	554	1498	10.88	312	943
2	12.43	398	1374	13.2	351	1287
3	12.32	358	1225	13.18	346	1267
4	13.77	226	865	14.25	126	499

Table 6 Oxygen demand and deficits $O_{2\text{defi}}^m$ both before and after training. D is the actual oxygen demand as calculated using our model of the performance in the constant speed test before and after training. We also show the percentage increase in oxygen demand $\% \Delta D$, in the time to exhaustion, $\% \Delta T$ and in $\dot{V}O_{2\text{max}}$, $\% \Delta \dot{V}O_{2\text{max}}$

Subject	D^b (ml/min/Kg)	$O_{2\text{defi}}^{bm}$ (ml/Kg)	D^a (ml/min/Kg)	$O_{2\text{defi}}^{am}$ (ml/Kg)	$\% \Delta D$	$\% \Delta T$	$\% \Delta \dot{V}O_{2\text{max}}$
1	43.96	35	52.43	36	19.20	-45.23	17.02
2	56.05	54	62.4	58	11.33	-39.02	8.33
3	55.12	53	60.03	59	8.91	-2.79	6.78
4	56.61	35	63.96	35	12.98	-44.74	0

$$O_{2\text{defi}} = \int_{t=t_0}^{t=t_f} [D(v, t) - \dot{V}O_2(t)] dt. \quad (9)$$

As this is a run to exhaustion in which the subjects are exhausted in greater than 2 minutes, then the $O_{2\text{defi}}$ can be assumed to be an estimate of the anaerobic capacity if we believe that the individual was truly exhausted (Medbo et al., 1988; Saltin 1987, 1990).

By looking at the relative increases of $\% \Delta D$ and $\% \Delta \dot{V}O_{2\text{max}}$ and combining this with the information regarding $\% \Delta T$, it becomes easy to see who will increase their $O_{2\text{defi}}^m$. In Table 6, an increase in oxygen deficit as shown by Subjects 1, 2, and 3, is correlated with a larger $\% \Delta D$ in comparison to $\% \Delta \dot{V}O_{2\text{max}}$ and a sufficiently small drop in $\% \Delta T$. No change in oxygen deficit (i.e., Subject 4) occurred when the reduction in the time to exhaustion given by $\% \Delta T$ was too much for the increased demand $\% \Delta D$ to result in an increased oxygen deficit, even though there was a substantial increase in the oxygen demand.

Table 6 shows that Subject 4 showed no change in $O_{2\text{defi}}^m$, whilst Subjects 1, 2, and 3 all increased their oxygen deficits to some degree. However, the increase in oxygen deficit for Subject 1 is minimal. It can also be seen that both tests of Subject 2 and Subject 3 can be considered as runs to exhaustion. Looking at the size of the oxygen deficit and the run time to exhaustion for Subject 2 and Subject 3, we can assume this is a good indication of their anaerobic capacity. What is interesting, however, is that Subject 4 and to an approximation Subject 1, both accumulate very similar oxygen deficits at the point at which they stop due to exhaustion even though the tests were done before and after the training period, and the run speeds and durations are substantially different. This reproducibility at different

Table 7 Time to achieve 95% of $\dot{V}O_{2\max}^b$ both before and after training (i.e., $TA95\%_{1^b}^b$ and $TA95\%_{1^b}^a$, respectively). D_s^a corresponds to the normalized after training demand for a subject running at a demand $D = \dot{V}O_{2\max}^b$ following a period of training in which has resulted in a change in the maximum oxygen uptake to $\dot{V}O_{2\max}^a$. $\lambda_{2_{1^b}}^a$ is the eigenvalue of the fixed point at $\dot{V}O_2 = D = \dot{V}O_{2\max}^b$ following training. Before training, $\lambda_{2_{1^b}}^b = 0$ for all subjects

Subject	$\dot{V}O_{2\max}^b$ (ml/min/Kg)	$\dot{V}O_{2\max}^a$ (ml/min/Kg)	D_s^a	$TA95\%_{1^b}^b$ (s)	$TA95\%_{1^b}^a$ (s)	$\lambda_{2_{1^b}}^a$
1	47	55	0.84	218	64	-0.0118296
2	60	65	0.92	573	136	-0.0030853
3	59	63	0.93	527	207	-0.0016980
4	60	60	1	253	253	0

oxygen demand suggests that maybe their values for the oxygen deficit are also good approximations of their anaerobic capacity.

3.2.2. The parameters and their effect on the time to achieve 95% of $\dot{V}O_{2\max}^b$, whilst running at $D = \dot{V}O_{2\max}^b$, following training

We integrate Eqs. (1) and (2) with respect to time to obtain the time series of the $\dot{V}O_2(t)$ kinetics. From this time series, we then calculate the time to achieve 95% of an oxygen demand equal to the before training $\dot{V}O_{2\max}^b$, (which we denote $TA95\%_{1^b}^b$ and $TA95\%_{1^b}^a$, for both before and after training, respectively, where the subscript 1^b refers to an oxygen demand equal to $\dot{V}O_{2\max}^b$). The time to achieve 95% of $\dot{V}O_{2\max}^b$ is a classical measure, see, for example, Billat et al. (2000), used to indicate changes in fitness.

Table 7 shows the time to achieve 95% of $\dot{V}O_{2\max}^b$ both before and after training (see also Fig. 7 for Subject 3 showing the $\dot{V}O_2(t)$ time series before and after training and the time to achieve 95% of $\dot{V}O_{2\max}^b$). The normalized value of a demand equal to $\dot{V}O_{2\max}^b$ for an individual who after training has a maximum oxygen uptake equal to $\dot{V}O_{2\max}^a$ is given by $D_s^a = \frac{\dot{V}O_{2\max}^b - 3.5}{\dot{V}O_{2\max}^a - 3.5}$. By comparing the values of $TA95\%_{1^b}^b$ and $TA95\%_{1^b}^a$, Table 7 allows us to see whether the kinetics has speeded up. Speeded oxygen kinetics is signified by a lower $TA95\%_{1^b}^a$ (i.e. it takes less time to achieve 95% of $\dot{V}O_{2\max}^b$). As can be seen in Table 7, three of the subjects have a speeding up of the kinetics following training (i.e., Subjects 1, 2, and 3) while one of the subjects (i.e., Subject 4) show no change as a result of no change in the optimized parameters of our model. Note that as the demand equals $\dot{V}O_{2\max}^b$, then in the before training state $\lambda_{2_{1^b}}^b = 0$, however, for those who increased their $\dot{V}O_{2\max}$ following training (i.e., $\dot{V}O_{2\max}^a > \dot{V}O_{2\max}^b$), the corresponding value of $\lambda_{2_{1^b}}^a$ decreases and becomes more negative. This makes the solution more attracting, and hence explains the decrease in $TA95\%_{1^b}$.

3.2.3. The parameters and their effect on the time limit to exhaustion at a standardized oxygen demand, $D = \dot{V}O_{2\max}^b$ following training

In this section, we look more closely at the oxygen deficits calculated in the previous section (see Table 6). We use this value of the oxygen deficit as a measure of the anaerobic capacity; we then calculate the time to exhaust this capacity, which we call t_{lim} .

Table 8 Time limit to exhaustion $t_{\lim D=\dot{V}O_{2\max}^b}$ at a standardized real oxygen demand equal to the before training $\dot{V}O_{2\max}^b$ and a standardized initial condition of $\dot{V}O_2(0) = 6.3 \text{ ml/min/Kg}$. This is calculated using the assumption that the subject will be exhausted when the accumulated oxygen deficit becomes equal to the maximum oxygen deficit obtained in the constant speed run test to exhaustion

Subject	$O_{2\text{defi}}^b$ (ml/Kg) accumulated	$t_{\lim D=\dot{V}O_{2\max}^b}^b$ (s)	$O_{2\text{defi}}^a$ (ml/Kg) accumulated	$t_{\lim D=\dot{V}O_{2\max}^b}^a$ (s)	D_s^a
1	35	169	36	359	0.84
2	54	76	58	708	0.92
3	53	90	59	179	0.93
4	35	100	35	100	1

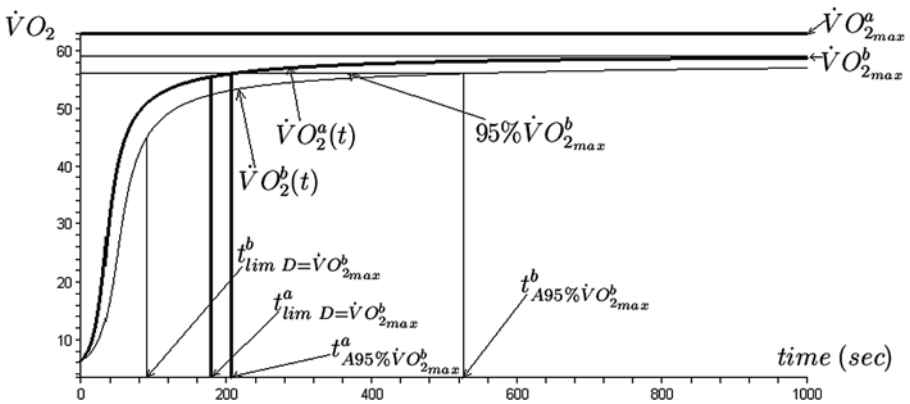


Fig. 7 Using Subject 3 as an example, we present the time to achieve 95% of $D = \dot{V}O_{2\max}^b$ after training in comparison to the time to achieve 95% of $\dot{V}O_{2\max}^b$ before training. We also show the time limit to exhaustion at a standardized real oxygen demand equal to the before training $\dot{V}O_{2\max}^b$. The times $t_{\lim D=\dot{V}O_{2\max}^b}^a$ and $t_{\lim D=\dot{V}O_{2\max}^b}^b$ represent the time limits to exhaustion before and after training, respectively. $T_{A95\%_1^b}$ and $T_{A95\%_1^a}$ represent the times to achieve 95% $\dot{V}O_{2\max}^b$ before and after training, respectively. The thin curve corresponds to the before training state and the thick to the after training state.

In Table 8, we look at the predicted increased time to exhaustion following training by comparing the before and after values of oxygen deficit and parameters at a standard value of the oxygen uptake equal to the before training value of $\dot{V}O_{2\max}$, $\dot{V}O_{2\max}^b$. This time to exhaustion at $\dot{V}O_{2\max}^b$ both before and after training (i.e., $t_{\lim D=\dot{V}O_{2\max}^b}^b$ and $t_{\lim D=\dot{V}O_{2\max}^b}^a$, respectively) is shown graphically in Fig. 7 for Subject 3. We make the assumption that subject will be exhausted when the accumulated oxygen deficit becomes equal to the maximum oxygen deficit obtained in the constant speed run test to exhaustion. Or in other words, we calculate the predicted time taken for the subject to use up all of their anaerobic capacity, at a specific real value of oxygen demand both before and after training.

In Table 8, it can be seen that three subjects (Subjects 1, 2, and 3) increased their time limit to exhaustion while running at a demand equal to $\dot{V}O_{2\max}^b$. The subject who did not

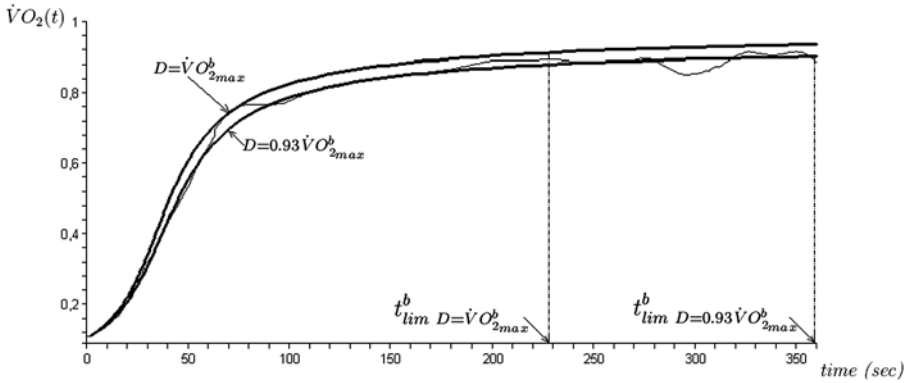


Fig. 8 Graph for before training, showing for Subject 3 the predicted time limit to exhaustion for a demand $D = \dot{V}O_{2max}^b$ and the actual time to exhaustion for a demand (i.e., $D = 0.93\dot{V}O_{2max}^b$) equal to that required for the subject to complete the constant velocity test. The predicted time to exhaustion at a demand $D = \dot{V}O_{2max}^b$ is calculated as the time required to use up all of the oxygen deficit or anaerobic capacity (i.e., the time to accumulate the same oxygen deficit as in the constant velocity run to exhaustion). The thin curve shows the Fourier filtering of the data obtained during the constant velocity run to exhaustion, to which model was fit. The two thick curves correspond to the oxygen uptake kinetics given by the model for the two different oxygen demands.

increase his $\dot{V}O_{2max}$ following training (i.e., Subject 4) also showed no increase in the time limit to exhaustion as there was no change in his anaerobic capacity with training.

In Fig. 8, we show how the model of Stirling et al. (2005) can also be used to predicted the decrease in time to exhaustion (given by $\Delta t_{lim}^b = t_{lim D=\dot{V}O_{2max}^b}^b - t_{lim D=0.93\dot{V}O_{2max}^b}^b$) as one increases the intensity of the exercise. This is obviously of much use when predicting, for a given fitness level, time limits to exhaustion at exercise intensities other than those for which we have data.

3.3. Summary regarding improvements in fitness

In Table 9, we look at the relative improvements of the previously measured values following training. With the use of this table, it will be possible to see who improved what aspects of their physiology (as measured during the constant speed run to exhaustion) and the effect this had on the free race time T_f .

It can be seen in Table 9 that Subject 2 and Subject 3 can be seen to have shown large improvements in $\% \dot{V}O_{2max}$, $\% T_f^b$, $\% O_{2defi}^m$, $\% \lambda_{2,0.95}^b$, $\% TA95\%_{0.95}^b$, $\Delta \lambda_{2,1}^b$, $\% TA95\%_{1}^b$, and $\% t_{lim,1}^b$. Subject 1 shows large improvements in all but the $\% \Delta O_{2defi}^m$ where the improvement is smaller. This could be a result of not running to exhaustion in the second test (or in other words setting off too fast and stopping prematurely). As can be seen in Table 6, the increase in demand is the largest of the four subjects, but so is the increase in $\dot{V}O_{2max}$, however, the percentage decrease in run time is the least of the four subjects. However, it could also be said that for Subject 1 the training just did not improve his anaerobic capacity very much.

Subject 4 shows no improvement in the $\% \dot{V}O_{2max}$ or $\% O_{2defi}^m$, or any of the other measured values (due to the fact his optimal model parameters were found to remain constant),

Table 9 Summarizing table showing the percentage of the after training value relative to the before training value, for $\%T_f^b$, $\%\dot{V}O_{2\max}^b$, $\%O_{2\text{defi}}^b$, $\%\lambda_{2,0.95}^b$, $\%TA95\%_{0.95}^b$, $\%TA95\%_{1b}^b$, and $\%T_{1b}^b$. For $\lambda_{2,1b}$, we calculate $\Delta\lambda_{2,1b}$ as $\lambda_{2,1b}^b = 0$

Subject	$\%T_f^b$	$\%\dot{V}O_{2\max}^b$	$\%O_{2\text{defi}}^b$	$\%\lambda_{2,0.95}^b$	$\%TA95\%_{0.95}^b$	$\Delta\lambda_{2,1b}$	$\%TA95\%_{1b}^b$	$\%t_{\text{lim}1b}^b$
1	90.6	117.0	102.9	496.0	40.0	-0.0118296	29.4	212.4
2	94.9	108.3	107.4	615.6	33.2	-0.0030853	23.7	931.6
3	94.7	106.8	111.3	367.0	53.9	-0.0016980	39.3	198.9
4	93.7	100	100	100	100	0	100	100

however, a significant improvement in $\%T_f^b$ can be observed. This leads to the conclusion that Subject 4 did not actually get fitter following training; he just ran the post training test harder, or in other words, he put in more effort and ran at a high oxygen demand. This is also backed up by the two curves in Fig. 3 which show fit of the model to the before and after data sets. It is also interesting to notice that even though Subject 4 ran at a higher oxygen demand and for less time in the second test the oxygen deficit that was accumulated at the point of exhaustion was identical in each test, suggesting that his anaerobic capacity had also not improved.

4. Conclusions

In this paper, we apply techniques from dynamical systems (Guckenheimer and Holmes, 1983) and time series analysis (Kantz and Schreiber, 1999) to the study of oxygen uptake kinetics. This is the first time that the modeling and analysis procedures presented in Stirling et al. (2005) have been applied to raw unedited and unaveraged oxygen uptake data from a group of subjects. The tools and concepts we use allow for a more in depth and far reaching understanding of the subjects' current fitness levels than was previously possible for the type of data we studied. These tools also allow us to make predictions about the subjects capabilities for exercise intensities for which we do not have data. This is obviously a very powerful feature which will be of much practical use.

We also for the first time (with real data) use the method suggested in Stirling et al. (2005) to calculate anaerobic capacity. We use this and the model of Stirling et al. (2005) to make predictions of the uptake kinetics and time limit to exhaustion at intensities other than those in the tests. This shows the power of the model. We also use the model of Stirling et al. (2005) to show how to analyze performance so as to obtain an in depth understanding of changes in the subject brought about via training.

We used the classic parameters of fitness, these being the time to cover a set distance in an all out race with free speed, T_f and $\dot{V}O_{2\max}$. The $\dot{V}O_{2\max}$ of each subject was found from the peak $\dot{V}O_2$ of either the free race or constant velocity runs to exhaustion. We also used other classic parameters of fitness, such as the anaerobic capacity, which is defined as the maximum accumulated oxygen deficit $O_{2\text{defi}}$ in a run to exhaustion lasting longer than 2 minutes. However, the oxygen deficit was calculate applying for the first time a new technique proposed in Stirling et al. (2005).

The model of Stirling et al. (2005) was also used to make predictions of the oxygen kinetics at exercise intensities other than those in which we have data. This is possible

because the parameters fit in this model are constant for the continuum of exercise intensities at a given level of fitness. This then allowed us to calculate other classic parameters such as the time to achieve 95% of a certain constant oxygen demand (i.e., $\%T A95\%_{0.95^b}$ and $\%T A95\%_{1^b}$, where the oxygen demands were $95\% \dot{V}O_{2\max}^b$ and $\dot{V}O_{2\max}^b$, respectively) and the time limit to exhaustion $\%t_{\lim_{1^b}}^b$ at $\dot{V}O_{2\max}^b$.

The eigenvalues of the fixed points, as proposed in Stirling et al. (2005) were used to look at speeded oxygen uptake kinetics. The change in these eigenvalues allows one to see whether the fixed point solutions, (i.e., those solutions corresponding to $\ddot{V}O_2(t) = 0$, the condition when the oxygen uptake kinetics reaches a steady state equilibrium) have become more attracting following training. We showed this for oxygen demands $95\% \dot{V}O_{2\max}^b$ and $\dot{V}O_{2\max}^b$ and showed how it correlated with the time to achieve 95% of these demands. It should also be noted that an increase in the strength of the attracting solution will also increase the time limit to exhaustion at that demand, assuming the anaerobic capacity remains constant. Hence, it can be seen that the eigenvalues give very important information regarding the subjects fitness levels.

The oxygen uptake kinetics were also presented in a different way to that usually used in exercise physiology by plotting $\ddot{V}O_2(t)$ vs. $\dot{V}O_2(t)$. This allows one to easily and graphically observe both the fixed points solutions and also the presence of speeded oxygen kinetics following training. We also presented a method of understanding the eigenvalues by plotting λ_2 vs. D . With this graph, we can observe where the maximum amplitude of the so-called slow component will be and also how the effects of training have changed the strength of the fixed point attractor for a particular demand. It should be noted that as the eigenvalue is always zero for fixed points of oxygen demands equal to both $\dot{V}O_{2\min}$ and $\dot{V}O_{2\max}$, then this is the place where the least attracting solutions exist, and hence this is the value of oxygen demand for which the amplitude of the so-called slow component will be greatest.

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